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Palms and trees resist extreme drought in Amazon forests with shallow water tables

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Abstract

1. The intensity and frequency of severe droughts in the Amazon region has increase in recent decades. These extreme events are associated with changes in forest dynamics, biomass and floristic composition. However, most studies of drought response have focused on upland forests with deep water tables, which may be especially sensitive to drought. Palms, which tend to dominate the less well-drained soils, have also been neglected. The relative neglect of shallow water tables and palms is a significant concern for our understanding of tropical drought impacts, especially as one third of Amazon forests grow on shallow water tables (<5m deep).

2. We evaluated the drought response of palms and trees in forests distributed over a 600 km transect in central-southern Amazonia, where the landscape is dominated by shallow water table forests. We compared vegetation dynamics before and following the 2015-16 El Nino drought, the hottest and driest on record for the region (-214 mm of cumulative water deficit).

3. We observed no change in stand mortality rates and no biomass loss in response to drought in these forests. Instead, we observed an increase in recruitment rates, which doubled to

6.78% y-1 ± 4.40 (mean ± SD) during 2015-16 for palms and increased by half for trees (to 2.92% y-1 ± 1.21), compared to rates in the pre-El-Nino interval. Within these shallow water table forests, mortality and recruitment rates varied as a function of climatic drought intensity and water table depth for both palms and trees, with mortality being greatest in climatically and hydrologically wetter environments and recruitment greatest in drier environments. Across our transect there was a significant increase over time in tree biomass.

4. Synthesis: Our results indicate that forests growing over shallow water tables – relatively under-studied vegetation that nonetheless occupies one-third of Amazon forests - are remarkably resistant to drought. These findings are consistent with the hypothesis that local hydrology and its interactions with climate strongly constrain forest drought effects, and has implications for climate change feedbacks. This work enhances our understanding of integrated drought effects on tropical forest dynamics and highlights the importance of incorporating neglected forest types into both the modeling of forest climate responses and into public decisions about priorities for conservation.

Keywords: water table, groundwater, Arecaceae, drought, extreme events, forest dynamics, tropical forest, climate change.

Introduction

There has been an increase in the frequency and intensity of severe droughts in the Amazon. The most recent three extreme drought events occurred at a very short interval (2005, 2010 and 2015-16) and the last two were possibly the most severe in a century (Anderson et al., 2018; Jiménez-Muñoz et al., 2016; Marengo et al., 2011). Due to its extensive area (≈6 million km^2), large carbon stores, and exceptional species richness (including as many as 15,000 tree species), the responses of the Amazon forests to extreme events is likely to affect not only the basin itself, but also global climates and biodiversity (Nobre et al., 2016; Saatchi et al., 2011; Ter Steege et al., 2013). It is already clear that the water deficits associated with recent droughts has slowed growth rates (e.g., Feldpausch et al., 2016) and increased tree mortality rates (e.g., Phillips et al., 2009; Zuleta et al., 2017), resulting in biomass loss (Brienen et al., 2015; Feldpausch et al., 2016; Leitold et al., 2018; Phillips et al., 2009). These evidences of vulnerability reinforce concerns that Amazon ecosystems may be vulnerable if drought frequency continues to increase (Esquivel-Muelbert et al., 2017). However, most assessments of drought effects have ignored the soil hydrological conditions and assumed that precipitation is the only source of water deficit to plants. The balance between precipitation and estimated evapotranspiration is the basis of the most used metrics to quantify drought, e.g. the maximum accumulated water deficit, and belowground water sources, such as provided by the water table, are not explicitly included. The water table may be the main source over considerable large expanses of the Amazon. Thousands of square kilometers of the Amazon basin are covered by poorly drained areas (Junk, 1993) and at least 36% of whole Amazonian basin is covered by forests over shallow water table (<5m deep) (Fan & Miguez-Macho, 2010). The belowground water source can be expected to minimize the effects of droughts on plants and change the predictions of forest vulnerability to drought.

Water table depth is an important driver of rooting depth and plant water uptake. Under deep water table conditions, the vegetation relies on local precipitation and rooting depth is determined by the depth of rainfall infiltration into the soil (Fan, Miguez-Macho, Jobbágy, Jackson, & Otero-Casal, 2017). On the other hand, shallow water table prevents drainage and creates frequently waterlogged soil conditions. Thus, roots remain shallow, to minimize the stress due to anaerobiosis (Fan et al., 2017; Fan & Miguez-Macho, 2011). In deep water table forests (DWTF), the drier and warmer climate conditions during extreme droughts decrease soil moisture leading to reduced photosynthesis and net primary production (Santos et al., 2018; Zhao & Running, 2010). However, this should not apply to shallow water table forests (SWTF), as the soil waterlogging tend to decrease during droughts in leading to an increase the growth window, and thus promote growth in a similar way to what has been observed in floodplain forests (Schöngart et al., 2004; Schöngart et al., 2005).

Our current understanding on the effect of drought on Amazonian forests have neglected how palms, a fundamental functional group within these forests, have responded to the changes in climate. Responses to drought have been mostly evaluated for dicotyledonous trees and lianas and have typically either excluded palms or included them within a broad category of 'trees' (e.g., Brienen et al., 2015; Fauset et al., 2012; Laurance et al., 1999; Lewis et al., 2011; Phillips et al., 2004). However, palm's xylem anatomy, architecture and growth strategies are fundamentally different from dicotyledonous trees (Castilho et al., 2006; Emilio et al., 2013; Tomlinson, 2006). Thus, the changing patterns in dynamics and biomass stocks described for trees across the Amazon may simply not apply to palms. The responses of palms to climate are likely to have important basin-wide implications, as palm-dominated forests cover 20% of the Brazilian Amazon and contribute up to 23% of the basal area in the western Amazon (Emilio et al., 2013; IBGE, 1997). Moreover, this group comprises no less than six of the top ten most abundant tree species of the Amazon basin (Ter Steege et al., 2013), being highly useful for people (Levis et al., 2018). To date the only analysis we are aware of in which the effect of Amazon climate drying on long-term population changes of Amazon trees has been probed, found that palms are especially drought-vulnerable, having declined in abundance in many long-term Amazon forest plots (Esquivel-Muelbert et al., 2019). Thus, forests on shallow water table (SWTF) and palms both represent important and currently neglected components that need to be understood to properly evaluate the future of Amazon forests under climate change.

Trees and arborescent palms differ in growth strategies, rooting and vascular systems (Gale & Barfod, 1999; Renninger et al, 2013). Furthermore, palms and trees are associated to different soil physical conditions, palms being more abundant on less structured soils, e.g. environments that limit root development. Moreover, palms are more physically stable due to characteristics of their stem anatomy that allows firm anchorage to the ground (Emilio et al., 2013; Tomlinson, 1990). Palms lack vascular cambium and thus, as opposed to trees, cannot add additional vessels to increase stem diameter and cannot replace embolized xylem vessels (Tomlinson, 2006). The palm root system is shorter than in trees, and therefore, is naturally restricted to superficial soil layers (Tomlinson, 1990). These morphological differences between palms and trees should affect their responses to droughts. Notably, the absence of secondary xylem vessels production and shallow roots could make palms more sensitive to drought-induced embolism (Renninger et al., 2013; Rich, 1987; Tomlinson, 2006).

Considering the limited understanding of forest dynamics in areas of shallow water table and the great importance of palms to the structure of the tropical forests, here we seek to address these gaps. Our study takes advantage of a unique permanent plot initiative, which has established and monitored sites accessible from the Central-southern Amazon BR-319 road. This made possible for the first time to track forest dynamics and biodiversity over a huge and otherwise largely inaccessible landscape. Using this plot network, we monitored the dynamics of palms and trees in forests along a 600 km transect, through landscapes dominated by shallow water table forests, and during a period that captures the intense 2010 and 2015-16 droughts. We specifically addressed the following questions: 1) Are palms more vulnerable to extreme drought than trees?; 2) What is the impact of different climatological drought intensities on palm and tree dynamics?; 3) How do local water table depth and soil properties interact with climatological droughts to influence palm and tree dynamics?

We considered two alternative hypotheses: 1) palms here will be more sensitive to droughts than trees, so that intense droughts (such as in 2015-16) cause strong reduction in water availability of these normally water saturated soils, leading to higher mortality and lower recruitment rates, and a consequent loss of biomass stocks; or 2) droughts will instead promote a decrease in the water table level and a consequent reduction in the stressful soil anoxic condition, and so ameliorate the growing conditions for both palms and trees. In this scenario, plants will benefit from droughts, with no changes in their mortality and an increase in recruitment rates would be expected. In addition, independent of the drought events, higher soil physical constraints, i.e., shallow, compact and anoxic soils, will promote greater recruitment and lower palm mortality, given the palms preference for these conditions (Emilio et al., 2013).

Materials and methods

Study area and sampling design

The study was conducted along a 600 km transect along the interfluvial region between the Purus and Madeira rivers, south of the Amazon River in Central-southern Amazonia. The water table is shallow (2.81 m ± 2.38 deep (mean ± SD)), and topography in the region is generally flat with elevation above sea level varying from 30–80 m over large distances (estimated by Shuttle Radar Topography Mission - SRTM data) (Rodríguez, Morris, & Belz, 2006). Mean annual precipitation in this area varies from 2100–2700 mm

(Hijmans etal., 2005), with on average two to three consecutive months with less than 100 mm rainfall (dry months) per year (Sombroek, 2001). Soils are predominantly Plinthosols and Gleysols, the predominant texture is silt to fine sand, with poor drainage, and varying degrees of soil water saturation and anoxic conditions (Martins et al., 2014; Sombroek, 2000). Soils physical structure is generally dense and restrictive to root growth, with varying degrees of hardness and effective soil depth (Quesada et al., 2010).

We sampled 25-1 ha plots systematically distributed in 8 research sites along 600 km of the BR-319 highway. In each site, two to five plots were sampled in regular grids of 5 x 1 km, keeping a 1 km minimum distance among plots (Fig. 1). Plots were established at least 1 km distance from the road to avoid sampling forests which had been recently disturbed by human activity. Permanent plots were 250 m long and followed the terrain altitudinal contour, in order to reduce edaphic and hydrological variation within plots (Magnusson et al., 2005).

Vegetation data

Diameter at breast height (dbh) of approximately 1,700 palm stems and 15,000 trees were measured in the 25 plots. We used a nested design to measure palms and trees along the 250 m plot main axis (Magnusson et al., 2005). All stems with dbh ≥ 30 cm were sampled in the full 1 ha (250 x 40 m), stems with 10 cm ≤ dbh < 30 cm were measured in a subplot of 0.5 ha (250 x 20 m) and stems with 1 cm ≤ dbh < 10 cm were measured in a subplot of 0.025 ha (250 x 1 m). Each stem from clonal species (mostly palms) was considered as an individual stem in the analyses. The three censuses for vegetation monitoring were conducted during dry season in the years 2010 (Schietti et al., 2016), 2015 and 2016. All palms and trees with above-ground stems measured were considered in the analyses. Palm and tree data were uploaded and curated in the ForestPlots.net data management system (Lopez-Gonzalez et al, 2011).

Above-ground biomass of individual palms was calculated based on dry mass fraction (dmf), stem diameter (dbh) and stem height (H_{stem}), according to the family-level allometric equation for Amazonian palms developed by Goodman et al. (2013):

$$\text{Palm biomass} = 0.55512^4 \times (\text{dmf} \times \text{dbh}^2 \times H_{stem})$$

The Goodman et al. (2013) equation is largely supported by local studies such as Silva et al. (2015) and Avalos et al. (2019) who both studied a subset of the species in our dataset. Palm heights were measured using a Vertex hypsometer (Vertex Laser VL400 Ultrasonic-Laser Hypsometer III, Haglöf of Sweden). Stem heights could only be estimated during the second census in 2015, when 70% of the total number of palms registered in the plots had their height measured. For those stems that did not had their height measured, we used species-level means, either the site-level mean height for the most abundant species (*Lepidocaryum tenue* and *Oenocarpus bataua*) or the overall mean height for remaining species. We disregarded changes in palm height over time and used the height measurements from 2015 for all censuses (2010, 2015 and 2016).

Our evaluation of changes in the palm biomass stock is based on only on the population changes, i.e. recruitment and mortality. We assumed zero stem diameter growth, as palm diametric variations are mostly governed by fluctuations in water content (Stahl et al., 2010). We note that palm growth occurs via increasing height, with the addition of new metamers (Tomlinson, 1990), so quantifying biomass increases in individual palms requires repeated height measurements which were not possible here.

Above-ground biomass of individual trees was calculated based on diameter (D), wood density (ρ) and tree height (H), according to the pantropical allometric model developed by Chave et al. (2014):

$$\text{Tree biomass} = 0.0673 \text{ x } (\rho D^2 H)^{0.976}$$

Tree height was estimated using D-H allometric equations adjusted for each of the 8 research sites along the transect (Schietti et al., 2016). Species wood density was obtained from the global wood-density data base (Chave et al., 2009; Zanne et al., 2009).

Annual mortality rates (λ) were calculated as: $\lambda = \left[\ln(N_0) - \ln(N_s)\right]/t$, where N_0 and N_s are the number of stems counted of the initial population, and the number of stems surviving to time t, respectively (Sheil, Burslem, & Alder, 1995). Annual recruitment rates (μ) were calculated following Phillips et al (1994) equation: $\mu = [\ln(N_f/N_s)]/t$, where N_f is the final number of stems, N_s is the original number of stems surviving to final inventory and t is the number of years between inventories. Mortality and recruitment rates were calculated for the intervals 2010-2015 and for 2015-2016. In this paper stand mortality and stand recruitment were treated as mortality and recruitment rates, respectively.

Long and irregular census intervals may lead to some underestimation of mortality and recruitment rates, since they have a greater probability of including unobserved mortality and recruitment especially of fast turnover sub-populations (Lewis et al., 2004). The proposed correction factor $\lambda_{corr} = \lambda \times t^{0.08}$, where λ is the rate and t is time between censuses in years, was applied for all the demographic rates calculated in this study.

Environmental data

To assess meteorological drought, i.e., atmospheric drought based on the balance between precipitation and evapotranspiration, we estimated maximum cumulative water deficit (MCWD) between census intervals, considering the month of the initial and final census of each plot. MCWD corresponded to the maximum value of the monthly accumulated climatic water deficit reached for each location. This metric represents the sum of water deficit values (i.e. the difference between precipitation and estimated evapotranspiration for the forest) over consecutive months when evapotranspiration is greater than precipitation (Aragão et al., 2007). Precipitation data were extracted from the Tropical Rainfall Measuring Mission satellite (TRMM, 3B43 7A) (Huffman et al., 2007) produced from 2010 to 2016, at 0.25º spatial resolution. Monthly evapotranspiration was assumed fixed at 100 mm month^{-1}, considering that moist tropical canopies have approximately constant evapotranspiration rate (Rocha et al., 2004; Shuttleworth, 1988).

As a proxy to the plant access to belowground water, which can affect the hydrological drought experienced by roots, we characterized the local hydrological condition as the average water table depth (WTD) monitored using piezometers between the years of 2010 and 2013 in all plots (Fig. S1). Each plot had one piezometer 7 m deep in the ground, monitored every one or four months in this period. Although the hydrological drought would be more correctly described by WTD values measured along the full census period, this concomitant temporal data was not available. However, the seasonal fluctuation of WTD in each plot is similar across years, i.e. plots with shallow minimum and maximum values along the year (thus shallow WTD average) in general do not attain deeper WTD values in dry years than plots with deeper min, max and average WTD (Fig. S6). This means that we can use these average values to rank plots along a gradient of WTD that is indicative of the potential hydrological drought experienced by plants.

Since forest dynamics is known to be linked not only to climate but also to soil properties (Quesada et al., 2012), we included an index of soil physical restriction developed by Quesada et al. (2010) in our analyses, to represent the magnitude of soil physical limitation. This semi-quantitative index is based on soil effective depth, soil structure, anoxic conditions and topography. Higher scores denote more limited soil conditions for plant roots. Soil physical classification was determined in 2 m deep pits dug in each research site and in soil-profile samples from all plots (Martins et al., 2014). As a proxy of soil fertility we used the available phosphorus content (extracted with Mehlich-1) (EMBRAPA, 2011) determined from a compound sample derived from 6 subsamples from the first 30 cm soil depth (Schietti et al., 2016).

Data analyses

All analyses were conducted in R version 3.4.2 software (The R Core Team, 2018). To evaluate the changes in recruitment and mortality over time on a plot basis we used paired *t-tests* between the moderate (2010-2015) and severe (2015-2016) droughts, this was also applied to assess changes in rates considering different diameter size classes. Biomass stock were analyzed by repeated-measures ANOVA between the years of 2010, 2015 and 2016. To investigate the relationships of palm and tree dynamics with environmental conditions, we used generalized linear mixed models, with package GAMLSS (Stasinopoulos & Rigby, 2007), assuming a Beta distribution for demographic rates. Site was included in the models as a random effect, to control for potential spatial autocorrelation between plots nested in the same site. We tested models relating palms and trees demographic rates to a set of combinations of environmental variables describing hydrology and soil constraints (Supporting information Tables S3 and S4). Hydrological conditions were represented by meteorological drought (maximum cumulative water deficit: MCWD) and water in soil (average water table depth); soil constraints were represented by an index of soil physical restriction and available phosphorus. We hypothesized that water table depth would modulate the effects of the drought intensity on demographic rates, so we included the interactions among these factors. The models were built and evaluated based on the continuous values of MCWD, however for visualization of interactions our outputs were categorized into “more negative” and “less negative”. The classification of MCWD in these two classes was data-driven based on the frequency distribution of values observed in the plots - thus in the moderate drought the MCWD threshold was -90 mm, while in strong drought MCWD threshold was -130 mm (Fig. S2). Best models were selected according to the Akaike’s information criterion (AIC). Models with lower AIC, fewer parameters and significant relationships between the response and the predictor variables were selected as the best models.

Results

In our dataset we recorded 19 palm species distributed in 13 genera, with *Lepydocaryum tenue* and *Oenocarpus bataua* being the most abundant species (Supporting information Table S1). According to precipitation data recorded from 1998 to 2016, the study region experienced MCWD annual anomalies up to -1σ in 2010 (MCWD = 107 mm; accumulated annual precipitation = 2438 mm) and MCWD annual anomalies up to -3σ in

2015 (MCWD = 308 mm; accumulated annual precipitation = 2053mm) (Fig. 1). Due to the MCWD anomalies recorded in the years 2010 and 2015 in relation to the historical series, the first interval can be considered as a moderate drought (2010-2015) and the second interval as a severe drought (2015-2016) for this study region.

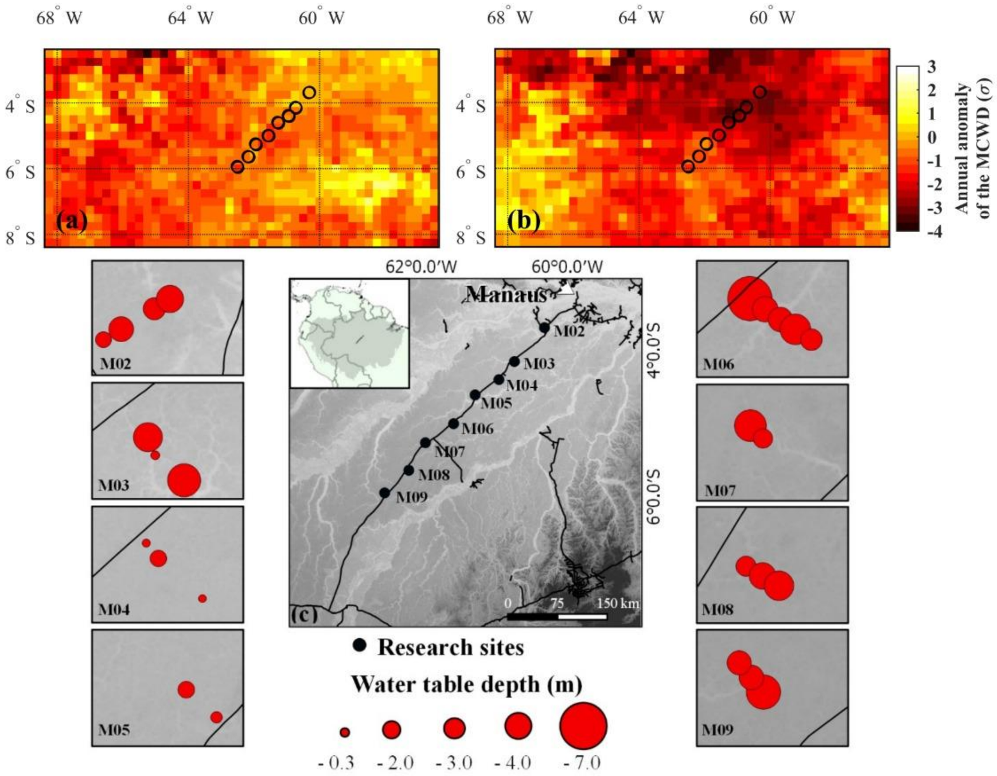

FIGURE 1. Characterization of the drought intensity (MCWD, in mm) across the study region in 2010 (a), and 2015 (b), and the average water table depth of the plots in each of the 8 research sites along the Purus–Madeira interfluve, in central-southern Amazonia (c)

Palm and tree annual recruitment dynamics changed between moderate and strong droughts. There was a strong increase in palm annual recruitment rates from the first to the second period ($t = -4.02$; $df = 24$; $p < 0.001$). Palm recruitment averaged 3.30% ± 1.94 (mean ± SD) per year in the period 2010 to 2015 and doubled to 6.78% ± 4.40 (mean ± SD) per year during 2015-2016 (Fig. 2a). Annual recruitment rates also increased among trees from the first to the second interval ($t = -4.70$; $df = 24$; $p < 0.001$), averaging 1.85% ± 0.52 (mean ± SD) per year from 2010 to 2015, and was 1.5 times greater between 2015 and 2016 (2.92% ± 1.21, mean ± SD) (Fig. 2c). However, there was no change in annual mortality rates over the same intervals for palms (3.67% ± 1.93, 2010-2015 and 4.28% ± 3.69, 2015-2016) or trees (1.56% ± 0.62, 2010-2015 and 1.69% ± 0.91, 2015-2016) (Figs. 2b-2d). Considering the variation among diameter classes, we find that annual recruitment rates increased from the first to the second interval only for small diameter classes (1 cm ≤ dbh < 10 cm), for both trees and palms. On the other hand, annual mortality rates do not differ among size classes between intervals, i.e. large trees (dbh ≥ 30 cm) did not have higher mortality in years of severe drought (Fig. S5).

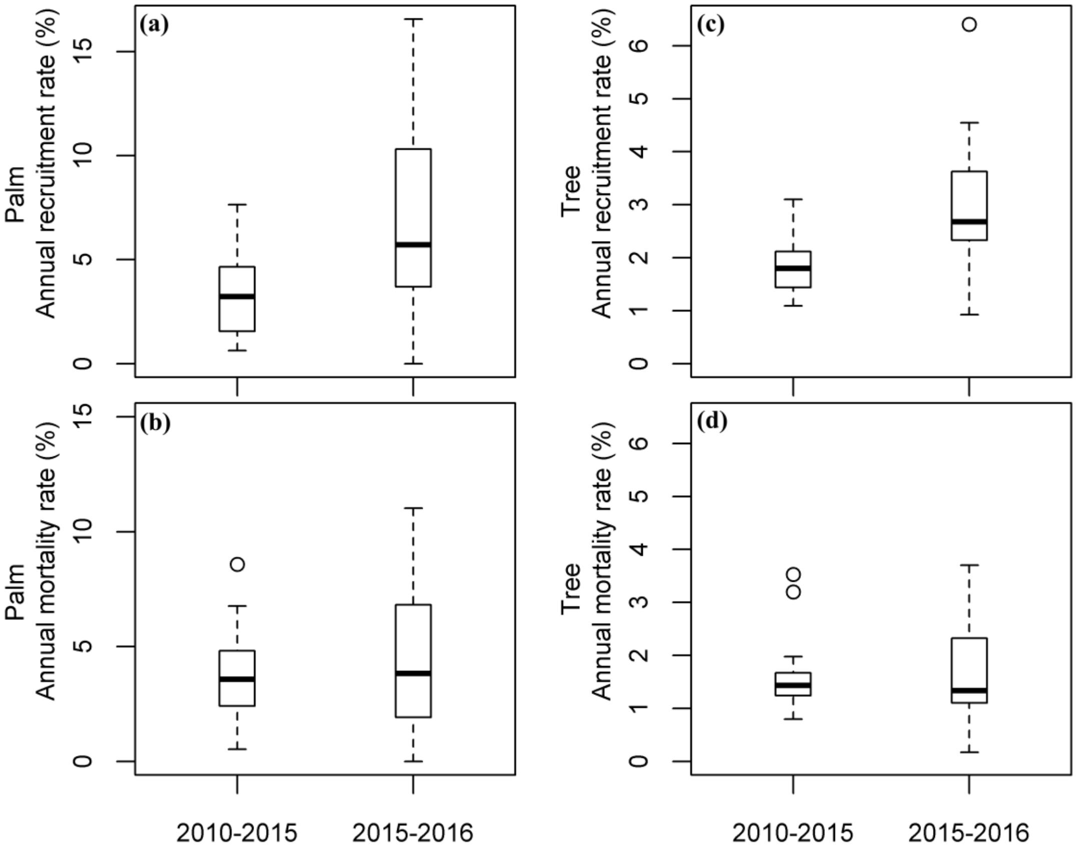

FIGURE 2. Palm annual recruitment (a) and mortality rates (b); Tree annual recruitment (c) and mortality rates (d), between the two censuses in forests along the Purus–Madeira interfluve, in central-southern Amazonia

The association between demographic rates of both palms and trees (described by the models below) and environmental predictors varied across time periods (Supporting information Tables S3 and S4). Variation in mortality rates was significantly associated to the environmental conditions only in the period with moderate drought (2010-2015), while variation in recruitment was significantly associated to environment only in the period with the strongest drought (2015-2016).

The best model to explain palm mortality rates included the interaction between cumulative water deficit and average water table depth, and soil physical restriction index (Table 1). In the interval from 2010 to 2015, sites that experienced less negative water deficit (MCWD > -90 mm) and with shallowest water table (Fig. 3a, grey points on the right of the dashed line) had higher palm annual mortality rate (x̄ = 4.12%). In contrast, forests sites that experienced more negative water deficit (MCWD < -90 mm) and shallowest water table (Fig. 3a, black points on the right dashed line) had lower palm mortality rates (x̄ = 2.36%). Palm mortality was also higher in soils with lower physical constraints (Fig. 3b).

The best model for palm recruitment included only hydrological variables, i.e. an interaction between the maximum cumulative water deficit and average water table depth in the interval from 2015 to 2016 (Table 1). On average, during this interval, palm annual recruitment rates did not differ between plots that experienced less negative water deficit (MCWD > -130 mm) (x̄ = 7.06%) and those that experienced more negative water deficit (MCWD < -130 mm) (x̄ = 6.52%). However, recruitment was lower (1.68%) in plots with shallower water table (< 2.5 m deep) and under strong drought (Fig. 3e, black points on the right of dashed line). Plots on the same shallow water table level, but experiencing less negative water deficit, had higher recruitment rates (5.98%, Fig. 3e, grey points on the right of dashed line).

For trees, in the interval from 2010 to 2015, models with higher support to explain mortality rates included the average water table depth and the available soil phosphorus (Table 1). Tree mortality was higher in soils with shallowest water table and greater fertility (Figs. 3c-3d). During the 2015- 2016 interval, the best recruitment rates model included an interaction between maximum cumulative water deficit and average water table depth (Table 1). In this period, recruitment rates were lower in plots that experienced less negative water deficit (MCWD > -130 mm) (x̄ = 2.28%) than in those that experienced more negative water deficit (MCWD < -130 mm) (x̄ = 3.50%). Among plots with higher water deficit, recruitment increased with water table depth, and the decreased for plots with lower water deficit (Fig. 3f).

TABLE 1. Statistical summary of the best generalized mixed models to explain the relationship between palm and tree dynamics and environmental variables. Intercept and slopes of each predictor included in the regressions are presented; ΔAIC is the difference between the model with the lowest AIC and the model chosen.

Models	Predictors	p	ΔAIC	R2
Palm mortality (2010-2015)	0.02 MCWD	0.002	0	0.84
	0.47 average water table depth	0.001		
	-0.13 soil physical restriction index	<0.001		
	0.005 MCWD*average water table	0.004		

Models	Predictors	p	ΔAIC	R2
	depth			
Palm recruitment (2015-2016)	0.05 MCWD 1.37 average water table depth 0.01 MCWD*average water table depth	< 0.001 0.001 0.0004	-0.64	0.70
Tree mortality (2010-2015)	0.12 average water table depth 0.08 available soil phosphorus	<0.001 0.05	0	0.61
Tree recruitment (2015-2016)	0.004 MCWD 0.43 average water table depth 0.003 MCWD*average water table depth	0.34 0.02 0.04	0	0.52

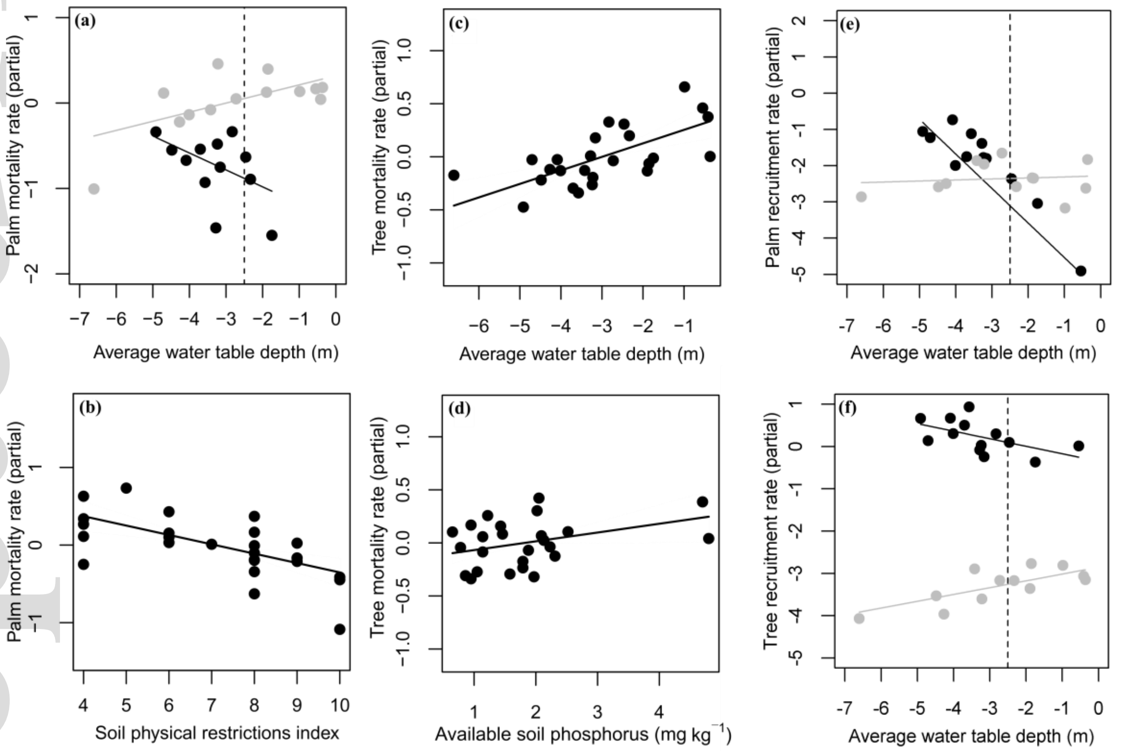

FIGURE 3 Partial regressions derived from the multiple regression models investigating the effects of maximum cumulative water deficit (MCWD), average water table depth (m), soil physical restriction index and available soil phosphorus on mortality and recruitment in Central-Southern Amazonia. (a) Partial effect of the interaction between MCWD and average water table depth and (b) partial effect of the soil physical restriction index on palm mortality, during the 2010 to 2015 interval; (c) Partial effect of the average water table depth (m) and (d) partial effect of available soil phosphorus on tree mortality, during 2010 to 2015 interval;

(e) Partial effect of the interaction between MCWD and average water table depth on palm recruitment, and (f)) partial effect of the interaction between MCWD and average water table depth on tree recruitment, during the 2015 to 2016 interval. For mortality, grey points are plots that experienced less negative MCWD (> -90 mm) in the analyzed period, black points are plots that experienced more negative MCWD (< -90 mm). For recruitment, grey points are plots that experienced less negative MCWD (> -130 mm) in the analyzed period, black points are plots that experienced more negative MCWD (< -130 mm). Dashed lines indicate 2.5 m water table depth

Spatially, palm biomass stocks (AGB) varied widely from 1.12 to 12.33 Mg ha^{-1} (Fig. 4a) and contributed with 1% to 5% per hectare to the total amount of alive above-ground biomass (Table S2). Biomass stocks were respectively 5.84 ± 3.17 (mean ± SD) in 2010, 5.84 ± 3.18 in 2015 and 5.86 ± 3.17 in 2016 for palms, and 227.94 ± 55.39, 233.95 ± 55.73 and 234.48 ± 56.57 (mean ± SD) for trees. There was no significant change in palm biomass stock between the three censuses (F= 0.014; p= 0.91) considering the balance between recruitment and mortality of individuals. For trees, biomass varied spatially from 97.15 to 328.75 Mg ha^{-1} (Fig. 4b). However, unlike palms, trees had an increase in the biomass stock from the 2010 to 2015 (F= 17.69; p < 0.001). Analyzing plot-by-plot 80%, of them had biomass gain in this interval (Fig. S4b).

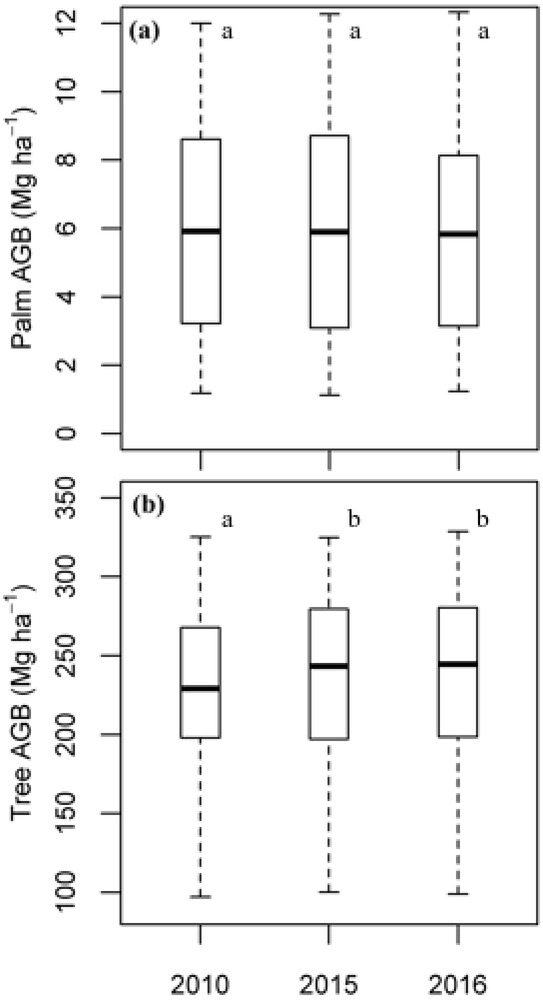

FIGURE 4 Variation in palm (a) and tree (b) biomass stocks (AGB) in 25 plots measured along the Purus–Madeira interfluve, in Central-southern Amazonia. Different letters indicate significant differences in biomass stock between years ($p < 0.001$; Tukey method)

Discussion

We analyzed for the first time the effect of droughts of different intensities over shallow water table Amazonian forests (SWTF). Our results show that palms were no more vulnerable to extreme droughts than trees in these forests. The strong drought of 2015 did not increase palm or tree mortality rates, but instead, promoted increased recruitment rates. The drought responses in terms of recruitment and mortality were mediated by the local hydrological conditions, soil fertility and soil physical restriction. There was an increase in tree above-ground biomass stock from 2010 to 2015, but no significant change over time of palm AGB. Overall, extreme droughts did not have a negative impact on either trees or palms growing over shallow water table. Our study reveals the complex interplay between climatological droughts and belowground water access on forest dynamics. Our results indicate the crucial need to incorporate the interaction between precipitation and belowground properties for a more realistic estimation of local hydrological conditions on environmental impact evaluations and models to forecast drought effects in the Amazon.

We hypothesized that more intense droughts could sufficiently reduce water availability of these normally water-saturated soils, leading to higher mortality and lower recruitment rates, resulting in biomass loss, particularly of palms. However, our results did not support this hypothesis. Palms and trees have structural differences in their vascular anatomy, which are reflected on different sensitivities to drought. Palms tend to have large vessels, high hydraulic conductivity and high demand for water (Aparecido et al. 2015; Kunert et al. 2013), which could be expected to generate a larger vulnerability to drought, however this was not what observed in SWTF. Our results are partially in accordance with our alternative hypothesis: droughts are likely to lead to moderate soil drying, which is enough to reduce the anoxic conditions of waterlogged soils and hence promote palm and tree growth, with increased recruitment and no increase in mortality rates. This suggests that both palms and trees on shallow water table forests are resistant to extreme droughts because the belowground hydrological environment buffers climatological water deficit. Thus, shallow water table may offer a relief from the atmospheric water stress projected by climate models for decades to come, functioning as hydrologic refugia (McLaughlin et al., 2017; Pokhrel, Fan, & Miguez-Macho, 2014).

Higher tree mortality in soils with higher phosphorus concentration may be related to the functional properties selected by fertile soils and the resulting vegetation dynamics. Low wood density is selected on fertile soils, which generally have high phosphorus availability and physical restrictions, leading to high turnover rates (Baker et al., 2004; Phillips et al., 2004) and low biomass stock (Quesada et al., 2012; Schietti et al., 2016).

Higher recruitment rates observed during the 2015-16 interval are likely to be directly associated with climatological changes, though they could potentially be an indirect result of previous disturbances that increase light. The importance of light availability to forest growth and dynamics is well known (Augspurger, 1984; Bentos et al. 2017; Jakovac et al. 2012), however responses still depend on specific requirements of each species (Ley-López, Avalos, & Chacón-Madrigal, 2016). Our study did not include direct metrics of light availability, however, we evaluated whether previous disturbances (i.e., the mortality rates in the previous period, a proxy for canopy openness) could be leading to increased recruitment. We found no effect of previous disturbances on recruitment rates on the following period (Fig. S3), thus it is likely that the higher recruitment in 2015-16 is associated with the environmental conditions during the 2015-16 El Niño event. In seasonally flooded forests, drought prolongs the non-flooded period, which is when plants grow due to the reduction of anoxic stressful conditions (Schöngart et al., 2002). Under the drier conditions observed in El Niño years, floodplain forests show increased wood growth (Schöngart et al., 2004). Our findings of increased recruitment in the 2015-16 El Niño in SWTF are consistent with those observations on floodplain forests. However, this increase in recruitment during the strongest drought cannot be solely attributed to the temporal decrease in stress due to anoxia. Forest plots that experienced higher climatological water deficits and deeper water table had higher recruitment rates than plots that experienced similar drought condition but located in shallow water table. It must be acknowledged that all sites studied here have shallower water table (average depth < 7m; Fig. S1) than most other studied plots in the Amazon (i.e. from 10 to more than 40 m deep, S. Chen personal communication). We can speculate that during the strong drought, anoxia was sufficiently reduced in soils with water table deeper than 3 m, but not enough where the water table was shallow. However, detailed monitoring of belowground water level fluctuation during drought periods is still required, through field monitoring and / or eco-hydrological modeling (Chitra-Tarak et al., 2018). This information may provide additional support to our hypothesis or elucidate other mechanisms that may be involved on forest responses.

Over our 600 km of monitored forests, there was no increase in mortality from the moderate to the strong drought periods, and neither larger mortality rates associated to sites that experienced the strongest climatic water deficits. We expected stronger negative drought effects on palms, as their anatomy and growth form are likely to make this group more drought-vulnerable (Tomlinson, 2006). Indeed highly increased mortality (7%) of the most abundant palm species of a *terra firme* forest over deep water table was observed after the strong 1997 drought (Williamson et al., 2000), and a long-term decline trend of wet-affiliated palms was detected across the Amazon basin as climate becomes drier (Esquivel-Muelbert et al., 2019). Surprisingly, we found no evidence that palms are more vulnerable to drought than trees in the wet conditions experienced by SWTF. This is consistent with the findings of no increases in palm mortality after droughts in wet forests of western Amazonia (Olivares et al. 2017) and Central America (Condit et al. 2004). Our results suggest that even if Amazon palms are intrinsically susceptible to drought, their response to drought events can be highly variable and contingent to local belowground hydrological conditions. The fact that even the more drought-sensitive palms did not suffer increased mortality in the strong 2015 drought supports the assertion that forests with shallowest water table are more resistant to drought than forest with deep water table.

Our result of an increase in the tree biomass stock is the contrary of what has been observed (biomass loss) on most tropical forests after droughts. Studies in Amazon forests have evidenced its vulnerability to drought through the reduction in above-ground biomass along the last decades (Brienen et al., 2015; Phillips et al., 2009). In the 2010 drought, the estimated biomass loss of Amazon forests was on average 1.45 Mg ha^{-1}, leading to a projected reduction of carbon uptake of 1.1 Pg (Feldpausch et al., 2016). Biomass stock of the Amazon has a wide spatial variation, from 200 to 350 Mg ha^{-1}, according to the geographic region (Baker et al., 2004; Lewis et al., 2013). In the present study, forest biomass stock was comparable to that of the Southwestern region, which has lower biomass compared to Central and Eastern Amazonia (Baker et al., 2004). Although palms do not contribute heavily to biomass in most dense *terra firme* forests (~ 1%) (Castilho et al., 2006), their contribution is often considerably greater in other environments as open forests and swampy conditions (Kahn et al., 1990; Lähteenoja et al., 2009), as represented in our plots. More stable biomass stocks in the shallow water table forests, which cover around a third of the Amazon basin (Junk et al., 2011), may thus provide a counterbalance to losses on the deep water table forests during droughts.

We have shown here that, contrary to the previous results from studies conducted at forest over deep water table across the Amazon basin (Brienen et al., 2015; Feldpausch et al., 2016; Phillips et al., 2009), palms and trees on SWTF are more resistant to drought. Therefore, it is important to consider the local belowground hydrological environment for a better assessment of drought effects on tropical forests. In addition, as previously reported for lianas (Lewis et al., 2004; Nepstad et al., 2007; Phillips et al., 2002; Van Der Heijden et al., 2013), different life forms may respond differently to global climate changes according to their biology and the effect on these should be investigated separately. Considering the progression of climate change, SWTF can be considered as potential refuges for biodiversity, conservation of the Amazon forest and may provide an important counterbalance to the biomass loss in forests affected by both atmospheric and soil moisture deficits. Given the extent of these forests, and their differential responses to drought, more research in shallow water table tropical forests is urgently needed. Not only will it be important to better account for soil water supply in modeling the dynamics and carbon fluxes of tropical forests, but a wider recognition of the importance of these systems can contribute to the development of public policies including prioritizing conservation areas on SWTF, which may be best-suited to help Amazonia resist climate change.

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Authors' contributions:

TRS, FRCC and JS conceived the ideas; TRS, FCS, AEM, JS and TE collected the data; TRD, IOR and PACLP analysed the data; TRS led the writing of the manuscript; FRCC and OP made important intellectual contributions. All authors revising and contributed critically to the drafts and gave final approval for publication.

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