



## Multiple drivers of aboveground biomass in a human-modified landscape of the Caatinga dry forest



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### ABSTRACT

Aboveground biomass is an important predictor of net primary productivity and provision of ecosystem services such as carbon storage and food supply. However, biomass can be a complex and multi-driven ecosystem feature, particularly in tropical forests experiencing human disturbances. Here we examine the potential effects of forest successional stage, species richness, plant assemblage functional composition, rainfall, grazing and soil fertility as drivers of biomass in a human-modified landscape of the Caatinga dry forest. We recorded 8911 stems ( $DSH \geq 3$ ) across 35 0.1-ha plots and calculated the aboveground biomass adopting allometric model developed specifically for Caatinga dry forest. Caatinga flora was dominated by species bearing moderate to heavy wood, with aboveground biomass concentrated into a few dominating species and narrow stems. Biomass averaged  $28.48 \pm 23.32 \text{ Mg ha}^{-1}$  with a high cross-stand variation as it resulted from a complex interaction of age of forest stand, rainfall and species richness; i.e. old-growth forest stands supported twice as much biomass ( $38.81 \pm 25.08 \text{ Mg ha}^{-1}$ ) than successional stands ( $14.68 \pm 10.52 \text{ Mg ha}^{-1}$ ). Drivers of plot-level biomass also affected biomass at species level as well as the abundance of the species which contributed most for forest biomass. Our results confirm that slash-and-burn agriculture supports the emergence of biomass mosaics associated to the presence of old-growth and successional forest stands of varying age. In this context, Caatinga supports reduced forest biomass, which responds to both natural and human-driven forces and their complex interactions. Moreover, biomass persistence in human-modified landscapes requires not only long fallow periods, but also the protection of species-rich forest assemblages.

### 1. Introduction

Aboveground biomass is a key attribute of tropical forests as it correlates directly with ecosystem productivity and several globally relevant ecological services such as carbon storage (Beer et al., 2010; Poorter et al., 2015). Although tropical forests cover only 7–10% of the terrestrial surface, they account for 35% of land net primary productivity and 25% of biomass, with approximately  $195 \text{ PgC}^{-\text{yr}}$  (Poorter et al., 2015; Alamgir et al., 2016). In other words, tropical forests are powerful carbon sinks (Saatchi et al., 2011; Brienen et al., 2015; Sullivan et al., 2017) with impacts on climate regulation and mitigation of climate changes (Phillips et al., 2009). Moreover, expressive part of plant biomass can be used as forest products (e.g. timber, charcoal, fodder), which are exploited for subsistence and commercial purposes

affecting people's livelihood (Sánchez-Azofeifa et al., 2014).

Overall, this is particularly the case of seasonally dry tropical forests (STDF) in human-modified landscapes dominated by forest-dependent people (Sánchez-Azofeifa et al., 2014). Biomass is also involved with nutrient cycling and long-term viability of slash-and-burn agriculture, as it usually operates with low external inputs (Sanchez, 2002). Particularly in seasonally tropical dry forests, secondary or regenerating forests frequently emerge in response to post-cultivation fallows. Accordingly, second growth forests comprise almost a half of the original cover by tropical forests (FAO, 2010). Thus, it is fundamental to understand forest recovery, biomass gain and the services/functions provided by secondary forests in landscapes in which such forest products are vital to livelihood.

In dry tropical forests, aboveground biomass is affected by a large

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number of drivers. There is robust evidence that soil water availability and rainfall are primary limiting factors (Maass, 1995; Becknell et al., 2012; Poorter et al., 2016) by affecting forest productivity since both seasonality and intensity of leaf production correlate with photosynthetic rates and thus to carbon storage (Chapin III et al., 1990, 2000). Additionally, water influences and regulates soil microbial dynamics, organic matter decomposition and mineralization, changing label carbon availability (Anaya et al., 2007), as well as phosphorus concentration (Read and Lawrence, 2003). These processes provide organic and inorganic nutrients to plants after rain events (Jaramillo et al., 2011). In fact, it has supported the notion that increased soil fertility could, influence biomass gain since plants can grow faster (Pastor et al., 1984; Quesada et al., 2012).

In addition to physical drivers, the niche complementarity hypothesis states that primary productivity and biomass gain/storage would be affected by niche trade-off models of species competition and coexistence (Tilman et al., 1997, 2014). Precisely, authors postulate that primary productivity and biomass increase as the number of plant species increases (Cavanaugh et al., 2014; Tilman et al., 1997, 2014). In addition to species richness, plant functional traits correlate with individual growth rate and thus they have been recognized as predictors of primary productivity and biomass dynamics (Cardinale et al., 2007; Finegan et al., 2015; Lohbeck et al., 2014, 2015). In this perspective, plant biomass patterns in non-disturbed old growth forests can be attributed to the presence of late successional tree species with more conservative resource-use strategies (Laurance et al., 2011; Sullivan et al., 2017). Particularly, specific leaf area and leaf dry matter content are good predictors for biomass storage, since these traits are usually related to resource use by plants (Finegan et al., 2015; Ali et al., 2017).

Finally, acute and chronic anthropogenic disturbances (*sensu* Singh, 1998) can also be important aboveground biomass drivers (e.g. Conti et al., 2014), particularly in human-modified landscapes supporting forest-dependent people. Frequently, slash-and-burn fallow may not permit the full recovery of aboveground biomass (Guariguata and Ostertag, 2001; Chazdon et al., 2007). Moreover, biomass removal via forage, firewood, timber and other forest products increases nutrient exportation exceeding some resilience thresholds, becoming forests increasingly degraded (Melito et al., 2018). Additionally, secondary succession after disturbances and land abandonment drives aboveground biomass recovery in space and time because successional pathways allow increments in the complexity of forest structure [i.e. basal area, species richness, species composition, taxonomic and functional changes (Guariguata and Ostertag, 2001; Chazdon et al., 2007; Lebrija-Trejos et al., 2010)]. Furthermore, a complex set of interactions during succession (e.g. seed sources, disturbance history, species life histories) leads to environmental changes (e.g. light and soil nutrients availability, temperature) providing gradual replacement of pioneer/acquisitive species by the dominance of old-growth/conservative species that are fundamental to biomass accumulation during secondary succession (Guariguata and Ostertag, 2001; Pinho et al., 2017). Although patterns and mechanisms of biomass dynamics in tropical forest have raised attention in the context of carbon dynamics and global climatic changes (Urquiza-Haas et al., 2007; Conti et al., 2014; Liu et al., 2015; Poorter et al., 2016), the relationships among biomass, resilience, livelihood and sustainability are intrinsically complex into a large portion of dry tropical regions, which deserves additional attention (Conti et al., 2014; Melito et al., 2018).

The Brazilian Caatinga is one of the largest and species-rich seasonally dry tropical forests worldwide (DRYFLOR et al., 2016; Silva et al., 2017). Similar to other seasonally dry tropical forests, most of the Caatinga region has been converted into human-modified landscapes with the predominance of smallholding farming devoted to slash-and-burn agriculture and extensive cattle breeding based on native vegetation as the main source of forage (Sampaio, 1995; Silva et al., 2017; ,). Accordingly, the remaining vegetation can be described as the combination of old growth and successional forest patches of different ages

and permanently exposed to chronic anthropogenic disturbances (Silva et al., 2017). Disturbances can eliminate useful large trees and change the relative contribution of traits and consequently the functional composition of plant assemblages by the proliferation of disturbance-adapted species (Ribeiro et al., 2016; Sfair et al., 2018). However, the way this myriad of drivers affects aboveground biomass remains unexplored.

Here we describe aboveground biomass distribution and examine potential drivers of biomass across a 670-km<sup>2</sup> landscape covered by the Caatinga dry forest, including both old growth and successional forest patches of varying age. We adopted the structural equation modeling (SEM) to test direct and indirect relationships among forest successional stage (i.e. years since land abandonment and old-growth forest stands), plant community attributes (i.e. species richness and assemblage functional composition) and environmental gradients (i.e. rainfall, chronic anthropogenic disturbance and soil fertility) on aboveground biomass. We also examine how particular plant species respond to these drivers and then affect forest biomass. Based on previous findings in our focal and other human-modified Caatinga landscapes (Ribeiro et al., 2016; Rito et al., 2016; Sfair et al., 2018) we expected a flora dominated by hard woods and low scores of forest biomass. Moreover, biomass should be concentrated into few dominant species and narrow stems. Finally, all selected drivers should contribute to forest biomass, particularly forest successional stage and precipitation (i.e. globally recognized drivers) as well as to the abundance of those plant species contributing most for forest biomass.

## 2. Materials and methods

### 2.1. Study site

This study was carried out in the Catimbau National Park (8°23'17"–8°36'35" S; 37°11'00"–37°33'32"W; Fig. 1), covering 607 km<sup>2</sup> of the Caatinga dry forest in the Northeast Brazil. The annual rainfall ranges from 500 to 1000 mm, concentrated between March and July. The annual mean temperature is 23 °C with low seasonality (from 21 °C in July and 25 °C in December). The forest is dominated by Leguminosae, Euphorbiaceae and Cactaceae species (Rito et al., 2016). This protected area is still home for over 400 families whose livelihood relies on subsistence agriculture (i.e. slash-and-burn agriculture), goat breeding and collection of forest products, such as firewood, timber and fodder (Tabarelli et al., 2017a).

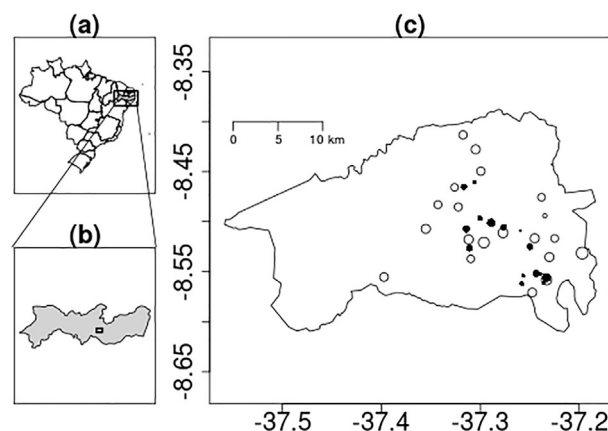


Fig. 1. Study site location in (a) Brazil, and (c) in the Catimbau National Park (b) in the Pernambuco state. The circle size represents the biomass of successional (black) and old growth (white) stands. The x and y axes in (c) are the longitude and latitudes coordinates, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 2.2. Biomass of woody plant species

We used the species-abundance dataset by Rito et al. (2016), Paula (2017) and Barros (2018), which consists of 35 20 × 50 m or 0.1-ha plots, summing up 3.5 ha of sampling area. All shrubs and trees with diameter at soil height (DSH) ≥ 3 cm and total height ≥ 1 m were sampled and classified at species level following the Angiosperm Phylogeny Group III. We used the allometric model proposed for Caatinga vegetation by Sampaio and Silva (2005) to estimate woody plant living biomass using basal area at soil level ( $AGL = \pi \cdot (DSH^2)/4$ ), in which DSH = diameter at soil height (cm) to calculate the AGB:  $AGB = 0.0832 \cdot (AGL \cdot h \cdot SSD)^{0.9224}$ , in which h = stem height and SSD = stem specific density ( $g\ cm^{-3}$ ). To calculate SSD, we sampled a portion of ~5 cm of the wood branch from one to 10 individuals of all species in each plot, following the protocol by Pérez-Harguindeguy et al. (2013). Biomass estimates by the equation of Sampaio and Silva (2005) did not differ ( $P > 0.05$ ) of other formula, such as the equation proposed by Chave et al. (2014).

## 2.3. Predictor variables

Plant species richness (S), rainfall (RF), community weighted mean (CWM) of specific leaf area (SLA) and leaf dry matter content (LDMC), livestock pressure index (LPI), soil fertility (SEF) and years since land abandonment (hereafter, “successional” or “age” stands) were used as predictors of plot-level aboveground biomass. Rainfall (RF) within each plot was obtained from the interpolation of the updated WorldClim global climate data repository (Hijmans et al., 2005) at 1 km resolution. Data was collected using the “raster” package (Hijmans, 2016) of R version 3.4 (R Core Team 2017). Cross-plot mean annual rainfall ranged from 510 to 940 mm, and it was strongly related to other climatic variables, such as mean annual temperature (Sfair et al., 2018). We measured SLA and LDMC following the protocol by Pérez-Harguindeguy et al. (2013) for the most abundant shrub and tree species, which represent nearly 75% of all individuals recorded in the plots. For each plot, we calculated the CWM for these traits (Garnier et al., 2004). Although other traits can be adopted to predict biomass (e.g. wood density, leaf area and plant height), these traits have been proven to be the most effective as they correlate with primary productivity (Chapin III et al., 2000; Finegan et al., 2015) and are statistically correlated to CWM of other traits, such as leaf area and plant height (Sfair et al., 2018).

We considered the livestock pressure index (LPI) as the grazing pressure caused mainly by goat and cattle. In four 2 × 2 m subplots within each plot, we counted all goat dung pellets, while cattle dung and the goat trail length were measured with odometer in the whole 0.1 ha plot area. To compute such a proxy of goat herbivory, we used the first axis of a PCA calculated by goat trail length and their dung counts (the first coordinate explained 86% of the variance). Goat herbivory and cattle dungs were used to calculate LPI according to the formula proposed by Arnan et al. (2018). LPI varies from 0 (no livestock pressure in the plot) to 100 (maximum livestock pressure in the plot).

We considered nine samples of 10 × 10 cm<sup>2</sup> of superficial soil (20 cm deep) for each plot. Micronutrients, water content, organic matter and acidity were estimated following the official Brazilian protocol for soil agronomic analyses (Embrapa, 1997). Further, we calculated the soil evaluation factor, a measure of soil fertility (SEF; Lu et al., 2002) as follows:  $SEF = [Ca + Mg + K - \log(1 + Al)] \cdot OM + 5$ ; where SEF = soil fertility, Ca = exchangeable calcium (cmolc dm<sup>-3</sup>), Mg = exchangeable magnesium (cmolc dm<sup>-3</sup>), K = exchangeable potassium (cmolc dm<sup>-3</sup>), Al = exchangeable aluminum (cmolc dm<sup>-3</sup>) and OM = organic matter ( $g\ kg^{-1}$ ). Ca, Mg, and K are considered nutrients, Al is toxic to plant growth and OM is related to other soil fertility factors, e.g., nutrient availability, soil structure, air infiltration and water infiltration and retention (Lu et al., 2002).

The age of forest stands was established by interviews with local

residents. Plots without record of shift cultivation by locals for the last 100 years were considered as old growth forest and arbitrarily set with 150 years old. Successional stands were previously used for small crops, such as corn, bean and cassava, and were abandoned after lack of financial return and soil nutrient depletion. These plots ranged from four to 70 years of abandonment (Paula, 2017; Barros, 2018).

## 2.4. Data analyses

To understand the complex relationships among the environmental and community variables and biomass, the total biomass of the plots was ln-transformed to achieve the assumptions of the test (normality and homogeneity of variance). Then, we used Structural Equation Modelling (SEM) to understand how the number of species, rainfall, CWM of SLA and LDMC, LPI, soil fertility and forest age influenced the total aboveground biomass at plot level. We ln-transformed the biomass to achieve normality following Mardia's Multivariate Normality test in MVN package using R ( $P > 0.05$ ; Korkmaz et al., 2014). Firstly, we built an *a priori* hypothetical model in which the number of species, rainfall, CWM of SLA and LDMC, LPI, soil fertility and age could influence directly the total biomass of stands. The conceptual model also considers that environmental variables (rainfall, LPI, soil fertility and time since abandonment) may directly influence the number of species and the CWM of SLA and LDMC. These correlations are supported in previous studies conducted in the studied area that correlated environmental variables with biodiversity (Rito et al., 2016; Arnan et al., 2018; Sfair et al., 2018). To optimize the conceptual model, we systematically removed the terms with low and non-significant z values until achieving the best model describing the data (Appendix A, B). Two ways to evaluate whether the model represents the data adequately have been proposed: the  $\chi^2$  and the Root Mean Square Error of Approximation (RMSEA). If the  $\chi^2$  is non-significant ( $P > 0.05$ ) and the RMSEA is close to zero, the model representing the data can be considered satisfactory (Grace, 2006). As all tested models had a non-significant and a RMSEA < 0.05 (Appendix A), we adopted the Akaike Information Criterion (AIC) to identify the best model representing the data. In this approach, multiple competing hypotheses are tested and based on model parsimony the best statistical model is the one with the lowest value of AIC. If the difference of the best and the second-best model is lower than two, then there is substantial evidence in favor of both models. Intermediate differences (between three and seven) indicate that the model has considerably less support. However, high differences, such as higher than ten, indicate that the model is very imprecise as compared to a model with the lowest AIC (Burnham and Anderson, 2002; Mazerolle, 2006). For the most parsimonious model, we standardized the estimated coefficient ( $\beta$ ), and its P-value was used to assess the parameter significance, whereas the coefficient of determination ( $R^2$ ) was represented as the variance of endogenous variables ( $\varphi$ ). The SEM analysis was performed by the lavaan package in R (Rosseel, 2012).

As complementary approach to identify the forest biomass drivers, we performed a Canonical Correspondence Analysis (CCA) between the biomass of each species in each plot and the following predictor variables: number of species, rainfall, CWM of SLA and LDMC and soil fertility (Legendre and Legendre, 2012). We performed CCA for old growth and successional stands separately and together. The significance of each CCA was tested by analysis of variance with 999 permutations (Legendre and Legendre, 2012). In the same perspective, we also performed generalized linear models with Poisson distribution corrected by overdispersion (Crawley, 2012) for the abundance of the top four species with the highest biomass (hereafter, the biomass-relevant species: *Poincianella microphylla*, *Pityrocarpa moniliformis*, *Senegalia bahiensis* and *Syagrus coronata*, Appendix C). The predictors of the statistical models were LPI, SF and forest age.

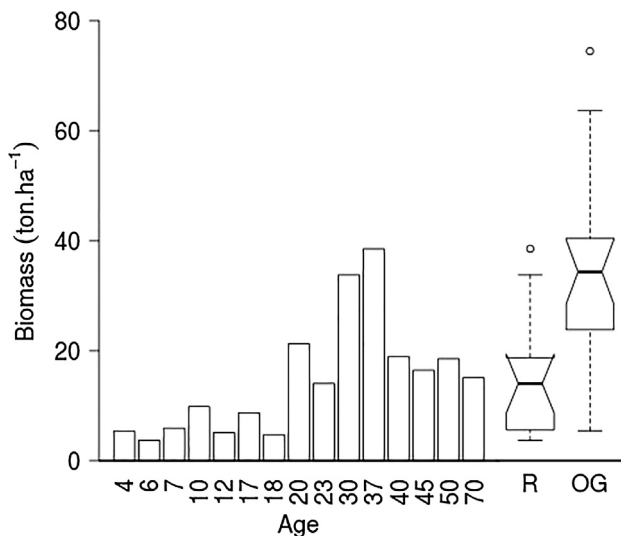


Fig. 2. Aboveground biomass according across successional (R) and old growth (OG) forest stands in the Catimbau National Park, Brazil.

### 3. Results

We recorded 8911 individuals from 144 trees and shrubs species across all 35 plots, with stem specific density ranging from 0.200 to 1.468  $\text{g cm}^{-3}$ . Species with intermediate scores of stem specific density (0.60–0.79  $\text{g cm}^{-3}$ , Fig. S1) predominated, particularly among successional stands. High levels of species dominance were recorded by collapsing all plots: collectively, *Pityrocarpa moniliformis* ( $n = 1136$ ), *Poincianella microphylla* ( $n = 702$ ), *Jatropha mutabilis* ( $n = 671$ ) and *Croton tricolor* ( $n = 645$ ) accounted for 3,154 (37.3%) stems. Accordingly, total biomass was influenced by a small set of species, but not necessarily by the most abundant ones (Fig. S2). Total biomass was also concentrated in narrow stems, with little contribution from stems > 40 cm DSH (Fig. S3).

Plot-level biomass averaged ( $\pm$  standard deviation)  $28.48 \pm 23.32 \text{ Mg ha}^{-1}$ , with a large cross-plot variation ( $3.72\text{--}122.60 \text{ Mg ha}^{-1}$ ). Old growth stands had twice as much biomass in average ( $38.81 \pm 25.08 \text{ Mg ha}^{-1}$ ) than successional stands ( $14.68 \pm 10.52 \text{ Mg ha}^{-1}$ , Fig. 2). All SEMs were satisfactory (all with  $\chi^2$  test at  $P > 0.05$  and RMSEA > 0.05; Appendix A), then we adopted the best model according to AIC to represent our data. This best model included forest stand age, rainfall, species richness, LDMC and biomass connected by five significant pathways, explaining 62% of the total biomass in the plots as follows: plant richness positively influenced biomass ( $\beta = 0.34$ ), which, in turn, was directly affected by time since abandonment ( $\beta = 0.77$ ), but also positively affected by rainfall ( $\beta = 0.58$ ). Areas abandoned for longer time also had higher biomass ( $\beta = 0.37$ ). The CWM of LDMC was positively related to rainfall ( $\beta = 0.42$ ), but biomass suffered little influence of livestock pressure, soil fertility and CWM of SLA and LDMC (Fig. 3, Appendix B).

Overall, CCA indicated that the total biomass of the species among plots responded to the predictors ( $F_{7,27} = 1.85$ ;  $P < 0.05$ , Fig. 4a). Particularly, forest stand age ( $F = 2.03$ ;  $P < 0.05$ ), species richness ( $F = 1.81$ ;  $P < 0.05$ ), CWM of SLA ( $F = 2.41$ ;  $P < 0.05$ ) and LDMC ( $F = 2.39$ ;  $P < 0.05$ ), livestock pressure ( $F = 1.55$ ;  $P = 0.03$ ) and rainfall ( $F = 1.75$ ;  $P = 0.02$ ). Soil fertility had non-significant effect on biomass ( $F = 1.00$ ;  $P = 0.43$ ). When performed separately by forest successional stage (old growth vs successional stands), environmental variables also influenced biomass in both old growth ( $F_{6,13} = 1.79$ ;  $P < 0.05$ , Fig. 4b) and successional stands ( $F_{6,8} = 1.52$ ;  $P < 0.05$ , Fig. 4c), particularly the richness of species ( $F = 1.62$ ;  $P = 0.04$ ), CWM of SLA ( $F = 2.36$ ;  $P < 0.05$ ) and LDMC ( $F = 2.40$ ;  $P < 0.05$ ) and livestock pressure ( $F = 1.57$ ;  $P = 0.04$ ; Fig. 4b) in old growth, while

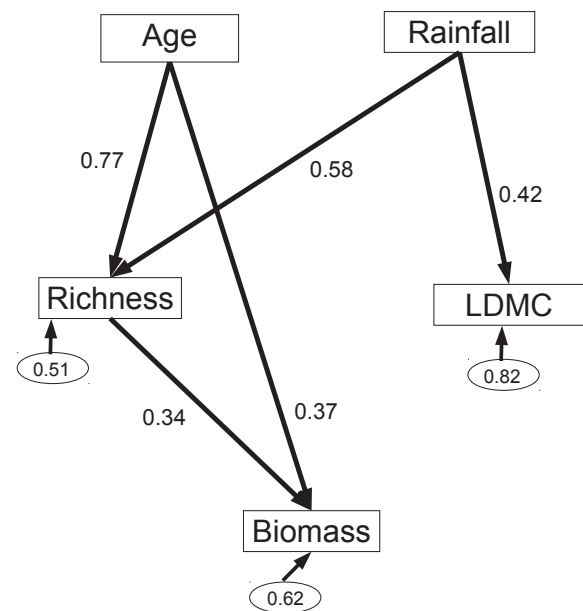


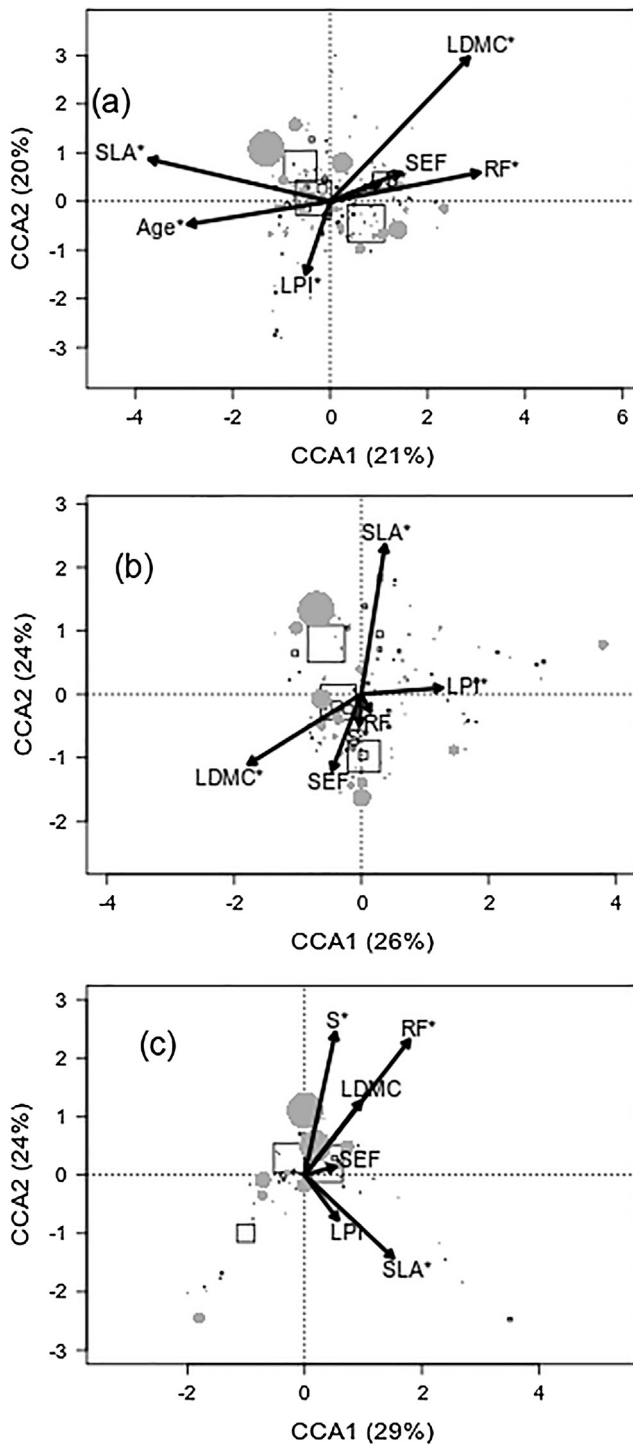
Fig. 3. The best structural equation model for forest biomass in the Catimbau National Park, Brazil. Dashed lines indicate non-significant relation, whereas continuous lines mean a significant relation. The number beside the large arrows indicates standardized estimated coefficient ( $\beta$ ) and the number inside the ellipse is the  $R^2$ . “LDMC” is the community weighted mean of leaf dry matter content, and “Age” is the years since the plot. We only show the significant paths, i.e., livestock pressure, soil fertility and community weighted mean of specific leaf area are not represented.

species number ( $F = 1.81$ ;  $P < 0.05$ ), CWM of SLA ( $F = 1.79$ ;  $P < 0.05$ ) and rainfall ( $F = 1.88$ ;  $P < 0.05$ , Fig. 4c) affected biomass in successional stands.

The plot-level biomass response to focal variables was confirmed by the abundance response exhibited by several species, particularly to rainfall, but also to livestock pressure (Appendix C shows the correlation ranks between species abundance and rainfall or LPI in the plot). Overall, species abundance in this focal plant group responded mainly to rainfall, while soil fertility and time since abandonment played a minor role. While *P. microphylla* was more abundant in drier areas regardless of the type of stand (mature forests or successional stands), *S. coronata* had a higher abundance in wetter stands and in successional stands (Table 1, Fig. 5). Although *S. bahiensis* and *P. moniliformis* had a higher abundance in wetter areas, the former species had only significant values in old growth stands, and *P. moniliformis* only in successional stands (Table 1, Fig. 5).

### 4. Discussion

Our results suggest the Caatinga flora is dominated by species bearing moderate to heavy wood, with aboveground biomass concentrated into a few widespread and dominating species and narrow stems. Furthermore, the Caatinga biomass is highly variable as it results from a combination of the age of forest stands, rainfall (i.e. total annual rainfall) and species richness: older forest stands exposed to high rainfall support a high number of species, which in turn, influences biomass positively. In other words, species-rich old growth forests in humid sites support the highest amounts of biomass rather than species-poor, early successional stands in the Caatinga landscapes. These drivers also affect both the abundance and the biomass of the species that contribute most for Caatinga forest biomass (i.e. biomass-relevant species). In contrast to our initial expectation, livestock pressure, soil fertility and community-level plant traits appear to play a minor role on forest biomass although they affect the abundance and the biomass supported by relevant species. It implies that the Caatinga forest



**Fig. 4.** Canonical Correspondence Analysis (CCA) between the community assemblages considering biomass of each species in each plot in the Catimbau National Park, Brazil. Age = years since abandoned after soil depletion in shifting agriculture system, RF = Rainfall, LPI = Livestock Pressure Index, S = Species Richness, SEF = Soil Fertility, SLA = community weighted mean of specific leaf area, LDMC = community weighted mean of leaf dry matter content. The square size represents the proportional biomass of each species, whereas the circle size means the proportional biomass of each plot. (a) All plots, (b) old growth, and (c) successional stands. \* The significant environmental variables.

**Table 1**

Generalized linear models for abundance of species that contributed the most to the total biomass in the Catimbau National Park, PE, Brazil. The regressions used Poisson distribution with correction for overdispersion.

	Degree of freedom	Deviance	Degrees of freedom of the residual deviance	Residual Deviance	P
<i>Pityrocarpa moniliformis</i>					
Null	34	2030.50	34	2030.50	
Stand	1	10.01	33	2020.50	0.69
Rainfall	1	59.22	32	1961.20	0.33
Livestock pressure	1	15.08	31	1946.20	0.63
Soil fertility	1	60.90	30	1885.20	0.33
<i>Poincianela microphylla</i>					
Null	34	972.36	34	972.36	
Stand	1	37.03	33	935.33	0.16
Rainfall	1	433.80	32	501.54	< 0.001
Livestock pressure	1	28.80	31	472.74	0.21
Soil fertility	1	4.39	30	468.35	0.63
<i>Senegalia bahiensis</i>					
Null	34	1306.58	34	1306.58	
Stand	1	6.20	33	1300.38	0.70
Rainfall	1	215.97	32	1084.41	0.02
Livestock pressure	1	1.15	31	1083.26	0.87
Soil fertility	1	165.22	30	918.04	0.05
<i>Syagrus coronata</i>					
Null	34	245.85	34	245.85	
Stand	1	65.32	33	180.53	< 0.001
Rainfall	1	48.19	32	132.34	< 0.001
Livestock pressure	1	2.45	31	129.89	0.46
Soil fertility	1	2.18	30	127.71	0.48
Control					
<i>Pityrocarpa moniliformis</i>					
Null	19	1071.96	19	1071.96	
Rainfall	1	0.00	18	1071.96	1.00
Livestock pressure	1	4.67	17	1067.29	0.78
Soil fertility	1	203.23	16	864.06	0.06
<i>Poincianela microphylla</i>					
Null	19	337.98	19	337.98	
Rainfall	1	145.25	18	192.73	< 0.001
Livestock pressure	1	25.85	17	166.88	0.05
Soil fertility	1	31.74	16	135.15	0.03
<i>Senegalia bahiensis</i>					
Null	19	649.08	19	649.08	
Rainfall	1	142.82	18	506.26	0.04
Livestock pressure	1	0.36	17	505.90	0.92
Soil fertility	1	42.92	16	462.98	0.26
Successional					
<i>Pityrocarpa moniliformis</i>					
Null	14	956.41	14	956.41	
Rainfall	1	273.86	13	682.55	0.03
Livestock pressure	1	6.83	12	675.72	0.73
Soil fertility	1	0.04	11	675.68	0.98
<i>Poincianela microphylla</i>					
Null	14	625.01	14	625.01	
Rainfall	1	360.11	13	264.90	< 0.001
Livestock pressure	1	9.31	12	255.60	0.62
Soil fertility	1	11.01	11	244.59	0.58
<i>Syagrus coronata</i>					
Null	14	116.11	14	116.11	
Rainfall	1	20.93	13	95.17	0.08

(continued on next page)

Table 1 (continued)

	Degress of freedom	Deviance	Degrees of freedom of the residual deviance	Residual Deviance	P
Livestock pressure	1	1.77	12	93.40	0.61
Soil fertility	1	4.97	11	88.43	0.40

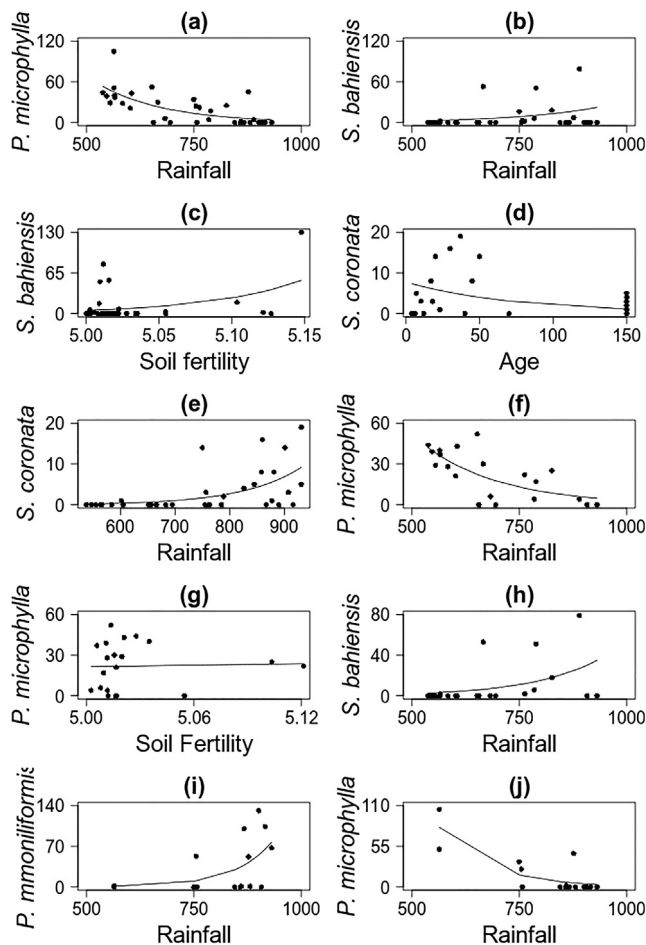


Fig. 5. Significant responses of species abundance to gradients (years since abandonment (Age), rainfall ( $\text{mm year}^{-1}$ ), soil fertility and livestock pressure) based on correlations considering old growth and successional stands combined (a, b, c, d, e) and separately (old growth: f, g, h; successional: i, j) in the Catimbau National Park, Brazil. For all relationships, see Table 1. *P. microphylla* = *Poincianella microphylla*; *S. coronata* = *Syagrus coronata*; *P. moniliformis* = *Pityrocarpa moniliformis* and *S. bahiensis* = *Senegalia bahiensis*.

biomass responds to interacting natural and human-driven forces.

The biomass exhibited by some Caatinga forest stands in our focal landscape lies on the range of other seasonally dry tropical forests, i.e.  $35\text{--}140 \text{ Mg ha}^{-1}$ , averaging  $77.4 \pm 30.5 \text{ Mg ha}^{-1}$  (mean  $\pm$  SD; Jaramillo et al., 2011). However, the Caatinga average biomass is out of the range posed by SDTF, although the Caatinga flora supports several plant species exhibiting intermediate to high woody density (see also Sampaio et al., 2010). It is important to notice that stem specific density is correlated to carbon storage (Baker et al., 2004; Prado-Junior et al., 2016) and hard-wood species are less prone to cavitation (Chave et al., 2009), which reinforces the role played by water availability as an ecological driver in seasonally dry tropical forests.

In fact, there is a strong debate about the underlying mechanisms affecting the biomass of tropical forests across multiple spatial scales,

with most studies focusing on either old growth (Baraloto et al., 2011; Finegan et al., 2015; Prado-Junior et al., 2016) or secondary forests (Urquiza-Haas et al., 2007; Chazdon et al., 2007; Becknell and Powers 2014; Lohbeck et al., 2015; Poorter et al., 2016). However, a non-integrative approach may be inadequate to properly address forest biomass in human-modified landscapes inhabited by forest-dependent people, since forests tend to be converted into successional mosaics due to shifting agriculture (Chazdon et al., 2007; Tabarelli et al., 2017b) and experience chronic disturbances such as browsing by livestock, firewood collection and timber harvesting (Silva et al., 2017).

In this context, our results suggest that slash-and-burn agriculture supports the emergence of mosaics of biomass associated to the presence of old-growth and successional forest stands of varying age at landscape spatial scale (Schacht et al., 1988; Pereira et al., 2003; Urquiza-Haas et al., 2007). Moreover, the Caatinga forest biomass is affected by factors interacting in a complex way. Positive relationships between time since land abandonment, recovery of forest biomass, species richness and rainfall are not a novelty (Becknell et al., 2012; Chazdon et al., 2016, Poorter et al., 2015, 2016). As the time since land abandonment and succession advances, plants grow and accumulate biomass, but species richness increases and biomass accumulates due to establishment and growth of novel species, including many hardwood and long-lived, large tree species (Brown and Lugo, 1990; Guariguata and Ostertag, 2001; Sobrinho et al., 2016). Elapsed several decades both species richness and biomass tend to approach the scores supported by old growth stands (Guariguata and Ostertag, 2001; Arroyo-Rodriguez et al., 2015). Rainfall also correlates positively with plant species richness and biomass in dry tropical forests (Adler and Levine, 2007; Rito et al., 2016; Becknell et al., 2012; Poorter et al., 2016). Particularly in the case of dry forests, increased water availability is associated to the establishment of large and evergreen trees (Bullock et al., 1995; Rito et al., 2016) resulting in increased leaf production, leaf area and carbon gain (Chapin III et al., 2000; Jaramillo et al., 2011). This could directly affect the gain of forest biomass by increasing ecosystem productivity associate to particular plant groups such as long-lived large trees. In our focal landscape, many large tree species are restricted to humid patches such as *Senegalia bahiensis* (Rito et al., 2016).

Ecosystem productivity and, consequently, forest biomass can also be affected by species richness, what represents an additional mechanism/hypothesis for the patterns we documented in the Catimbau landscape. According to niche complementarity hypothesis (Tilman et al., 1997, 2014), there is a positive relationship between species number, community-level functional diversity and better use of resources, resulting on more productive assemblages (Chisholm et al., 2013; Cavanaugh et al., 2014; Lohbeck et al., 2014; Ali et al., 2017). Specifically, this hypothesis postulates that biomass and carbon storage are, associated to species number and niche complementarity, (Tilman et al., 1997, 2014). Moreover, this mechanism is expected to be stronger in more stressful environments (Paquette and Messier, 2011) and has been confirmed elsewhere (e.g. Tilman et al., 2001; Cardinale et al., 2007; Ruiz-Jaen and Potvin, 2010; Cavanaugh et al., 2014). Increased niche complementary resulting in higher productivity has also been advocated as crucial mechanism operating during secondary succession: as succession proceeds, resources become limited, making niche complementarity the major driver shaping communities at late successional stages (Lohbeck et al., 2014). Accordingly, fluxes and stocks of energy and matter (i.e. carbon storage, nutrient dynamics) over spatial scales (see Chazdon et al., 2007; Guariguata and Ostertag, 2001) are increased in late successional stages. Note that the biomass supported by several species in our focal landscape was influenced by plant species richness at plot level.

Although soil fertility, functional composition of plant assemblages (Finegan et al., 2015; Lohbeck et al., 2015; Ali et al., 2017; van der Sande et al., 2018) and chronic disturbances (e.g. livestock pressure, Rito et al., 2016) can potentially affect forest biomass, we did not find

evidence supporting this potential influence. However, some of these variables proved to affect the abundance/biomass of the biomass-relevant species in our focal landscape, such as *P. moniliformis*, the most abundant species in the landscape and able to be taller in humid areas (Rito et al., 2016, M; Tabarelli personal observation). It is in accordance with previous findings in the Caatinga suggesting that chronic disturbances impose specie-specific effects (Ribeiro et al., 2016; Sfair et al., 2018) and plant assemblage attributes (such as the presence of rare species) are more influenced by changes in the precipitation level than by chronic disturbances (Rito et al., 2016). Furthermore, species-level response to rainfall not only reinforces water as an important driver of forest biomass, but also indicates that the relationship between forest successional stage, precipitation, species richness and forest biomass is mediated by some few species.

Seasonally dry tropical forests represent one third of the tropical forest coverage and has been identified as a conservation priority for biodiversity, cultural heritage, ecological services and livelihood for millions of people (Pennington et al., 2009; Silva et al., 2017). We argue that forest biomass in human-modified landscapes is patchy or organized into mosaics as it responds to forest successional stage (Urquiza-Haas et al 2007; Conti et al., 2014, Chazdon et al., 2016), water availability (Jaramillo et al., 2011, Poorter et al., 2016) and species richness (Poorter et al., 2015). Increments on forest productivity apparently represents the underlying mechanism, with a weak effect of other potential driving forces, such as livestock pressure, soil fertility and changes in the functional composition of plant assemblages relative to leaf-economic spectrum in response to rainfall. As the species richness emerges as a key driver, further studies are required to identify how increased species richness positively affects ecosystem productivity and biomass. Our findings imply that forest biomass persistence in human-modified landscapes requires long fallows and the protection of species-rich forest assemblages in the most suitable patches for agriculture (i.e. humid spots). It is a challenging perspective, since human disturbances tend to intensify land use and impoverish plant assemblages (Lugo, 2013), while climate changes will expose many seasonally dry tropical forests, such as the Caatinga vegetation, to increased aridity (Santos et al., 2014).

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.12.042>.

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