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1   **Title:** Palms and trees resist extreme drought in Amazon forests with shallow water

2   tables

3

4   **Abstract**

5   1. The intensity and frequency of severe droughts in the Amazon region has increase in

6   recent decades. These extreme events are associated with changes in forest dynamics,

7   biomass and floristic composition. However, most studies of drought response have

8   focused on upland forests with deep water tables, which may be especially sensitive to

9   drought. Palms, which tend to dominate the less well-drained soils, have also been

10   neglected. The relative neglect of shallow water tables and palms is a significant

11   concern for our understanding of tropical drought impacts, especially as one third of

12   Amazon forests grow on shallow water tables (<5m deep).

13   2. We evaluated the drought response of palms and trees in forests distributed over a

14   600 km transect in central-southern Amazonia, where the landscape is dominated by

15   shallow water table forests. We compared vegetation dynamics before and following the

16   2015-16 El Nino drought, the hottest and driest on record for the region (-214 mm of

17   cumulative water deficit).

18   3. We observed no change in stand mortality rates and no biomass loss in response to

19   drought in these forests. Instead, we observed an increase in recruitment rates, which

20   doubled to 6.78% y-1 ± 4.40 (mean ± SD) during 2015-16 for palms and increased by

21   half for trees (to 2.92% y-1 ± 1.21), compared to rates in the pre-El-Nino interval.

22   Within these shallow water table forests, mortality and recruitment rates varied as a

23   function of climatic drought intensity and water table depth for both palms and trees,

24   with mortality being greatest in climatically and hydrologically wetter environments

25 and recruitment greatest in drier environments. Across our transect there was a

26 significant increase over time in tree biomass.

27 4. Synthesis: Our results indicate that forests growing over shallow water tables –

28 relatively under-studied vegetation that nonetheless occupies one-third of Amazon

29 forests - are remarkably resistant to drought. These findings are consistent with the

30 hypothesis that local hydrology and its interactions with climate strongly constrain

31 forest drought effects, and has implications for climate change feedbacks. This work

32 enhances our understanding of integrated drought effects on tropical forest dynamics

33 and highlights the importance of incorporating neglected forest types into both the

34 modeling of forest climate responses and into public decisions about priorities for

35 conservation.

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 ($\approx$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).

62 The belowground water source can be expected to minimize the effects of droughts on

63 plants and change the predictions of forest vulnerability to drought.

64   Water table depth is an important driver of rooting depth and plant water uptake.

65 Under deep water table conditions, the vegetation relies on local precipitation and

66 rooting depth is determined by the depth of rainfall infiltration into the soil (Fan,

67 Miguez-Macho, Jobbágy, Jackson, & Otero-Casal, 2017). On the other hand, shallow

68 water table prevents drainage and creates frequently waterlogged soil conditions. Thus,

69 roots remain shallow, to minimize the stress due to anaerobiosis (Fan et al., 2017; Fan

70 & Miguez-Macho, 2011). In deep water table forests (DWTF), the drier and warmer

71 climate conditions during extreme droughts decrease soil moisture leading to reduced

72 photosynthesis and net primary production (Santos et al., 2018; Zhao & Running,

73 2010). However, this should not apply to shallow water table forests (SWTF), as the soil

74 waterlogging tend to decrease during droughts in leading to an increase the growth

75 window, and thus promote growth in a similar way to what has been observed in

76 floodplain forests (Schöngart et al., 2004; Schöngart et al., 2005).

77   Our current understanding on the effect of drought on Amazonian forests have

78 neglected how palms, a fundamental functional group within these forests, have

79 responded to the changes in climate. Responses to drought have been mostly evaluated

80 for dicotyledonous trees and lianas and have typically either excluded palms or included

81 them within a broad category of 'trees' (e.g., Brienen et al., 2015; Fauset et al., 2012;

82 Laurance et al., 1999; Lewis et al., 2011; Phillips et al., 2004). However, palm's xylem

83 anatomy, architecture and growth strategies are fundamentally different from

84 dicotyledonous trees (Castilho et al., 2006; Emilio et al., 2013; Tomlinson, 2006). Thus,

85 the changing patterns in dynamics and biomass stocks described for trees across the

86 Amazon may simply not apply to palms. The responses of palms to climate are likely to

87 have important basin-wide implications, as palm-dominated forests cover 20% of the

88 Brazilian Amazon and contribute up to 23% of the basal area in the western Amazon

89 (Emilio et al., 2013; IBGE, 1997). Moreover, this group comprises no less than six of

90 the top ten most abundant tree species of the Amazon basin (Ter Steege et al., 2013),

91 being highly useful for people (Levis et al., 2018). To date the only analysis we are

92 aware of in which the effect of Amazon climate drying on long-term population changes

93 of Amazon trees has been probed, found that palms are especially drought-vulnerable,

94 having declined in abundance in many long-term Amazon forest plots (Esquivel-

95 Muelbert et al., 2019). Thus, forests on shallow water table (SWTF) and palms both

96 represent important and currently neglected components that need to be understood to

97 properly evaluate the future of Amazon forests under climate change.

98   Trees and arborescent palms differ in growth strategies, rooting and vascular

99 systems (Gale & Barfod, 1999; Renninger et al, 2013). Furthermore, palms and trees are

100 associated to different soil physical conditions, palms being more abundant on less

101 structured soils, e.g. environments that limit root development. Moreover, palms are

102 more physically stable due to characteristics of their stem anatomy that allows firm

103 anchorage to the ground (Emilio et al., 2013; Tomlinson, 1990). Palms lack vascular

104 cambium and thus, as opposed to trees, cannot add additional vessels to increase stem

105 diameter and cannot replace embolized xylem vessels (Tomlinson, 2006). The palm root

106 system is shorter than in trees, and therefore, is naturally restricted to superficial soil

107 layers (Tomlinson, 1990). These morphological differences between palms and trees

108 should affect their responses to droughts. Notably, the absence of secondary xylem

109 vessels production and shallow roots could make palms more sensitive to drought-

110 induced embolism (Renninger et al., 2013; Rich, 1987; Tomlinson, 2006).

111   Considering the limited understanding of forest dynamics in areas of shallow

112   water table and the great importance of palms to the structure of the tropical forests,

113   here we seek to address these gaps. Our study takes advantage of a unique permanent

114   plot initiative, which has established and monitored sites accessible from the Central-

115   southern Amazon BR-319 road. This made possible for the first time to track forest

116   dynamics and biodiversity over a huge and otherwise largely inaccessible landscape.

117   Using this plot network, we monitored the dynamics of palms and trees in forests along

118   a 600 km transect, through landscapes dominated by shallow water table forests, and

119   during a period that captures the intense 2010 and 2015-16 droughts. We specifically

120   addressed the following questions: 1) Are palms more vulnerable to extreme drought

121   than trees?; 2) What is the impact of different climatological drought intensities on palm

122   and tree dynamics?; 3) How do local water table depth and soil properties interact with

123   climatological droughts to influence palm and tree dynamics?

124   We considered two alternative hypotheses: 1) palms here will be more sensitive

125   to droughts than trees, so that intense droughts (such as in 2015-16) cause strong

126   reduction in water availability of these normally water saturated soils, leading to higher

127   mortality and lower recruitment rates, and a consequent loss of biomass stocks; or 2)

128   droughts will instead promote a decrease in the water table level and a consequent

129   reduction in the stressful soil anoxic condition, and so ameliorate the growing

130   conditions for both palms and trees. In this scenario, plants will benefit from droughts,

131   with no changes in their mortality and an increase in recruitment rates would be

132   expected. In addition, independent of the drought events, higher soil physical

133   constraints, i.e., shallow, compact and anoxic soils, will promote greater recruitment

134   and lower palm mortality, given the palms preference for these conditions (Emilio et al.,

135   2013).

136

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 $\geq$ 30

cm were sampled in the full 1 ha (250 x 40 m), stems with 10 cm $\leq$ dbh < 30 cm were

measured in a subplot of 0.5 ha (250 x 20 m) and stems with 1 cm $\leq$ 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):

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 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):

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 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: $\lambda = [\ln(N_0) - \ln(N_s)]/t$, 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.

209   Long and irregular census intervals may lead to some underestimation of

210   mortality and recruitment rates, since they have a greater probability of including

211   unobserved mortality and recruitment especially of fast turnover sub-populations (Lewis

212   et al., 2004). The proposed correction factor $\lambda_{corr}=\lambda \times t^{0.08}$, where λ is the rate and t is

213   time between censuses in years, was applied for all the demographic rates calculated in

214   this study.

Environmental data

216   To assess meteorological drought, i.e., atmospheric drought based on the balance

217   between precipitation and evapotranspiration, we estimated maximum cumulative water

218   deficit (MCWD) between census intervals, considering the month of the initial and final

219   census of each plot. MCWD corresponded to the maximum value of the monthly

220   accumulated climatic water deficit reached for each location. This metric represents the

221   sum of water deficit values (i.e. the difference between precipitation and estimated

222   evapotranspiration for the forest) over consecutive months when evapotranspiration is

223   greater than precipitation (Aragão et al., 2007). Precipitation data were extracted from

224   the Tropical Rainfall Measuring Mission satellite (TRMM, 3B43 7A) (Huffman et al.,

225   2007) produced from 2010 to 2016, at 0.25º spatial resolution. Monthly

226   evapotranspiration was assumed fixed at 100 mm month^{-1}, considering that moist

227   tropical canopies have approximately constant evapotranspiration rate (Rocha et al.,

228   2004; Shuttleworth, 1988).

229   As a proxy to the plant access to belowground water, which can affect the

230   hydrological drought experienced by roots, we characterized the local hydrological

231   condition as the average water table depth (WTD) monitored using piezometers

232   between the years of 2010 and 2013 in all plots (Fig. S1). Each plot had one piezometer

233   7 m deep in the ground, monitored every one or four months in this period. Although

234   the hydrological drought would be more correctly described by WTD values measured

235   along the full census period, this concomitant temporal data was not available.

236   However, the seasonal fluctuation of WTD in each plot is similar across years, i.e. plots

237   with shallow minimum and maximum values along the year (thus shallow WTD

238   average) in general do not attain deeper WTD values in dry years than plots with deeper

239   min, max and average WTD (Fig. S6). This means that we can use these average values

240   to rank plots along a gradient of WTD that is indicative of the potential hydrological

241   drought experienced by plants.

242   Since forest dynamics is known to be linked not only to climate but also to soil

243   properties (Quesada et al., 2012), we included an index of soil physical restriction

244   developed by Quesada et al. (2010) in our analyses, to represent the magnitude of soil

245   physical limitation. This semi-quantitative index is based on soil effective depth, soil

246   structure, anoxic conditions and topography. Higher scores denote more limited soil

247   conditions for plant roots. Soil physical classification was determined in 2 m deep pits

248   dug in each research site and in soil-profile samples from all plots (Martins et al., 2014).

249   As a proxy of soil fertility we used the available phosphorus content (extracted with

250   Mehlich-1) (EMBRAPA, 2011) determined from a compound sample derived from 6

251   subsamples from the first 30 cm soil depth (Schietti et al., 2016).

252

253   **Data analyses**

254   All analyses were conducted in R version 3.4.2 software (The R Core Team,

255   2018). To evaluate the changes in recruitment and mortality over time on a plot basis

256   we used paired *t-tests* between the moderate (2010-2015) and severe (2015-2016)

257   droughts, this was also applied to assess changes in rates considering different diameter

258   size classes. Biomass stock were analyzed by repeated-measures ANOVA between the

259 years of 2010, 2015 and 2016. To investigate the relationships of palm and tree

260 dynamics with environmental conditions, we used generalized linear mixed models,

261 with package GAMLSS (Stasinopoulos & Rigby, 2007), assuming a Beta distribution

262 for demographic rates. Site was included in the models as a random effect, to control for

263 potential spatial autocorrelation between plots nested in the same site. We tested models

264 relating palms and trees demographic rates to a set of combinations of environmental

265 variables describing hydrology and soil constraints (Supporting information Tables S3

266 and S4). Hydrological conditions were represented by meteorological drought

267 (maximum cumulative water deficit: MCWD) and water in soil (average water table

268 depth); soil constraints were represented by an index of soil physical restriction and

269 available phosphorus. We hypothesized that water table depth would modulate the

270 effects of the drought intensity on demographic rates, so we included the interactions

271 among these factors. The models were built and evaluated based on the continuous

272 values of MCWD, however for visualization of interactions our outputs were

273 categorized into "more negative" and "less negative". The classification of MCWD in

274 these two classes was data-driven based on the frequency distribution of values

275 observed in the plots - thus in the moderate drought the MCWD threshold was -90 mm,

276 while in strong drought MCWD threshold was -130 mm (Fig. S2). Best models were

277 selected according to the Akaike's information criterion (AIC). Models with lower AIC,

278 fewer parameters and significant relationships between the response and the predictor

279 variables were selected as the best models.

280

281 **Results**

282   In our dataset we recorded 19 palm species distributed in 13 genera, with

283 *Lepydocaryum tenue* and *Oenocarpus bataua* being the most abundant species

284 (Supporting information Table S1). According to precipitation data recorded from 1998

285 to 2016, the study region experienced MCWD annual anomalies up to -1σ in 2010

286 (MCWD = 107 mm; accumulated annual precipitation = 2438 mm) and MCWD annual

287 anomalies up to -3σ in 2015 (MCWD = 308 mm; accumulated annual precipitation =

288 2053mm) (Fig. 1). Due to the MCWD anomalies recorded in the years 2010 and 2015 in

289 relation to the historical series, the first interval can be considered as a moderate

290 drought (2010-2015) and the second interval as a severe drought (2015-2016) for this

291 study region.
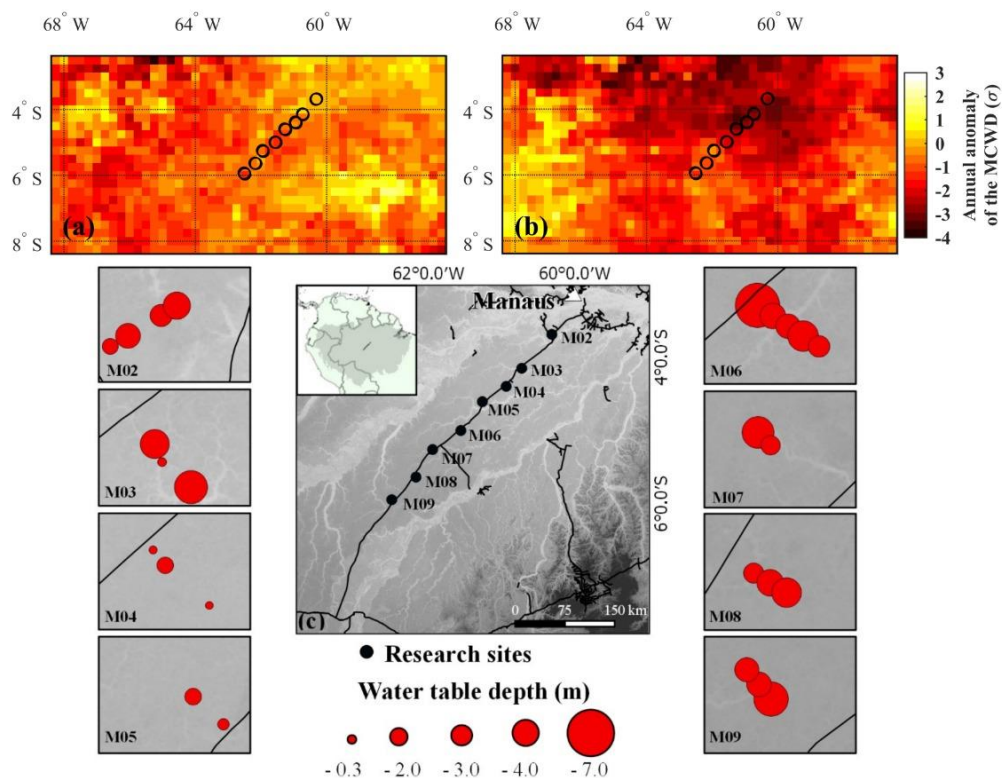
292

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

297   Palm and tree annual recruitment dynamics changed between moderate and

298 strong droughts. There was a strong increase in palm annual recruitment rates from the

299 first to the second period (t = -4.02; df = 24; p < 0.001). Palm recruitment averaged

13

300   3.30% ± 1.94 (mean ± SD) per year in the period 2010 to 2015 and doubled to 6.78% ±

301   4.40 (mean ± SD) per year during 2015-2016 (Fig. 2a). Annual recruitment rates also

302   increased among trees from the first to the second interval (t = -4.70; df = 24; p <

303   0.001), averaging 1.85% ± 0.52 (mean ± SD) per year from 2010 to 2015, and was 1.5

304   times greater between 2015 and 2016 (2.92% ± 1.21, mean ± SD) (Fig. 2c). However,

305   there was no change in annual mortality rates over the same intervals for palms (3.67%

306   ± 1.93, 2010-2015 and 4.28% ± 3.69, 2015-2016) or trees (1.56% ± 0.62, 2010-2015

307   and 1.69% ± 0.91, 2015-2016) (Figs. 2b-2d). Considering the variation among diameter

308   classes, we find that annual recruitment rates increased from the first to the second

309   interval only for small diameter classes (1 cm ≤ dbh < 10 cm), for both trees and palms.

310   On the other hand, annual mortality rates do not differ among size classes between

311   intervals, i.e. large trees (dbh ≥ 30 cm) did not have higher mortality in years of severe

312   drought (Fig. S5).
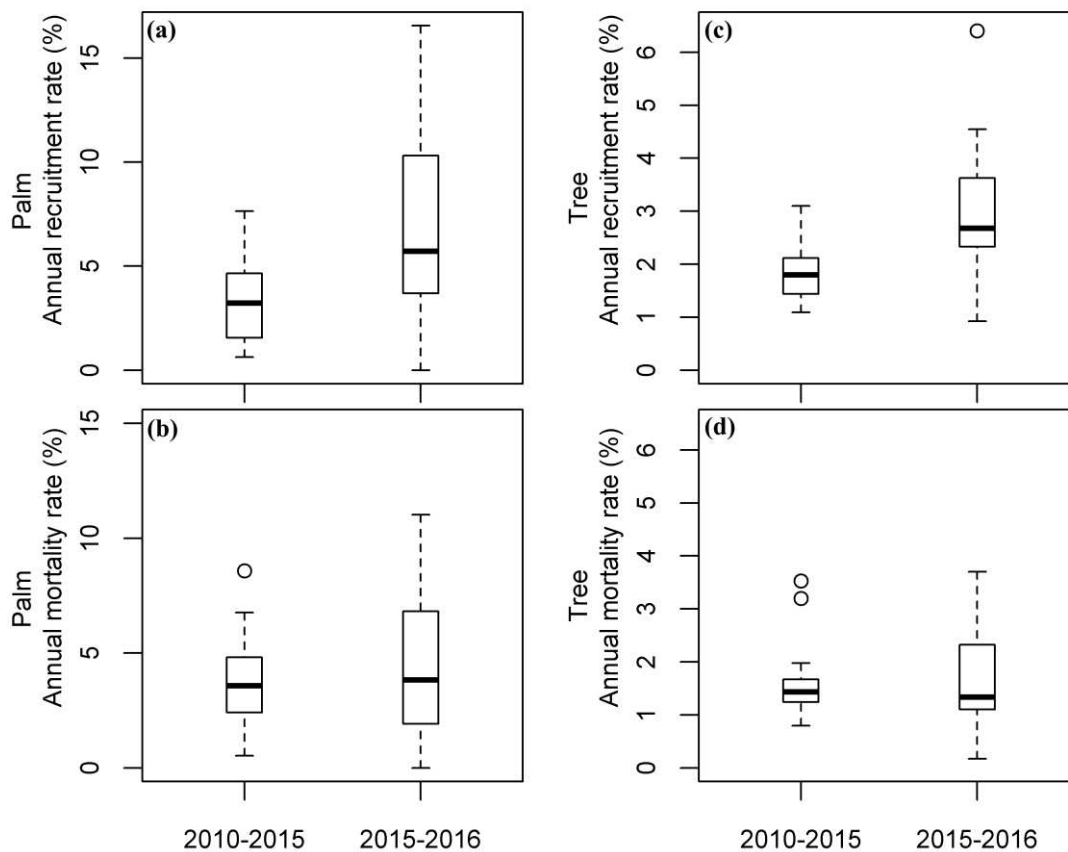
FIGURE 2. Palm annual recruitment (a) and mortality rates (b); Tree annual recruitment (c) and mortality rates (d), between the two censuses in forests along the Purus–Madeira interfluve, in central-southern Amazonia

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 ($\bar{x}$ = 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 ($\bar{x}$ = 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) ($\bar{x}$ = 7.06%) and those that experienced more negative water deficit (MCWD < -130 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 (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) ($\bar{x}$ = 2.28%) than in those that experienced more negative water deficit (MCWD < -130 mm) ($\bar{x}$ = 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
355 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 depth	0.004		
Palm recruitment (2015-2016)	0.05 MCWD	< 0.001	-0.64	0.70
	1.37 average water table depth	0.001		
	0.01 MCWD*average water table depth	0.0004		
Tree mortality (2010-2015)	0.12 average water table depth	<0.001	0	0.61
	0.08 available soil phosphorus	0.05		
Tree recruitment (2015-2016)	0.004 MCWD	0.34	0	0.52
	0.43 average water table depth	0.02		
	0.003 MCWD*average water table depth	0.04		

356
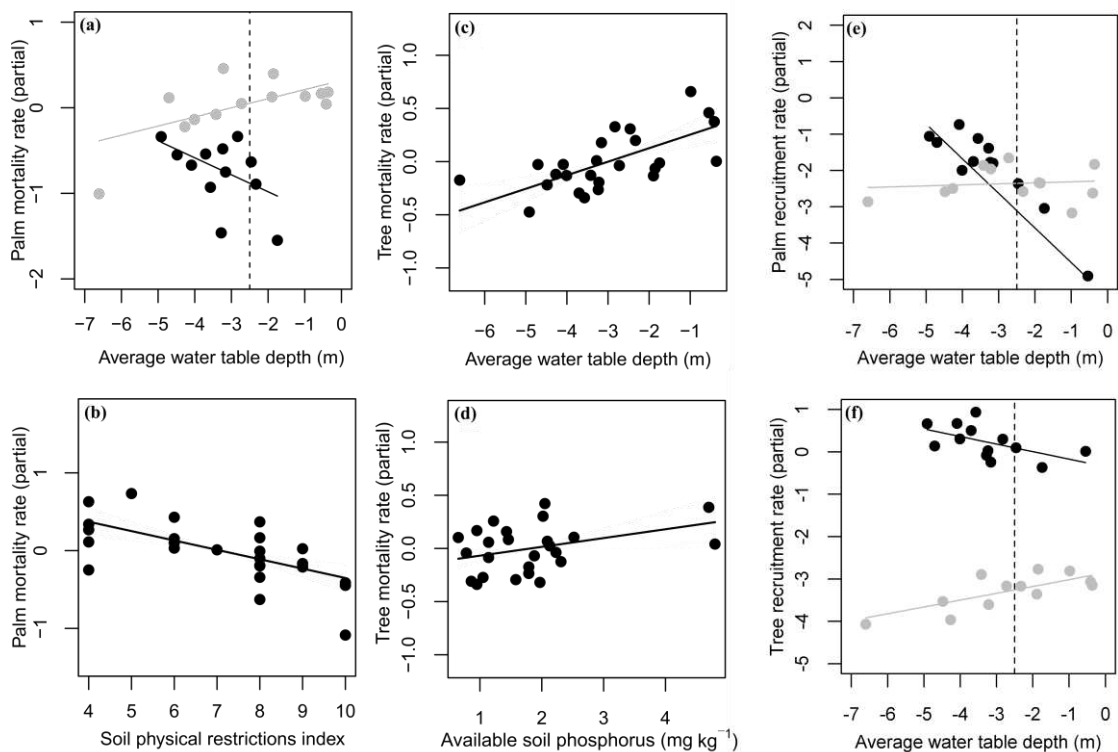
FIGURE 3 Partial regressions derived from the multiple regression models
investigating the effects of maximum cumulative water deficit (MCWD), average water
table depth (m), soil physical restriction index and available soil phosphorus on
mortality and recruitment in Central-Southern Amazonia. (a) Partial 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

364 phosphorus on tree mortality, during 2010 to 2015 interval; (e) Partial effect of the
365 interaction between MCWD and average water table depth on palm recruitment, and (f)
366) partial effect of the interaction between MCWD and average water table depth on tree
367 recruitment, during the 2015 to 2016 interval. For mortality, grey points are plots that
368 experienced less negative MCWD (> -90 mm) in the analyzed period, black points are
369 plots that experienced more negative MCWD (< -90 mm). For recruitment, grey points
370 are plots that experienced less negative MCWD (> -130 mm) in the analyzed period,
371 black points are plots that experienced more negative MCWD (< -130 mm). Dashed
372 lines indicate 2.5 m water table depth

373 Spatially, palm biomass stocks (AGB) varied widely from 1.12 to 12.33 Mg ha^{-1}

374 (Fig. 4a) and contributed with 1% to 5% per hectare to the total amount of alive above-

375 ground biomass (Table S2). Biomass stocks were respectively 5.84 ± 3.17 (mean ± SD)

376 in 2010, 5.84 ± 3.18 in 2015 and 5.86 ± 3.17 in 2016 for palms, and 227.94 ± 55.39,

377 233.95 ± 55.73 and 234.48 ± 56.57 (mean ± SD) for trees. There was no significant

378 change in palm biomass stock between the three censuses (F= 0.014; p= 0.91)

379 considering the balance between recruitment and mortality of individuals. For trees,

380 biomass varied spatially from 97.15 to 328.75 Mg ha^{-1} (Fig. 4b). However, unlike

381 palms, trees had an increase in the biomass stock from the 2010 to 2015 (F= 17.69; p <

382 0.001). Analyzing plot-by-plot 80%, of them had biomass gain in this interval (Fig.

383 S4b).
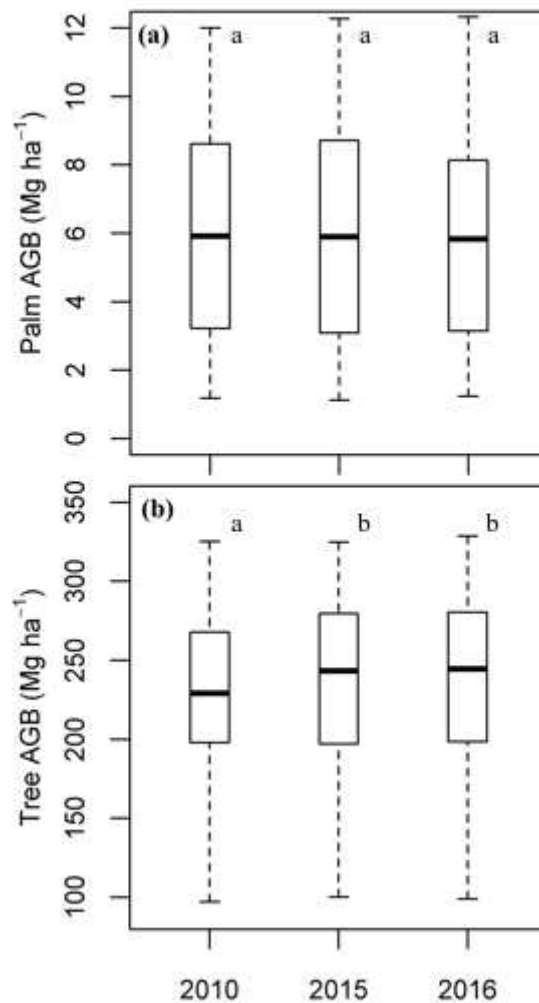
FIGURE 4 Variation in palm (a) and tree (b) biomass stocks (AGB) in 25 plots
measured along the Purus–Madeira interfluve, in Central-southern Amazonia. Different
letters indicate significant differences in biomass stock between years ($p < 0.001$; Tukey
method)

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

19

395   mediated by the local hydrological conditions, soil fertility and soil physical restriction.

396   There was an increase in tree above-ground biomass stock from 2010 to 2015, but no

397   significant change over time of palm AGB. Overall, extreme droughts did not have a

398   negative impact on either trees or palms growing over shallow water table. Our study

399   reveals the complex interplay between climatological droughts and belowground water

400   access on forest dynamics. Our results indicate the crucial need to incorporate the

401   interaction between precipitation and belowground properties for a more realistic

402   estimation of local hydrological conditions on environmental impact evaluations and

403   models to forecast drought effects in the Amazon.

404   We hypothesized that more intense droughts could sufficiently reduce water

405   availability of these normally water-saturated soils, leading to higher mortality and

406   lower recruitment rates, resulting in biomass loss, particularly of palms. However, our

407   results did not support this hypothesis. Palms and trees have structural differences in

408   their vascular anatomy, which are reflected on different sensitivities to drought. Palms

409   tend to have large vessels, high hydraulic conductivity and high demand for water

410   (Aparecido et al. 2015; Kunert et al. 2013), which could be expected to generate a larger

411   vulnerability to drought, however this was not what observed in SWTF. Our results are

412   partially in accordance with our alternative hypothesis: droughts are likely to lead to

413   moderate soil drying, which is enough to reduce the anoxic conditions of waterlogged

414   soils and hence promote palm and tree growth, with increased recruitment and no

415   increase in mortality rates. This suggests that both palms and trees on shallow water

416   table forests are resistant to extreme droughts because the belowground hydrological

417   environment buffers climatological water deficit. Thus, shallow water table may offer a

418   relief from the atmospheric water stress projected by climate models for decades to

419   come, functioning as hydrologic refugia (McLaughlin et al., 2017; Pokhrel, Fan, &

420   Miguez-Macho, 2014).

421   Higher tree mortality in soils with higher phosphorus concentration may be

422   related to the functional properties selected by fertile soils and the resulting vegetation

423   dynamics. Low wood density is selected on fertile soils, which generally have high

424   phosphorus availability and physical restrictions, leading to high turnover rates (Baker

425   et al., 2004; Phillips et al., 2004) and low biomass stock (Quesada et al., 2012; Schietti

426   et al., 2016).

427   Higher recruitment rates observed during the 2015-16 interval are likely to be

428   directly associated with climatological changes, though they could potentially be an

429   indirect result of previous disturbances that increase light. The importance of light

430   availability to forest growth and dynamics is well known (Augspurger, 1984; Bentos et

431   al. 2017; Jakovac et al. 2012), however responses still depend on specific requirements

432   of each species (Ley-López, Avalos, & Chacón-Madrigal, 2016). Our study did not

433   include direct metrics of light availability, however, we evaluated whether previous

434   disturbances (i.e., the mortality rates in the previous period, a proxy for canopy

435   openness) could be leading to increased recruitment. We found no effect of previous

436   disturbances on recruitment rates on the following period (Fig. S3), thus it is likely that

437   the higher recruitment in 2015-16 is associated with the environmental conditions

438   during the 2015-16 El Niño event. In seasonally flooded forests, drought prolongs the

439   non-flooded period, which is when plants grow due to the reduction of anoxic stressful

440   conditions (Schöngart et al., 2002). Under the drier conditions observed in El Niño

441   years, floodplain forests show increased wood growth (Schöngart et al., 2004). Our

442   findings of increased recruitment in the 2015-16 El Niño in SWTF are consistent with

443   those observations on floodplain forests. However, this increase in recruitment during

444   the strongest drought cannot be solely attributed to the temporal decrease in stress due

445   to anoxia. Forest plots that experienced higher climatological water deficits and deeper

446   water table had higher recruitment rates than plots that experienced similar drought

447   condition but located in shallow water table. It must be acknowledged that all sites

448   studied here have shallower water table (average depth < 7m; Fig. S1) than most other

449   studied plots in the Amazon (i.e. from 10 to more than 40 m deep, S. Chen personal

450   communication). We can speculate that during the strong drought, anoxia was

451   sufficiently reduced in soils with water table deeper than 3 m, but not enough where the

452   water table was shallow. However, detailed monitoring of belowground water level

453   fluctuation during drought periods is still required, through field monitoring and / or

454   eco-hydrological modeling (Chitra-Tarak et al., 2018). This information may provide

455   additional support to our hypothesis or elucidate other mechanisms that may be

456   involved on forest responses.

457   Over our 600 km of monitored forests, there was no increase in mortality from

458   the moderate to the strong drought periods, and neither larger mortality rates associated

459   to sites that experienced the strongest climatic water deficits. We expected stronger

460   negative drought effects on palms, as their anatomy and growth form are likely to make

461   this group more drought-vulnerable (Tomlinson, 2006). Indeed highly increased

462   mortality (7%) of the most abundant palm species of a *terra firme* forest over deep

463   water table was observed after the strong 1997 drought (Williamson et al., 2000), and a

464   long-term decline trend of wet-affiliated palms was detected across the Amazon basin as

465   climate becomes drier (Esquivel-Muelbert et al., 2019). Surprisingly, we found no

466   evidence that palms are more vulnerable to drought than trees in the wet conditions

467   experienced by SWTF. This is consistent with the findings of no increases in palm

468   mortality after droughts in wet forests of western Amazonia (Olivares et al. 2017) and

469   Central America (Condit et al. 2004). Our results suggest that even if Amazon palms are

470   intrinsically susceptible to drought, their response to drought events can be highly

471   variable and contingent to local belowground hydrological conditions. The fact that

472   even the more drought-sensitive palms did not suffer increased mortality in the strong

473   2015 drought supports the assertion that forests with shallowest water table are more

474   resistant to drought than forest with deep water table.

475   Our result of an increase in the tree biomass stock is the contrary of what has

476   been observed (biomass loss) on most tropical forests after droughts. Studies in

477   Amazon forests have evidenced its vulnerability to drought through the reduction in

478   above-ground biomass along the last decades (Brienen et al., 2015; Phillips et al., 2009).

479   In the 2010 drought, the estimated biomass loss of Amazon forests was on average 1.45

480   Mg ha^{-1}, leading to a projected reduction of carbon uptake of 1.1 Pg (Feldpausch et al.,

481   2016). Biomass stock of the Amazon has a wide spatial variation, from 200 to 350 Mg

482   ha^{-1}, according to the geographic region (Baker et al., 2004; Lewis et al., 2013). In the

483   present study, forest biomass stock was comparable to that of the Southwestern region,

484   which has lower biomass compared to Central and Eastern Amazonia (Baker et al.,

485   2004). Although palms do not contribute heavily to biomass in most dense *terra firme*

486   forests (~ 1%) (Castilho et al., 2006), their contribution is often considerably greater in

487   other environments as open forests and swampy conditions (Kahn et al., 1990;

488   Lähteenoja et al., 2009), as represented in our plots. More stable biomass stocks in the

489   shallow water table forests, which cover around a third of the Amazon basin (Junk et

490   al., 2011), may thus provide a counterbalance to losses on the deep water table forests

491   during droughts.

492   We have shown here that, contrary to the previous results from studies

493   conducted at forest over deep water table across the Amazon basin (Brienen et al., 2015;

494   Feldpausch et al., 2016; Phillips et al., 2009), palms and trees on SWTF are more

495   resistant to drought. Therefore, it is important to consider the local belowground

496   hydrological environment for a better assessment of drought effects on tropical forests.

497   In addition, as previously reported for lianas (Lewis et al., 2004; Nepstad et al., 2007;

498   Phillips et al., 2002; Van Der Heijden et al., 2013), different life forms may respond

499   differently to global climate changes according to their biology and the effect on these

500   should be investigated separately. Considering the progression of climate change,

501   SWTF can be considered as potential refuges for biodiversity, conservation of the

502   Amazon forest and may provide an important counterbalance to the biomass loss in

503   forests affected by both atmospheric and soil moisture deficits. Given the extent of these

504   forests, and their differential responses to drought, more research in shallow water table

505   tropical forests is urgently needed. Not only will it be important to better account for

506   soil water supply in modeling the dynamics and carbon fluxes of tropical forests, but a

507   wider recognition of the importance of these systems can contribute to the development

508   of public policies including prioritizing conservation areas on SWTF, which may be

509   best-suited to help Amazonia resist climate change.

510   .

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Data Availability Statement:

530 Dryad, Dataset, https://doi.org/10.5061/dryad.kh189322m

531

Authors' contributions:

533 TRS, FRCC and JS conceived the ideas; TRS, FCS, AEM, JS and TE collected the data;

534 TRD, IOR and PACLP analysed the data; TRS led the writing of the manuscript; FRCC

535 and OP made important intellectual contributions. All authors revising and contributed

536 critically to the drafts and gave final approval for publication.

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