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


1 Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; 2 Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; 3 School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK; 4 School of Geography, University of Leeds, Leeds, UK; 5 Programa de Pós-Graduação em Clima e Ambiente (CLIAMB, INPA/UEA), Manaus, Brazil; 6 Programa Nacional de Pós-Doutorado (PNPD), Programa de Pós-Graduação em Ecologia, Instituto de biologia, Universidade de Campinas, Campinas, Brazil and 7 Programa de Pós-Graduação em Recursos Naturais, Universidade Federal de Roraima, UFRR, Boa Vista, Brazil

Correspondence
Thaiane R. Sousa
Email: thaianesousar@gmail.com

Funding Information
Amazonas State Research Foundation (FAPEAM); Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Grant/Award Number: 307579/2013-1 and 142166/2015-4; Newton Fund, Grant/Award Number: NE/M022021/1; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES), Grant/Award Number: 88887.141433/2017-00; PPBio Manaus, INCT CENBAM and RAINFOR; Cuomo Foundation

Handling Editor: Crystal McMichael

Abstract
1. The intensity and frequency of severe droughts in the Amazon region have increased in the 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 (<5 m 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 (SWTF). We compared vegetation dynamics before and following the 2015–2016 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% year$^{-1}$ ± 4.40 (M ± SD) during 2015–2016 for palms and increased by half for trees (to 2.92% year$^{-1}$ ± 1.21), compared to rates in the pre-El-Nino interval. Within these SWTF, 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 modelling of forest climate responses and into public decisions about priorities for conservation.

### KEYWORDS
Areceae, climate change, drought, extreme events, forest dynamics, groundwater, tropical forest, water table

### 1 | 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 2015–2016) and the last two were possibly the most severe in a century (Anderson et al., 2018; Jiménez-Muñoz et al., 2016; Marengo, Tomasella, Alves, Soares, & Rodriguez, 2011). Due to its extensive area (>6 million km²), large carbon stores, and exceptional species richness (including as many as 15,000 tree species), the responses of the Amazon forests to extreme events are 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 have slowed growth rates (e.g. Feldpausch et al., 2016) and increased tree mortality rates (e.g. Phillips et al., 2009; Zuleta, Duque, Cardenas, Muller-Landau, & Davies, 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, for example, 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 kilometres 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 (<5 m 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 (WTD) 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 & Miguez-Macho, 2011; Fan et al., 2017). 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 tends 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, Piedade, Wittmann, Junk, & Worbes, 2005).

Our current understanding on the effect of drought on Amazonian forests has 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, Brando, Phillips, Heijden, & Nepstad, 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; Instituto Brasileiro de Geografia e Estatística, 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 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 & Barfold, 1999; Renninger, McCulloh, & Phillips, 2013). Furthermore, palms and trees are associated to different soil physical conditions, palms being more abundant on less structured soils, for example, 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 SWTF, and during a period that captures the intense 2010 and 2015–2016 droughts. We specifically addressed the following questions: (a) Are palms more vulnerable to extreme drought than trees? (b) What is the impact of different climatological drought intensities on palm and tree dynamics? (c) How do local WTD and soil properties interact with climatological droughts to influence palm and tree dynamics?

We considered two alternative hypotheses: (a) palms here will be more sensitive to droughts than trees, so that intense droughts (such as in 2015–2016) 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 (b) 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, that is, shallow, compact and anoxic soils, will promote greater recruitment and lower palm mortality, given the palms preference for these conditions (Emilio et al., 2013).

2 MATERIALS AND METHODS

2.1 Study area and sampling design

The study was conducted along a 600 km transect along the inter-fluvial 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 [M ± SD]), and topography in the region is generally flat with elevation above sea level varying from 30 to 80 m over large distances (estimated by Shuttle Radar Topography Mission data; Rodriguez, Morris, & Belz, 2006). Mean annual precipitation in this area varies from 2,100 to 2,700 mm (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), with on average two to three consecutive months with <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 eight research sites along 600 km of the BR-319 highway. In each site, two to five plots were sampled in regular grids of 5 × 1 km, keeping a 1 km minimum distance among plots (Figure 1). Plots were established at 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).

2.2 Vegetation data

Diameter at breast height (dbh) of approximately 1,700 palm stems and 15,000 trees was 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 × 40 m), stems with 10 cm ≤ dbh < 30 cm were measured in a subplot of 0.5 ha (250 × 20 m) and stems with 1 cm ≤ dbh < 10 cm were measured in a subplot of 0.025 ha (250 × 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, Lewis, Burkitt, & Phillips, 2011).

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

\[
Palm\ biomass = 0.55512^{4} \times (dmf \times dbh^{2} \times H_{stem}).
\]

The Goodman et al. (2013) equation is largely supported by local studies such as Da 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 have 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 require repeated height measurements which were not possible here.

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

\[
Tree\ biomass = 0.0673 \times (\rho D^{2}H)^{0.976}.
\]

Tree height was estimated using \( D-H \) allometric equations adjusted for each of the eight research sites along the transect (Schietti et al., 2016). Species wood density was obtained from the global wood-density database (Chave et al., 2009; Zanne et al., 2009).
Annual mortality rates ($\lambda$) were calculated as: $\lambda = \frac{\ln(N_f) - \ln(N_i)}{t}$, where $N_i$ and $N_f$ are the number of stems counted at the initial population, and the number of stems surviving to time $t$, respectively (Shiel, Burslem, & Alder, 1995). Annual recruitment rates ($\mu$) were calculated following Phillips, Hall, Gentry, Sawyer, and Vassquez (1994) equation: $\mu = \frac{\ln(N_i/N_f)}{t}$, where $N_f$ is the final number of stems, $N_i$ 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 subpopulations (Lewis, Phillips, et al., 2004). The proposed correction factor $\lambda_{corr} = \lambda \times 1^{0.09}$, where $\lambda$ is the rate and $t$ is time between censuses in years, was applied for all the demographic rates calculated in this study.

### 2.3 Environmental data

To assess meteorological drought, that is, 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 (3B43 7A; Huffman et al., 2007) produced from 2010 to 2016, at 0.25° spatial resolution. Monthly evapotranspiration was assumed fixed at 100 mm/month, 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 WTD monitored using piezometers between the years of 2010 and 2013 in all plots (Figure S1). Each plot had one piezometer 7 m deep in the ground, monitored every 1 or 4 months in this period. Although the hydrological drought would be more correctly described by WTD values measured along the full census period, these concomitant temporal data were 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 (Figure 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 six subsamples from the first 30 cm soil depth (Schietti et al., 2016).

### 2.4 Data analyses

All analyses were conducted in R version 3.4.2 software (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 was analysed 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 gams (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 auto-correlation 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 (Tables S3 and S4). Hydrological conditions were represented by meteorological drought (MCWD) and water in soil (average WTD); soil constraints were represented by an index of soil physical restriction and available phosphorus. We hypothesized that WTD 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 (Figure 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.

### 3 Results

In our dataset, we recorded 19 palm species distributed in 13 genera, with Lepidocaryum tenue and Oenocarpus bataua being the
most abundant species (Table S1). According to precipitation data recorded from 1998 to 2016, the study region experienced MCWD annual anomalies up to $-1\sigma$ in 2010 (MCWD = 107 mm; accumulated annual precipitation = 2,438 mm) and MCWD annual anomalies up to $-3\sigma$ in 2015 (MCWD = 308 mm; accumulated annual precipitation = 2,053 mm; Figure 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.

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 $3.30\% \pm 1.94 (M \pm SD)$ per year in the period 2010–2015 and doubled to $6.78\% \pm 4.40 (M \pm SD)$ per year during 2015–2016 (Figure 2A). Annual recruitment rates also increased among trees from the first to the second interval ($t = -4.70; df = 24; p < 0.001$), averaging $1.85\% \pm 0.52 (M \pm SD)$ per year from 2010 to 2015, and was 1.5 times greater between 2015 and 2016 ($2.92\% \pm 1.21, M \pm SD$; Figure 2C). However, there was no change in annual mortality rates over the same intervals for palms ($3.67\% \pm 1.93, 2010–2015$ and $4.28\% \pm 3.69, 2015–2016$ or trees ($1.56\% \pm 0.62, 2010–2015$ and $1.69\% \pm 0.91, 2015–2016$; Figure 2B–D). 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 ($1 \text{ cm} \leq \text{dbh} < 10 \text{ cm}$), for both trees and palms. On the other hand, annual mortality rates do not differ among size classes between intervals, that is, large trees ($\text{dbh} \geq 30 \text{ cm}$) did not have higher mortality in years of severe drought (Figure S5).

The association between demographic rates of both palms and trees (described by the models below) and environmental predictors varied across time periods (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 WTD, and soil physical restriction index (Table 1). In the interval from 2010 to 2015, sites that experienced less negative water deficit (MCWD > $-90 \text{ mm}$) and with shallowest water table (Figure 3A, grey points on the right of the dashed line) had higher palm annual mortality rate ($\bar{x} = 4.12\%$). In contrast, forests sites that experienced more negative water deficit (MCWD < $-90 \text{ mm}$) and shallower water table (Figure 3A, black points on the right dashed line) had lower palm mortality rates ($\bar{x} = 2.36\%$). Palm mortality was also higher in soils with lower physical constraints (Figure 3B).

The best model for palm recruitment included only hydrological variables, that is, an interaction between the MCWD and average WTD 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 > $-130 \text{ mm}$; $\bar{x} = 7.06\%$) and those that experienced more negative water deficit (MCWD < $-130 \text{ mm}$; $\bar{x} = 6.52\%$). However, recruitment was lower (1.68%) in plots with shallower water table (<2.5 m deep) and under strong drought (Figure 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%, Figure 3E, grey points on the right of dashed line).
**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.

<table>
<thead>
<tr>
<th>Models</th>
<th>Predictors</th>
<th>p</th>
<th>ΔAIC</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palm mortality (2010–2015)</td>
<td>0.02 MCWD</td>
<td>0.002</td>
<td>0</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td>0.47 average WTD</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>−0.13 soil physical restriction index</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.005 MCWD × average WTD</td>
<td>0.004</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palm recruitment (2015–2016)</td>
<td>0.05 MCWD</td>
<td>&lt;0.001</td>
<td></td>
<td>0.70</td>
</tr>
<tr>
<td></td>
<td>1.37 average WTD</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.01 MCWD × average WTD</td>
<td>0.0004</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree mortality (2010–2015)</td>
<td>0.12 average WTD</td>
<td>&lt;0.001</td>
<td>0</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>0.08 available soil phosphorus</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree recruitment (2015–2016)</td>
<td>0.004 MCWD</td>
<td>0.34</td>
<td>0</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>0.43 average WTD</td>
<td>0.02</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.003 MCWD × average WTD</td>
<td>0.04</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Abbreviations: AIC, Akaike's information criterion; MCWD, maximum cumulative water deficit; WTD, water table depth.

**FIGURE 3** Partial regressions derived from the multiple regression models investigating the effects of maximum cumulative water deficit (MCWD), average water table depth (WTD; 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 WTD and (B) partial effect of the soil physical restriction index on palm mortality, during the 2010–2015 interval; (C) Partial effect of the average WTD (m) and (D) partial effect of available soil phosphorus on tree mortality, during 2010–2015 interval; (E) Partial effect of the interaction between MCWD and average WTD on palm recruitment, and (F) partial effect of the interaction between MCWD and average WTD on tree recruitment, during the 2015–2016 interval. For mortality, grey points are plots that experienced less negative MCWD (>−90 mm) in the analysed 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 analysed period, black points are plots that experienced more negative MCWD (<−130 mm). Dashed lines indicate 2.5 m WTD.
For trees, in the interval from 2010 to 2015, models with higher support to explain mortality rates included the average WTD and the available soil phosphorus (Table 1). Tree mortality was higher in soils with shallowest water table and greater fertility (Figure 3C,D). During the 2015–2016 interval, the best recruitment rates model included an interaction between MCWD and average WTD (Table 1). In this period, recruitment rates were lower in plots that experienced less negative water deficit (MCWD > -130 mm; \( x = 2.28\% \)) than in those that experienced more negative water deficit (MCWD < -130 mm; \( x = 3.50\% \)). Among plots with higher water deficit, recruitment increased with WTD, and the decreased for plots with lower water deficit (Figure 3F).

Spatially, palm biomass stocks (AGB) varied widely from 1.12 to 12.33 Mg/ha (Figure 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 (M ± 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 (M ± 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 (Figure 4B). However, unlike palms, trees had an increase in the biomass stock from the 2010 to 2015 (\( F = 17.69; p < 0.001 \)). Analysing plot-by-plot 80% of them had biomass gain in this interval (Figure S4b).

4 | DISCUSSION

We analysed 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 sensivities to drought. Palms tend to have large vessels, high hydraulic conductivity and high demand for water (Aparecido, Santos, Higuchi, & Kunert, 2015; Kunert, Barros, & Higuchi, 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 SWTF 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., 2004a, 2004b; Phillips et al., 2004) and low biomass stock (Quesada et al., 2012; Schietti et al., 2016).

Higher recruitment rates observed during the 2015–2016 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, Nascimento, Vitzcarra, & Williamson, 2017; Jakovac, Bentos, Mesquita, & Williamson, 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 (Figure S3), thus it is likely that the higher recruitment in 2015–2016 is associated with the environmental conditions during the 2015–2016 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, Piedade, Ludwigshausen, Horna, & Worbes, 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 2015–2016 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 <7 m; Figure S1) than most other studied plots in the Amazon (i.e. from 10 to more than 40 m deep, S. Chen, pers. comm.). 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 modelling (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 (Oliveiras, Svanning, Bodegom, Valencia, & Balslev, 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, 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, according to the geographic region (Baker et al., 2004a, 2004b; 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., 2004a, 2004b). 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 & Mejia, 1990; Lähteenoja, Ruokolainen, Schulman, & Oinonen, 2009), as represented in our plots. More stable biomass stocks in the SWTF, which cover around a third of the Amazon basin (Junk et al., 2011), may thus provide a counterbalance to losses on the DWTF 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, Mali, & Phillips, 2004; Nepstad, Tohver, Ray, Moutinho, & Cardinot, 2007; Phillips et al., 2002; Van Der Heijden, Schnitzer, Powers, & Phillips, 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 modelling 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.

ACKNOWLEDGEMENTS
This work was part of the PhD thesis of the first author developed at the Graduate Program in Ecology of the National Institute of Amazonian Research (INPA) and was partly sponsored by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brazil (CAPES)—Finance Code 001, (88887.141433/2017-00). The authors also thank the financial and research support of the Conselho Nacional de Desenvolvimento Científico e Tecnológico— CNPq (Productivity grant 307579/2013-1 to F.R.C.C.; PELD grant 142166/2015-4), Amazonas State Research Foundation (FAPEAM) and the Newton Fund via the Natural Environment Research Council (NE/M022021/1 to O.P. and F.R.C.C.), PPBio Manaus, INCT CENBAM and RAINFOR. We thank the field assistants and residents of the BR-319 highway who helped in the logistics and data collection, and without whom this research would not be possible; Fernando Figueiredo for support on the statistical analyses and Karina Melgaço for curating and managing ForestPLOTS data-base. The fifth author (Igor O. Ribeiro) has the financial support of the Cuomo Foundation. The content of this document is solely the liability of IOR and under no circumstances may be considered as the reflection of the position of the Cuomo Foundation and/or the Intergovernmental Panel on Climate Change Scholarship (IPCC).

AUTHORS’ CONTRIBUTIONS
T.R.S., F.R.C.C. and J.S. conceived the ideas; T.R.S., F.C.d.S., A.E.-M., J.S. and T.E. collected the data; T.R.S., I.O.R. and P.A.C.L.P. analysed the data; T.R.S. led the writing of the manuscript; F.R.C.C. and O.P. made important intellectual contributions. All authors revised and contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.kh189322m (Sousa et al., 2020).

REFERENCES


**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Sousa TR, Schietti J, Coelho de Souza F, et al. Palms and trees resist extreme drought in Amazon forests with shallow water tables. *J Ecol.* 2020;00: 1-13. [https://doi.org/10.1111/1365-2745.13377](https://doi.org/10.1111/1365-2745.13377)