Drought-induced mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian Amazon

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Abstract. Extreme climatic events affecting the Amazon region are expected to become more frequent under ongoing climate change. In this study, we assessed the responses to the 2010 drought of over 14,000 trees ≥10 cm dbh in a 25 ha lowland forest plot in the Colombian Amazon and how these responses varied among topographically defined habitats, with tree size, and with species wood density. Tree mortality was significantly higher during the 2010–2013 period immediately after the drought than in 2007–2010. The post-drought increase in mortality was stronger for trees located in valleys (+243%) than for those located on slopes (+67%) and ridges (+57%). Tree-based generalized linear mixed models showed a significant negative effect of species wood density on mortality and no effect of tree size. Despite the elevated post-drought mortality, aboveground biomass increased from 2007 to 2013 by 1.62 Mg ha^{-1} yr^{-1} (95% CI 0.80–2.43 Mg ha^{-1} yr^{-1}). Biomass change varied among habitats, with no significant increase on the slopes (1.05, 95% CI −0.76 to 2.85 Mg ha^{-1} yr^{-1}), a significant increase in the valleys (1.33, 95% CI 0.37–2.34 Mg ha^{-1} yr^{-1}), and a strong increase on the ridges (2.79, 95% CI 1.20–4.21 Mg ha^{-1} yr^{-1}). These results indicate a high carbon resilience of this forest to the 2010 drought due to habitat-associated and interspecific heterogeneity in responses including directional changes in functional composition driven by enhanced performance of drought-tolerant species that inhabit the drier ridges.

Key words: aboveground biomass dynamics; Amazon forest; carbon; climate change; forest dynamics plot; forest microhabitats; forest resilience.

INTRODUCTION

The frequency and intensity of extreme climatic events affecting the Amazon region are expected to increase this century as a consequence of climate change (Cox et al. 2008, Malhi et al. 2008, Duffy et al. 2015). A recent study reported a reduction in the rate of the net biomass gain in Amazon forests due to tree mortality triggered by two intense droughts in 2005 and 2010 (Brienen et al. 2015). The associated reduction in biomass carbon uptake across the Amazon has been estimated at 1.6 petagrams of carbon (Pg C) for the 2005 drought (Phillips et al. 2009), and 1.1 Pg C for the 2010 drought (Feldpausch et al. 2016). In general, increased tree mortality decreases forest carbon stocks in aboveground biomass (AGB) (e.g., Phillips et al. 2009). Because the Amazon basin harbors approximately 50% of all tropical forests and 10% of terrestrial carbon stocks, increases in tree mortality and decreases in AGB due to extreme climatic events are important for the global carbon cycle (Zhao and Running 2010, Wang et al. 2014).

The susceptibility of trees to water stress varies with their size and species functional traits (Corlett 2016). Species with low wood density are expected to suffer greater increases in mortality rates during droughts (Slik 2004, Phillips et al. 2009). In contrast, slow-growing species with high wood density are generally more resistant to cavitation or carbon starvation caused by water deficits (McDowell et al. 2008, Poorter et al. 2008, Wright et al. 2010). Likewise, it has been shown that ecological and physiological mechanisms make large trees quite vulnerable to drought (Ryan et al. 2006, Phillips et al. 2010). Although tall trees may be deeply rooted, which may be an advantage under drought conditions (Wright 1992), they also have to lift water to leaves at tall heights and are exposed to higher evaporative demand (Bennett et al. 2015). Thus, given that large trees are responsible for a disproportionately large share of biomass carbon stores and productivity (Stephenson et al. 2014), these vulnerabilities imply potentially dramatic negative feedbacks due to the high amount of carbon large trees may release to the atmosphere through death and/or the reduced amounts of carbon they may sequester owing to reductions in photosynthetic and growth rates.

Local variation in climate and soils also play an important role in defining tree sensitivity to water stress (Johnson et al. 2016, Levine et al. 2016). The Amazon terra firme tropical forest, one of the most diverse ecosystems on earth (ter Steege et al. 2003, Duque et al. 2017), exhibits systematic variation in AGB stocks and mortality rates among different topographic habitats - e.g., ridges and valleys (Chave et al. 2003, Valencia et al. 2009, Detto et al. 2013). Valleys have higher moisture availability than hills or ridges, and thus trees in valleys may have less tolerance to water shortage than those on slopes or ridges (Condit et al. 1995, Harms et al. 2001, Itoh et al. 2012). Hence, we might expect that droughts disproportionately increase mortality rates of trees in valleys and valley-associated tree species. In combination with increased mortality, reduced growth of more vulnerable species is expected to further reduce forest carbon stores in the medium to long term (Engelbrecht et al. 2007).

Here, we use censuses of over 14,000 trees ≥10 cm dbh in the 25 ha Amacayacu forest dynamics plot before and after the 2010 drought to evaluate the impact of that drought on tree mortality and biomass dynamics in this lowland terra firme Amazonian forest. We ask (1) Did tree mortality increase after the 2010 drought? (2) Did tree mortality and the impact of drought on mortality vary with (a) topographically defined habitats, (b) tree size, and/or (c) species wood density? (3) Did the Amacayacu forest plot act as a source or as a sink of carbon during the 2007–2013 study period encompassing the 2010 drought? Answering these questions will help us better understand the response of Amazon terra firme forests to climate variation and climate change.

Methods

Study area

This study was carried out at the Amacayacu forest dynamics plot (AFDP), located in Amacayacu National Natural Park in the Colombian Amazon (3°48′33.02″ S and 70°16′04.29″ W). The AFDP has an area of 25 ha (500 m × 500 m). This plot is part of the Center for Tropical Forest Science - Forest Global Earth Observatory (CTFS-ForestGEO; Anderson-Teixeira et al. 2015), a network that comprises >60 forest plots worldwide that were established and are monitored following the same protocols (Condit 1998). The life zone of the AFDP corresponds to a Tropical wet forest (Holdridge 1978) located on terra firme that is not subjected to direct flooding of the Amazon River. The plot sits on the Pebas geological formation, which has an Andean origin (Hoorn 1994) and is characterized by hilly and moderately dissected topography. In general, soils in the Amacayacu Park have low fertility, high acidity and low base saturation due to the dominance of minerals such as kaolinite and quartz, which are generally poor in nutrients (Chamorro 1989). The mean annual temperature is 25.8°C, mean annual precipitation is 3,216 mm,

and mean relative humidity is ca. 86% (climate statistics for the weather station at the airport at Leticia, 55.39 km away from the plot; Prieto 1994).

We evaluated the effects of the 2010 drought on climate at the AFDP through analyses of precipitation and potential evapotranspiration (PET). In addition, we calculated the water deficit in the AFDP as the balance between the cumulative rainfall and PET for each month of the 2010 yr (following Aragão et al. 2007). This water deficit is a measure of drought intensity that has been shown to be related to tree mortality in Amazonian forests (Phillips et al. 2009). Precipitation was quantified using satellite-derived rainfall data for the period 1998–2010 (Tropical Rainfall Measuring Mission, 3B42 v7, 0.25° resolution; Goddard Earth Sciences Data and Information Services Center, 2016) (sensu Aragão et al. 2007). PET was obtained from the Global Land Data Assimilation System Version 2 (GLDAS-2), at 0.25° spatial resolution (Rodell, M. and Beaudoing, H. K. NASA/GSFC/HSL, 2015).

We divided the AFDP into 625 quadrats of 20 × 20 m and assigned each quadrat to a habitat class based on elevation, slope, and convexity calculated at the 20-m scale using the CTFS R Package (http://ctfs.si.edu/). For each quadrat, elevation was calculated as the mean elevation of its four corners, and convexity as the mean elevation of the focal quadrat minus the mean elevation of its eight neighboring quadrats. For edge quadrats, convexity was defined internally as the elevation of the center point minus the mean elevation of the four corners. The slope was estimated by dividing the four corners of a quadrat into four groups, calculating the slope from three random elevations in each of the four groups, and averaging the resulting slope values. We then applied Ward's minimum variance method of hierarchical clustering analysis to quadrat slope, elevation, and convexity variables to classify the main topographic habitats in the AFDP.

Forest censuses and species wood density

Analyses presented here were based on information from three censuses of trees with diameter at breast height (dbh) ≥10 cm in the AFDP. The first census corresponds to plot establishment in 2007. In this census, all shrubs, trees, palms, and tree ferns with dbh ≥10 cm were mapped, tagged, measured, and collected for species identification following the standardized methods for long-term tropical forest dynamics plots (Condit 1998, Anderson-Teixeira et al. 2015). Voucher specimens were deposited and identified in the Herbario Amazónico Colombiano (COAH) of the Instituto Amazónico de Investigaciones Científicas (SINCHI). A second mortality-only census was performed between November and December of 2010. In the 2010 census, all individuals ≥10 cm dbh in the 2007 census were visited and recorded as either alive or dead. Finally, a third complete census of trees ≥10 cm dbh was carried out from March 2013 to December 2014, in which

recruitment, mortality and dbh growth were assessed. In the second and third censuses, a tree was recorded dead if: (1) it had no living leaves or sprouts at all and was without signs of life (e.g., rotted trunk); (2) it was found fallen with no living resprouts; or (3) it was completely missing (sensu Condit 1998). The mean census intervals for the pre-drought (2007–2010) and post-drought (2010–2013) periods were 3.4 (SD = 0.3) and 3.1 (SD = 0.5) years, respectively (means taken over trees).

Wood density for each species in the AFDP was obtained from the literature (Chave et al. 2006, Zanne et al. 2009), giving priority to the studies or data nearest to the Amacacyacu plot. When species-level values were not available, we used genus- or family-level averages (Chave et al. 2006).

Data analysis

To quantify drought effects on tree mortality and test for variation in these effects across topographic habitats (questions 1 and 2a), we calculated quadrat-based mortality rates for the pre-drought (2007–2010) and post-drought (2010–2013) census intervals for the whole plot and for each habitat. Tree mortality was calculated as $m = (\log(N0)–\log(N1))/t$, where $N0$ is the number of trees alive in the initial census, $N1$ is the number of those trees still alive in the final censuses, and t is the average time between the two censuses. We calculated confidence intervals of mortality rates from 1,000 bootstraps over quadrats, following Valencia et al. (2009).

We employed tree individual-based analyses to investigate how habitat, tree size, and species wood density affect mortality and the influence of drought on mortality (question 2). We constructed Generalized Linear Mixed-Effects Model (GLMM) by maximum likelihood estimation (Laplace approximation) using the lme4 package in R (Bates et al. 2011). Tree mortality (m) was modeled at the tree level using the logit link function with fixed effects of (1) period (pre-drought or post-drought), (2) habitat (valley, slope, or ridge), (3) tree size ((log(dbh), a continuous variable), species wood density (WD, a continuous variable), and (4) the second-order interactions among them. We included random effects for quadrat, species, and individual. We simplified the full model using model selection based on removing the least significant term starting with the highest order interactions and refitting the GLMM without that term. This process was repeated until we achieved the best model, defined as that containing only variables significant at the 5% level (Crawley 2007). For the final GLMM, we assessed overdispersion (Venables and Ripley 2002), spatial autocorrelation of the residuals (Diggle and Ribeiro 2007), homogeneity of variance, and linearity of Pearson residuals with respect to the independent variables.

Finally, we quantified the AGB stocks and fluxes for the complete study period (2007–2013) (question 3). (Note that we could not separately quantify the AGB dynamics for the pre- and post- drought study periods

because dbh was not measured in the second census). Individual tree AGB was estimated using the general AGB model without tree height developed by Chave et al. (2014), defined as AGB = exp(−1.803−0.976*E+0.976*log(WD) + 2.673*log(dbh) −0.0299*(log(dbh)^2), where AGB is in kg and dbh is in cm. This model includes a site-specific environmental stress variable, E. that takes the value of −0.075 for Amacacyacu. AGB dynamics components were estimated based on the AGB in the initial (B_0) and final census (B_1), the AGB of dead trees (D), the AGB of recruits (R), and the average annualized time between the two censuses (t). Relative AGB mortality (mAGB) for the complete study period was estimated as mAGB = $(\log(B_0/(B_0 − D))/t$. Relative AGB recruitment (rAGB) was calculated as rAGB = log $((B_0–D+R)/(B_0–D))/t$. Relative AGB growth (gAGB) was estimated as gAGB = log $((B_1–R)/(B_0–D))/t$, and, the AGB net change (nAGB) was estimated as nAGB = $\log(B_1/B_0)/t$. Mean wood density at each census was calculated with weighting by basal area. We calculated these metrics for the plot as a whole and for each habitat type separately, and estimated confidence intervals from 1,000 bootstraps over quadrats. All analyses were conducted using R 3.2.3 (R Core Team 2015).

Results

Effects of the 2010 drought on local climate

The AFDP experienced a drought in 2010. During 5 months (April, May, August, September, and October), rainfall in the plot was among the lowest values of the previous 12 yr (1998–2009), which included the 2005 extreme drought (Phillips et al. 2009) (Fig. 1a). Precipitation in April, May, August and September of 2010 was more than one standard deviation (SD) below the mean (Appendix S1: Fig. S1b). The water deficits in August and September of 2010 were −34.11 and −43.91 mm month^{-1}, respectively, which were second in severity only to the 2005 drought year for comparisons over the previous 12 yr (Fig. 1b). The PET was not excessively high in 2010; indeed, it was close to or below average for the entire year (Appendix S1: Fig. S1).

Topographic habitats

Elevation in the AFDP ranged from 88.5 to 110.9 m a.s.l. Ward's classification identified three topographic habitats in the AFDP: ridges, slopes, and valleys (Fig. 2a, Appendix S1: Fig. S2). A plurality of 44.2% of the quadrats were classified as valley, 30.7% as slopes, and 25.1% as ridges (Fig. 2b).

Drought effects on mortality

We tracked survival of 14,408 trees belonging to 86 families, 286 genera and 828 species during the study period (2007–2013). Tree mortality was significantly higher in the
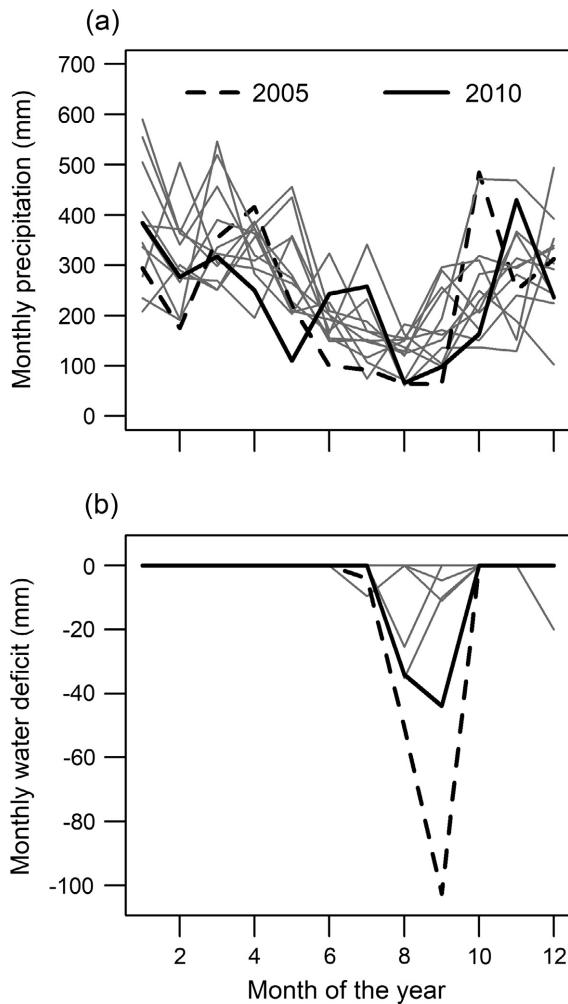
FIG. 1. Seasonal variation in rainfall (a) and water deficit (b) for the Amacayacu forest dynamics plot for each year from 1998 to 2010 (Tropical Rainfall Measuring Mission, 3B42 v7, 0.25° resolution; Goddard Earth Sciences Data and Information Services Center, 2016). Individual years other than 2005 and 2010 are shown with thin lines.

found significant negative effects of species wood density ($P < 0.001$), but no significant effect of tree size ($P > 0.05$) (Table 1). There were no significant interactions of wood density with drought or habitat, meaning these effects were purely additive (Fig. 3b, Appendix S1: Fig. S3). That translated to expected annual pre-drought mortality of 1.47 and 0.58% for species with wood density of 0.33 and 0.85 (5th and 95th percentiles), respectively, compared with expected post-drought mortality of 4.82 and 1.97%. Note that the slightly shorter census interval for the post-drought period means that the total impact of the drought on annual mortality rates (as calculated here and graphed in Fig. 3b, Appendix S1: Fig. S3 after
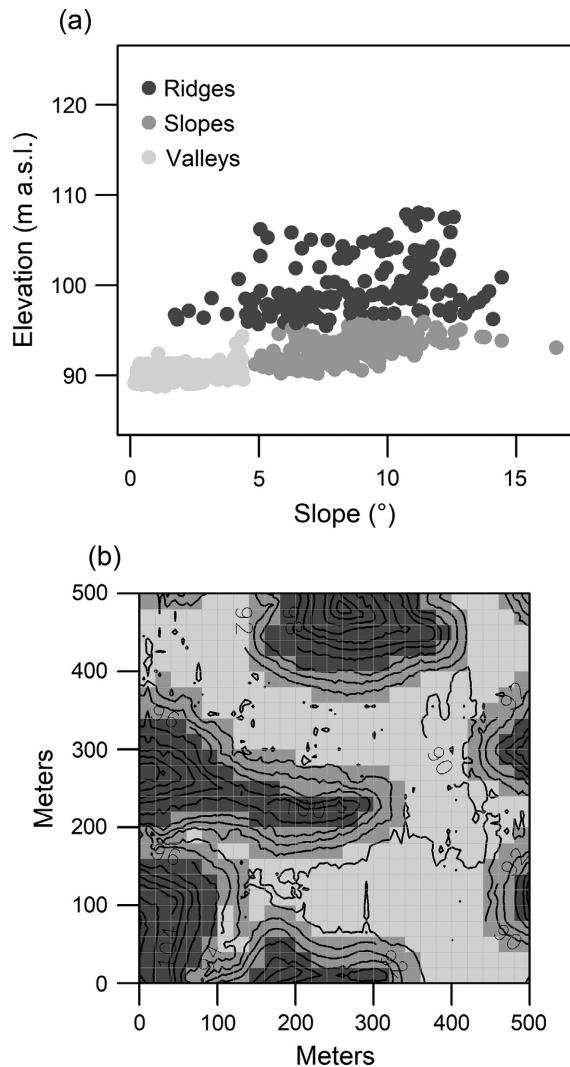

FIG. 2. (a) Elevation and slope of the 625 20 × 20 m quadrats in the Amacayacu forest dynamics plot, with shading indicating their topographic habitat classification. Additional pairwise scatterplots including convexity are shown in the supporting information (Appendix S1: Fig. S2). (b) Map of the Amacayacu forest plot showing the topographically defined habitats (ridges: dark gray, slopes: gray, and valley: light gray). Gray squares indicate the 20 × 20 m quadrats.
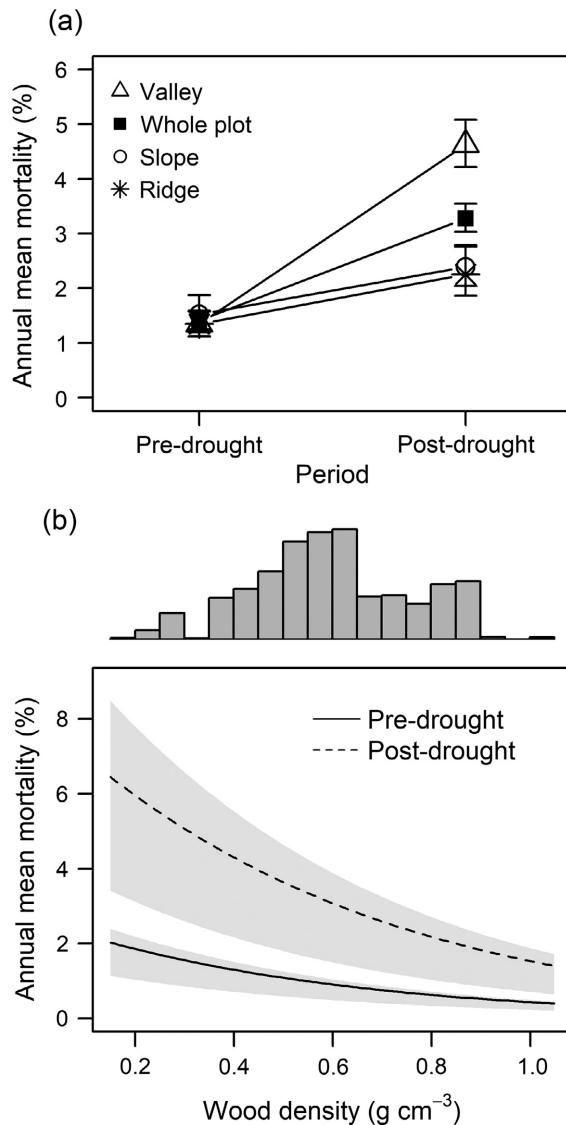
post-drought interval (2010–2013) than in the pre-drought interval (2007–2010) (Fig. 3a). Post-drought mean mortality rose to 3.28% per yr (95% CI 3.03–3.55% per yr) compared with 1.42% per yr (1.25–1.59% per yr) pre-drought. This result was consistent when we modeled mortality at the tree level ($P < 0.001$, Table 1). The increase in tree mortality in the post-drought period was evident in all habitat types (Fig. 3a). The relative increase in the valleys (243.2%) was much higher than for ridges (67.3%), and slopes (56.8%). Interestingly, trees in the valley had somewhat lower mortality than those on the ridge in the pre-drought period ($P = 0.03$, Table 1).

Wood density and tree size in relation to mortality

Tree-level analyses (GLMM) confirmed the interacting effects of drought and habitat on mortality and also

(a)

(b)

Fig. 3. (a) Annual mean mortality before and after the 2010 drought for trees with dbh ≥10 cm on the ridges, slopes, valleys, and the whole 25 ha Amacayacu forest dynamics plot. Vertical bars show the 95% confidence intervals based on bootstrapping over 20 × 20 m quadrats. (b) Annual mean mortality estimated from the average marginal probability of tree death before and after the 2010 drought in the Amacayacu forest dynamics plot as a function of species wood density. Shaded areas span the 25th to 75th percentiles of the predicted values. Upper histogram in panel (b) shows the distribution of trees across wood density in the plot.

correcting for the census interval) was stronger than is apparent from the model terms themselves (Table 1).

Aboveground biomass dynamics

Over the study period as a whole (2007–2013), high relative AGB mortality (2.25% per yr, Fig. 4a) was more than balanced by high AGB recruitment and growth (Fig. 4b,

c), such that the total estimated AGB in the AFDP increased significantly (+0.66% per yr, Fig. 4d, or 1.62 Mg ha^{-1} yr^{-1}, Table 2). Biomass dynamics tended to differ among the habitats, with ridges exhibiting lower mortality fluxes; valleys higher mortality, recruitment and growth fluxes; and thus the most positive net change in ridges, with valleys intermediate and slopes lowest (Fig. 4). However, these differences were not statistically significant ($P > 0.05$) given high spatial variation among quadrats.

DISCUSSION

The 2010 drought, which had a strong impact on the water deficit in Amacayacu, led to a significant two-fold increase in tree mortality in the 25-ha Amacayacu forest dynamics plot. Interestingly, the observed tree mortality rate of 1.42% per yr (1.25–1.59 per yr) for the pre-drought period in the 25-ha AFDP plot is lower than the recently reported mean for the Amazon basin between 1995 and 2009 (1.96 ± 0.08% per yr, $n = 167$ plots of ~1 ha), and much lower than the mean for the western Amazon (2.62 ± 0.12% per yr, $n = 76$ plots of ~1 ha) (Johnson et al. 2016). The strong effect of the drought on mortality in Amacayacu highlights the potential importance of severe and continuous droughts for forest dynamics and functioning in the coming decades (Malhi et al. 2008, Duffy et al. 2015).

Post-drought mortality was much higher in valleys than on slopes and ridges of the plot, even though there was no significant difference in pre-drought mortality among these habitats (Fig. 3a). This is consistent with our expectation that trees in valleys are less adapted to moisture stress, because valleys are generally wetter (Harms et al. 2001, Itoh et al. 2012), and suffer disproportionately during drought. These results suggest that tree dieback is largely associated with local fine-scale processes that differentiate water availability among habitats, which, in turn, may determine the aboveground biomass dynamics at the landscape scale (Valencia et al. 2009, Gonzalez-Akre et al. 2016, Levine et al. 2016). One clear implication of these results is that data on tree

TABLE 1. Summary of the best generalized linear mixed-effects model for tree mortality in the 25 ha Amacayacu permanent plot, Northwest Amazon.

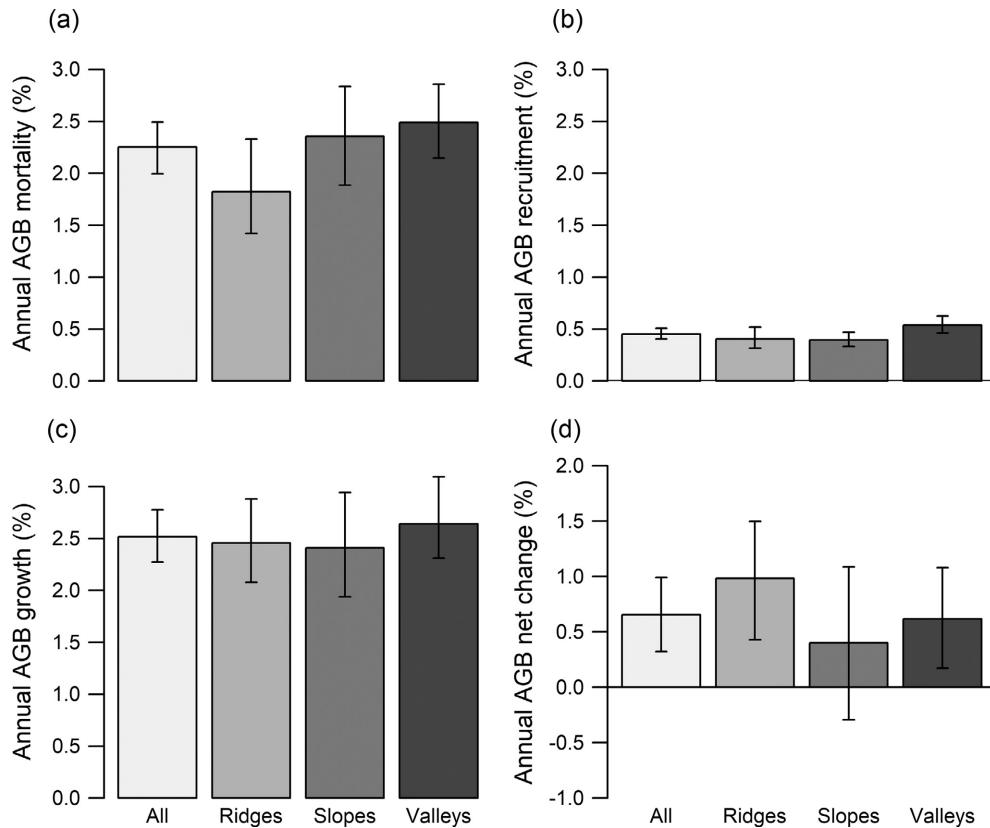|	Estimate	SE	z-value	P-value
Intercept	−2.336	0.225	−10.376	<0.001***
Post-drought period	0.573	0.113	5.089	<0.001***
Habitat slope	−0.056	0.138	−0.404	0.686
Habitat valley	−0.293	0.137	−2.141	0.032*
Wood density	−1.894	0.335	−5.656	<0.001***
Pre-drought period × Habitat slope	0.185	0.151	1.224	0.221
Pre-drought period × Habitat valley	1.244	0.145	8.588	<0.001***

***$P < 0.001$, *$P < 0.05$.

FIG. 4. Relative aboveground biomass fluxes in (a) mortality, (b) recruitment, (c) growth, and (d) net change for the 25 ha Amacayacu forest dynamics plot and for habitats within it, calculated as a percentage of initial biomass (% per yr) between 2007 and 2013 for trees with dbh ≥10 cm. Vertical bars show the 95% confidence limits based on bootstrapping over 20 × 20 m quadrats. Values are presented in Appendix S1: Table S1.

TABLE 2. Aboveground biomass carbon stocks and fluxes for trees ≥10 cm dbh in the AFDP between 2007 and 2013 (census 1 and 3, respectively), for the entire 25-ha plot and by topographically defined habitats. Changes in the number of individuals (n) and in the mean species wood density (weighted - WDw - and unweighted - WDuw - by basal area) are shown. 95% confidence intervals from bootstrapping over 20 × 20 m quadrats are shown in parentheses.

	All plot	Ridge	Slope	Valley
$n1$ (ha^{-1})	576 (567–586)	618 (600–638)	603 (585–620)	534 (520–548)
$n3$ (ha^{-1})	581 (571–591)	645 (626–666)	613 (596–630)	522 (508–537)
AGB1 (Mg ha^{-1})	241.4 (231.7–251.1)	275.1 (255.2–296.1)	257.6 (241.0–274.7)	210.9 (197.7–224.2)
AGB3 (Mg ha^{-1})	250.4 (240.4–261.0)	291 (270.5–313.0)	263.5 (247.5–279.6)	218.2 (204.5–232.1)
AGB Mortality rate (Mg ha^{-1} yr^{-1})	5.1 (4.6–5.7)	4.8 (3.7–6.1)	5.7 (4.5–6.9)	4.9 (4.3–5.6)
AGB Recruitment rate (Mg ha^{-1} yr^{-1})	0.977 (0.892–1.086)	1.017 (0.823–1.278)	0.905 (0.763–1.049)	1.005 (0.880–1.141)
AGB Growth rate (Mg ha^{-1} yr^{-1})	5.8 (5.3–6.3)	6.5 (5.6–7.7)	5.8 (4.7–7.2)	5.2 (4.6–6.1)
AGB Net change (Mg ha^{-1} yr^{-1})	1.62 (0.80–2.43)	2.79 (1.20–4.21)	1.05 (−0.76 to 2.85)	1.33 (0.37–2.34)
WDw1 (g cm^{-3})	0.594 (0.590–0.599)	0.600 (0.592–0.610)	0.587 (0.580–0.594)	0.595 (0.588–0.602)
WDw3 (g cm^{-3})	0.595 (0.591–0.600)	0.602 (0.593–0.611)	0.586 (0.579–0.593)	0.599 (0.591–0.606)
WDuw1 (g cm^{-3})	0.590 (0.588–0.593)	0.594 (0.590–0.599)	0.587 (0.583–0.591)	0.590 (0.586–0.594)
WDuw3 (g cm^{-3})	0.593 (0.590–0.595)	0.595 (0.591–0.600)	0.588 (0.584–0.592)	0.595 (0.591–0.599)

mortality rates should always be accompanied by information on the relative topographic position of trees, in order to enable proper scaling up to the landscape scale. This is especially important when small plots (≤1 ha) are used, as these are unlikely to provide representative samples of local topographic variation.

Species wood density was negatively related to mortality, consistent with previous studies (Condit et al. 1995, Kraft et al. 2010). Lower wood density species are at a particular disadvantage during droughts, as they have higher probability of hydraulic failure or cavitation under water stress (Phillips et al. 2010). Higher mortality rates for lower wood density species could shift species composition towards higher wood densities. However, such a shift is not a necessary consequence of differential mortality, as lower wood density species generally have faster dynamics, and their higher recruitment rates may compensate for their higher mortality. In the AFDP, plot-level mean wood density showed a slight but non-significant increase during the 2007–2013 census period (0.590 to 0.593), with the valley showing the largest trend (0.590 to 0.595). If droughts tend to disproportionately negatively impact species with low wood density, then increasing frequency and/or severity of droughts (Cox et al. 2008, Malhi et al. 2008, Duffy et al. 2015) would be expected to result in a gradual shift in composition towards species that are more drought tolerant, likely having higher wood density (e.g., Feeley et al. 2011). The implications of any such directional changes for forest structure and functioning remain highly uncertain and much debated (Phillips et al. 2009, 2010, Feeley et al. 2011, Finegan et al. 2015).

One obvious question is whether the higher drought-related mortality in the valleys was associated with habitat differences in species composition. The valleys do show slightly lower wood densities than the ridges on average, but the slopes show even lower wood densities (Table 2), and all the habitat-associated differences in mean wood density are very small, so they cannot explain the among-habitat variation in mortality. A post hoc analysis showed that the species random effect on mortality in the GLMM was not significantly correlated with an indicator of species habitat association, namely the proportion of individuals that inhabits the valleys ($P > 0.05$ for a regression weighted by the log of the species abundance, Appendix S1: Fig. S4). This finding indicates that the probability of tree death is independent of the proportion of individuals a species has in the valleys (Appendix S1: Fig. S4), once wood density has been accounted for, and so, that species compositional differences cannot explain habitat differences in mortality.

We found no significant effect of tree size on the probability of tree death, contrary to our expectations (e.g., Bennett et al. 2015), although consistent with some other studies (e.g., Greenwood et al. 2017). Thus, our findings are not in line with observational and experimental studies that have shown how large trees have to deal with ecological and physiological mechanisms that

make them more vulnerable to drought conditions (Ryan et al. 2006, da Costa et al. 2010, Phillips et al. 2010, Bennett et al. 2015). For the Amacayacu forest dynamics plot, the lack of a disproportionate effect of the 2010 drought on the mortality of the largest trees implies that the high amounts of carbon stored by them as well as their high productivity rates (Stephenson et al. 2014) were largely maintained during and after this water shortage event.

Given that mortality rates in the valleys of the Amacayacu plot in the post-drought period were two- to three-times higher than mean mortality reported for wet tropical forests (Condit et al. 2006), we expected this forest to be acting as a carbon source during the study interval that included the drought (Phillips et al. 2009). However, aboveground biomass in the plot increased from 2007 to 2013, even in the valley habitat, with an overall average increase of 1.62 Mg ha^{-1} yr^{-1} and the valley habitat increasing by 1.33 Mg ha^{-1} yr^{-1} (Table 2). From our data alone, it is not possible to separate biomass fluxes before and after the drought, and thus we cannot determine if the forest was a carbon sink or a source in the immediate post-drought period. Other studies of Amazon forests have found contrasting results regarding their carbon balances after drought events, with some forests acting as carbon sinks even after drought events (da Costa et al. 2010, Feldpausch et al. 2016), and others changing from carbon sinks to sources after drought (Phillips et al. 2009, Gatti et al. 2014, Brienen et al. 2015). The net biomass change in the Amacayacu plot varied strongly among habitats, with ridges showing more than twice the absolute AGB increase as valleys, consistent with the much more modest impact of the drought on mortality losses in the ridges (Figs. 3a, 4). The ongoing carbon sequestration in this forest during 2007–2013 could be explained by the CO_2 fertilization hypothesis, and/or by longer-term recovery from previous disturbances, of which the exceptional 2005 drought may have had a particularly strong effect on the Amacayacu forest (Laurance et al. 2004, Wright 2005).

In conclusion, our analyses of tree mortality and aboveground biomass dynamics in a large permanent plot located on terra firme in Colombian Amazonia yield new insights into the responses of tropical forest functioning to changing climates. Firstly, our finding of highly differential drought effects between ridges and valleys highlights the importance of measuring and reporting local topographic position in studies of tree mortality and forest dynamics more generally. It also reinforces the importance of ongoing efforts to include drought's local fine-scale processes and microhabitat characteristics in vegetation models used to predict forest responses to climate (Anderegg et al. 2015). Secondly, our work demonstrates a high carbon resilience of this forest to the 2010 drought, as manifested by the forest constituting a strong carbon sink over the study period as a whole, especially in the relatively drier terrain

of the ridges. This suggests that northwestern Amazon forests might be relatively resilient to this sort of extreme climatic event, although we cannot tell if they will be similarly resilient to the more frequent and extreme droughts predicted for the future (Brienen et al. 2015).

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