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Impacts of Fire on Forest Biomass Dynamics at the Southern Amazon Edge

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Summary

Over recent decades, biomass gains in remaining old-growth Amazonia forests have declined due to environmental change. Amazonia's huge size and complexity makes understanding these changes, drivers, and consequences very challenging. Here, using a network of permanent monitoring plots at the Amazon–Cerrado transition, we quantify recent biomass carbon changes and explore their environmental drivers. Our study area covers 30 plots of upland and riparian forests sampled at least twice between 1996 and 2016 and subject to various levels of fire and drought. Using these plots, we aimed to: (1) estimate the long-term biomass change rate; (2) determine the extent to which forest changes are influenced by forest type; and (3) assess the threat to forests from ongoing environmental change. Overall, there was no net change in biomass, but there was clear variation among different forest types. Burning occurred at least once in 8 of the 12 riparian forests, while only 1 of the 18 upland forests burned, resulting in losses of carbon in burned riparian forests. Net biomass gains prevailed among other riparian and upland forests throughout Amazonia. Our results reveal an unanticipated vulnerability of riparian forests to fire, likely aggravated by drought, and threatening ecosystem conservation at the Amazon southern margins.

Introduction

The single largest repository of biodiversity and biomass carbon on Earth is the Amazon forest, still covering almost 5.3 million km^2 and representing a uniquely large and relatively contiguous tropical forest (Aragão et al. 2014). Around the margins of Amazonia are additional, distinctive global biodiversity centres with endemic biota and conservation challenges (Myers et al. 2000). Amazonia holds significant remaining terrestrial biodiversity, provides ecosystem services and economic goods (Gardner et al. 2009) and contributes to the regulation of ecosystem functions such as South American and global hydrological cycles, climates and carbon storage (Aragão et al. 2014).

Amazonia carbon storage (e.g., Malhi et al. 2006) and net carbon sinks (e.g., Phillips & Brienen 2017) are at risk due to environmental change. The evidence of a multi-decadal biomass carbon sink from ground-based measurements (e.g., Phillips et al. 1998, Pan et al. 2011) and atmospheric analyses (e.g., Stephens et al. 2007) indicates a long-term decline in the rate of net carbon accumulation into Amazon biomass (Brienen et al. 2015). The mechanisms related to this decline involve both shortening carbon residence times due to increased mortality rates and levelling off of growth rate increases (Brienen et al. 2015). These long-term basin-wide changes are consistent with drought sensitivity and multiple anthropocentric environmental threats (Phillips et al. 2009, Aragão et al. 2014, Gatti et al. 2014, Anderson et al. 2015). Nevertheless, the potential impact of climate change and its interaction with anthropogenic disturbances (e.g., fragmentation and fire) on South American forests remains highly uncertain (Aragão et al. 2014, Tollefson 2016), and how these ecosystems will feed back on climate change is poorly understood (e.g., Davidson et al. 2012, Aragão et al. 2014).

Regionally, recent droughts and fire have especially impacted forests at the southern Amazon border (Brienen et al. 2015, Doughty et al. 2015, Feldpausch et al. 2016), which have experienced four major droughts over the past two decades allied to abnormalities such as El Niño and other extreme climatic events (Anderson et al. 2015). Thus, before the 2005 drought, long-term monitoring of permanent forest plots indicated significant accumulation of carbon in forest biomass in the order of 0.45 MgC ha^{-1} year^{-1} (Phillips et al. 2009). The decline in the net sink in the last decade has been linked to the increasing frequency of droughts, especially in the south (Phillips & Brienen 2017), accompanied by enhanced fire-mediated carbon emission with land-use intensification (Anderson et al. 2015).

Recent climate trends (e.g., Jiménez-Muñoz et al. 2016) and climate model projections (e.g., Chen et al. 2016) indicate more frequent and intense droughts with hotter dry seasons in southern Amazonia interacting synergistically with fire (Brando et al. 2014, Aragão et al. 2018). During the 2010 drought, for instance, up to c. 13 000 km^2 or c. 4.5% of the remaining pristine old growth forest and 60 000 km^2 or c. 28% of remaining Brazilian Cerrado burned in Mato Grosso, releasing c. 56 Tg of carbon into the atmosphere according to analysis of multi-temporal satellite-derived data (Anderson et al. 2015).

The extensive Amazon–Cerrado Transition Zone (hereafter, ZOT) supports a wide range of different vegetation types, including savanna and various forest formations (Ratter et al. 1973, Marimon et al. 2006, Marimon et al. 2014). Understanding the transitions in vegetation structure and composition here has been the focus of several recent studies (e.g., Marimon et al. 2006, Marimon et al. 2014, Morandi et al. 2016), with soil properties, fragmentation, frequency of fire, and local water supply all playing a role (e.g., Brando et al. 2014, Veenendaal et al. 2015). While the ZOT has experienced more frequent droughts in the last two decades (Anderson et al. 2015), lack of long-term monitoring here has prevented an evaluation of their ecosystem impacts. The ZOT also lies within the 'arc of deforestation', where the new agricultural frontiers that opened in the late twentieth century continue to advance and consolidate (Morandi et al. 2016). It is plausible that the interactive outcome of drought intensity, deforestation and burning at the ZOT will intensify tree mortality and carbon release to the atmosphere (Anderson et al. 2015), with unpredictable feedbacks on regional and global climate change (e.g., Nepstad et al. 2008, Nobre et al. 2016).

A key conservation challenge within the ZOT, therefore, is to understand the current trajectory of ecosystem change and which factors may help – or hinder – efforts to protect remaining ecosystems. While forests in the ZOT are exceptionally dynamic and variable compared to other forests in Amazonia and beyond in the tropics (Phillips et al. 1994, Marimon et al. 2014), and in spite of modelling and experimental work on the drivers of vegetation dynamics in the ZOT (e.g., Hirota et al. 2010, Dionizio et al. 2018, Silverio et al. 2019), there has been little attempt to actually assess on the ground how remaining vegetation here has fared. However, a state-wide network of monitoring plots capable of assessing ecosystem functions and change in relation to environmental impacts is now available in the ZOT of Mato Grosso (Marimon et al. 2014, Morandi et al. 2016). Plots with up to a decade or more of careful tree-by-tree records from across the region provide an opportunity to track and analyse forest responses to the changing environment. Here, we attempt to analyse for the first time whether forests here have actually accumulated biomass and to explore the likely environmental drivers of changes, with a particular focus on the threats of fire and drought, as well as the potential for forests with local riverine water sources to mitigate these threats.

Our approach involves evaluating the stocks, net balance and gross fluxes of biomass among the forest ecosystems in the ZOT, both as a whole and when analysed at the level of different vegetation types. We hypothesize that forests here have gained biomass, in parallel with other parts of Amazonia (Brienen et al. 2015), but that there will be significant variation in carbon balance between forest types (Brienen et al. 2015, Flores et al. 2017). In particular, we expected that this will be related to the distinctive susceptibility of vegetation types to fire in the ZOT, as occurs elsewhere in Amazonia (Flores et al. 2017). Furthermore, given that the ZOT is climatically susceptible to moisture deficiencies, we expect riparian forests to behave differently from upland formations – either losing biomass over time as a consequence of greater sensitivity to the impacts of drought and fire (e.g., Flores et al. 2017) or gaining it if their locally enhanced water supply mitigates these threats. In summary, we aimed to: (1) estimate the long-term biomass change rate; (2) determine the extent to which forest changes are influenced by forest type and fire; and (3) use these results to evaluate drivers of biomass change and to assess the threat to forests from upcoming environmental change in the ZOT.

Methods

Study Area

Our study is based on forest in the ZOT between Amazon and Cerrado in eastern Mato Grosso (Brazil). Vegetation inventories were conducted from as early as 1996 to as recently as 2016, with most censuses occurring between 2007 and 2016. Among the 30 permanent monitoring plots, 18 represent terra firme (upland forest) and 12 riparian forests, and each was sampled at least twice between 1996 until 2016 (Supplementary Table S1, available online). The plots span 1200 km of spatial extent in the ZOT (Supplementary Fig. S1). The climate in our study area varies from typical savanna (Aw), with a rainy summer and a dry winter, to wet tropical monsoon (Am) according to the Köppen classification (Peel et al. 2007, Alvares et al. 2013). Average annual precipitation varies from 1508 to 2353 mm, and average temperature from 24.1°C to 27.3°C.

Our data set represents the most complete, standard and systematic information yet acquired from permanent monitoring of different vegetation types in any neotropical forest–savanna transition zone. It includes a range of phytophysiognomies – riparian forests, flooded forests (known locally as 'impucas'), seasonal perennial forests, seasonal deciduous forests, open ombrophyllous evergreen forests, monodominant forests and cerradão forests. We classified each forest plot according to association with water courses, including riparian and floodplain forest as one category and all upland forests as another (hereafter, riparian and terra firme, respectively). We also recorded the occurrence of burning events for comparative analysis of dynamics of aboveground biomass (AGB). Burning evidence was identified at each census by field observation of fire scars and burned stems, and any damage and death due to fire was recorded during the census. Burning events were observed at least once in eight riparian forests, while four of them did not burn. On the other hand, fire occurred only in one upland cerradão forest.

In each plot, vegetation was sampled in 25 subplots of 20 × 20 m each, totalling 1 ha, with some minor exceptions (Supplementary Table S1). All trees were identified, tagged with a specific number and measured in terms of their diameter following standard RAINFOR protocols (Phillips et al. 2010), representing more than 20 000 trees in the 30 ZOT plots. The average number of censuses

Table 1. Means and standard errors of net aboveground biomass change (Mg ha⁻¹ year⁻¹), evaluated by vegetation type and burning occurrence among plots for the whole period and within plots for specific intervals before and after the 2010 drought. Paired t-tests compare non-burned versus burned census intervals within plots.

	All plots	Terra firme	Riparian
Whole period	−0.66 ± 0.99 (n = 30)	+1.12 ± 0.64* (n = 18)	−3.32 ± 2.11 (n = 12)
Unburned	+1.37 ± 0.57* (n = 21)	+1.09 ± 0.68 (n = 17)	+2.56 ± 0.40* (n = 4)
Burned	−5.39 ± 2.45[a] (n = 9)	+1.67[b] (n = 1)	−6.268 ± 2.59* (n = 8)
Pre-2010[c]	+0.20 ± 1.10 (i = 13)	+0.52 ± 1.38 (i = 8)	−0.32 ± 2.01 (i = 5)
Unburned	+0.91 ± 3.75 (i = 9)	+0.10 ± 4.39 (i = 6)	+2.53 ± 1.53 (i = 3)
After mid-2010[c]	+0.27 ± 0.63 (i = 53)	+0.58 ± 0.73 (i = 35)	−0.35 ± 1.22 (i = 18)
Unburned	+1.13 ± 4.29* (i = 46)	+0.72 ± 4.62 (i = 36)	+2.57 ± 2.47* (i = 10)

[a] Marginally significant values, possibly due to small sample size (p < 0.10).
[b] Indicates absolute value due to only one sample.
[c] Full comparisons of pre-2010 and during and after the 2010 drought are not shown in the main text, given that they follow the same patterns observed for the whole period and there are not enough degrees of freedom for all burned combinations.
*Significant difference from a mean of 0 according to one-sample t-tests (or Wilcoxon rank tests for non-normal data).
'i' denotes the number of inventories (or censuses) within each class in the table, which may reflect remeasurements for multiple plots.

per plot was 3.2 (range: 2–8). Species were identified based on voucher collection and direct expert observation, and all names were checked for synonymy according to Brazilian Flora 2020 (http://floradobrasil.jbrj.gov.br) using the *flora* package in R; plot census data were rigorously reviewed for consistency and potential measuring errors, and they were deposited in the ForestPlots.net database (Lopez-Gonzalez et al. 2012; https://www.forestplots.net).

AGB Estimation

To enable standardized and accurate comparative analysis of the biomass change of multiple vegetation inventories at plot scale, we used recently developed allometric models to estimate biomass, accounting for tree diameter, woody specific gravity and tree height. Thus, we employed the Chave Moist equation, where AGB is calculated according to the following log–log model (Chave et al. 2014): $\ln(AGB) = \alpha + \beta \ln(\rho \times D^2 \times H) + \varepsilon$, where ρ, D^2 and H are woody specific gravity, tree diameter at breast height and tree height, respectively, and the ε error term is assumed to be normally distributed. The parameters α and β are model coefficients estimated from ordinary least squares regression, yielding 0.0673 and 0.9760, respectively, in the AGB estimation model: $AGB_{est} = 0.0673 \times (\rho \times D^2 \times H)^{0.976}$ (details in Chave et al. 2014). Height was estimated using a Weibull regional equation parameterized for Brazilian shield forests (Feldpausch et al. 2011, 2012). AGB was estimated using functions available in the online version of the ForestPlots.net platform (Lopez-Gonzalez et al. 2012; https://www.forestplots.net).

Data Analysis

Net biomass change rates were derived and analysed both at the level of each interval and for each plot as the difference between total standing biomass at the final census and the first census divided by the interval length. Gains of woody biomass ('tree growth' plus 'recruitment') and biomass loss ('mortality') were computed at the stand level for each interval between successive censuses and for each plot using methods described elsewhere (Talbot et al. 2014, Brienen et al. 2015). To describe overall trends, we report averages and standard errors considering multiple sample plots and censuses along with one of the categorical factors: riparian or terra firme; burned or unburned; pre-2010 or during and after 2010. The one-sample Wilcoxon test was used to compare mean AGB net change rate variation from zero, after checking for non-normality with a Shapiro–Wilk test (Supplementary Fig. S2(a)); otherwise, a one-sample Student t-test was used.

Welch's t-tests were used to compare mean AGB net change rates among burned and non-burned forests and among riparian and terra firme forests, and as an alternative to the normal sample distribution, we used two-sample Wilcoxon tests after checking for normality, unequal sample sizes or heterogeneous variances. For the comparison between pre-2010 and during and after 2010 drought, we used only unburned plots to disentangle the direct effect of fire from drought. The same procedures were used for statistical analysis of productivity and mortality rates. All analyses were conducted in R (R Core Team 2017).

Results

Long-Term AGB Dynamics

Among all forest plots monitored in our study, we estimate a net overall biomass balance (mean ± standard error) of −0.66 ± 0.99 Mg ha⁻¹ year⁻¹ (Table 1 and Supplementary Table S2). Despite substantial plot-to-plot variation in biomass dynamics (5.43 standard deviations; Supplementary Fig. S2(a) and S2(b)), overall changes in net AGB among plots remained at balance over the monitored period (V = 260, p = 0.584). Terra firme forests gained 1.12 ± 0.64 Mg ha⁻¹ year⁻¹, while riparian forests lost −3.32 ± 2.11 Mg ha⁻¹ year⁻¹. Despite similar rank net AGB change among two forest types (W = 75, p = 0.171), only terra firme had gains greater than zero (V = 133, p = 0.038).

Determinants of AGB Net Change

Markedly divergent net AGB change among plots was due to burning effects (W = 31, p = 0.003). Thus, for example, while unburned forests had net gains (+1.37 ± 0.56 Mg ha⁻¹ year⁻¹; t = 2.42, df = 20, p = 0.025), there were significant losses of −5.39 ± 2.45 Mg ha⁻¹ year⁻¹ in burned forests (t = −2.20, df = 8, p = 0.059). Moreover, the burning effect was much more severe in riparian burned forest (−6.27 ± 2.59; t = −2.42, df = 7, p = 0.046), contrasting with average gains in unburned riparian forests (+2.56 ± 0.40; t = 6.36, df = 3, p = 0.008) or the average balance in terra firme forests (1.09 ± 0.68; t = 1.61, df = 16, p = 0.128) (Fig. 1).

The difference in biomass change between unburned and burned forests was entirely driven by mortality processes, since neither forest type nor fire had any effect on AGB productivity (gain plus recruitment by Mg ha⁻¹ year⁻¹; W = 314, p = 0.800 and W = 552, p = 0.5507, respectively; Fig. 2(a)). Instead, AGB mortality was closely associated with burning occurrence (W = 580, p < 0.001), with mortality in riparian burned forests being on average

8.26 ± 1.33 Mg ha^{-1} year^{-1}, while it was only 2.10 ± 0.32 Mg ha^{-1} year^{-1} in riparian unburned forests, 3.42 ± 0.41 Mg ha^{-1} year^{-1} in terra firme unburned forests and 4.45 ± 1.03 Mg ha^{-1} year^{-1} in terra firme burned forests (Fig. 2(b)). Rates of tree mortality were not related to forest type in isolation (W = 578, p = 0.348). Overall, increased tree mortality associated with burning occurrence has driven rapid biomass loss in riparian forests but not in terra firme forests over the average time of monitoring, which spanned from *c.* 1 to 7 years between inventories (Supplementary Table S1).

There was no effect of the 2010 drought in isolation on the biomass balance, woody productivity or mortality in terms of AGB. However, there was a significant relationship between burning occurrence and the 2010 drought (t = –2.19, df = 26.65, p = 0.037; Supplementary Fig. S3). Despite this, no relation was found between maximum climatological water deficit (MCWD) and biomass change (R^2 = 0.001, F$_{(1, 28)}$ = 0.018, p = 0.894), which we attribute to broad year-to-year variation in the effects of climate on vegetation dynamics (including biomass gains and losses).
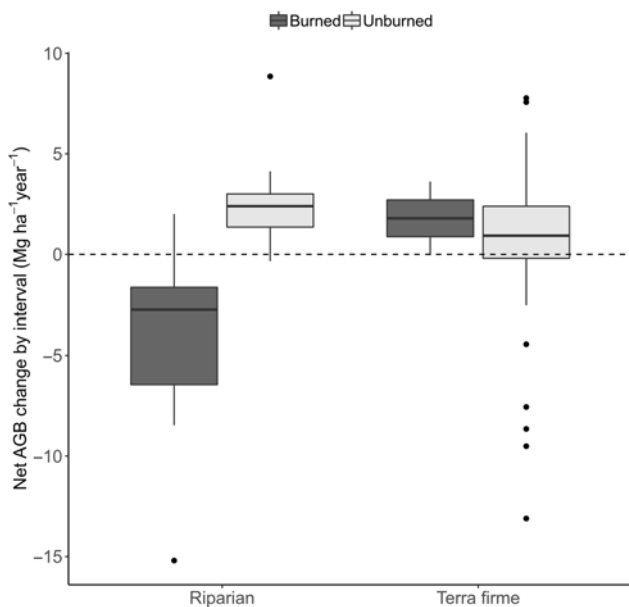

Fig. 1. Box-and-whisker chart showing variation in whole period net biomass change rates in Mg ha^{-1} year^{-1}, calculated as the aboveground biomass (AGB) difference within plots divided by the total time elapsed (averaged over the years) and plotted against forest type and burning occurrence.
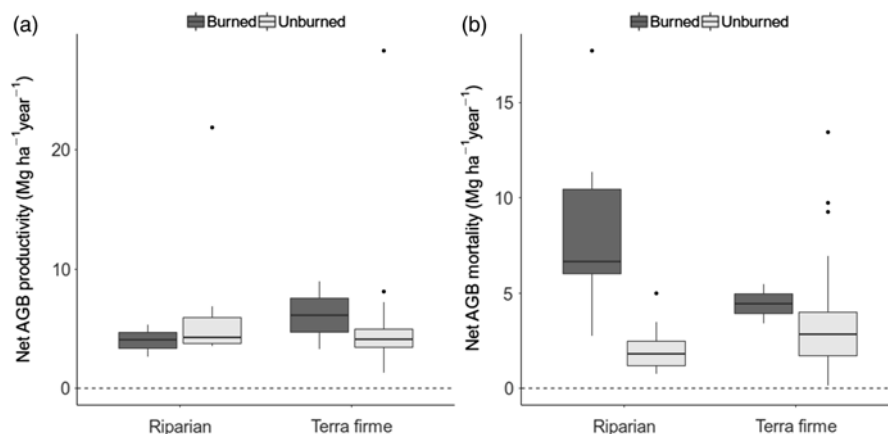
Plot-Scale Variation in AGB

At the individual plot scale, there was substantial variation; however, every plot with magnified loss of biomass was burned at least once in the studied period (Fig. 3 and Supplementary Table S2). For instance, PEA-06 lost biomass at the fastest rate, decreasing by –15.20 Mg ha^{-1} year^{-1} in one interval between 2008 and 2016, followed by GAU-01 with –8.47 Mg ha^{-1} year^{-1} between 1999 and 2013. Among unburned plots, net losses in ALF-02 (–5.67 ± 4.90 Mg ha^{-1} year^{-1} from 2008 to 2013) are associated with a low productivity of 4.60 ± 4.91 Mg ha^{-1} year^{-1} and a high mortality -8.78 ± 4.66 Mg ha^{-1} year^{-1} over the monitored period (Supplementary Table S2). Despite not being burned, TAN-03 lost –2.98 Mg ha^{-1} year^{-1} from 2009 to 2015, where a low productivity 3.60 ± 1.37 Mg ha^{-1} year^{-1} and a high mortality –6.19 ± 1.78 Mg ha^{-1} year^{-1} appear consistent with expectations of drought impacts. Large net increases were found elsewhere, such as in FLO-02 (+5.94 ± 0.12 Mg ha^{-1} year^{-1} between 2010 and 2015), POA-01 (+5.17 ± 5.16 Mg ha^{-1} year^{-1} from 2014 to 2016) and ALF-01 (+1.56 ± 0.39 Mg ha^{-1} year^{-1} from 2002 to 2013) (Supplementary Fig. S2(b)). Overall, this suggests no consistent region-wide signal of impact of recent droughts.

Discussion

Long-Term Biomass Change

Firstly, our results indicate that forests in the ZOT remain in balance, taking up carbon from the atmosphere at the same rate as losing it. Permanent monitoring plots elsewhere in Amazonia indicate significant spatial variation in biomass and productivity (e.g., Johnson et al. 2016) and significant changes over time (e.g., Phillips et al. 2009, Brienen et al. 2015), showing that both spatial and time-variable environmental factors modulate Amazon forest dynamics. Nevertheless, substantial uncertainty on the future biomass balance of Amazon forest remains (Huntingford et al. 2013), and an oft-neglected source of uncertainty is the ecological diversity within Amazonia ecosystems themselves (Levine et al. 2016).

The apparent rate of change in AGB in unburned forests (net gain of *c.* 1.4 Mg ha^{-1} year^{-1}, albeit with substantial site-to-site variation) is comparable to values recorded for decades across the transitions zones of Amazon (Phillips & Brienen 2017) as well as African (Lewis et al. 2009) and Asian tropical forests (Qie et al. 2017). This suggests that the ultimate drivers of this sink may be the same widespread processes, possibly related to the planet-wide

Fig. 2. Box-and-whisker charts showing variation in rates of biomass gain (a: productivity) and loss (b: mortality) in Mg ha^{-1} year^{-1}, calculated by census-to-census aboveground biomass (AGB) change within plots and plotted according to forest type and burning occurrence.
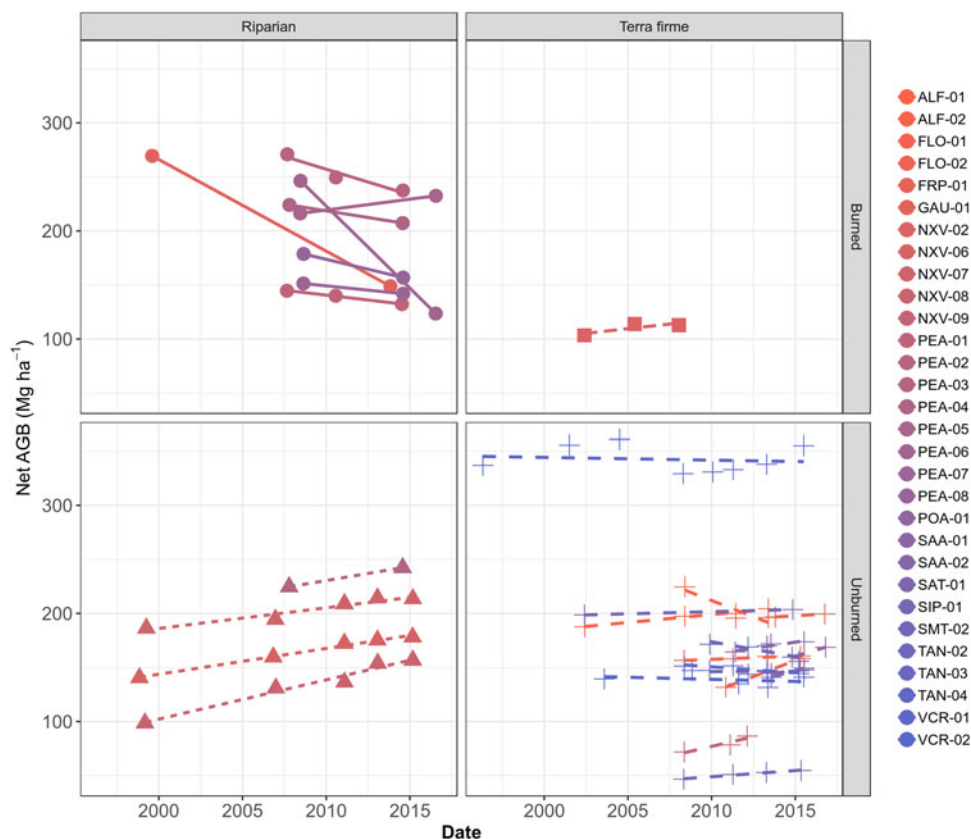
Fig. 3. Plot-scale temporal variation in above-ground biomass (AGB) in Mg ha⁻¹, split among forest types and according to burning occurrence over the monitored period.

increase in gross primary production of more than 30% over the past century (Campbell et al. 2017). However, at the ZOT, we observed that the net rate of biomass change was significantly greater (more positive) in terra firme forests than in riverine forests (1.12 ± 0.64 and –3.32 ± 2.11 Mg ha⁻¹ year⁻¹, respectively). To our knowledge, this is the first time a biomass dynamic comparison has been attempted anywhere in Amazonia using multiple permanent monitoring plot data, and the results show that the Amazon carbon sink conceals substantial long-term variation from one forest type to another.

Drivers of Biomass Change

Our results suggest that the different forest ecosystems here vary in their capacity to store and take up carbon, and that this is driven primarily by their sensitivity to fire, despite the potential interaction with drought (Brando et al. 2014, Alencar et al. 2015). In our study, overall, burned riparian forests lost biomass, but unburned riparian forests and terra firme forests gained biomass. Notably, it is likely that differing responses to ongoing environmental changes can be expected among these different forest ecosystems (Levine et al. 2016, Esquivel-Muelbert et al. 2017, Flores et al. 2017). However, although we could not demonstrate direct effects of the 2010 drought from our long-term data before this period, a partial correlation between burning occurrence and drought was evident, suggesting that fire-prone ecosystems may suffer most from a fire–drought interaction (Brando et al. 2014). Drought potentially increases the flammability of riparian forests, which seem much less resilient to burning events than upland forests at the scale analysed here and elsewhere (de Faria et al. 2017, Flores et al. 2017).

Our results show that riparian forests are losing their capacity to take up carbon because fire is causing high biomass mortality

rather than impacting forest regrowth. The impacts of fire presumably extend well beyond the forest biomass balance, including also the plant and animal species compositions of the forests, grass invasion and edge effects (Silvério et al. 2013). The comparison among forest types suggests that riparian forests are not sensitive to direct drought effects – gaining biomass even during and after the severe drought event of 2010 – but instead they are more impacted by burning events. Despite this, some of our plots have suffered biomass loss not associated with burning occurrence (Supplementary Fig. S2(b)), and we suggest that a combination of drought and edge effects due to forest fragmentation may also be playing a role here as in another parts of Amazonia (Alencar et al. 2015, de Faria et al. 2017, Rappaport et al. 2018).

Amazon-wide, fire is associated with drought, and remote sensing analyses show that this is much more frequent during extreme drought events (Chen et al. 2013, Aragão et al. 2014, 2018, Brando et al. 2014). Thus, indirect effects related to enhanced forest flammability caused by drought are also plausible here in the ZOT, given that MCWD seemed to vary widely after the 2010 drought and was associated with plots where burning had occurred (Supplementary Fig. S3). In riparian forests, fires deliberately set to stimulate grass regrowth (Silvério et al. 2013) may invade forest areas more frequently and intensively in drier years. Associated with organic fuel sources of riparian forests, soils may magnify burning intensity, causing biodiversity erosion and biomass loss with a clear tendency towards the biotic homogenization of tree taxonomic composition (Da Silva et al. 2018).

The long-term association between drought and fire (e.g., Chen et al. 2013) and the recent 2015–2016 El Niño spike in fire frequency (Aragão et al. 2018) show that this is an ongoing threat at the ZOT. Remote sensing analyses also suggest that elsewhere in Amazonia floodplain forests are more sensitive to the joint

effects of drought and fire (Flores et al. 2017). Floodplain forests seem more vulnerable because of naturally higher flammability compared with upland forests, with larger masses of exposed root mats or fine litter in the soils that may burn and spread fire easily in drier years. Our long-term monitoring on the ground thus validates and advances our understanding of the trends identified by satellite and previous field reports for Amazon riparian forests in relation to fire sensitivity (de Resende et al. 2014, Maracahipes et al. 2014, de Almeida et al. 2016).

Overall, our results suggest that the synergistic effects of ongoing climate change and widespread fires (Chen et al. 2013, Brando et al. 2014) are the main threats to Amazonia's stability, especially along riparian and flooding forests, corroborating other studies (e.g., Alencar et al. 2015, Flores et al. 2017). In this respect, the forests at the southern Amazon edge are at particular risk because of the large area of contact edges between riparian forest ecosystems and adjacent savannas and agriculture, which increase incidental burning risk (Chen et al. 2013). The existence of extensive variability among floodplain forests (Schöngart et al. 2017), and also regarding upland forest floristic composition and structure (Alencar et al. 2015), should be extensively considered in future analysis of biomass and carbon dynamics in the face of ongoing environmental threats throughout the Amazon basin.

Implications for Forest Conservation

The pathway to potential 'biomass collapse' (Laurance et al. 1997) may take different forms in different ecosystems of Amazonia. Here at the southern edge, the joint effects of ongoing climate change and widespread and uncontrolled burning for land clearance and pasture management represent twin threats. Our long-term plots provide substantial evidence that riparian forests are sensitive to uncontrolled fires that are widespread over the southern Amazonia edge in most dry seasons and especially during drought years. Conserving the crucial ecosystem functions of the remaining riparian forests requires both stopping deforestation and reducing the occurrence of accidental fires. In addition, the ongoing small carbon sink into unburned forests in the region and the lack of an obvious direct impact of drought show that the ecosystems of the region retain substantial resilience to environmental change – including the heating and drying that has occurred here already (Brando et al. 2014, Marimon et al. 2014). If these forests can be protected from burning, then there is every chance that they can thrive and continue to sustain their unique biodiversity (Flores et al. 2017, Sullivan et al. 2017) and continue to provide critical regional and global ecosystem services. Whether or not they will be protected is less clear, as they are profoundly threatened by the greatly weakened protection laws for riverine forests embodied in recent changes in the Brazilian Forest Code.

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