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Amazon forest response to repeated droughts

Running title: Amazon forest response to droughts

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Keywords: climate change; carbon; plant water stress; soil water deficit; productivity; mortality; TRMM

Key Points:

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- Amazon forests, regardless of drought status, on average lost biomass during the 2010 drought
- Biomass losses were partially driven by a decline in productivity related to precipitation anomalies
- Pre-2010 droughts did not compound the effects of the 2010 drought

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Abstract

The Amazon Basin has experienced more variable climate over the last decade, with a severe and widespread drought in 2005 causing large basin-wide losses of biomass. A drought of similar climatological magnitude occurred again in 2010; however, there has been no basin-wide ground-based evaluation of effects on vegetation. We examine to what extent the 2010 drought affected forest dynamics using ground-based observations of mortality and growth utilizing data from an extensive forest plot network. We find that during the 2010 drought interval, forests did not gain biomass (net change: −0.43 Mg ha^{-1}, CI: −1.11, 0.19, n=97), regardless of whether forests experienced precipitation deficit anomalies. This loss contrasted with a long-term biomass sink during the baseline pre-2010 drought period (1998 − pre-2010) of 1.33 Mg ha^{-1} yr^{-1} (CI: 0.90, 1.74, p<0.01). The resulting net impact of the 2010 drought (i.e., reversal of the baseline net sink) was −1.95 Mg ha^{-1} yr^{-1} (CI:−2.77, −1.18; p<0.001). This net biomass impact was driven by an increase in biomass mortality (1.45 Mg ha^{-1} yr^{-1} CI: 0.66, 2.25, p<0.001), and a decline in biomass productivity (−0.50 Mg ha^{-1} yr^{-1}, CI:−0.78, −0.31; p<0.001). Surprisingly, the magnitude of the losses through tree mortality was unrelated to estimated local precipitation anomalies, and was independent of estimated local pre-2010 drought history. Thus, there was no evidence that pre-2010 droughts compounded the effects of the 2010 drought. We detected a systematic basin-wide impact of drought on tree growth rates across Amazonia, with this suppression of productivity driven by moisture deficits in 2010, an impact which was not apparent during the 2005 event [*Phillips et al.*, 2009]. Based on these ground data, both live biomass in trees and corresponding estimates of live biomass in roots, we estimate that intact forests in Amazonia were carbon neutral in 2010 (−0.07 PgC yr^{-1} CI:−0.42, 0.23), consistent with results from an independent analysis of airborne estimates of land-atmospheric fluxes during 2010 [*Gatti et al.*, 2014]. Relative to the long-term mean, the 2010 drought resulted in a reduction in biomass carbon uptake of 1.1 PgC, compared to 1.6 PgC for the 2005 event [*Phillips et al*. 2009].

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Introduction

The Amazon Basin has seen increased climatic variability over recent decades. Precipitation records and long-term river levels show that, while in some regions there is an overall trend towards increased annual precipitation [*Gloor et al.*, 2013], the dry season in the south of the basin appears to becoming longer [*Marengo et al.*, 2011] and drier [*Chou et al.*, 2013]. In addition, temperature has increased over recent years [e.g., *Jiménez-Muñoz et al.*, 2013]. There are large uncertainties in predictions of 21st century climate, with some models suggesting an increase in extreme dry events [*Cox et al.*, 2008], and a tendency for increasingly dry conditions during the dry season [*Malhi et al.*, 2009], while recent multi-model comparisons suggest an increase in total precipitation concentrated in the wet season [*Kitoh et al.*, 2013]. It is highly uncertain how forests of the Amazon Basin will respond to these changes. As the most extensive tropical forest on Earth, a biome storing more than 100 billion tonnes of carbon in biomass [*Feldpausch et al.*, 2012], changes in the Amazon forest may have large and global consequences. To date, there has been no basin-wide analysis based on long-term permanent forest plot data of tree-by-tree response to the 2010 event and to repeated precipitation anomalies.

River level and precipitation records indicate that parts of the Amazon Basin have experienced several anomalously dry periods over the last two decades [*Coelho et al.*, 2012; *Espinoza et al.*, 2011; *Lewis et al.*, 2011; *Marengo et al.*, 2008]. The most recent events in 2005, 2007, and 2010 left large regions of Amazonia anomalously dry, with each having a distinctive and complex spatial pattern (SI Figure S1). These recent droughts are not individually exceptional in the long-term as river gauge data indicate dry years of similar or greater magnitude over the last century in 1916, 1926, and 1963 [*Coelho et al.*, 2012; *Williams et al.*, 2005]. Nevertheless, forest response to the 2005 dry-period resulted in a reversal of a multi-decadal trend in above-ground biomass gain, with the forests on average losing biomass [*Phillips et al.*, 2009]. The main cause of this loss was increased tree mortality, not a reduction in tree growth.

Climatologically, the 2010 event differed from 2005. While 2005 was bracketed by climatologically average years, the 2010 event was preceded by one of the wettest years in recent history (annual precipitation > 0.975 quantile) [*Gloor et al.*, 2013]. Spatial footprints also differed, with 2005 drying being most pronounced in southwestern Amazonia, 2007 in

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southeastern Amazonia, and 2010 precipitation anomalies being more spatially dispersed (SI Figure S1). The 2010 drought occurred immediately following a number of anomalously hot dry seasons [*Jiménez-Muñoz et al.*, 2013], representing a possible intensification of climate stress for Amazonian forests. Inverse modeling of airborne-measurements of carbon dioxide and carbon monoxide concentrations above Amazonia and weather reanalysis products indicated that the Amazon Basin neither gained nor lost carbon during 2010, while it was a net carbon sink in the relatively wet 2011 year for which measurements were also made [*Gatti et al.*, 2014; *Laan-Luijkx et al.*, 2015]. Data from a small number of plots indicated that mortality increased during the 2010 drought, but that productivity was unaffected [*Doughty et al.*, 2015].

Tropical forest trees' physiological response to drought affects their carbon assimilation and allocation, as well as their mortality risk. Recent work has suggested a strong interdependence of hydraulic function, and metabolism, with drought affecting the ability of trees to mobilize and transport carbohydrates, produce defense compounds, and refill embolized xylem [*McDowell et al.*, 2011]{O'Brien, 2014 #3787}. Much of the existing work focuses on seedlings and temperate regions rather than the tropics, leaving major gaps in understanding of the physiological response to drought and the potential role of carbon starvation for tropical trees [*Parker and Patton*, 1975; *Sala et al.*, 2010], although recent research from one experimental drought plot suggests hydraulic stress plays a larger role than carbon starvation in initiating tree mortality [*Rowland et al.*, 2015]. At the tree-level, by monitoring changes in carbon allocation to different tree components, there is some evidence to suggest that following drought, trees shift carbon allocation towards the canopy, and later, to fine roots [*Doughty et al.*, 2014]. The interaction of drought with high temperatures also appears to reduce tree growth [*Clark et al.*, 2010; *Vlam et al.*, 2014]. When stress becomes too great due to drought, tree mortality increases [*Wang et al.*, 2012]. Regardless of the exact mechanisms involved, it is clear that tree-level physiological responses to drought substantially altered the carbon cycle of Amazonian forests during both the 2005 and the 2010 drought [*Brando et al.*, 2008; *Gatti et al.*, 2014; *Phillips et al.*, 2009; *Potter et al.*, 2011].

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If the climate of many tropical forests is shifting to one in which drought is a more frequent and/or intense phenomenon, we need to understand not only the impacts of single events, but also the cumulative effects of repeated droughts. Two potentially opposing outcomes might be reasonably anticipated. First, if unusually severe water deficits result in increased mortality rates for already weakened trees 'naturally' in decline (e.g., those that are competitively suppressed, drought intolerant, disease-affected, or individuals reaching the end of their lifespan) then it may simply accelerate pre-destined mortality. In this scenario, the effect of the drought would be to concentrate mortality over short anomalously dry periods, and thus potentially leave a forest of more vigorous, faster-growing individuals more likely to resist future physiological challenges once more normal rainfall patterns return. We call this the 'inoculation' hypothesis, because the effect of the first drought (e.g., 2005, 2007) is to (indirectly) confer on the remaining forest some resistance to the impact of future droughts.

Alternatively, it could also be argued that successive droughts might act in concert, for example through repeated episodes of irreversible damage from embolism [*Anderegg et al.*, 2014], and hydraulic fatigue [*Rowland et al.*, 2015], or by continual drawdown of carbohydrate reserves as a result of reduced photosynthetic rates [*Doughty et al.*, 2015]. In such a scenario, the first drought may weaken but not kill a large number of trees, making them vulnerable to repeated droughts of similar magnitude [*Brando et al.*, 2008]. We call this the 'degradation' hypothesis, because the initial drought is expected to degrade trees' ability to respond to later physiological challenges. This is conceptually similar to the "mortality spiral" towards tree death suggested by Franklin et al. 1987. Consistent with this, experimental drought studies showed drought effects may take a number of years to be expressed, with the mortality impacts of two drought experiments in eastern Amazonia only becoming clear after two or three seasons of experimental moisture depletion [*Brando et al.*, 2008; *da Costa et al.*, 2010; *Rowland et al.*, 2015].

Forest demography studies [*Condit*, 1995; *Phillips et al.*, 2010b; *Williamson et al.*, 2000] have consistently reported that short-term tropical droughts increase tree mortality. By temporarily raising mortality rates over large areas, relatively small local impacts of droughts can scale to have significant impacts on the carbon cycle, of the order of ≈1 Pg C at the scale of the Amazon Basin, mostly via longer-term committed atmospheric releases from

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necromass as a result of temporarily elevated mortality [*Phillips et al.*, 2009], and with potentially long-lasting impacts on the forest canopy [*Saatchi et al.*, 2013].

While plot-based studies have characterized the effect of natural tropical forest drought on tree mortality, they have failed to detect a clear impact on tree growth rates [*Doughty et al.*, 2015; *Phillips et al.*, 2009], suggesting that any such impacts are either minor, or not easily detected in nature due to problems of small sample sizes, inadequate temporal resolution, or measurement precision. Furthermore, the effect of repeated droughts at the basin-level on mortality and growth remains unknown. The occurrence in 2010 of a second major Amazon Basin-wide drought after a five-year interval, and the 2007 drought over a large area of southeastern Amazonia, combined with the increasing sampling intensity of the RAINFOR plot network, provided a unique opportunity to now address these questions.

Here, we present the first basin-scale, ground-based evaluation of the impact of the 2010 drought and repeat droughts on Amazon forest biomass dynamics using a set of measurements of biomass, growth, and mortality. Specifically, we test whether, H1) the net effect of drought alters stand-level biomass, H2) drought affects tree mortality and growth, and H3) previous droughts (or the plot drought history) affects the response of the forest to the 2010 event.

To address these questions, we first quantify the magnitude of the climatological drought for each plot based on previously used [*Aragão et al*. 2007; *Phillips et al*. 2009] and alternative metrics of drought stress. We then estimate the impact of the 2010 event on plots by calculating the change in biomass loss (through tree mortality) and productivity (defined as the growth gains of stems plus recruitment) during the drought interval against the long-term (pre-2010) baseline of mortality and productivity for these plots (i.e, mortality and productivity anomalies). Finally, we evaluate whether plots undergoing single, repeat, or no drought differ in biomass dynamics in 2010, evaluating changes for each of nearly 100 plots (mean size = 1.2 ha) distributed across 38 geographically distinct South American tropical forest locations (SI Table S2). Using a subset of plots with short census intervals that span the 2010 drought, we evaluate results in the context of a long-term baseline in forest biomass

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dynamics in South American mature forests with a net positive biomass sink that has gradually declined over time [*Brienen et al.*, 2015].

Methods

Forest census data

Forests had been sampled using established plot recensus protocols, over multiple census intervals across the Amazon Basin over three decades as part of the RAINFOR plot network, [*Phillips et al.*, 2010a] (Figure 1). In brief, all live tree stems with diameter (D) ≥10 cm were measured at 1.3 m height or above buttresses and deformities. 'Emergency' post-drought recensus campaigns were conducted across the basin to evaluate the effect of both the 2005 and 2010 droughts. For 2010, a total of 97 plots were selected for recensus that provided a maximum census length of <3.5 years and spanned the 2010 event. The mean (median) plot area was 1.2 (1.0) ha and mean (median) census length 2.3 (2.1) years. This census interval is similar to that used for the 2005 drought analysis (mean = 2.0 years) [*Phillips et al.*, 2009]. Data are curated within the ForestPlots.net web application and database [*Lopez-Gonzalez et al.*, 2011; *Lopez-Gonzalez et al.*, 2009]. For treatment of changes in the diameter point of measurement, we follow the recommendations of Talbot *et al*. [2014], as used in the recent pan-Amazonian study of Brienen *et al*. [2015] (Supplemental Information).

Biomass dynamics and anomaly

Above ground biomass (B) was estimated for each tree stem for all plots and summed per hectare (Mg/ha) from queries within ForestPlots.net based on a pan-tropical moist forest equation [*Chave et al.*, 2005]:

$$B = 0.0509 \times \rho D^2 H \quad (1)$$

where D is tree bole diameter in cm, ρ wood specific gravity (g cm^{-3}), and H tree height in m. Individual tree ρ was assigned based on taxonomy from values compiled in a global wood density database [*Chave et al.*, 2009; *Zanne et al.*, 2009]. In the absence of taxonomic information for a tree, the mean ρ from all stems in the plot was applied. Additional details of level of taxonomic determination and protocols are included in the SI. Tree H for a given D varies among geographic region and with environment [*Banin et al.*, 2012; *Feldpausch et al.*,

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2011] and was included in all estimates of *B*. Tree height was estimated with South America region-level Weibull models of the form:

$$H = a(1\text{-}\exp(\text{-}bD^c) \quad (2)$$

with coefficients and regions from Feldpausch et al. [2012]. These regions have been chosen based on substrate geological age [*Fittkau*, 1971]. The net change in *B* (and thus carbon) per hectare was estimated as the sum of biomass gained by recruitment of individuals into the 10 cm *D* class plus the gain in *B* of surviving trees, minus the *B* loss due to mortality. Biomass values were converted to carbon estimates using the fraction 0.5.

Long-term plot measurements used as the pre-2010 baseline data were previously reported in detail [e.g., *Brienen et al.*, 2015; *Phillips et al.*, 2009]. Censuses corresponding to the 2010 event were defined as those spanning the dry season of 2010 with <3.5 years in total census length. The year 1998 was chosen as the start of the reference period for the practical reason that it represents the start of precipitation data availability from the Tropical Rainfall Monitoring Mission (TRMM). The scale of the sampling and funding limitations makes it impossible to synchronize all measurements, or conduct annual census work everywhere. Therefore, census start and end dates vary, as do census lengths.

To evaluate the effect of drought(s) on biomass dynamics, we used absolute values of net change, mortality and gains in biomass (*B*) between the various census intervals, and also calculated the anomalies in net change, mortality and gains (using notation: Delta, Δ) from a baseline mean value for 1998-2010. For instance, the net biomass change anomaly (Δ*B*) was calculated for each plot as the net change *B* during the drought census minus the plot mean baseline net *B* change since 1998 to pre-2010, excluding the 2010 plot census interval. To gain insights in the drivers of change in biomass, we also analyzed data on plot-level changes in wood density (g cm^{-3}), number of trees dying (ha^{-1}), and tree basal area (m^2 ha^{-1}). These metrics were compared between 2010 and the mean of all previous measurements for a plot. Since we specifically focus on drought impacts, and need plots that allow comparisons pre- and post-drought having census intervals that bracket the 2010 drought, our dataset is substantially smaller than that used in the recent Brienen *et al*. [2015] analysis (n=321 plots). That dataset includes plots that have longer census intervals that may span drought and non-

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drought periods and multiple droughts for a single census. The Brienen *et al*. [2015] dataset is more appropriate for basin-wide estimates of biomass dynamics over long periods, while our data selection is tailored to capture 2010 drought-specific effects.

Precipitation anomalies and drought

Precipitation time-series data from 1998 to 2012 were sourced from the Tropical Rainfall Monitoring Mission (TRMM) product 3B43 version 7 [*NASA*, 2012] derived mainly from satellite and some ground values. Monthly precipitation (*P*) estimates, calculated from hourly average precipitation rates of 0.5° × 0.5° longitude by latitude grid cells, were extracted for each plot location.

We classified drought stress for each plot based on the maximum census climatological water deficit (*W*) modified from Aragão et al. [2007]. In addition, we evaluated two alternative drought indices, the Standard Precipitation Index (*SPI*) and the Standard Precipitation Evapotranspiration Index (*SPEI*) [*Vicente-Serrano et al.*, 2010](Supplemental Information). SPI and SPEI are multi-scalar drought indices that measure drought severity according to intensity and duration, and can distinguish the start and end of drought episodes; SPEI, unlike SPI, accounts for variation in potential evapotranspiration. *W* is based on the approximation that moist tropical forest canopy transpires ~100 mm/month, the mean evapotranspiration value (*E*) obtained from ground measurements over different seasons and for different regions of Amazonia [*da Rocha et al.*, 2004; *Shuttleworth*, 1988; *von Randow et al.*, 2004]. When *P* is <100 mm, the forest enters into water deficit. In calculating *W* on a plot-by-plot basis, the following rules were applied for each month (*n*):

$$If\ W_{n-1} - E + P_n < 0; \quad (3)$$

$$then\ W_n = W_{n-1} - E + P_n; \quad (4)$$

$$else\ W_n = 0 \quad (5)$$

Where *E* is evapotranspiration (100 mm), *P* is precipitation in a given month, and W_n is ≤ 0. The annual maximum climatological water deficit (*annual W*) was obtained for each forest plot as the most negative value of the climatological water deficit among all the months in each year, with year being based on the start of the rainy season (October) to the end of the

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dry season (September). Since we mostly lack annual recensus data, taking the mean annual W across multi-year census intervals [*Phillips et al.*, 2009] would have obscured the drought for 2010. Preliminary tests showed there was no significant relationship between the mean annual W as computed in Phillips et al. (2009) and forest change dynamics during the 2010 event. We therefore also calculated and used in the analysis the *absolute* maximum census W for each plot for a given census interval that may span several years. As a reference baseline, the long-term mean W was calculated for each plot from all historic census data from 1998 to the most recent census (but excluding the 2005 and 2010 drought). To quantify the intensity and duration of drought during a given census period relative to long-term mean values, water stress was calculated as the difference (Δ) of the census interval maximum climatological water deficit (Wt) from the long-term mean from 1998 to 2012 (excluding 2005 and 2010) ($\overline{W}_{1998\text{-}2012}$). Plots were first classified as 'droughted' during a census interval if the difference $\Delta W < -25$mm, for comparison with Phillips et al. 2009. In addition, we used a second threshold based on Z-scores, δW, by classifying plots as droughted when $\Delta W/\sigma_{1998-2012}$ was < -1.6, where $\sigma_{1998-2012}$ is the standard deviation of W from 1998 to 2012 (excluding 2005 and 2010). This latter threshold takes into account the background variability in W that the forest experiences, with $-1.6\ \sigma$ corresponding to a 90% confidence interval. To evaluate the effect of repeated droughts (e.g., 2005, 2007, 2010) on vegetation dynamics in 2010, the time since last drought was calculated for each plot as the census interval from the last time instance when $\delta W < -1.6$ to the date of the recensus that spanned the 2010 drought. An evaluation of errors associated with TRMM estimates of precipitation indicate that TRMM data provide accurate estimates for areas with precipitation <300 mm month^{-1} but may overestimate rainfall for the most extreme water deficits (e.g., < −300 mm) [*Aragão et al.*, 2007]. This indicates that estimates of water deficits using TRMM are likely to be conservative.

Scaling drought effects to the basin

The Amazon forest area was estimated based on the evergreen and closed deciduous classes of the Global Forest Cover 2000 data [*Bartholomé et al.*, 2002]. These data were updated for Brazil using the deforestation data through 2010 obtained from the INPE Assessment of Deforestation in Brazilian Amazonia project (PRODES) (http://www.inpe.br/) (Table 1). To estimate the total basin-wide effect of the 2010 drought in these forest areas, we scaled ΔB values to the Amazon Basin as follows. The ΔB mean and 95% bootstrapped confidence

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intervals were multiplied by the area considered as having been exposed to precipitation anomalies ($\delta W < -1.6$; SI: $\Delta W < -25$mm, as in Phillips *et al*. [2009]) and multiplied by the mean census period spanning the 2010 drought, 2.29 years, to estimate the change during the census interval. To estimate the effect on unmeasured *B,* we used several ratios of above ground *B* to liana *B*, small tree B, and belowground B. We applied 0.099 as the estimated ratio of trees <10 cm *D* and lianas >1 cm D to trees >10 cm *D* in Amazonia, and for the below-ground *B* applied the ratio 0.37 for *B* belowground to *B* aboveground [*Phillips et al.*, 2008], and summed all *B* converted to carbon (0.5) by Amazon region [*Feldpausch et al.*, 2012].

Statistical analysis

Plot census level changes in *B* dynamics, including net change, growth, and mortality, were examined for the pre- and post-drought census intervals, and in comparison to the long-term mean (ΔB values: difference from the long-term mean) as using two- and one-sample Wilcoxon signed rank tests and Welch two sample weighted t-tests. Bootstrapped 95% confidence intervals were estimated by resampling the data 1000 times. The relationship between ΔB and ΔW was examined using weighted linear regression and rank estimation [*Kloke and McKean*, 2013]. Tests were conducted at the un-weighted plot-level and weighted cluster level. Clusters represent plots in close proximity (<100 km) with similar climatic conditions. Weighting follows Brienen *et al*. (2015) with weights calculated as the square root of the plot or total cluster area times the census interval length. Regression analysis at the cluster-level also uses these same weights (i.e., procedure of weighted means for clusters and weighted mean regression, whereby a large plot monitored for many years would contribute more to a given cluster mean). Processing of TRMM data and forestplots.net vegetation data, and all statistical analyses and maps were conducted with the R Statistical Platform [*R Development Core Team*, 2013] version 3.1.0. TRMM netCDF files were manipulated with the 'raster' package [*Hijmans and van Etten*, 2013]. The 'Rfit' package was used for rank estimation for linear models [*Kloke and McKean*, 2013].

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Results

Drought spatial patterns

For the 2010 event, approximately 30-60% of each of the five Amazon regions was classified as being drought affected according to the criterion $\delta W \leq -1.6$ (Table 1). A total of 3.16 million km^2 (~50%) of the entire Amazon Basin experienced water deficits of $\delta W \leq -1.6$ (Figure 1). As a consequence, 65 of the 97 plots sampled were estimated as having experienced cumulative water deficits, ΔW, more severe than the long-term mean.

Biomass changes over droughted and non-droughted periods

Absolute biomass change

During both the 2010 (Figure 2) and 2005 events (Table 2), plots on average did not gain above-ground biomass, regardless of whether they experienced precipitation anomalies. These results were in contrast to the same plots having positive net change in biomass (i.e., a net sink) during the designated full pre-2010 drought baseline period, and for the period between 2004 and pre-2010, and for the period following the 2005 drought and prior to the 2010 drought (2007 to pre-2010), and for the period that spanned both the 2005 and the 2010 droughts (2003 to post-2010).

Biomass change anomaly

Independent of drought classification, the mean net biomass change anomaly, ΔB (i.e. 2010 minus long-term mean), was strongly and significantly negative during the 2010 census interval, confirming that biomass change was much lower in 2010 compared to the long-term mean of positive biomass change (Figure 2d). In terms of underlying biomass fluxes, the 2010 drought interval also showed significantly lower total tree productivity (i.e., growth plus recruitment) (Figure 2e), and greater biomass losses due to mortality (Figure 2f) compared to the long-term mean.

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Biomass change and drought intensity

Our data suggest that (H1) the magnitudes of anomalies (ΔB) in net biomass change and productivity for the 2010 event were significantly related to the severity of the drought (measured as the change in W during the drought period). Thus, forests more heavily droughted in 2010 gained less biomass in 2010 (Figure 3a) and (H2) trees on average grew less (Figure 3b) compared to the pre-2010 baseline that spanned multiple droughts.

In contrast, (H2) anomalies in mortality during 2010 did not covary with the severity of the drought (Figure 3c). The intercepts for net ΔB change were negative when ΔW was zero (Figure 3) indicating that even for plots that were not considered to be anomalously dry in 2010, net ΔB was lower than during the baseline period (1998 - pre-2010). The results for the anomalies in net biomass change and mortality were consistent (while anomalies in productivity were not) with results with ΔW when using an alternative metric, SPI, to quantify drought anomalies (SI Figure S3).

Wood density, number, and size of trees dying

We detected weak impacts of the 2010 drought in terms of trees which died. On average, there was a weak but significant tendency in the more strongly droughted plots for lighter wood-density taxa to be more at risk of death (SI Figure S4a). There was, however, no clear pattern for the drought to kill larger trees, on average, at higher drought intensity (SI Figure S4b). For plots undergoing the greatest precipitation anomalies (δW < -1.6) (n = 48), the number of stems dying per year increased by 30% during the 2010 event compared to the pre-2010 mean [mean number of trees dying increased from 10.1 to 13.2 (p<0.001)] (SI Table S1).

Effect of repeated drought

The TRMM-based analysis indicates that parts of Amazonia experienced anomalously high water stress anomalies over the past decade in addition to the 2010 event (e.g., during 2005 and 2007) (SI Figure S1, δW annual time series). The total combined area classified as droughted in 2005 *or* 2007 covered large areas of the Amazon Basin based on δW Z-scores ≤ −1.6 (Figure 4a). The 2005 event most affected an area in western, central, and northeastern Amazonia, while the most severe δW anomalies in 2007 were more dispersed throughout

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Amazonia. The 2010 event, having affected a much larger area than either 2005 or 2007 (Figure 4b), spanned areas droughted in 2005 or in 2007, but rarely in both (Figure 4a). Thus a large part of western and southern Amazonia that was droughted in 2010 was also droughted in *either* 2005 *or* 2007 (Figure 4c).

Interestingly, we found (H3) no significant difference in net change, productivity, or mortality during the 2010 event between plots that experienced droughts before or plots that were never droughted (Figure 5). However, there were patterns that highlight the 2010 drought effect and indicate a potential lag in effects from previous droughts. For example, on average, stands that had the most negative ΔB productivity anomaly were classified as droughted in pre-2010 and 2010, suggesting an interaction between pre-2010 and the 2010 drought. Plots classified as never droughted during the study period also had negative ΔB net change, negative productivity, and positive mortality anomalies. Mortality was extremely 'noisy' in 2010, having high standard deviation in plots (Figure 5).

The time since last drought (the interval from the last δW Z-score < -1.6 to the current interval) failed to explain any differences in ΔB, B net change, or B gains due to growth or loss due to mortality in 2010. This was the case whether all continuous time since last drought data were combined (Figure 6), or when examining discrete periods corresponding to the time since the 2007, 2005, and pre-2005 droughts (SI Figure S6).

Regional patterns and basin-wide scaling

Our data show that intact forests during the 2010 drought lost biomass in three of the five regions, and that forests in none of the regions, on average, gained biomass (Table 1). Furthermore, those plots performing poorly in 2010 compared to the long-term mean (negative ΔB changes in plot dynamics) were not confined to a single region (Figure 1). Plots having the most negative ΔB net change values and largest ΔB loss due to mortality in 2010 corresponded to regions with the greatest δW anomaly, which was the southern half of Amazonia. The northwest and Guiana Shield had ΔB net change values that did not differ significantly from the long-term mean.

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Scaling field measurements by region from intact non-anthropogenically degraded plots and the unmeasured above-and below-ground components for forest census spanning the 2010 event, we estimated the basin was carbon neutral during 2010 (−0.07 CI: −0.42, 0.23 PgC yr^{-1}) (Table 1). In comparison to the long-term mean, we estimated a reduction in carbon uptake (ΔC net change) in 2010 of −0.47 PgC yr^{-1} (or, −1.1 PgC during the average 2.3-year 2010 census interval). Of this, −0.14 PgC yr^{-1} (CI: −0.27, −0.03), or ca. 30% was due to a reduction in growth (ΔC growth). This ΔC net change represents the reversal in the previous long-term carbon sink, i.e., reduction in growth, and the carbon to be released from tree mortality and decomposition.

Discussion

We have analyzed tree growth and mortality across the Amazon using forests censuses which cover the 2010 drought period. Similar to the 2005 event, we found (H1) an effect of precipitation anomalies on the net biomass change of the forests. In contrast to 2005, in 2010 we detected (H2) the first clear evidence for a widespread reduction in forest productivity (growth) in the Amazon due to drought. Mortality was (H2) also elevated in 2010, but not related to estimated precipitation anomalies. We found (H3) no evidence for the hypothesis that repeated droughts ledled to an enhanced impact.

Net change in biomass

The 2010 drought was one of the most geographically extensive of the last few decades. On average, our plots did not gain biomass in 2010, regardless of drought classification (Figure 2). The lack of net biomass gain was widespread, and not confined to one region (Figure 1). This reversal was in contrast to the same plots previously acting as a carbon sink [*Baker et al.*, 2004; *Phillips et al.*, 2009]. Our results are consistent with reported long-term decline of the Amazon forest carbon sink [Brienen et al. 2015], which has been most marked during the last decade.

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Growth and mortality impacts

In contrast to the 2005 event, which only saw elevated mortality [*Phillips et al.*, 2009], we now find that the net reduction in carbon uptake during the 2010 event was caused by a combination of both higher mortality *and* slower tree growth (Figure 2). The significantly elevated mortality rates during the 2010 drought interval indicate that drought is only partially responsible for the earlier reported long-term increase in mortality rates found by Brienen et al. [2015]. In addition, we show that significant reductions in growth contributed a further 30% to a weakening of the sink capacity of the basin during the 2010 drought. However, because the slowdown in growth and the increase in mortality began well before the 2005 event, additional processes may contribute to the long-term sink decline [cf. *Brienen et al*. 2015].

We found that changes in growth or recruitment (but not mortality) relate to the intensity of the drought (Figure 3, SI Figure S3). While the effects of the drought on net biomass changes are broadly in line with results from the 2005 event [*Phillips et al.*, 2009], we find two important differences: *i*) on average, trees in plots more intensely droughted grew less in 2010 compared to the long-term mean, and *ii*), there was no relation between biomass losses due to mortality and drought severity in 2010. And, related to this, there was no difference in biomass net change between plots classified as droughted or non-droughted [*Phillips et al.*, 2009]. Thus, even plots that were not droughted showed elevated mortality during the 2010 event.

Experimental rainfall exclusion has been shown to cause a reduction in growth. Drying of Amazonian forest under throughfall exclusion experiments (TFE) indicated that wood productivity can decline substantially with a sustained precipitation reduction [*Brando et al.*, 2008; *da Costa et al.*, 2010; *Nepstad et al.*, 2007; *Rowland et al.*, 2015]. The multi-year TFE experiments and natural drought are not directly comparable, since artificial droughts induce different artificially induced soil deficits, and lack the pattern of lower atmospheric humidity typical of natural droughts. Despite these differences, results from the two TFE experiments, both in eastern Amazonia, appear broadly in line with our observations of plots across the Amazon Basin. For example, not only were net biomass change anomalies for basin-wide plots similar during the 2005 and 2010 events, but also the basin-wide plots now exhibited a clear reduction in growth due to drought, as has been seen in the TFE. Further, plots lost

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biomass and had growth reductions in response to drought throughout the Amazon Basin (Figure 1), despite large difference in precipitation, soil texture, depth, and drainage in plots, and despite basin-scale fertility gradients [*Quesada et al.*, 2011]. The TFE experiments also showed that drought-related tree mortality can take several years to occur, so that basin-wide forest inventories following the 2010 event may only capture part of the mortality.

Fast-growing trees with low wood density may be most sensitive to drought [*McDowell et al.*, 2008; *Phillips et al.*, 2009]. In line with predictions, during the 2010 event trees with lower wood density were most affected by the greatest water deficits (Figure S4a). However, in contrast to the results from the TFE [*da Costa et al.*, 2010] and from the 2005 event [*Phillips et al.*, 2009], we did not find strong evidence that the size of trees that died in plots with most sever water deficit anomalies during the 2010 event was on average larger than in previous intervals. This may suggest different mortality mechanism for the largest trees during the 2010 event.

The lack of a significant relationship between mortality and our measured drought intensity in our study contrasts with results from the 2005 drought [*Phillips et al.*, 2009] and the TFE experiments [*Brando et al.*, 2008; *da Costa et al.*, 2010; *Nepstad et al.*, 2007]. The TFE experiments found that mortality rates under experimental drought were higher than those observed in plots undergoing natural droughts of lower intensity. Stem mortality rates in the TFE peaked in the year with the greatest water deficit (2005) for all stem size classes, indicating that drought effects on mortality can be detected within the year of severe water deficits [*da Costa et al.*, 2010]. Following the peak, mortality may continue to be elevated for some size classes (e.g., >40 cm in da Costa et al. 2010). A lack of a relationship between mortality and drought intensity in 2010 may be partially explained by several factors: 1) by pre-drought conditions, and limitations of the metric *W*. For example, the drought mortality relationship may be partially obscured by the record precipitation in 2009; 2) there may be a lag in tree mortality until water deficits become extreme [*da Costa et al.*, 2010]; 3) the metric *W* is insufficient to capture the drought stress experienced by trees growing on widely varying soils and under varying climatic conditions. However, using two other drought metrics that account for additional climate variables we similarly failed to detect an effect on mortality during this time period (Supplemental Information). This is both mechanistically and ecologically interesting, suggesting that other factors may also be affecting mortality in

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our plots.

Nevertheless, mortality was on average generally higher in our Amazon plots in 2010 (Figure 2); and, higher mortality during drought years has been reported for other biomes and may have longer-term impacts such as species compositional change via the selection of more drought-adapted species. For example, forests in parts of western and central Africa have recently changed compositionally in response to drought [*Fauset et al.*, 2012; *Ouédraogo et al.*, 2013]. Increased mortality due to drought is not restricted to tropical forests [e.g., *Allen et al.*, 2010; *van Mantgem et al.*, 2009]. Boreal forests of Canada, for example, have undergone an increase of 4.7% yr^{-1} in mortality over the last 40 years, with this increase attributed to regional decline in precipitation [*Peng et al.*, 2011].

Repeated drought impacts

Our analysis is the first ground-based Amazon Basin-wide study to examine effects due to the 2010 drought and interactive effects of repeat drought. Our results show that variation in precipitation significantly affects the carbon balance of intact tropical forest in the Amazon Basin. However, we find (H3) no evidence for the hypothesis that repeated droughts leads to enhanced impact, suggesting that drought effects in 2010 were largely independent from previous droughts. While mortality increased significantly in 2010, we find that drought effects are not substantially compounded in 2010 for those forests undergoing pre-2010 droughts. Thus net change in biomass during the 2010 event was approximately the same and independent as to whether a plot was or was not considered as having been droughted in recent history, prior to 2010 (Figure 5). Thus the hypothesis, that earlier drought impacts may have simply weeded out trees destined to die (i.e., pre-2010 droughts advanced mortality events, thereby 'inoculating' forests to later droughts) is not validated by our results. Overall, there was neither an additional effect (degradation) nor was there interfering effect (inoculation) of repeated droughts. Variable census length, and 2010 following an anomalously wet year are two factors that may limit the ability to detect either effect; therefore, these are cautious interpretations. That the Amazon trees proved sensitive to two major droughts in five years suggests these forests will continue to exhibit reduced growth and enhanced mortality rates in response to any future periods of drought severity similar to the 2005, 2007, and 2010 events studied here. Finally, Amazonian forests appear to have a

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degree of forest-level resilience in terms of their demonstrated ability to return to be a net above-ground carbon sink. Thus, results from experimentally droughted forests [*Brando et al.*, 2008; *da Costa et al.*, 2010] and from our natural drought observations showing that plots returned to acting as net sinks following the 2005 event (Table 1), both suggest that the reduction in growth following drought may be short-term.

The effects of precipitation anomalies can also be interpreted through the "mortality spiral" proposed by Franklin [1987]. For example, drought-stressed trees may undergo a series of stress events such as hydraulic fatigue [*Rowland et al.*, 2015] and non-structural carbohydrate depletion [*Doughty et al.*, 2014] leading to death, with reductions in growth one proximate cause of death. Trees may also shift their allocation of carbon in response to drought. A recent study found that during and after drought, trees adapt carbon allocation strategies by shifting allocation between wood, canopy, and roots, and reducing autotrophic respiration [*Doughty et al.*, 2015; *Doughty et al.*, 2014]. Our results of a consistent and drought-associated reduction in growth during the 2010 event contrast with the report of Doughty *et al*. [2015] that productivity remained constant. This contrast may be due to differences in the number of plots sampled, and spatial and temporal differences between the two studies. Doughty *et al*. [2015] focused on intensive 1-3-month measurements in thirteen plots representing dry and humid forests, and had one year of pre-2010 baseline data, while the current study mobilizes two decades of baseline data. Understanding regional variation and how response plasticity may allow some trees to better respond to repeated droughts will help to understand factors that delay or accelerate the onset of death. There is also a need to improve understanding of the interaction between recent anomalously hot dry seasons [*Jiménez-Muñoz et al.*, 2013] and precipitation anomalies.

Stand- and basin-scale effects

Our ground-based measurements permit evaluation of space-, airborne-, and flux tower-based observations of drought. Based on analysis of TRMM and gauge-based precipitation data [*Lewis et al.*, 2011; *Marengo et al.*, 2011], the 2010 drought was reported to have extended across a much larger area than the 2005 drought. Our ground-based measurements confirm that forests in these regions lost biomass compared to the long-term mean; however, the mechanisms by which forests lost biomass due to drought differ from 2005. Satellite data have suggested that some areas affected by the drought in 2005 had persistent changes in tree

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canopies up to several years after the drought that were attributed to changes in structure and water content of the forest upper canopy [*Saatchi et al.*, 2013]. Our plots lack the synoptic coverage that remote sensing permits, and so long-term impacts in some parts of the Amazon may not be inconsistent with our analysis. Nevertheless, our direct measurements of forest dynamics show that the carbon balance impacts of Amazon previous droughts have been rather short-lived, since after the losses of the 2005 event forests quickly returned, on average, to carbon sink status. In addition, we did not observe any evidence for an inoculation effect nor for an additive effect of previous droughts on the effect of the 2010 drought.

Our 'bottom-up' basin-wide results are in line with 'top-down' estimates based on regional atmospheric inversion using airborne measurements of gas concentrations. Thus, after taking into account carbon losses due to forest loss and fire in 2010, the Amazon Basin vegetation was estimated to be carbon neutral (−0.03 ± 0.22 PgC yr^{-1}) [*Gatti et al.*, 2014] or a source (−0.1 to −0.4 PgC yr^{-1}) [*Laan-Luijkx et al.*, 2015]. This compares to a ground-based estimate from this study including estimates of above and belowground commitments that the basin was biomass carbon neutral during 2010 (−0.07 PgC yr^{-1} CI: −0.42, 0.23) (Table 1). This represents a marked reduction in carbon uptake when compared to either pre-2005 ground-based estimates (0.39 ± 0.10 PgC yr^{-1}) [*Phillips et al.*, 2009] or to atmospheric inversion estimates for 2011 (0.25 ± 0.14 PgC yr^{-1}) [*Gatti et al.*, 2014]. It is important to note that estimates by different techniques are not fully comparable in process or in time – ground plots 'see' the response of above-ground forest biomass, while atmospheric measurements of carbon dioxide emissions are also affected by autotrophic and heterotrophic respiration, and decay of necromass produced by drought-induced mortality will not be seen immediately. Scaling vegetation response to the 2010 event is also limited by uncertainty in total carbon storage in roots and uncertainty in shifts in carbon allocation during and following the event [*Doughty et al*. 2015]. Notwithstanding these caveats, it is remarkable how closely the bottom-up and top-down estimates compare for the 2010 carbon balance.

Challenges in evaluating drought response: alternative drivers and limitations

There are a number of challenges in evaluating response for the Amazon Basin to the 2010 drought including, and not limited to, *i*) vegetation dynamics show long-term (decadal scale) changes (Brienen et al. 2015), and separating specific changes during the 2010 drought from such long-term changes is challenging ; *ii*) the 2010 drought was bracketed by some of the

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wettest years on record and there are interactions among several factors; *iii*) some, but not all, of drought versus climate relationships observed for the 2005 drought apply to the 2010 event.

There are long-term changes occurring in Amazonian forests, with increasing levels of turnover, even before the 2005 drought [*Brienen et al.*, 2015; *Phillips and Gentry*, 1994]. This long-term increase in mortality may be due to other drivers in addition to drought, such as faster growth leading to shorter tree live-spans [*Bigler and Veblen*, 2009; *Di Filippo et al.*, 2015], increasing liana abundance [*Phillips et al.*, 2002] leading to increased tree death [*van der Heijden et al.*, 2015], and increasing climate variability other than droughts [*Gloor et al.*, 2013; *Jiménez-Muñoz et al.*, 2013]. The reduction in the rate that Amazon forests are gaining carbon over the last three decades [*Brienen et al.*, 2015] results in a challenge in evaluating drought responses, since the baseline itself is changing (i.e., increasing mortality and decreasing net change). In this study we used the baseline 1998 to pre-2010, which corresponds to the TRMM time window. As expected, since the rate of carbon gain has declined [*Brienen et al.*, 2015], when we run the same analysis using all available pre-2010 baseline data back to the 1980's, the biomass loss due to the 2010 drought (ΔB net change) was greater still as the net biomass gains in the baseline back to the 1980's were greater (values not reported).

Furthermore, the exceptional wet years both preceding and following the 2010 drought represent an underlying intensification of the Amazon climate system, with annual precipitation on average increasing [*Gloor et al.*, 2013]. The 2010 drought may have been less intense compared to previous droughts due to the effect of the higher than average precipitation in 2009 [*Chen et al.*, 2013]. The changes required different approaches in analyzing the 2010 drought compared to the 2005 drought. These wet years may have dampened the drought effect on trees, with soil moisture being on average higher prior to onset of the drought, and soils rapidly rewetting following the drought. Because the 2010 drought was preceded by record rainfall in 2009, it was necessary to use the *maximum W* for a given census interval that may span several years, rather than the mean [e.g., *Aragão et al.*, 2007; *Phillips et al.*, 2010b; *Phillips et al.*, 2009]. Site-specific estimates of precipitation and soil moisture would also improve understanding of drought response. Our finding of different drivers of change in net biomass (reduction in productivity) in the 2010 event than the 2005

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event suggests that attempts to use results from one drought (e.g., 2005) to extrapolate to another using TRMM rather tree census data [e.g., *Lewis et al.*, 2011] may not accurately represent pathways and responses. We found consistent relationships for some but not all of the changes in vegetation dynamics anomalies versus water deficits using alternative metrics (e.g., SPI, Supplemental Information. Ultimately, these impacts can be best understood by directly measuring them on-the-ground, and not simply by extrapolation from previous drought responses.

Future considerations

Our findings have a number of implications. Amazonian forests appear to have a moderate level of resilience to repeated droughts, with fast post-drought returns to net carbon gains; however, the decline in productivity in 2010 shows a new response that was not recorded in the previous drought. Forests responded in a similar way across a large precipitation gradient (Figure 1). If trends in climate over the past few decades continue, the future climate of the Amazon Basin is liable to be one with greater extremes [*Gloor et al.*, 2013], including greater dry season water deficits [*Fu et al.*, 2013]. It is unclear how these dual extremes may affect forests. Our results, and those from Phillips et al. (2009) for the 2005 drought, show that forest responses per unit area are usually rather small, but that the extent over which they can act is vast, so that they have notable carbon cycle implications at regional and global scales. Finally, our finding of a reduction in productivity due to drought has important implications for estimating the longevity of the Amazon carbon sink (Brienen et al. 2015).

Based on these results, it is possible to make a number of recommendations:

1) *Suite of physiological, carbon cycling, and composition measurements*: The presence of a large, extensive plot network with long-term plot-based data has allowed us to partition drought response into growth and mortality. However, more work is needed to understand the underlying tree physiological responses involved and potential shifts in species composition.
2) *Soil-effects*: Additional studies are required to understand interaction between drought and soil (e.g., Supplemental Information), since variation in soils affects structure and productivity [*Aragão et al.*, 2009; *Quesada et al.*, 2012].
3) *Reducing uncertainty*: Assessing changes in belowground processes due to water deficits

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remains a major challenge and source of uncertainty. A lack of relationship between changes in aboveground *B* and drought metrics derived from TRMM suggest a need for better weather data collected at each plot.

4) *Interaction among multiple factors*. Alternative water deficit metrics evaluated in this study (Supplemental Information) such as the SPEI include indirect effects of temperature via the Penman-Monteith equation to estimate evapotranspiration. However, the interaction between multiple factors such as temperature and water deficits requires greater attention
5) *Spatial representativeness*: The network of permanent forest plots has grown steadily and is dispersed across the basin, yet important regions are still underrepresented. There is a clear need for ground-based assessments of tree growth and dynamics to fill key spatial gaps (both standard census and 'intensive' plots), and thus also improve the prospects for validating large-scale observations of forest canopy properties made remotely from space. Droughts over the last two decades have tended to focus on the southern Amazon border; these forests may serve as critical indicators of potential forest die-back due to future droughts.

Greater, coordinated effort in both ground-based and air/space-borne observations will help better determine the stand-level processes and tree-level mechanisms involved in forest responses to drought. Plot-based observations will help interpret and refine Earth observation techniques [e.g., *Samanta et al.*, 2010], improve dynamic vegetation models [*Galbraith et al.*, 2010], constrain estimates of carbon emissions [*Gatti et al.*, 2014; *Phillips et al.*, 2009], and validate predictions of the fate of Amazonian forests [*Cox et al.*, 2004; *Huntingford et al.*, 2013].

Conclusions

Drought negatively impacts neotropical forest carbon storage, and our study shows for the first time that it can cause a large-scale reduction in tropical forest productivity. Our results suggest further that Amazon forest response is to some extent predictable, being of similar magnitude to the 2005 drought, but that pathways differ between events, with different results found for mortality and productivity in 2010 compared to 2005. Our estimates of basin-wide vegetation being carbon neutral in 2010 closely match estimates independently derived from a regional-scale inversion using airborne measurements of greenhouse gases [*Gatti et al.*, 2014]. Despite drought being a natural feature of the Amazonian climate regime, there is

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large uncertainty regarding changes in the frequency, intensity, and impact of these events in the future [*Huntingford et al.*, 2013]. However, the intensities of future droughts are likely exacerbated by elevated temperatures, and it is therefore crucial that we improve understanding of forest response to drought events. Forests were not 'inoculated' against a second major drought in five years, suggesting that, should there be a future climate regime characterized by ever greater dry season soil water deficits as predicted by some models [*Fu et al.*, 2013], then declining productivity and increasing mortality may begin to degrade forests.

Supplemental Information is available in the online version of the paper.

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Author Contributions

TRF performed analyses and wrote the paper with major input from OLP, RB, JL, and EG. OLP, JL, and YM conceived the RAINFOR forest census plot network programme, and EG, TRF, and RB contributed to its development. OLP, TRF, JL, YM, and EG conceived the study and received funding. OLP, TRF, RJWB, and AMM coordinated data collection with the help of most co-authors. TRF, RB, AMM, OLP, and GLG performed quality control on the data with the help of most co-authors. All remaining authors contributed data. All authors commented on the analysis, presentation of the data, and manuscript.

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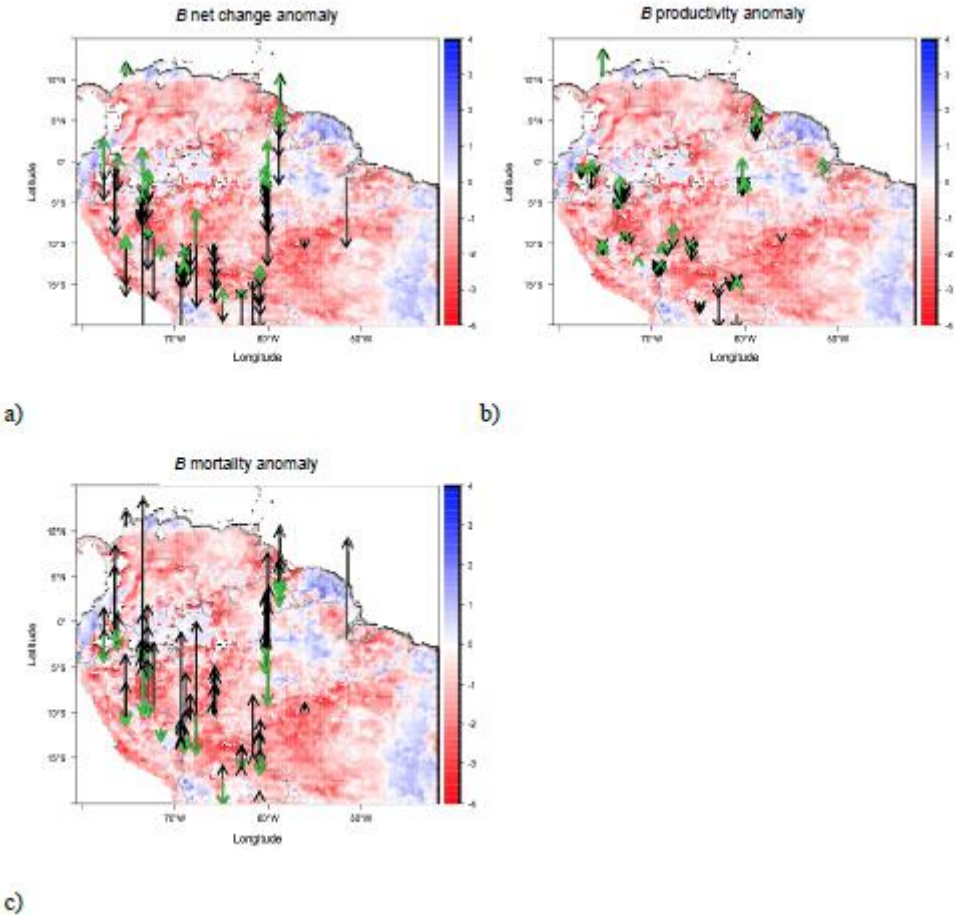

Figure 1: Spatial patterns in the 2010 biomass anomaly (ΔB) for plot clusters, including mean (a) net change, (b) productivity (recruitment + growth), and (c) mortality (all in Mg ha^{-1} yr^{-1}). Up (down) arrows indicate an increase (decrease) in values compared to the mean baseline 1998 to pre-2010. The background indicates the drought δW Z-scores.

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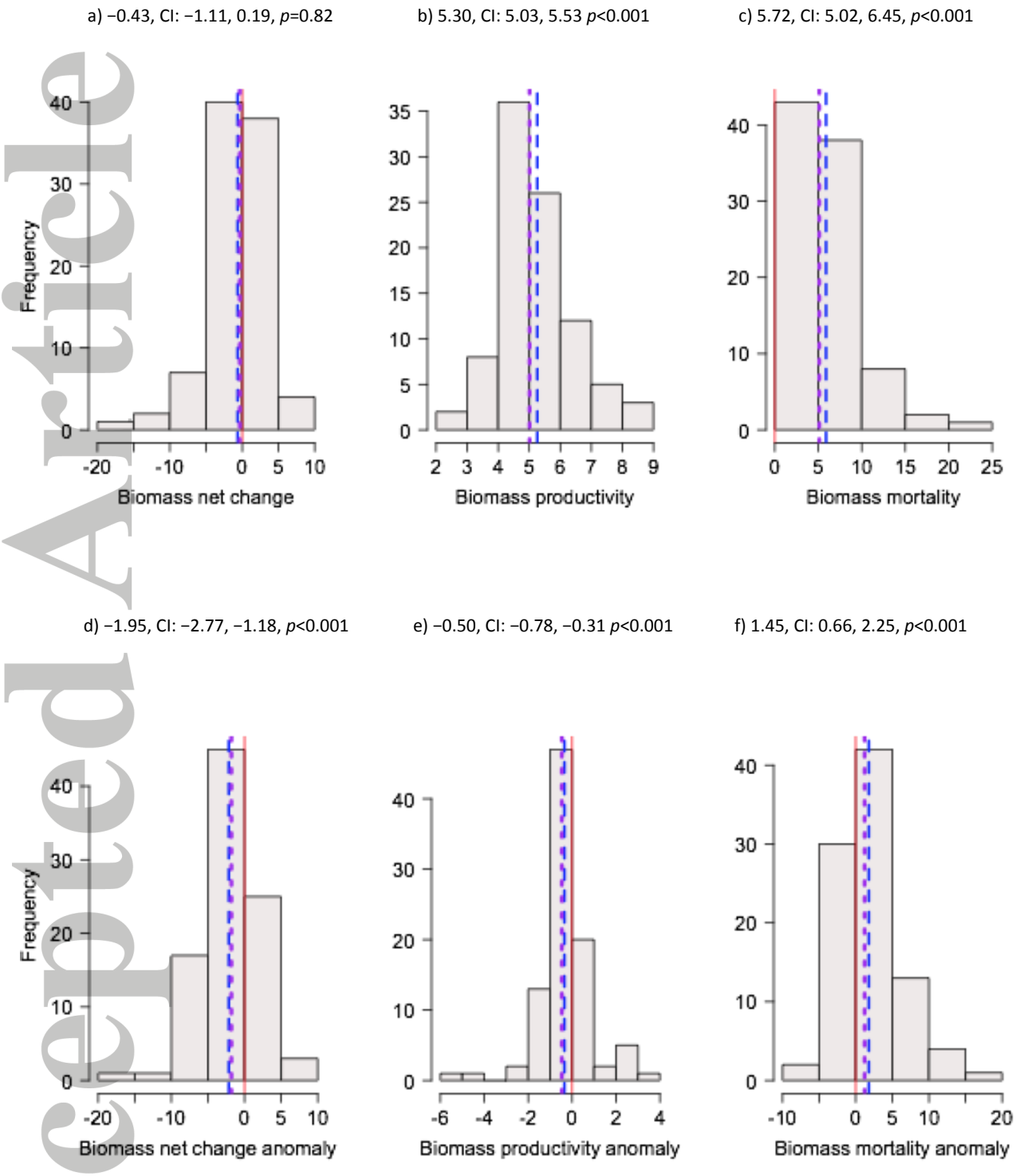

Figure 2: Plot-level biomass change in 2010 (mean, 95% bootstrapped confidence intervals) for: (a) net change, (b) productivity, (c) mortality, and mean ΔB (2010 – (mean pre2010 to 1998)), and for anomalies in (d) net change, (e) productivity, and (f) mortality. The dashed blue and purple lines represent the mean and median, and the solid red line is centered at zero (n=97). Units Mg ha^{-1} yr^{-1}.

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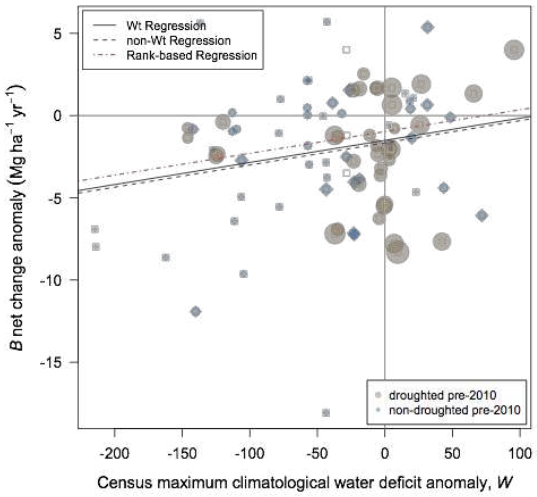

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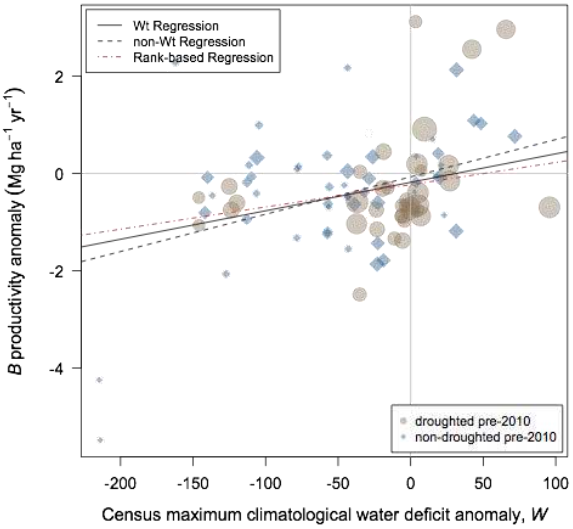

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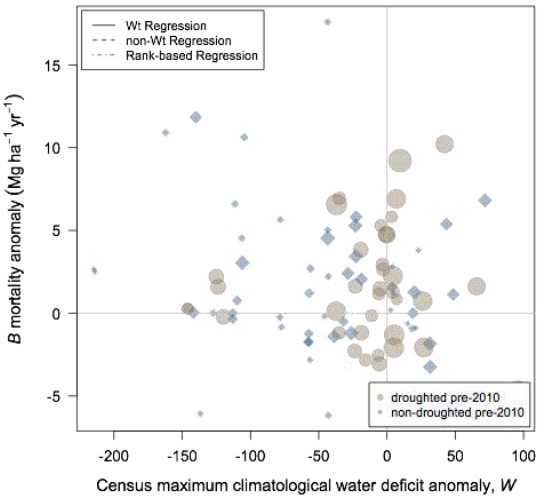

(c)

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Figure 3. Plot-level vegetation dynamics during the 2010 drought: a) ΔB net change (p = 0.026 weighted regression, p = 0.044 non-weighted regression, p = 0.036 Rank-based regression), b) ΔB productivity (growth + recruitment) (p = 0.002 weighted regression, p < 0.001 non-weighted regression, p = 0.015 Rank-based regression), c) ΔB mortality (all in Mg ha-1 yr-1) versus the ΔW (absolute W in 2010 census – mean of census absolute W values) for the pre-2010 to 1998 baseline. Symbol size is proportional to the intensity of the last pre-2010 δW, showing plots droughted (brown circles) and non-droughted from 2000 to pre-2010 (δW Z-score < −1.6) (blue diamonds).

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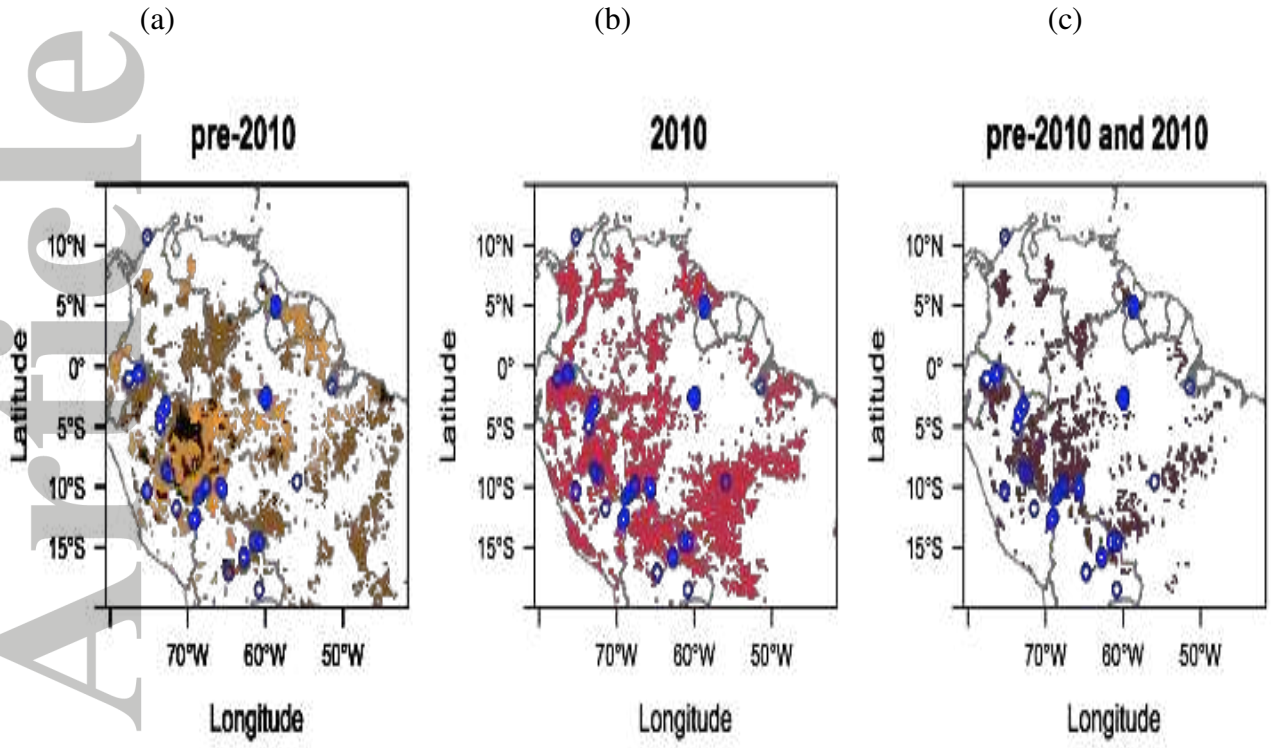

Figure 4: Areas droughted based on δW Z-score < -1.6 for a) pre-2010 (2005, orange or 2007, brown), b) 2010 (red), and c) pre-2010 (2005 or 2007) *and* 2010. A small percentage of the basin was droughted in both 2005 *and* 2007 (black in (a)). Blue circles show plot locations.

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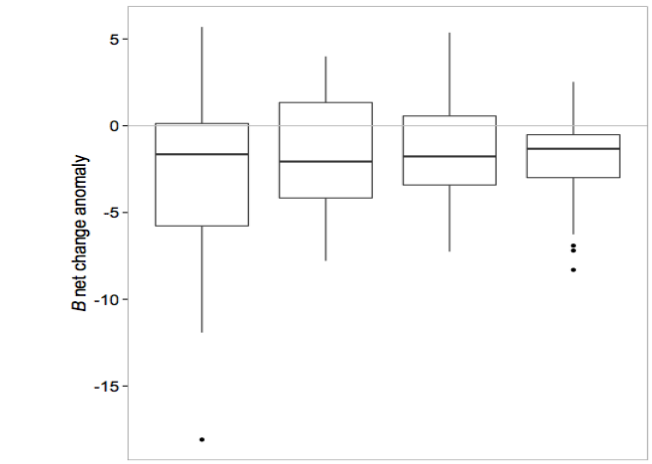

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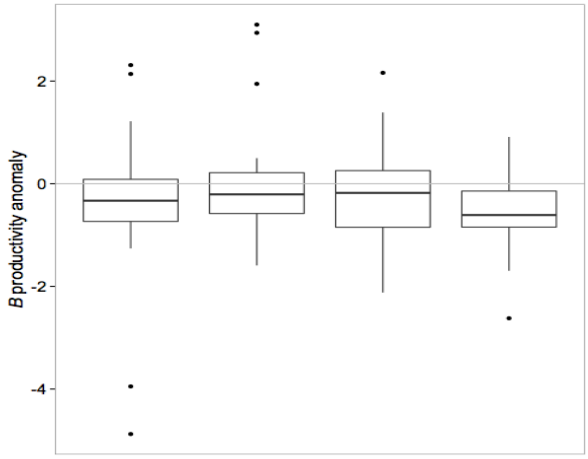

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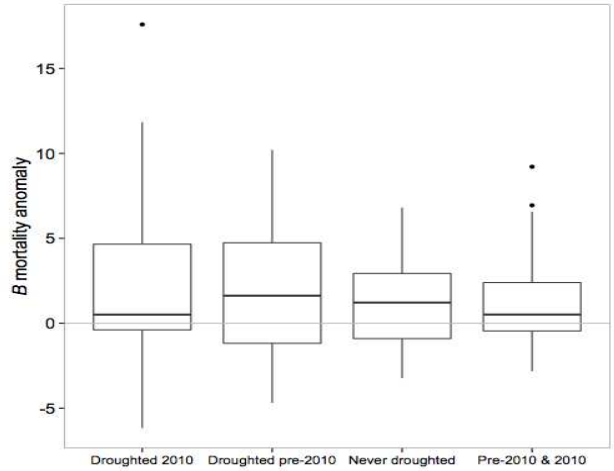

(c)

Figure 5: In 2010, biomass change anomaly (ΔB) (a) net change, (b) growth, and (c) mortality for plots undergoing or not undergoing drought in 2010 and in pre-2010 (2000 to <2010). All values in Mg ha^{-1} yr^{-1}. Plots with census δW Z-scores < −1.6 were classified as droughted. None of the classeses were significantly different (Tukey HSD p > 0.05)

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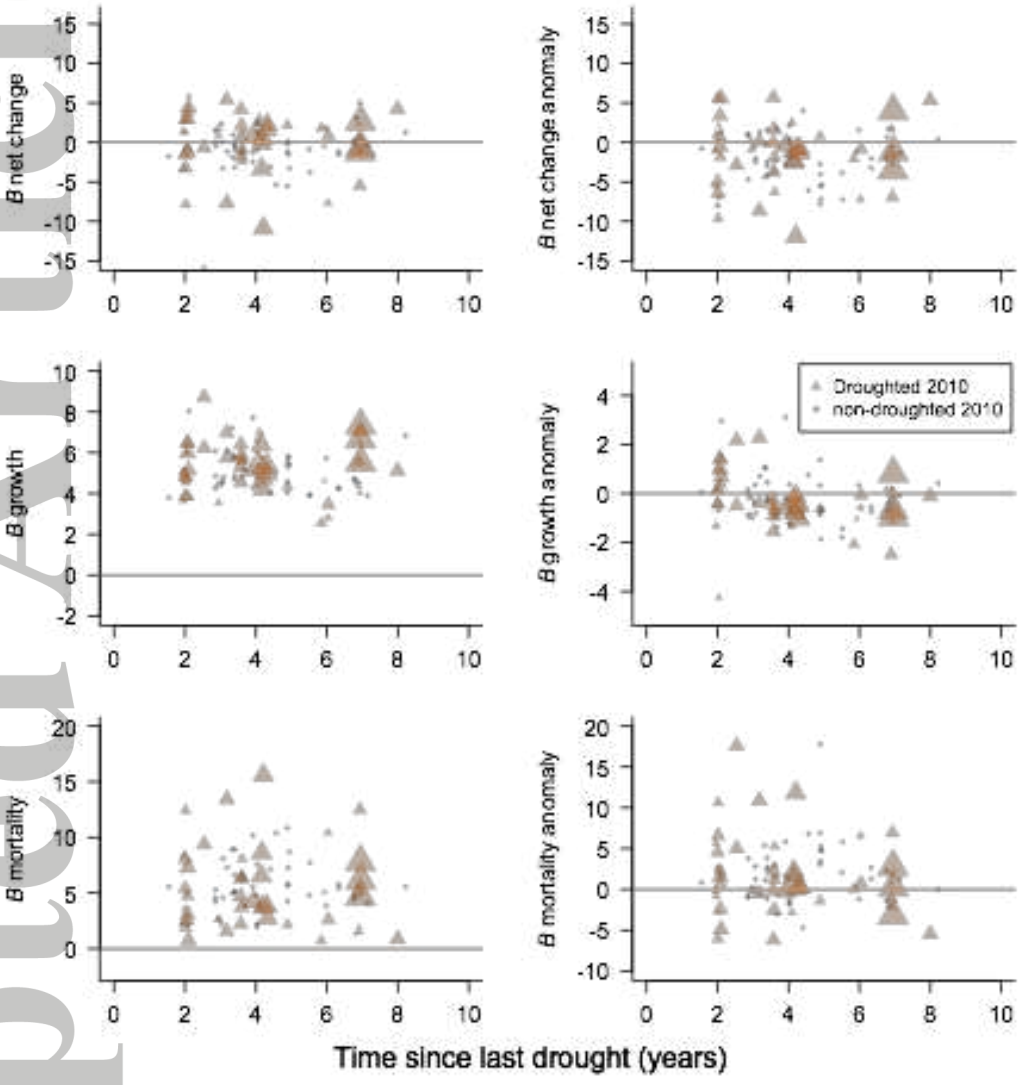

Figure 6: Tree growth and mortality dynamics in 2010 for plots droughted and non-droughted in 2010 versus time since last pre-2010 precipitation anomaly, $\delta W < -1.6$: (a) B net change and B net change anomaly (ΔB), (b) B growth and B growth anomaly, and (d) B mortality and B mortality anomaly, all in Mg ha^{-1} yr^{-1}. Symbol size is proportional to the intensity of the δW Z-score in 2010 and symbol color and shape corresponds to plots classified as droughted ($\delta W < -1.6$) or non-droughted in 2010. None of the relationships were significant ($p > 0.05$).

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Table 1: Total biomass change and ΔB change (including 95% bootstrap confidence intervals) during the 2010 drought interval (2.3 years) by region for the Amazon Basin for $\delta W < -1.6$.

Region	Forest area (10^6 ha)**	Area droughted[§]	Fraction Area droughted[§]	N plots	Total sample area (ha)	Mean ΔB (Mg ha^{-1} y^{-1})	(0.025-	0.975)	Mean B net change (Mg ha^{-1} y^{-1})	(0.025-	0.975)	Total change C in sink (Pg)*	(0.025-	0.975)	Estimated C sink (Pg)*	(0.025 -	0.975)
1. Northwest	125.6	66.2	0.53	25	21.7	-1.59	-3.49	0.10	0.21	-1.71	1.63	-0.18	-0.39	0.02	0.02	-0.19	0.18
2. Guiana Shield	153.3	50.7	0.33	12	30.5	-1.42	-3.57	0.83	0.88	-0.47	2.26	-0.12	-0.30	0.14	0.08	-0.04	0.19
3. Central east Amazon	110.3	47.6	0.43	12	20	-2.67	-4.99	-0.06	-1.88	-3.65	-0.15	-0.21	-0.40	-0.01	-0.15	-0.29	-0.01
4. South west Amazon	87.2	53.9	0.62	34	37.5	-2.00	-3.18	-0.84	-0.96	-2.00	-0.02	-0.18	-0.29	-0.15	-0.09	-0.18	0.00
5. Brazilian Shield	158.8	97.0	0.61	14	14	-2.30	-4.02	-0.73	-0.14	-1.60	1.02	-0.38	-0.66	-0.24	-0.02	-0.26	0.17
Whole Basin	635.2	315.5	0.50	97	123.64	-1.95	-2.77	-1.18	-0.43	-1.13	0.18	-1.07	-2.04	-0.24	-0.16	-0.97	0.53
Whole Basin PgC yr^{-1}												-0.47	-0.89	-0.57	-0.07	-0.42	0.23

*Including above ground B (≥10 cm D) and the unmeasured components (< 10 cm D, lianas, and roots)

**Forest cover area calculated by region [*Feldpausch et al*., 2012] using Global Forest Cover 2000 data [*Bartholomé et al*., 2002] [§] $\delta W < -1.6$

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Table 2: Net change in biomass (non-weighted mean, Mg ha^{-1} yr^{-1}) during, before, and spanning the 2010 event, and during the 2005 event (2004 - 2007), including 95% bootstrap confidence intervals and results of the t-test.

Period	**Net biomass change**	**CI**	***n***	***p*-value**
2010 event	−0.43	−1.11, 0.19	97	0.26
2005 event	0.91	−0.002, 1.81	45	0.07
baseline: 1998 − pre-2010	1.33	0.90, 1.74	97	<0.01
2004 − pre-2010	1.11	0.70, 1.46	89	0.01
2007 − pre-2010	1.36	0.50, 2.19	61	<0.05
2003 − post-2010	0.82	0.04, 1.60	63	<0.05

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