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A large-scale field assessment of carbon stocks in human-modified tropical forests

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Abstract

Tropical rainforests store enormous amounts of carbon, the protection of which represents a vital component of efforts to mitigate global climate change. Currently, tropical forest conservation, science, policies, and climate mitigation actions focus predominantly on reducing carbon emissions from deforestation alone. However, every year vast areas of the humid tropics are disturbed by selective logging, understory fires, and habitat fragmentation. There is an urgent need to understand the effect of such disturbances on carbon stocks, and how stocks in disturbed forests compare to those found in undisturbed primary forests as well as in regenerating secondary forests. Here, we present the results of the largest field study to date on the impacts of human disturbances on above and belowground carbon stocks in tropical forests. Live vegetation, the largest carbon pool, was extremely sensitive to disturbance: forests that experienced both selective logging and understory fires stored, on average, 40% less aboveground carbon than undisturbed forests and were structurally similar to secondary forests. Edge effects also played an important role in explaining variability in aboveground carbon stocks of disturbed forests. Results indicate a potential rapid recovery of the dead wood and litter carbon pools, while soil stocks (0–30 cm) appeared to be resistant to the effects of logging and fire. Carbon loss and subsequent emissions due to human disturbances remain largely unaccounted for in greenhouse gas inventories, but by comparing our estimates of depleted carbon stocks in disturbed forests with Brazilian government assessments of the total forest area annually disturbed in the Amazon, we show that these emissions could represent up to 40% of the carbon loss from deforestation in the region. We conclude that conservation programs aiming to ensure the long-term permanence of forest carbon stocks, such as REDD+, will remain limited in their success unless they effectively avoid degradation as well as deforestation.

Keywords: Amazon, biomass, forest degradation, logging, REDD+, secondary forests, soil, vegetation, wildfires

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Introduction

Anthropogenic forest degradation is the reduction in the overall capacity of a forest to supply goods and services including carbon storage, climate regulation, and biodiversity conservation. It can result from various types of human disturbances, such as selective logging, understory fires, fragmentation, and overhunting (Parrotta *et al*., 2012). These disturbances are known to impact vast areas of the tropics: for example, around 20 million hectares of humid tropical forests burned in 1997–1998 (Cochrane, 2003), while selective logging affected more than 20% of the world's tropical forests between 2000 and 2005 (Asner *et al*., 2009). In 2007, at its 13th Conference of the Parties, the UN Framework

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Convention on Climate Change (UNFCCC) recognized forest degradation as an important contributor to global carbon emissions by incorporating it into the Reducing Emissions from Deforestation and Forest Degradation (REDD+) mechanism (UNFCCC, 2008). However, limited progress has been made in quantifying carbon losses due to human disturbances (Parrotta *et al*., 2012) and, as a consequence, degradation remains largely overlooked by governments and civil society when compared to deforestation (e.g. Greenpeace, 2009; MCT, 2010).

In tropical forests, the degree of degradation of carbon stocks depends on the type of disturbance (e.g. logging, understory fires, edge effects), the intensity and frequency of disturbance events, and the time elapsed since their occurrence (Laurance *et al*., 2006; Barlow *et al*., 2012; Aragão *et al*., 2014). However, a lack of field data from disturbed forests means that our knowledge of the relative importance of these different factors in explaining changes in overall carbon stocks is very poor (Aguiar *et al*., 2012). Existing studies have focused on alterations of individual components of the total forest stocks (e.g. large trees, dead wood), or on the effects of single types of disturbance in relatively small areas (e.g. Barlow *et al*., 2003; Feldpausch *et al*., 2005; Balch *et al*., 2011; Paula *et al*., 2011). As a result, we still have a limited understanding of the combined effects of multiple forms of disturbance on different carbon pools, which constrains our ability to identify management priorities for avoiding further losses and restoring already degraded forests.

The Amazon is the world's largest tropical rainforest and stores approximately 86 Pg of carbon above and belowground, thereby playing a crucial role in global climate regulation (Saatchi *et al*., 2007; Betts *et al*., 2008). More than 60% of the Amazon lies within Brazil, making this country the world's largest repository of forest carbon (FAO, 2010). Recent government efforts to curb deforestation have led to a sharp decrease in rates of forest clearance, with annual deforestation falling by 79% from 2005 to 2013 (INPE, 2013a). Despite the good news, additional measures are urgently needed to reduce widespread forest degradation due (principally) to selective logging and wildfires: between 2007 and 2010, at least 6.4 million hectares of the region's forests were classified as newly degraded (INPE, 2013b). In 2008 alone, the area affected by logging and wildfires was more than twice the size of the area deforested in the same year (INPE, 2013a,b). Furthermore, the extent of forests disturbed by understory fires can be greatly exacerbated in years of El Niño or other severe drought episodes, due to increased flammability of forests (Alencar *et al*., 2006; Aragão *et al*., 2007; Silvestrini *et al*., 2011).

Here, we present the largest field study to date detailing the effects of anthropogenic forest disturbance (from selective logging, fire, and fragmentation) on the aboveground, dead wood, litter, and soil carbon pools. We use data from 225 forest plots distributed across two regions of the Brazilian Amazon, which together cover an area of more than 3 million hectares and represent different histories of human occupation and associated land-use change (see Gardner *et al*., 2013). We compare carbon stocks from disturbed primary forests (i.e. forests affected by logging and/or fire, but that do not exhibit any signs of having been clear-felled) to two contrasting reference states: undisturbed primary forests (stands with no detectable evidence of past anthropogenic disturbance) and secondary forests (forests regenerating after complete clearance). Specifically, we address the following questions: (i) What are the carbon stocks of human-modified tropical forests, and how do different types of disturbance affect individual carbon pools? (ii) Do different types of disturbance alter forest structure, and, if so, how? (iii) To what extent can variability in carbon stocks in primary forests be explained by differences in the history of forest disturbance, landscape context and topography? We use our results to discuss some of the challenges facing the long-term maintenance of carbon stocks in human-modified tropical forests.

Methodology

Study areas

This study was conducted in two different regions in the eastern Amazon: the municipalities of Santarém-Belterra and Paragominas (Fig. 1a). In each region, 18 study catchments (c. 5000 ha each) were distributed along a gradient of remaining forest cover (Fig. 1b). In each catchment, the number and location of the study plots (10 × 250 m, 0.25 ha) followed a stratified-random sampling design, with the number of plots being proportional to the forest cover of each study catchment, but without prior knowledge of the history of human-induced disturbance or clearance of the sites. Plots were located in evergreen nonflooded forests and were placed at least 1500 m aside from each other and no less than 100 m away from forest edges (Fig. 1c).

The 225 sampled plots encompassed undisturbed primary forests, secondary forests of different ages (from 6 to over 22 years old), and a gradient of primary forests that have been exposed to different levels of disturbance from logging, fire, and fragmentation. Study plots were separated into five different classes (Table 1) based on a combination of physical evidence of selective logging (debris and stumps) and understory fires

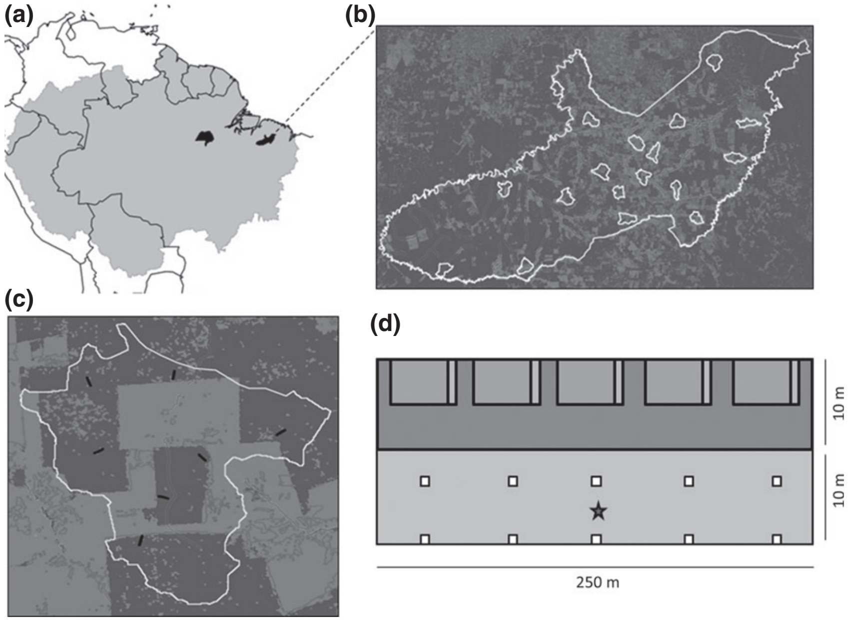

Fig. 1 Sampling design. (a) Location of the two study regions, Paragominas and Santarém, within the Amazon biome (in light gray), (b) Distribution of study catchments (in white outline) in Paragominas, (c) Plots distribution in a study catchment, (d) Carbon stocks assessment: Large dark gray rectangle – survey of live and dead trees, lianas, and palms ≥ 10 cm DBH. All individuals were identified to species level by experienced local parabotanists. Gray rectangles and small light gray rectangles attached – 5 × 20 m subplots for identification and measurement of all live and dead trees, lianas, and palms ≥2–10 cm DBH. Also, measurement of coarse woody debris (≥10 cm diameter in at least one extremity) was carried out in these subplots. Small light gray rectangles – 2 × 5 m subplots for fine woody debris sample (≥2–10 cm diameter in at least one extremity). Squares – 0.5 × 0.5 m quadrats for leaf litter sample. Underneath the first row of litter sampling (5 m away from the plot), composite soil samples were collected at three different depths: 0–10, 10–20, and 20–30 cm. Star – 30 × 30 cm trench for sampling of soil bulk density to calibrate soil carbon stocks. More details of sampling design can be found in the supporting information.

(charcoal and fire scars on stems; following Barlow *et al.*, 2010) found during field surveys, together with a visual inspection of a chronosequence of Landsat images (described below). Physical evidence of human-driven disturbance can remain in the environment for a long period after its occurrence: fire scars and charcoal can be found in forests even after 300 years of the fire event (Heinselman, 1973; Romme, 1982; Yocom & Fulé, 2012), while logging debris of tropical hardwoods may take up to 90 years to decompose (Harmon *et al.*, 1995; Filho *et al.*, 2004). As such, our ground surveys of human-driven disturbance cover a period of time longer than the existence of Paragominas (founded in 1965) and of the migratory boom to Santarém in the 1960s and 1970s. Finally, our extensive soil sampling found no evidence of pre-Columbian settlements (e.g. terra preta) in any of our study plots.

Table 1 Number of sampled plots (0.25 ha) per region according to forest class. In specific analysis where the full dataset could not be used, the sample size is indicated

Forest class	Paragominas	Santarém
Undisturbed	13	17
Logged	44	26
Burned	0	7
Logged-and-burned	44	24
Secondary	16	34
Total	117	108

Sampling and estimation of carbon stocks

The Intergovernmental Panel on Climate Change (IPCC) guidelines for national greenhouse gas inventories recommend that carbon assessments in forested lands should quantify five functionally distinct carbon pools (IPCC, 2006). We estimated carbon stocks in four of these pools (Fig. 1d): aboveground carbon (live trees, palms and lianas), dead wood (coarse woody debris and standing dead trees and palms), litter (fine woody debris and leaf litter), and soil (upper 30 cm; the default sampling depth established by the IPCC). Belowground biomass (i.e. coarse roots) is the only IPCC carbon pool that we did not sample. Carbon was assumed to be 50% of total biomass in the aboveground, dead wood, and litter pools (IPCC, 2006). As plots were laid out on

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the ground, we slope-corrected estimates of aboveground carbon stocks based on the percent incline of each individual study plot. However, results were not sensitive to slope as the relationship between slope-corrected and uncorrected estimates of aboveground carbon yielded a $R^2 > 0.99$. In total, we measured 70 293 stems of trees, palms, and lianas; 8 611 large pieces of coarse woody debris; and undertook 1 125 samples of fine woody debris, 2 250 litter samples, and 4 725 soil samples. Further details on the sampling and estimation of carbon stocks can be found in the supplementary online material.

Anthropogenic and natural drivers of carbon stocks

To further understand patterns of aboveground carbon stocks, we selected a suite of topographic, edaphic, landscape context and human disturbance variables, which have been previously shown to significantly influence aboveground stocks elsewhere in the Amazon (Castilho *et al*., 2006; Laurance *et al*., 2011; Barlow *et al*., 2012). Climate variables were assumed to be similar between and within regions and were not included in these analyses. Topographic variables included the average elevation and slope of all pixels in a 100 m buffer surrounding a study plot, obtained using a digital elevation model (STRM 90 m). Soil texture of each plot was assessed by estimating clay content (g kg^{-1}) of all soil samples through the densimeter method (Camargo *et al*., 2009). Variables related to the landscape context of the sampled plots included the average distance of all pixels that comprise a plot to the nearest forest edge (hereafter distance to edge) and the density of forest edges in a buffer of 250 m surrounding a plot. Both variables were estimated using ArcGIS 9.3 and a 2010 classified Landsat image. The history of human disturbance in the study plots covered by primary forest was estimated using five variables derived from both field and remote sensing information (using a 100 m buffer around the plot area): (i) the percent of total forest area that had been disturbed by logging or fire at least once, (ii) the time-since the last fire event, (iii) the time-since the last logging event, (iv) the number of fire events and (v) the number of logging events. Remote sensing analyses were carried out using a chronosequence of georeferenced 30 m spatial resolution Landsat images from 1988 to 2010 in Paragominas and 1990–2010 in Santarém. Images were first corrected for atmospheric haze and smoke interference and then classified using a decision tree algorithm (see Gardner *et al*., 2013). Where there was evidence of either fire or selective logging in the ground assessment but not in the time-series analyses, we attributed default values of 1 and 25 years for the number and time-since the event, respectively. Assigning a default time-since value of 25 assumes that the event occurred before the baseline of the satellite images and was not missed due to obstruction by clouds. For plots that did not experience a particular type of disturbance (e.g. undisturbed plots or logged but not burned plots), we attributed an arbitrary large default value of 50 years for the time elapsed since the last disturbance event. Finally, using the corrected Landsat images in the chronosequence, we also performed a visual inspection of the area around each study plot to help distinguish highly disturbed primary forests (never clear-cut) from secondary forests (previously cleared), as these can be confounded in ground surveys.

Data analysis and variable selection

We summed the carbon content of all sampled pools in each individual plot to estimate total carbon stocks and then averaged values by forest class (i.e. undisturbed, logged, burned, logged-and-burned, and secondary). Standard error of total stocks was estimated through the root of the sum of the squares of the error of each carbon pool (Pearson *et al*., 2005). We used one way ANOVA with *post hoc* Tukey tests to evaluate differences in the size of each carbon pool and their individual components between the different forest classes. We used *t*-tests on arcsine-transformed data to assess differences in the percentage of carbon stored in each of the aboveground components in disturbed primary forests in relation to the two reference states (i.e. undisturbed primary forests and secondary forests). To select explanatory variables for modeling aboveground carbon stocks, we first examined the correlation structure between all variables using Pearson's correlation coefficients and Variance Inflation Factors (VIF). When variables presented a high correlation ($r \geq 0.7$ and VIF ≥ 3), we only retained the variable that presented the strongest relationship with live aboveground carbon, excluding the others from the models (Zuur *et al*., 2009). This process resulted in the exclusion of edge density, number of fire events, and number of logging events from candidate models. We used generalized linear mixed-effect models (GLMMs) with a Gaussian error distribution to model differences in aboveground stocks. The nested sampling design (plots within catchments) was taken into consideration by setting catchment as a random effect. The distribution of the residuals of the global model (i.e. the model that contains all explanatory variables) was evaluated to confirm model validity. Subsequently, we ran all possible models using different combinations of the explanatory variables and ranked them by their AICc weights (Burnham & Anderson, 2002). Secondary forests were excluded from this analysis as we were only interested in the responses of aboveground carbon stocks in primary forests (disturbed or not) to the selected explanatory variables. The relative importance of each explanatory variable was calculated by summing the AICc weights of all models that included the variable of interest (Burnham & Anderson, 2002). The direction of the effect of individual explanatory variables on the aboveground pool was based only on models with a ΔAICc <2. Finally, to assess the recovery through time of the dead wood, litter, and soil carbon pools in primary forests, we used GLMMs with time-since the last disturbance (either fire or logging) as the only fixed factor and set catchment as the random effect. All analyses were done in R version 2.15.1 (R Core Development Team, 2012). We used the 'AED' package to examine the correlation structure between all variables, the 'nlme' package to build the global model, and the 'MuMin' package to generate the complete subset of models, as well as to assess models' AICc scores and the relative importance of each explanatory variable.

Results

Carbon stocks in human-modified tropical forests

Combining the four carbon pools we assessed, total carbon stocks (Mg C ha^{-1} ± SE) in undisturbed, logged, logged-and-burned, and secondary forests in Paragominas were 275.58 ± 14.09, 238.53 ± 7.62, 187.06 ± 7.50, and 125.58 ± 7.57, respectively. In Santarém, total stocks were 274.35 ± 21.72, 238.13 ± 13.05, 236.87 ± 28.74, 222.24 ± 18.17, and 132.66 ± 11.42 in undisturbed, logged, burned, logged-and-burned, and secondary forests, respectively.

The aboveground pool was particularly affected by human disturbance, exhibiting the largest decrease in stocks (Fig. 2a, Table S1). This was most notable in Paragominas where the amount of aboveground carbon in logged and logged-and-burned forests was 35% and 57% respectively lower than in undisturbed forests. In this region, logged-and-burned forests stored on average 116 Mg C ha^{-1} less than undisturbed forests and only 39 Mg C ha^{-1} more than secondary forests. The dead wood and litter carbon pools were seemingly unaffected by the type of forest disturbance in our comparisons in both study regions (Fig. 2b, c). The soil pool was significantly larger in logged forests than in undisturbed ones in Paragominas (Fig. 2d, Table S1), which was probably due to our undisturbed plots being concentrated in areas where soils were sandier (Figure S1). In Santarém, the soil pool did not present significant differences between forest classes (Fig. 2d). Despite undergoing the greatest reduction, the aboveground pool still held more carbon than any of the other pools across all forest disturbance classes (not considering deep soils).

Effects of disturbance on forest structure

Both selective logging and understory fires had a severe effect on trees ≥10 cm DBH in Paragominas, especially in the largest size class (≥50 cm DBH). Logged and logged-and-burned forests stored 47% and 75% respectively less carbon in trees this size, when compared to undisturbed primary forests (Fig. 3a). All size classes of trees ≥20 cm DBH in this region held significantly more carbon in undisturbed forests than the equivalent size class in disturbed primary forests (Fig. 3). Conversely, there was no significant difference in the amount of carbon stored in logged-and-burned vs. secondary forests for most tree size classes. In contrast to the patterns found in Paragominas, carbon stocks in all size classes of trees ≥10 cm DBH in Santarém were similar between primary forests, regardless of disturbance (Fig. 3).

The relative contribution of individual components to the aboveground carbon pool differed significantly between disturbance classes: trees ≥50 cm DBH were responsible for storing the largest fraction of aboveground carbon in undisturbed forests, but their contribution was markedly lower in logged and logged-and-burned forests. This decline was accompanied by an increase in the relative contribution of smaller trees and lianas (Fig. 4). For example, trees between 2 and 10 cm DBH increased their average contribution to aboveground stocks by 119% and 38% in logged-and-burned forests when compared to undisturbed forests in Paragominas and Santarém, respectively. When comparing disturbed primary forests with secondary forests, the latter stored significantly less carbon in trees ≥50 cm DBH than the former in both regions. The contribution of trees 20–50 cm DBH to aboveground stocks became increasingly similar between secondary and disturbed forests, as well as that of lianas ≥10 cm DBH (Figure S2). The structural similarity of disturbed primary and secondary forests was most pronounced in logged-and-burned forests in Paragominas, where six of 11 components of the aboveground pool had a statistically similar contribution to aboveground stocks to that of secondary forests (Figure S2).

Drivers of change in aboveground carbon stocks in primary forests

Distance to edge was the most important explanatory variable influencing aboveground carbon stocks in

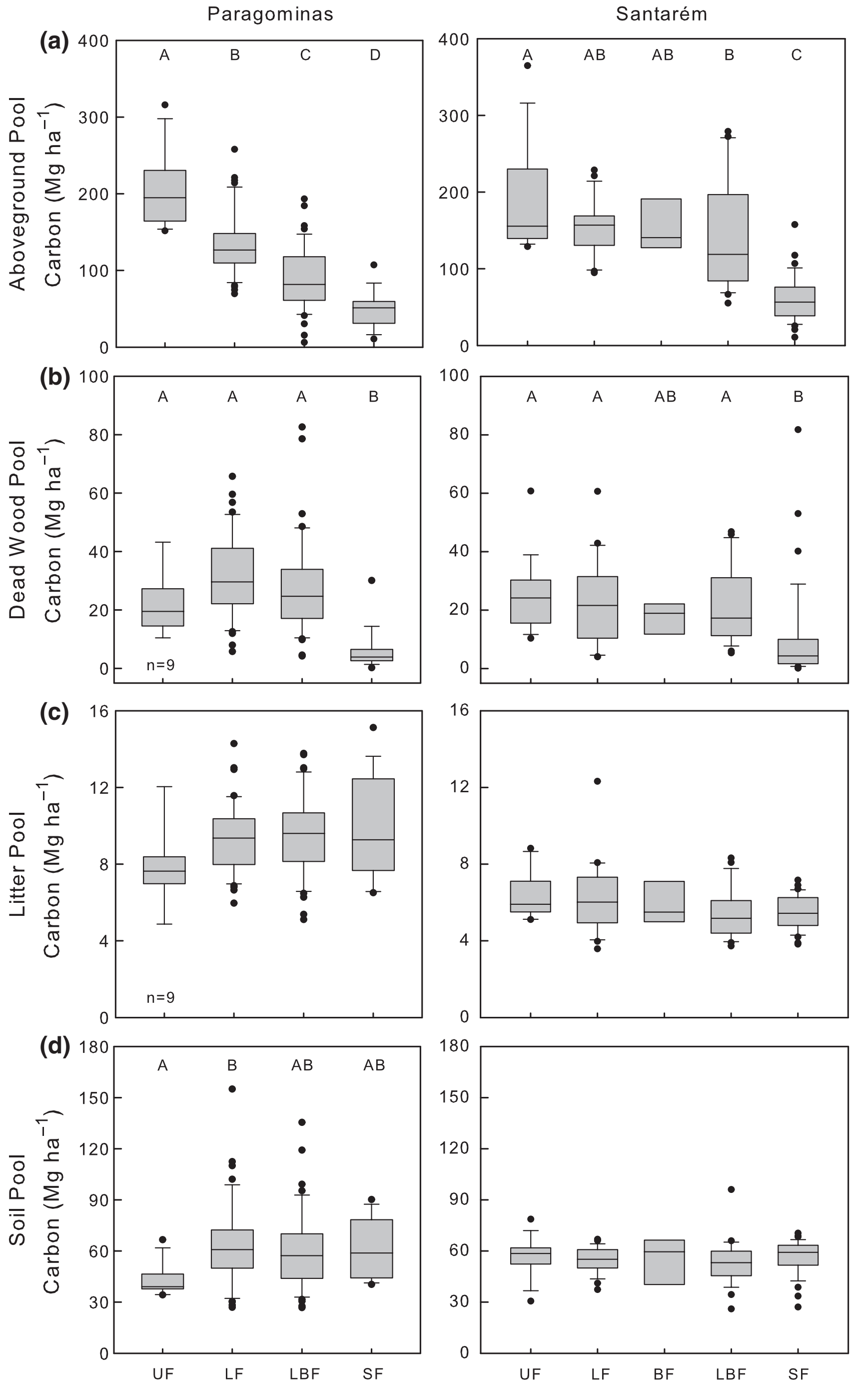

Fig. 2 Variation in the (a) Aboveground, (b) Dead wood, (c) Litter, and (d) Soil carbon pools in both study regions. Unless shown otherwise, sample sizes follow Table 1. Letters indicate forest classes with significantly different means following Tukey *post hoc* tests ($P < 0.05$). Dots represent outliers. UF = Undisturbed forests, LF = Logged forests, BF = Burned forests, LBF = Logged-and-burned forests, SF = Secondary forests.

primary forests of both regions and was positively associated with this pool (i.e. the highest aboveground stocks were recorded the furthest from forest edges; Fig. 5). In Paragominas, time-since the last fire event, terrain slope, and time-since the last logging event also had a strong influence on aboveground carbon (all had relative importance values >0.85; Fig. 5) and were all present in the best model (AICc weight of 0.54; Table S2). In Santarém, terrain slope was the second most important variable (relative importance value of 0.74),

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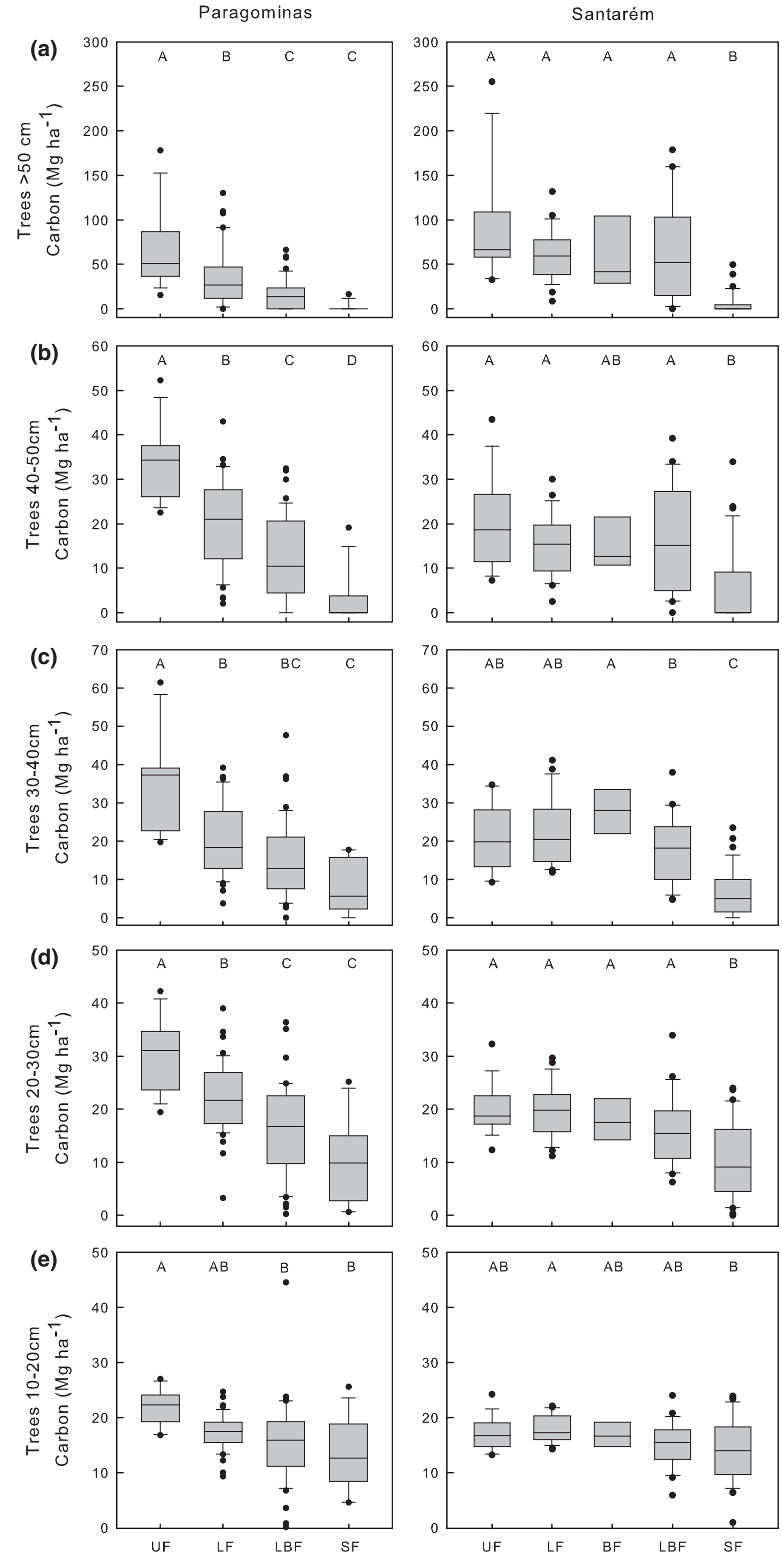

Fig. 3 Variation in the carbon content of the main components of the aboveground pool in Paragominas and Santarém. The main components are: (a) Trees ≥50 cm DBH, (b) Trees 40–50 cm DBH, (c) Trees 30–40 cm DBH, (d) Trees 20–30 cm DBH, and (e) Trees 10–20 cm DBH. DBH = 1.3 m from the ground. Letters represent significant differences ($P < 0.05$) in carbon stored between forest classes. Dots represent outliers. UF = Undisturbed forests, LF = Logged forests, BF = Burned forests, LBF = Logged-and-burned forests, SF = Secondary forests.

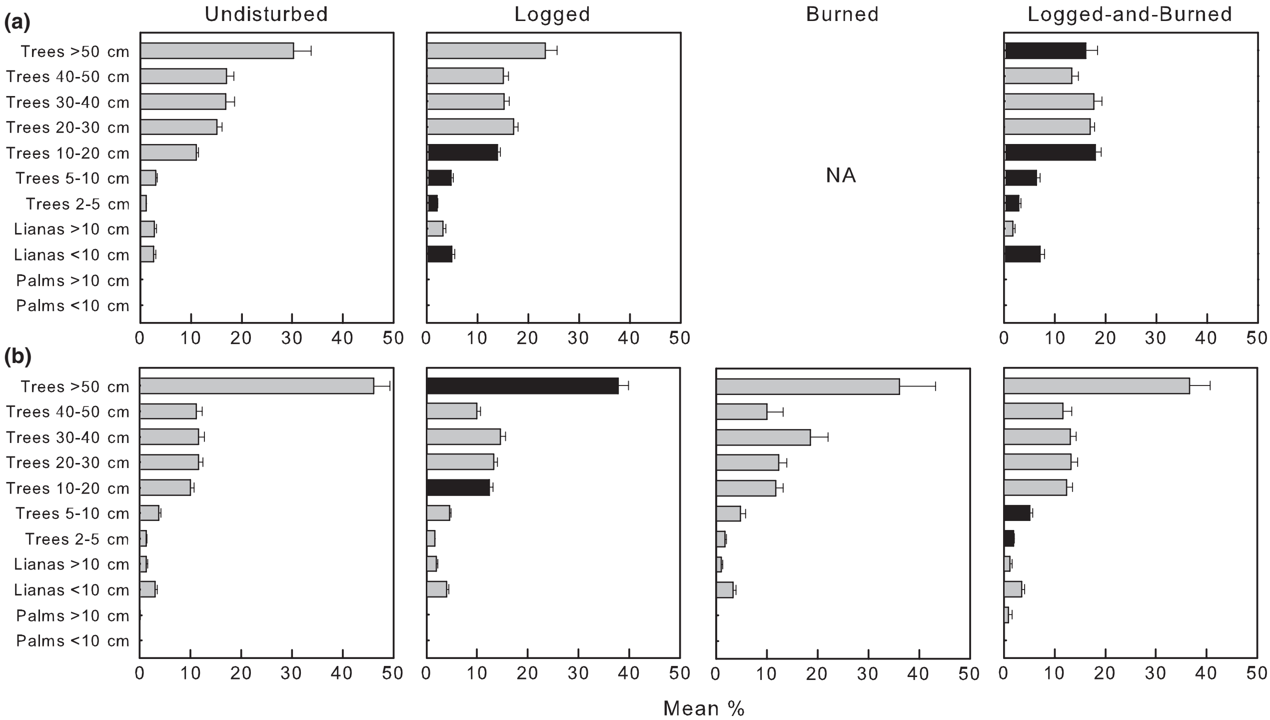

Fig. 4 Mean percentage contribution of 11 different components to the aboveground carbon pool. Results are separated by forest class in (a) Paragominas and (b) Santarém. Error bars indicate standard error. Black bars represent significant differences ($P < 0.05$) from undisturbed forests within the same region.

whereas percentage of area disturbed had a greater effect on aboveground stocks than either time-since the last fire or logging events (Fig. 5). Soil texture and plot elevation had a weak effect on the aboveground carbon pool of both Paragominas and Santarém. Model results were much less clear in Santarém as all the top nine ranked models had a ΔAICc <2 (Table S2).

Assessing the recovery through time of other carbon pools

As disturbance type had no effect on the dead wood, litter, and soil carbon pools (Fig. 2), we built GLMMs to investigate whether this lack of response could be attributed to a rapid recovery following disturbance. There was no effect of time-since the last disturbance

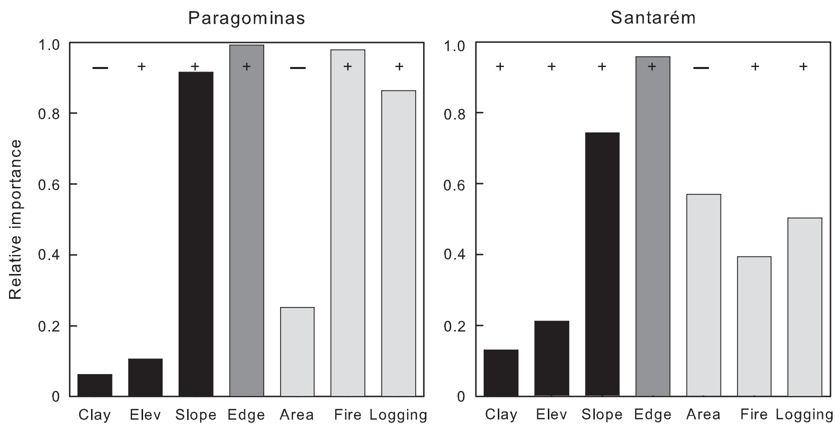

Fig. 5 The relative importance of edaphic, topographic, landscape context, and disturbance variables in determining differences in the size of the aboveground carbon pool. Edaphic and topographic variables (black bars) encompassed Clay = Mean soil clay content per plot, Elev = Mean plot elevation, and Slope = Mean plot slope. Landscape context (dark gray bar) included Edge = Average distance of the plot to the nearest forest edge. Anthropogenic disturbance variables (light gray bars) were Area = % of the plot that was degraded at least once in the satellite image analysis, Fire = Time-since the last wildfire occurrence, Logging = Time-since the last logging event. Signs indicate the direction of the effect of each variable on aboveground stocks.

on any of these three pools in either Paragominas or Santarém: the null model (intercept only) was consistently the highest ranked one, while the models including time-since the last disturbance always presented a ΔAICc >2 (Tables S3–S5).

Discussion

Most ecological research on carbon stocks of tropical rainforests has either focused on monitoring change in relatively undisturbed primary forests (e.g. Malhi *et al.*, 2006; Phillips *et al.*, 2008; Lewis *et al.*, 2009) or on quantifying deforestation and the effects of forest fragmentation on aboveground biomass (Laurance *et al.*, 2011; Paula *et al.*, 2011). We present the first large-scale ground study of changes in carbon stocks across multiple pools in human-modified tropical forests. We show that forest disturbance, particularly when resulting from a combination of both fire and logging, can severely alter forest structure (Fig. 3; Fig. 4), resulting in acute degradation of carbon stocks, with losses being more pronounced in live aboveground carbon than in dead organic matter or soil (Fig. 2). Alongside disturbance type, edge effects also play a major role in influencing aboveground stocks in primary forests (Fig. 5). Despite significant reductions in the carbon stored in disturbed forests, even the most degraded primary forests (i.e. logged-and-burned) still hold more carbon than secondary forests. We examine these findings in terms of the specific effects of disturbance on forest carbon stocks and structure, considering their implications for assessing and monitoring forest carbon, before finally discussing the prospects for carbon conservation in human-modified tropical forests.

Degradation of carbon stocks from anthropogenic disturbance

Human-modified forests are increasingly prevalent in the humid tropics (Achard *et al.*, 2002; Broadbent *et al.*, 2008; Melo *et al.*, 2013), hence understanding the effects of human disturbances on forest carbon stocks is crucial for better practices of forest management and conservation measures. The aboveground carbon pool was the most sensitive to human disturbances with disturbed primary forests containing between 18% and 57% less carbon than we observed in undisturbed forests (Fig. 2). Combining this observed range with Brazilian government remote sensing estimates of the extent of forest degradation (INPE, 2013b) suggests that, in 2010 alone, the Brazilian Amazon could have lost between 0.03 and 0.08 Pg of carbon from the 7 51 000 ha of forest impacted by fire and/or logging – c.40% of the loss from deforestation in the same year (INPE, 2013a). This substantial loss of carbon stocks remains unaccounted for in inventories of greenhouse gas emissions (e.g. MCT, 2010).

Previous studies have shown an increase in carbon stored in the dead wood and litter pools following human disturbances, but most sampling was carried out shortly after the disturbance had taken place (Uhl & Kauffman, 1990; Cochrane *et al.*, 1999; Gerwing, 2002; Keller *et al.*, 2004; Palace *et al.*, 2007). Surprisingly, our results do not show any significant difference between the dead wood and litter carbon pools found in undisturbed and disturbed primary forests. In addition, time-since the last disturbance event had no clear effect on the observed variability in these pools. Our findings could indicate a rapid recovery of both the dead wood and litter pools in disturbed forests, which happened over a shorter period of time than the one analyzed in our study.

The soil carbon pool is known to undergo significant change after tropical forest conversion into other land uses such as pastures (Cerri *et al.*, 2003), but little is known about its response to disturbances in standing forests. Our results show that the first 30 cm of the soil pool in disturbed primary forests contain a comparable amount of carbon as that of undisturbed areas of forest, suggesting that this pool is resistant to impacts from selective logging and understory fires. While impacts of human disturbances on the soil pool may be of particular concern in tropical forests located in peatlands (Page *et al.*, 2002), they appear less important in the nonpeat soils of the Amazon. However, it still remains unclear whether human-induced disturbances affect deeper soils.

Understanding changes in aboveground carbon stocks

In tropical forests, aboveground carbon stocks are influenced by a range of climatic, edaphic, topographic, and human-associated factors. Our understanding of the relative importance of these factors is highly dependent on both the spatial scale of the carbon assessment and the number of variables used to model changes in stocks (Baraloto *et al.*, 2011). At a regional scale (1000s km), variables known to be key in determining differences in plant biomass include total annual precipitation, dry season length, and soil fertility (Malhi *et al.*, 2006; Quesada *et al.*, 2012). At the landscape scale (10s km), elevation, terrain slope, soil texture, and soil fertility have been found to be significant predictors of aboveground carbon (Laurance *et al.*, 1999; Castilho *et al.*, 2006; Paoli *et al.*, 2008; Marshall *et al.*, 2012). Most research looking at the effects of anthropogenic disturbances on aboveground carbon has focused on landscape and plot-scale analysis, finding negative

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effects of selective logging (Lindsell & Klop, 2013), understory fires (Barlow *et al.*, 2012), distance to edge, fragment size (Laurance *et al.*, 1997), and hunting (Poulsen *et al.*, 2013) on this pool.

We assessed carbon stocks at the meso-scale (100s km) with sample sites distributed across more than one million hectares in each study region. Given the scale of our assessment and the similarities of climate both between and within our study regions, we expected that variables related to past plot-level human disturbances would outweigh both measures of landscape context and differences in topography. However, we found that distance to the nearest forest edge (a landscape context variable) was the most important predictor of aboveground carbon in primary forests of both regions (Fig. 5; Table S2). This result is probably because distance to edge acts as a proxy for a multitude of different effects that have negative impacts on plant biomass, such as increase in air temperature and in wind disturbance (Laurance *et al.*, 2002; Ewers & Banks-Leite, 2013). In addition, given the ease of access, forests close to edges are more susceptible to relatively low-intensity and small-scale selective logging and understory fires (Alencar *et al.*, 2006), which could have been cryptic to our remote sensing analysis. Although explanatory variables related to plot-level disturbances were more important in Paragominas than in Santarém, the main results were consistent between regions: aboveground carbon was lower in plots with a more recent history of fire or logging events (Figure S3), as well as in plots where a larger area was disturbed.

Context matters: regional differences in the effects of human disturbance on forest carbon stocks

Although there were some similarities across regions, such as the increase in contribution of small trees to aboveground stocks in highly degraded forests, there were also some important differences. For example, in Santarém only logged-and-burned forests stored significantly less aboveground carbon than undisturbed forests, compared to the situation in Paragominas where all disturbed forests had significantly less carbon. These regional differences are likely explained by their distinct histories and trajectories of human occupation (see Gardner *et al.*, 2013): Paragominas has a more recent history of severe forest disturbance and, in the 1980s, was one of the largest timber extraction centers in the world with 238 operating sawmills (Verissimo *et al.*, 1992). By contrast, 31% of the selective logged plots in Santarém were inside a national reserve where techniques of reduced-impact logging have been used. Although a simple on-the-ground classification of historical disturbance by type (i.e. logged, burned or logged-and-burned) can be of significant help in estimating changes in carbon stocks and forest structure, it also masks important differences regarding the intensity of past disturbances.

Secondarization of disturbed primary forests

In tropical rainforests, large trees are responsible for storing the greatest amount of aboveground carbon (Clark & Clark, 2000; Paula *et al.*, 2011; Marshall *et al.*, 2012). However, they are also exceptionally vulnerable to impacts from logging (Blanc *et al.*, 2009), fire (Barlow *et al.*, 2003), and fragmentation (Laurance *et al.*, 2000). The loss of large trees from disturbed primary forests affects forest structure (Fig. 4) and creates new openings in the canopy (Saatchi *et al.*, 2013), allowing more sunlight to penetrate the forest interior. Following anthropogenic disturbance and the subsequent collapse of vertical structure, there is a proliferation of small lianas and fast-growing pioneer tree species, and as a result, degraded Amazonian forests can shift from high-carbon environments to forests with dense understory and low-carbon content (Figure S4). Our results support previous studies that identified a similar 'secondarization' process, whereby increasingly disturbed primary forests become more and more similar to young secondary forests (Barlow & Peres, 2008; Santos *et al.*, 2008). In fact, our results are likely to be conservative, with large trees in disturbed forests storing even less carbon than reported here as the allometric equations used to estimate vegetation carbon stocks were developed in undisturbed forests, where trees present less crown damage (Clark & Kellner, 2012). Such severe changes in forest structure are likely to have detrimental impacts on biodiversity, potentially leading to cascading effects on ecosystem functions and services beyond carbon storage (Parrotta *et al.*, 2012). Nevertheless, on average these highly degraded primary forests still hold significantly more carbon than secondary forests. Investments in avoiding further disturbance (e.g. fire breaks) in low-disturbed forests can avoid structural shifts and ensure permanence of carbon in human-modified forests, hence constituting a great conservation opportunity.

Assessing and monitoring carbon stocks in degraded forests

Assessing and monitoring changes in forest carbon stocks following disturbance is fraught with difficulty (Parrotta *et al.*, 2012). Major challenges include a poor overall understanding of the responses of carbon stocks to forest disturbance, a lack of appropriate reference levels for deforestation and forest degradation, and uncertainty on how to effectively incorporate forest degradation when designing REDD+ projects (Aguiar *et al.*, 2012; Mertz *et al.*, 2012). The development of reliable, yet simple, protocols to assess and monitor changes in forest carbon is a critical step in addressing these challenges. These protocols should prioritize components of the stocks that both store the most carbon and are the most sensitive to human-associated disturbances and environmental change. Our data demonstrate that the aboveground pool meets both these criteria: it stores by far the largest amount of carbon in tropical forests (when deep soils are not considered) and it is also the most vulnerable carbon pool to human impacts (Fig. 2). Therefore, we recommend this pool to be the focus of initial forest inventories and subsequent monitoring procedures, even in landscapes not yet disturbed. By just measuring aboveground carbon, sampling protocols can account for virtually all the change in total forest stocks following disturbances, as well as assessing over 45% of total carbon stocks even in highly degraded areas (when excluding both roots stocks and soil carbon below 30 cm in depth). Moreover, the aboveground pool is relatively quick to measure when compared to others (Marshall *et al.*, 2012) and, if resources are severely limited, field assessments of stocks can focus only on trees ≥10 cm DBH: this involves identifying and measuring a smaller number of individuals, greatly reducing costs and time.

Assessment of historical disturbances should be viewed as a key component of any forest carbon inventory, as once-disturbed forests are more vulnerable to further disturbances, compromising the long-term permanence of stocks (Cochrane *et al.*, 1999; Alencar *et al.*, 2004; Ray *et al.*, 2005; Barlow *et al.*, 2012). However, to date implementation of REDD+ projects and monitoring of carbon stocks rely heavily on remote sensing analysis, given the impracticability of ground assessments over vast areas (e.g. country-wide). Even though remote sensing techniques to estimate anthropogenic disturbance in tropical forests are improving all the time (Asner, 2009), they will always be limited by the time period over which that sensor has been available. Despite using a 20 year time-series of Landsat images, our remote sensing estimates of fire and logging events are likely to have missed small-scale and low-intensity disturbances (e.g. nonmechanized logging), as well as events that occurred prior to our baseline year. In fact, careful visual inspection of the satellite image time-series was able to accurately match only 55% and 19% of the disturbance events identified through ground assessments in Paragominas and Santarém, respectively. Ground surveys of disturbance signals are therefore invaluable tools for providing basic information on the past disturbance regime in a given area of forest and can help decision makers to evaluate areas more likely to maintain carbon stocks in the long term.

The future of aboveground carbon stocks in human-modified Amazonian forests

In this century, the Amazon region is likely to experience a rise in temperature and an increase in the frequency and extent of drought events (Betts *et al.*, 2013). Severe droughts have already been reported in 1997–1998, 2005, 2007, and 2010, leading to widespread understory fires, which in turn led to an increase in tree mortality and subsequent greenhouse gas emissions (Aragão *et al.*, 2007; Lewis *et al.*, 2011). These fires also induce stress responses from the vegetation, increase fuel load on the forest floor, and render degraded forests more vulnerable to new fires (Cochrane *et al.*, 1999). Other contemporary threats include the growing demand for tropical timber, particularly from emerging economies (Liu & Diamond, 2005; Fearnside *et al.*, 2013), continued use of fire in agriculture (Aragão & Shimabukuro, 2010), and large-scale infrastructure developments in previously remote areas of the Brazilian Amazon (Fearnside *et al.*, 2012). These environmental and economic changes are likely to result in an expansion of degraded forests, especially if conservation efforts and policies remain predominantly focused on avoiding further deforestation.

Our data show that disturbances from logging and understory fires can lead to severely impoverished and degraded forests that store substantially less carbon. Highly degraded primary forests increasingly resemble young secondary forests (Barlow & Peres, 2008) constituting a simplified ecosystem, dominated by few low-stature, fast-growing pioneer species (Tabarelli *et al.*, 2012). To prevent further areas of remaining primary forests being similarly degraded, there is an urgent need to strengthen attempts to effectively incorporate avoided degradation measures in forest conservation and climate mitigation programs, such as REDD+. In addition, active ecological restoration of degraded forests (e.g. through enrichment planting) is a valuable but underused conservation strategy, which could considerably help maintenance of carbon stocks, as well as prevent cascading effects following degradation, such as biodiversity loss (Sasaki *et al.*, 2011; Parrotta *et al.*, 2012). The continuous neglect of the widespread impacts of forest degradation will result in additional, and unaccounted, greenhouse gases emissions from tropical countries, with consequent impacts on the world's climate.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Carbon sampling and biomass estimates.
Figure S1. Proportion of (a) coarse and (b) fine sand in the soil of primary forest plots in Paragominas. Letters indicate forest classes with significantly different means following Tukey *post hoc* tests ($P < 0.05$). Dots represent outliers. UF = Undisturbed forests, LF = Logged forests, LBF = Logged-and-burned forests. The methodology for estimating sand content is described elsewhere (See Gardner *et al*., 2013).
Figure S2. Mean percentage contribution of all the 11 different components of the aboveground carbon pool. Results are separated by forest class in (a) Paragominas and (b) Santarém. Error bars indicate SE. Black bars represent significant differences ($P < 0.05$) from secondary forests within the same region.
Figure S3. Relationship between the aboveground carbon pool and the time-since the last (a) logging event, and (b) fire event in primary forests of both study regions.
Figure S4. Changes in tropical rainforest structure from closed-canopy undisturbed primary forest to open forests with a dense understory dominated by lianas and fast-growing pioneers. All photos taken 10 m away from a 2 × 2 m tarpaulin by E.B. in Paragominas.
Table S1. Mean carbon content (Mg C ha^{-1}) and SE of the four carbon pools assessed in undisturbed, logged, burned, logged-and-burned, and secondary forests across Paragominas and Santarém.
Table S2. Top ranked models of factors driving aboveground carbon stocks in primary forests in Paragominas and Santarém. Generalized mixed-effects models were used, with Catchment set as a random factor and Percentage area disturbed (Area), Mean soil clay content (Clay), Distance to edge (Edge), Mean plot elevation (Elevation), Mean plot slope (Slope), Time-since the last fire event (Fire), and Time-since the last logging event (Logging) as fixed factors. Δ - AICc differences from Model 1 (e.g. Model 2 AICc – Model 1 AICc). Weight – Akaike weights.
Table S3. Results of generalized mixed-effects models using the dead wood carbon pool in primary forests as the response variable. Time-since the most recent disturbance (either selective logging or understory fire) was set as the only fixed factor and Catchment as a random factor. Results are separated by study region. Δ - AICc differences from Model 1 (e.g. Model 2 AICc – Model 1 AICc). Weight – Akaike weights.
Table S4. Results of generalized mixed-effects models using the litter carbon pool in primary forests as the response variable. Time-since the most recent disturbance (either selective logging or understory fire) was set as the only fixed factor and Catchment as a random factor. Results are separated by study region. Δ - AICc differences from Model 1 (e.g. Model 2 AICc – Model 1 AICc). Weight – Akaike weights.
Table S5. Results of generalized mixed-effects models using the soil carbon pool in primary forests as the response variable. Time-since the most recent disturbance (either selective logging or understory fire) was set as the only fixed factor and Catchment as a random factor. Results are separated by study region. Δ - AICc differences from Model 1 (e.g. Model 2 AICc – Model 1 AICc). Weight – Akaike weights.