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Loss of biodiversity and shifts in aboveground biomass drivers in tropical rainforests with different disturbance histories

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Abstract

Tropical forests account for more than half of the global carbon forest stock and much of the biological diversity on Earth. However, disturbances such as deforestation and forest degradation threaten the maintenance of these ecosystem services. This study aimed to understand how different disturbance histories affect the forest stand biomass, as well as species and functional diversity, and to what extent these differences can change the relationships between biomass and their drivers. We used data from forests with clear-cut and selectively logged disturbance histories, and from old-growth forests, situated in the Brazilian Atlantic forest. Forests with logging disturbances showed significant losses in their aboveground biomass compared to those of old-growth forests (50% loss in selectively logged forests and 80% loss in clear-cut forests). Interestingly, only clear-cut secondary forests showed differences in species and functional diversity, and were dominated by species with acquisitive trait values, commonly found early in succession. Shifts in stand biomass drivers were observed in selectively logged forests. The mass-ratio hypothesis (mainly through the functional trait of maximum height) was the most important biomass driver in clear-cut secondary and old-growth forests, whereas the importance of the niche complementarity hypothesis (through functional richness and dispersion) was higher in selectively logged forests. Our study highlights that disturbance histories can affect forest aboveground biomass and its drivers. Moreover, our results reinforce the need for conservation of intact forests but highlight the importance of including degraded forests in conservation mechanisms based in carbon stocks, as these forests retain high values of species and functional diversities that are crucial to biomass and consequently carbon stock acquisition.

Keywords Deforestation · Forest degradation · Clear-cut secondary forests · Selectively logged forests · Species and functional diversity · Niche complementarity · Mass-ratio · Carbon stocks

Introduction

The importance of tropical forests for worldwide biodiversity and their key role in global ecosystem services has been repeatedly highlighted by the scientific community (Alkama and Cescatti 2016), and is also reflected in global policies (UNFCCC 2015). Due to land-use activities and other environmental changes, more than half of the original tropical forest cover has been lost (FAO 2010), leading to a dramatic loss of species (Gibson et al. 2011) and high greenhouse gas emissions (Metz et al. 2007). Deforestation is the activity with the strongest human-triggered impact on these forests (Matos et al. 2017), and was responsible for an estimated net loss of 8 million ha year^{-1} in the tropics between 2000 and 2005 (FAO and JRC 2012). Moreover, during the same 5-year period, more than 20% of tropical forest area was degraded by some form of selective logging (Asner et al. 2009), which is currently taking place in at least 400 million ha of natural tropical forests (Blaser et al. 2011). In 2008, forest degradation was incorporated into the reducing emissions from deforestation and forest degradation (REDD+) mechanism (UNFCCC 2008), although the levels and the persistence of biomass loss in forests with different disturbance regimes or histories are still largely unknown (de Andrade et al. 2017).

The impact of forest degradation (e.g. selective logging) is commonly quantified as the amount of biomass lost due to the removal of large trees (with high economic value), neglecting the fact that other changes in the forest structure (e.g. stem density, basal area and canopy cover) and species diversity and composition may occur (Laurance et al. 2006; Berenguer et al. 2014). For instance, logging activities may increase plant mortality (through the damage of non-target and smaller trees) and forests gaps (thereby increasing the number of pioneer species), which can directly affect forests dynamics and light requirements for successful regeneration, contributing to further reductions in biomass and carbon stocks (Putz et al. 2008). Conversely, many deforested areas (clear-cut secondary forests) are regenerating in the tropics (Aide et al. 2013), giving rise to extensive areas of secondary forest that rapidly accumulate aboveground biomass, which may act to mitigate the impact of deforestation on tropical forest carbon stock (Poorter et al. 2016). Nevertheless, recent studies show that the annual losses from deforestation and forest degradation are still greater than the growth gains by forests regeneration (Baccini et al. 2017). New techniques, such as remote sensing, are improving the estimation of forest biomass at broad-landscape scales (Saatchi et al. 2011); however, its accuracy is strongly dependent on the knowledge of forest biomass at the community level (Grace et al. 2014).

While it has been well documented that anthropogenic disturbance histories affect aboveground biomass, it is still poorly understood how the underlying processes associated with disturbance (i.e. changes in forest structure and diversity) can also indirectly affect forests stand biomass (Magnago et al. 2015a). For instance, forests degradation may promote a gradual shift from dominance by late-successional species, with conservative trait values and high potential biomass accumulation (e.g., high wood density, high stature and large seed size) toward dominance by early-successional species, with acquisitive trait values and lower biomass storage potential (e.g., low wood density, lower stature, and small seed size). Therefore, in line with the mass-ratio hypothesis (Grime 1998), which predicts that the ecosystem processes (e.g., carbon stock) are driven by the most abundant species in the community, these changes in species composition would lead to a lower stand biomass in disturbed communities. Another impact related to disturbance is species loss, since the communities experience considerable simplification of species habitat structures (Floren and Linsenmair 2005), favouring generalist rather than specialist species (with

narrow ranges of niche amplitude). Then, according to the niche complementarity hypothesis, which predicts that an increase in biodiversity would allow more efficient use of available resources by species (Tilman 1999), the biodiversity loss would lead to lower stand biomass in forests under anthropogenic disturbance.

Several studies show that both hypotheses (mass-ratio and niche complementarity) are acting simultaneously as drivers of forest stand biomass (Finegan et al. 2015; Lohbeck et al. 2015a; Poorter et al. 2017). However, their relative importance might differ among anthropogenic disturbance histories because species are experiencing different environmental filters (e.g. resources availability) and species interactions (e.g. competition) (Cardinale et al. 2007; Lohbeck et al. 2014). For instance, in old-growth forests, where light is a strong limiting resource and competition is higher (Lohbeck et al. 2015a) the relative importance of the niche complementarity hypothesis as a biomass driver should be higher, since higher number of species (and functional diversity) should improve the uptake/use of the low available resources. Conversely, in degraded and regenerating forests, resources availability is higher and competition is lower (Weiher et al. 1998) which can favour local functional convergence, e.g. species with suitable similar traits may perform better. Thus, the relative importance of the mass-ratio hypothesis as a driver of biomass should be higher, because dominance of species with short-stature and low wood density values that have less biomass and carbon stocks per stem basal area (King et al. 2006a; Chave et al. 2009; Poorter et al. 2010; Prado-Junior et al. 2016b), would strongly decrease forest stand biomass. Such knowledge allows substantial information on which mechanisms are driving ecological processes in tropical forests (Mensah et al. 2016) and, therefore, might be an important conservation tool to understand the shifts in ecological processes over succession, and to manage disturbed forests to improve their ecosystem services.

Here, we investigated how aboveground biomass, species and functional diversity metrics are related to different anthropogenic disturbance histories (old-growth, selectively logged and clear-cut secondary forests). We addressed two questions: (1) To what extent forests under different disturbance histories differ in aboveground biomass, as well as species and functional diversity metrics?; and (2) Does the relative importance of the different biomass drivers (mass-ratio and niche complementarity hypotheses) differ between different forest disturbance histories? We predict that, in addition to decrease in stand biomass, forests with some form of logging disturbance (selective logging and clear-cut) will present an increase in the abundance of species with highly acquisitive traits and a decrease in the biodiversity measures (in terms of species and functional diversity indices). Moreover, we predict that after stronger anthropogenic disturbances, the relative importance of the niche complementarity hypothesis on forest stand biomass will decrease, and the relative importance of the mass-ratio hypothesis will increase.

Materials and methods

Study sites and sampling

This study was conducted in nine tropical rainforests located between the southern region of the state of Bahia and the northern region of the state of Espírito Santo along the Atlantic Coast of Brazil (Fig. S1 and Table S1). These forests are classified as Dense Ombrophylous Lowland Forest (IBGE 2012), occur in large and flat extensions over the northeast coast of Brazil, and are commonly called "tableland forests" due the characteristics of their

relief (Magnago et al. 2015b). All the sampled forests experience homogeneous climatic conditions, classified as tropical hot and humid climate ("Af" Megathermic climate of Köppen), with a mean annual rainfall of 1250 mm (ranges from 1050 to 1370 mm) and a mean temperature of 23–25 °C (Hijmans et al. 2005). The dominant soil type is Yellow Ultisol (Magnago et al. 2016).

The study forests are located in private areas within a landscape comprising mainly pastures, *Eucalyptus* spp. plantations, and annual croplands. Land use history of the forests was determined by interviewing local residents and from physical evidence found during our field surveys. Although chronological sequences of Landsat images were not available, physical evidence of human disturbance can remain in forests for long periods of time after their occurrence (e.g., logging debris might take up to 90 years to decompose; Harmon et al. 1995). The nine studied forests were classified into three categories of forest according with disturbance histories (three forests in each category): (a) old-growth forests, which had neither visual evidence of anthropogenic activities (e.g., logging or cattle grazing) nor a history of anthropogenic disturbance events; (b) selectively logged forests, which had evidence of silvicultural practices (e.g., tree stumps and post-harvest girdling of non-commercial trees), and (c) clear-cut secondary forests, which had a clear-cut disturbance history followed by nearly 40 years of succession. Plots were established in the core areas (i.e., ≥ 300 m from the forest edge) in each site, avoiding other possible effects (e.g. edge effect) in our results. In logged forests we established all plots close to logging signs and tree stumps. It was not possible to obtain the exact amount of timber extracted from the areas with selective logging history, nor the period and duration of these logging activities. This activity has occurred illegally in these forests and, therefore, such data was not available. It is likely that the logging is still occurring because we found signs of trees that have been recently logged.

In each forest, ten permanent plots (20×20 m) were established, yielding a total of 90 sample plots (3.6 ha). During sampling (which was carried out at different time periods for each forest, between 2011 and 2013), all living trees with a diameter at breast height (DBH) ≥ 5 cm were tagged, their diameters measured, heights estimated, and identification performed to the species level. Our plots comprised 4712 individuals, belonging to 360 species and 57 families.

Functional traits

The functional traits considered in this study are related to species standing biomass (Attri et al. 2015; Poorter et al. 2015): maximum height, wood density, and seed size. Species maximum height (Hmax, m) is an indicator of adult stature, and is potentially related to species longevity and life-history strategy (King et al. 2006b), and was calculated as the 95th-percentile of all trees of a given species. Species wood density (WD, g cm^{-3}) represents biomass per unit wood volume constructed (Chave et al. 2009), and was obtained from the global wood density database (filtered by Tropical South America, Zanne et al. 2009). For species without available WD values, we used mean values for the WD of the genus or family. Seed size (SS), although usually related to the competitive vigor of the seedlings (Kitagima 2007), is also an important life history trait for trees (Prado-Junior et al. 2016a), and is correlated with a suite of morphological and physiological traits of pioneer species (small seeds) and shade-tolerant species (large seeds) (Poorter and Rose 2005; Osuri and Sankaran 2016). Qualitative data for species SS were obtained from herbarium specimens, and the species were classified as small seed species (seed length < 0.6 cm),

medium seed species (length between 0.6 and 1.5 cm), large seed species (length between 1.6 and 3.0 cm), and very large seed species (length > 3.0 cm), following Tabarelli and Peres (2002) and Magnago et al. (2014). The information on species functional trait values can be found in supplementary material (Table S4).

Data analyses

For each individual tree with DBH ≥ 5 cm, the aboveground biomass (AGB) was calculated using the allometric formula of Chave et al. (2014) and the parameters, DBH (cm), height (H, m), and species wood density (WD, g cm^{-3}):

$$AGB = 0.0673 \times \left(WD \times DBH^2 \times H \right)^{0.976}$$

For each plot, the AGB stock was calculated as the sum of AGB values for all trees.

For each sample plot, four species and functional diversity metrics were calculated: Species richness (S, number of species per plot), Shannon diversity (H′, which incorporates species abundances), functional richness (FRic, a non-abundance-weighted index) and functional dispersion (FDis, an abundance-weighted index). Functional diversity indices were calculated based on species functional traits (Hmax, WD and SS). In addition, three community-weighted mean (CWM) trait values (that represents functional composition weighted by species abundance) were calculated per plot: CWM maximum height (CWM$_{Hmax}$), CWM wood density (CWM$_{WD}$) and CWM seed size (CWM$_{SS}$). CWM trait values and functional diversity indices were calculated using the 'FD' package in R (Laliberté et al. 2015).

To evaluate how aboveground biomass (AGB), CWM trait values, species richness and diversity, and functional diversity indices differ among forests with different disturbance histories (old-growth forests, selectively logged forests, and clear-cut secondary forests), linear mixed models were fitted, including site as a random factor (to account for the possible lack of independence of plots within the sites). The AGB was ln transformed prior to analysis to address the normality and homoscedasticity assumptions, reduce the effect of outliers and account for possible nonlinear relationships between variables. Models were fitted using a Gaussian error distribution with identity link function (normality was tested and confirmed by the Shapiro–Wilk test). Tukey's post hoc test was used to assess the differences in AGB and in species and functional diversity metrics among forests disturbance histories.

To evaluate the relative importance of the different biomass drivers in forests with different disturbance histories, we used AGB as the response variable and species and functional diversity metrics (S, H′, FRic and FDis) as well as CWM trait values (CWM$_{Hmax}$, CWM$_{WD}$ and CWM$_{SS}$) as explanatory variables, including forests disturbance history in interaction factor with each variable. The full model is therefore:

$$\ln AGB = DH*(S + H' + FRic + FDis + CWM_{Hmax} + CWM_{WD} + CWM_{SS}$$

where lnAGB is the ln transformed aboveground biomass; DH is the disturbance history (old-growth, selectively logged and clear-cut secondary forests) with interaction with all other fixed terms; S, H′ FRic and FDis are species richness, Shannon diversity index, functional richness and functional dispersion, respectively (where positive slopes support the niche complementarity hypothesis); CWM$_{Hmax}$, CWM$_{WD}$ and CWM$_{SS}$ are the community weighted mean trait values for species maximum height, wood density and seed

size, respectively (where positive or negative significant slopes support the mass-ratio hypothesis).

Subsequently, we ran all possible subsets of the full model using different combinations of the explanatory variables and ranked them based on the Akaike Information Criterion of the Second Order (AICc). The set of best models (models equally supported) were considered as those with $\Delta AICc \leq 2$ (Burnham and Anderson 2002). Candidate models were excluded when they had more than ten degrees of freedom (df), taking into account that models would be overfitted by too many explanatory variables considering our sample size (90 plots), and the random effect was considered to consume one df. In explanatory studies, it is usually recommended one degree of freedom for every 10 replicates.

The relative importance of each explanatory variable (and their respective ecological hypothesis, i.e., mass ratio and niche complementary) was evaluated by summing the Akaike weights of all models that included the variable of interest (Burnham and Anderson 2002; Burnham et al. 2011) and the direction of the effect of each explanatory variable on AGB was based on the set on best models ($\Delta AICc \leq 2$).

The analyses were performed using the platform R (R Core Team 2015) and the following packages: multcomp (Bretz et al. 2015), lme4 (Bates et al. 2014), lmerTest (Kuznetsova et al. 2016), MuMIn (Barton 2016), and ggplot2 (Wickham and Chang 2016).

Results

Forests disturbance history and AGB

The mean aboveground biomass (AGB) differed significantly among forest disturbance histories (one-way ANOVA, $p < 0.001$, Fig. 1, Tables S2 and S3), and was 276.53 34.68 Mg ha^{-1} (mean standard error) for old-growth forests, 138.95 17.42 Mg ha^{-1} for selectively logged forests, and 65.11 8.34 Mg ha^{-1} for clear-cut secondary forests. These values indicated a reduction in AGB stock of around 50% for selectively logged forests and 80% for clear-cut secondary forests, in comparison with old-growth forests.

Fig. 1 The effect of disturbance history on aboveground biomass (AGB) in the study site. *OG* old-growth forests, *SL* selectively-logged forests, *CC* clear-cut secondary forests. The fitted means were back-transformed from ln. Different letters are significantly different at $p < 0.05$, as per Tukey's test after GLMM. Errors bars represent the 95% of confidence intervals
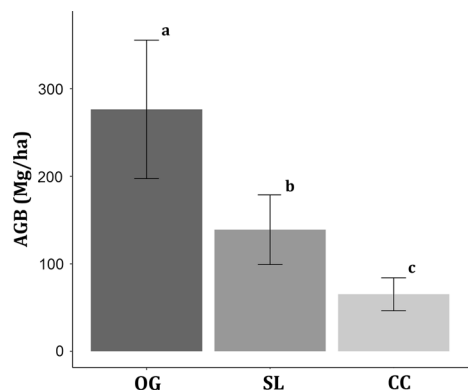
Forests disturbance history and species and functional diversity metrics

Species and functional diversity metrics differed significantly between clear-cut secondary and old-growth forests and between clear-cut secondary forests and selectively logged forests, except for CWM_{WD}. Clear-cut secondary forests had the lowest values of CWM_{Hmax}, CWM_{SS}, species richness, species diversity, functional richness and functional dispersion. Conversely, among the seven forests attributes evaluated, none were significantly different between the old-growth and selectively logged forests (Fig. 2 and Tables S2 and S3). These results indicate that selectively logged forests maintained species and functional diversity equivalent to those of old-growth forest, whereas clear-cut secondary forests had a strong reduction in species and functional diversity and significant shifts toward dominance by early-successional species, with acquisitive trait values and lower biomass storage potential (e.g., lower adult stature and small seed size).

Anthropogenic disturbance histories and the relative importance of biomass drivers

There was only one candidate model with $\Delta AICc \leq 2$ (AICc weight $\approx 23\%$) which contained five first-order explanatory variables and one interaction effect (between disturbance history and FDis) (Table 1). Disturbance history was an important explanatory variable related to forest AGB (relative importance value, RIV $\approx 86\%$, Table 1 and Fig. 4), indicating a strong reduction of AGB in selectively logged and clear-cut secondary forests compared to old-growth forests. Regardless of forests disturbance history, AGB was positively related to CWM_{Hmax} (RIV $\approx 100\%$) and functional richness (RIV $\approx 74\%$) (Figs. 3, 4). When accounting for the effect of disturbance history in the relationships between AGB and forests attributes (i.e., the interaction terms of the best model), functional dispersion was positively related to AGB in selectively logged forests (RIV $\approx 39\%$, Figs. 3, 4). Our results indicate that the mass-ratio hypothesis is a stronger driver of AGB stock independent of forests disturbance history (CWM_{Hmax} was present in all possible models), although the importance of the niche complementarity hypothesis was also supported by the positive coefficient of FRic (for all disturbance histories) and FDis (only in selectively logged forests).

Discussion

We examined how forests under different anthropogenic disturbance histories differ in forest stand biomass, species richness and diversity, and functional diversity metrics, and to what extent these differences can change the relationships of their biomass drivers. We found that clear-cut and selective logging have negative and significant consequences on forest aboveground biomass. However, species and functional diversity of selectively logged forests did not differ in comparison with the old-growth forests. Clear-cut secondary forests had lower values of species and functional diversity metrics, and were dominated by species with acquisitive trait values (e.g., lower adult stature and seed size). Our results suggest that the mass-ratio hypothesis plays a stronger role as driver of AGB compared to the niche complementarity hypothesis, although the importance of the niche

complementarity hypothesis seems to increase in forests under intermediate disturbance intensity (selectively logged forests compared to clear-cut secondary and old-growth forests).

Loss of stand biomass in selectively logged and clear-cut secondary forests

As hypothesized, stand biomass was 50% lower in selectively logged forests and 80% lower in clear-cut secondary forests compared with old-growth forests (Fig. 1). Decrease in stand biomass of forests under selective logging activities is expected because target trees (large and with high economic value) are responsible for most of the biomass (Marshall et al. 2012). However, considering that our selectively logged forests are under low logging intensity, other additional factors might be responsible for reducing stand biomass. For example, the removal of large trees increases light incidence in the lower strata, which can increase the density of lianas and fast-growing pioneer species (with higher growth rates but lower biomass accumulation over time; Poorter et al. 2010). Moreover, the cutting, fall, and transport of trees can damage non-target trees (usually small trees), thus increasing mortality and reducing overall biomass, in addition to delaying the recovery of selectively logged forests (Putz et al. 2012).

Stand biomass in the clear-cut secondary forests reached only 20% of the value of old-growth forests biomass, even after 40 years of regeneration. In a recent study of tropical biomass resilience, Poorter et al. (2016) found that stand biomass in secondary dry forests (< 1.500 mm rainfall, comparable with our study areas) after 20 years after land abandonment was around 70 Mg ha^{-1}, similar to our clear-cut secondary forests with twice the time of regeneration (65.11, 8.34 Mg ha^{-1}). A potential explanation for this slow biomass recovery is that our clear-cut secondary forests are located in a non-forest matrix, i.e., surrounded by croplands and pastures, while the secondary forests evaluated by Poorter et al. (2016) were located in a landscape matrix with mean forest cover of 70% (range from 31 to 100%). Such isolated forests are more vulnerable to diffused disturbances, showing severe changes in environmental conditions, and reduced plant colonization and survival (Poorter et al. 2016). Our result is in agreement with other studies, highlighting that actual biomass and carbon losses from deforestation and forest degradation are still greater than the growth gains by forests regeneration (Baccini et al. 2017), after half a century of secondary succession.

Biodiversity in disturbed forests

As hypothesized, clear-cut secondary forests showed significant shifts in terms of composition and diversity, compared with old-growth forests (Fig. 2 and Tables S2 and S3), which confirms that biodiversity loss is commonly accompanied by losses in functional composition (Allan et al. 2015). The observed reduction in CWM$_{Hmax}$ and CWM$_{SS}$ values reflects the dominance of acquisitive-trait species in the clear-cut secondary forests. The prevalence of these traits is expected in communities under intense disturbance regimes
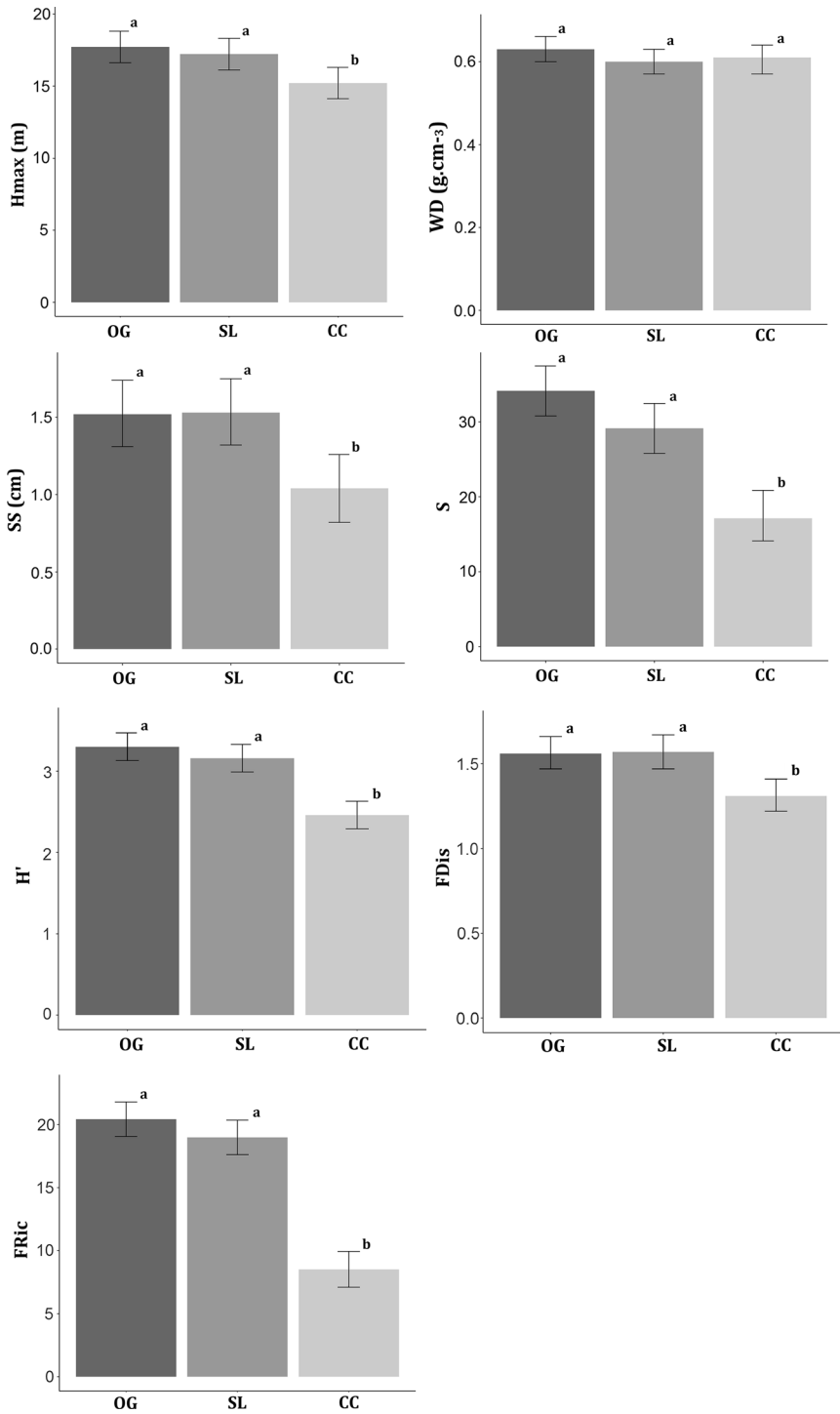
Table 1 The variables included in each of the top 20 models for AGB (aboveground biomass); *df* degrees of freedom, *ΔAICc* difference between the AICc of a given model and that of the best model, *Wt* Akaike weights, ×interaction term, *DH* disturbance history (categorical variable), *FDis* functional dispersion, *FRic* functional richness, *H'* Shannon index, *Hmax* maximum height, *S* species richness, *SS* seed size, *WD* wood density

DH	FDis	FRic	H'	Hmax	S	SS	WD	DH×FDis	DH×FRic	DH×S	DH×SS	df	ΔAICc	Wt
+	+	+		+				+				10	0.000	0.238
+		+		+								7	3.373	0.044
+		+		+					+			9	3.502	0.041
+		+		+			+		+			10	3.877	0.034
+		+		+			+					8	4.379	0.027
+		+		+		+			+			10	4.668	0.023
+		+		+		+						8	5.093	0.019
+		+		+		+	+					9	5.290	0.017
		+		+			+					6	5.311	0.017
+				+	+					+		9	5.318	0.017
+	+	+		+								8	5.500	0.015
+		+		+	+	+					+	10	5.654	0.014
+		+		+	+							8	5.689	0.014
+			+	+								6	5.716	0.014
+	+	+		+		+						8	5.735	0.014
+	+	+		+	+							9	5.922	0.012
+	+			+		+		+				10	5.952	0.012
+		+	+	+					+			10	6.040	0.012
+	+	+		+					+			10	6.041	0.012
+		+		+	+				+			10	6.052	0.012

The pluses mean that the variable/interaction with DH is included in the model

The complete table of parameter estimates (the intercept, standardized variable effects and standard error) can be found in Supplementary material (Table S5)
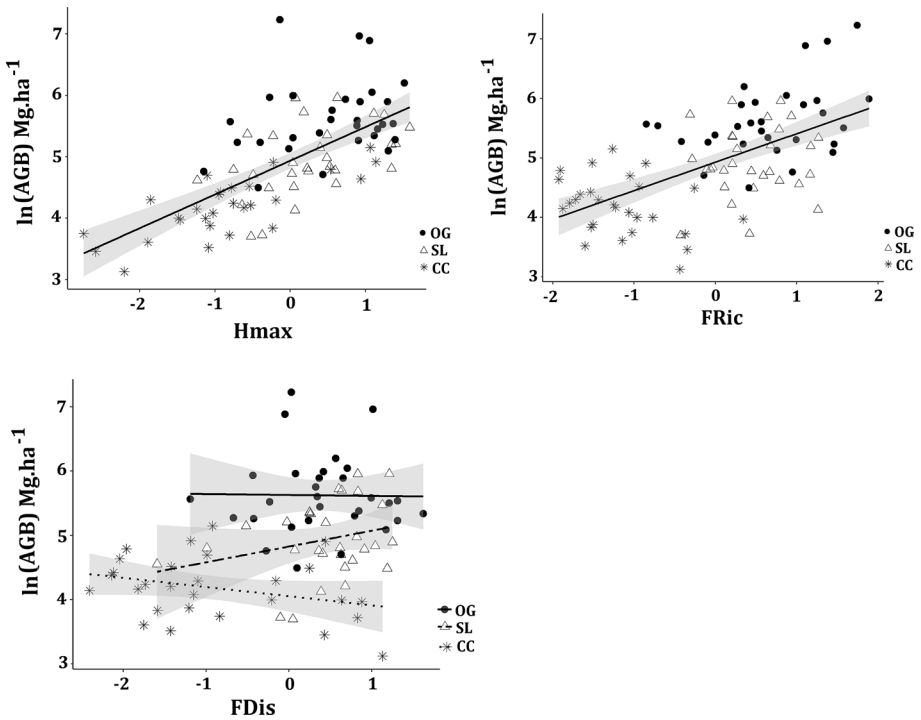
Fig. 3 Aboveground biomass (ln transformed) in relation to variables (standardized) selected in the best model (Hmax, FRic and FDis). *Hmax* maximum height, *FRic* functional richness, *FDis* functional dispersion, *OG* old-growth forests, *SL* selectively-logged forests and *CC* clear-cut secondary forests
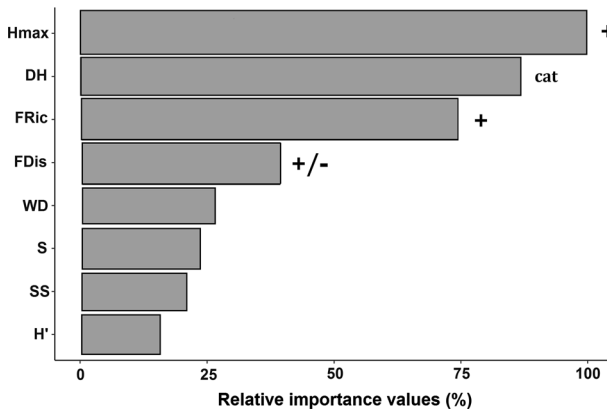
Fig. 4 Relative importance value (RIV) of biomass drivers on AGB, calculated from the sum of AICc weights of all models that included the variable. The directions of effects of explanatory variables present in the best model are indicated by the signs: (+) positive effect and (±) effect dependent on disturbance history. DH does not show effect direction because it is a categorical variable (cat). *DH* disturbance history, *FDis* functional dispersion, *FRic* functional richness, *H′* Shannon index, *Hmax* maximum height, *S* species richness, *SS* seed size, *WD* wood density

(Carreño-Rocabado et al. 2012). With shorter and more open canopies, light becomes a non-limiting resource, so tree species may invest in earlier reproduction rather than increase in height (Ruiz-Jaen and Potvin 2011), and small seed species have an advantage because they can persist longer in the soil seed bank and germinate under favourable conditions (Poorter and Rose 2005). However, the persistence of these tree life history traits, even after 40 years of regeneration, might indicate a loss of resilience, which could be induced by the lack of seed sources in the surrounding matrix (Bengtsson et al. 2003; Hooper et al. 2004), which may also explains their lower biodiversity. Clear-cut secondary forests with old-growth forests nearby tend to recover species richness and diversity faster than do isolated forests (Jakovac et al. 2015).

Our results showed that the differences in species and functional diversity between selectively logged and old-growth forests were not significant (Fig. 2 and Tables S2 and S3). This result was also found in other vegetation studies (Kariuki et al. 2006; Berry et al. 2008, 2010), and shows that even with strong reduction in some ecosystem services (e.g., carbon storage in terms of biomass), these forests can maintain high species conservation values. Especially under low selective logging intensity, i.e. without strong changes in forest structure, the new small gaps can increase light availability and allow new species less adapted to light limitation to coexist with shade-tolerant species, increasing communities species and functional diversity (Peña-Claros et al. 2008; Toledo et al. 2011; Finegan et al. 2015; Rozendaal and Chazdon 2015). Our results indicate that forests under low logging intensity can harbour high species and functional diversity, and the inclusion of degraded forests in REDD+ mechanisms is crucial for the role of these forests in biodiversity conservation.

Shifts in stand biomass predictors among different disturbance histories

Regardless of disturbance history, we found significantly higher AGB in plots with a wider niche range (higher FRic) and dominated by species with high adult stature (CWM$_{Hmax}$) (Table 1 and Fig. 3). These results support both ecological hypotheses (mass-ratio and niche complementarity) as drivers of biomass independent of forests disturbance history, but indicate that the role of the mass-ratio hypothesis is stronger, in line with other studies in tropical forests (Finegan et al. 2015; Lohbeck et al. 2015b; Prado-Junior et al. 2016b). Increase in functional richness should increase the stand biomass because a higher diversification in species traits represents different strategies for resource use, and thus coexisting species make more efficient use of available resources (Finegan et al. 2015). Conversely, the dominance of species with conservative traits (e.g. high maximum height) plays an important role to increase stand biomass. Species with high adult stature usually have a longer life span and typically experience brighter light conditions than small-statured species throughout most of their ontogenetic stages and, therefore, can accumulate more biomass (Poorter et al. 2005; Poorter and Bongers 2006).

We hypothesized that after stronger anthropogenic disturbances, the relative importance of the mass-ratio hypothesis will increase because species experience higher resource availability and lower competition, pressure which can favour local functional convergence (Weiher et al. 1998). However, in selectively logged forests functional dispersion was positively related to higher AGB (Fig. 3), indicating that the role of the niche complementarity as biomass driver is more important in selectively logged forests (intermediate anthropogenic disturbances) than in old-growth forests. Under low logging intensity, due to artificial gaps created when trees are logged, a more heterogeneous light environment is

expected (Nicotra et al. 1999; Fauset et al. 2017), allowing species with different attributes to increase performance according to their local environmental conditions. Conversely, in old-growth and clear-cut secondary forests (extremes of the disturbance history range), where usually the forest canopy is, respectively, taller and more closed or shorter and more open (also see Nicotra et al. 1999; Fauset et al. 2017), the dominance of species with traits related to high forest stand biomass should be more important, and therefore, the role of the mass-ratio hypothesis exceeds the niche complementarity in old-growth and clear-cut secondary forests.

We acknowledge that our study has some limitations; first is that we did not have the amount of timber extracted from the selectively logged forests (i.e. the effect of logging activities on the forests attributes must differ according to percentage of stem basal area removed during the logging), although we assume that the logging intensity is low. Second, we did not have data of species leaf traits (e.g., specific leaf area), which are inextricably linked to the storage of biomass (Poorter and Bongers 2006; Prado-Junior et al. 2016b) as good indicators of light interception and photosynthetic rates, and could improve our analysis of functional diversity, especially because a heterogeneous light environment is expected in forests under different disturbance histories. Third, the plot size (20×20 m) can be potentially too small to study stand biomass, although it is effective to evaluate biodiversity and species composition (Phillips et al. 2003) and, therefore, their relationships with stand biomass. Future studies could benefit from measuring anthropogenic disturbances (e.g. selective logging intensity) and leaf traits. Nevertheless, our results show clear trends that can be discussed in the light of current theory.

Concluding remarks and implications for conservation

This study presents three main results. First, after 40 years of regeneration, clear-cut secondary forests reached only 20% of the forest stand biomass in old-growth forests. Strong losses were observed in species and functional diversity, along with changes in species composition (i.e., dominance of early successional trait species), suggesting that clear-cut secondary forests surrounded by a non-forest matrix may take longer to recover. Second, although the selectively logged forests in this study showed similar species and functional diversity to those of old-growth forests, biomass was still only 50% of old-growth forest, probably due to the removal of large trees with high economic value. This finding highlights the need to expand protection of intact forests against unplanned and illegal selective logging because they reduce the potential value of these forests for mitigating global climate change. Finally, shifts in stand biomass drivers were found among forests with different anthropogenic disturbance histories. While the most abundant species seemed to be the main contributor to above-ground biomass (mass-ratio hypothesis), the importance of the niche complementarity (especially due to increases in functional diversity) seems to be high in forests under intermediate disturbance intensity (e.g., selectively logged forests). An increasing number of studies elsewhere have focused on the drivers of biomass, and our analysis shows that forests disturbance history must be taken into account to fully understand these relationships. Our results highlight that initiatives for biodiversity conservation are a crucial component of tropical forests ecosystem services (e.g., co-benefits between carbon stocks and biodiversity under REDD+), and are positively linked to higher biomass and carbon stocks, especially in forests under some type of anthropogenic disturbance, like most of the remaining Brazilian Atlantic Forest.

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