

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

Sousa, T.R.; Schietti, J.; Coelho de Souza, F.; Esquivel-Muelbert, A.; Ribeiro, I.O.; Emílio, T.; Pequeno, P.A.C.L.; Phillips, O.; Costa, F.R.C.

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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 $6.78\% \text{ y}^{-1} \pm 4.40$ (mean \pm SD) during 2015-16 for palms and increased by
21 half for trees (to $2.92\% \text{ y}^{-1} \pm 1.21$), 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.

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

38 **Introduction**

39 There has been an increase in the frequency and intensity of severe droughts in
40 the Amazon. The most recent three extreme drought events occurred at a very short
41 interval (2005, 2010 and 2015-16) and the last two were possibly the most severe in a
42 century (Anderson et al., 2018; Jiménez-Muñoz et al., 2016; Marengo et al., 2011). Due
43 to its extensive area (≈ 6 million km²), large carbon stores, and exceptional species
44 richness (including as many as 15,000 tree species), the responses of the Amazon
45 forests to extreme events is likely to affect not only the basin itself, but also global
46 climates and biodiversity (Nobre et al., 2016; Saatchi et al., 2011; Ter Steege et al.,
47 2013). It is already clear that the water deficits associated with recent droughts has
48 slowed growth rates (e.g., Feldpausch et al., 2016) and increased tree mortality rates
49 (e.g., Phillips et al., 2009; Zuleta et al., 2017), resulting in biomass loss (Brienen et al.,
50 2015; Feldpausch et al., 2016; Leitold et al., 2018; Phillips et al., 2009). These
51 evidences of vulnerability reinforce concerns that Amazon ecosystems may be
52 vulnerable if drought frequency continues to increase (Esquivel-Muelbert et al., 2017).
53 However, most assessments of drought effects have ignored the soil hydrological
54 conditions and assumed that precipitation is the only source of water deficit to plants.
55 The balance between precipitation and estimated evapotranspiration is the basis of the
56 most used metrics to quantify drought, e.g. the maximum accumulated water deficit,
57 and belowground water sources, such as provided by the water table, are not explicitly
58 included. The water table may be the main source over considerable large expanses of
59 the Amazon. Thousands of square kilometers of the Amazon basin are covered by
60 poorly drained areas (Junk, 1993) and at least 36% of whole Amazonian basin is
61 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

137 **Materials and methods**

138 **Study area and sampling design**

139 The study was conducted along a 600 km transect along the interfluvial region
140 between the Purus and Madeira rivers, south of the Amazon River in Central-southern
141 Amazonia. The water table is shallow ($2.81 \text{ m} \pm 2.38$ deep (mean \pm SD)), and
142 topography in the region is generally flat with elevation above sea level varying from
143 30–80 m over large distances (estimated by Shuttle Radar Topography Mission - SRTM
144 data) (Rodríguez, Morris, & Belz, 2006). Mean annual precipitation in this area varies
145 from 2100–2700 mm (Hijmans et al., 2005), with on average two to three consecutive
146 months with less than 100 mm rainfall (dry months) per year (Sombroek, 2001). Soils
147 are predominantly Plinthosols and Gleysols, the predominant texture is silt to fine sand,
148 with poor drainage, and varying degrees of soil water saturation and anoxic conditions
149 (Martins et al., 2014; Sombroek, 2000). Soils physical structure is generally dense and
150 restrictive to root growth, with varying degrees of hardness and effective soil depth
151 (Quesada et al., 2010).

152 We sampled 25-1 ha plots systematically distributed in 8 research sites along
153 600 km of the BR-319 highway. In each site, two to five plots were sampled in regular
154 grids of 5 x 1 km, keeping a 1 km minimum distance among plots (Fig. 1). Plots were
155 established at least 1 km distance from the road to avoid sampling forests which had
156 been recently disturbed by human activity. Permanent plots were 250 m long and
157 followed the terrain altitudinal contour, in order to reduce edaphic and hydrological
158 variation within plots (Magnusson et al., 2005).

159 **Vegetation data**

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

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

$$174 \text{ Palm biomass} = 0.55512^4 \times (\text{dmf} \times \text{dbh}^2 \times H_{\text{stem}})$$

175 The Goodman et al. (2013) equation is largely supported by local studies such as Silva
176 et al. (2015) and Avalos et al. (2019) who both studied a subset of the species in our
177 dataset.

178 Palm heights were measured using a Vertex hypsometer (Vertex Laser VL400
179 Ultrasonic-Laser Hypsometer III, Haglöf of Sweden). Stem heights could only be
180 estimated during the second census in 2015, when 70% of the total number of palms
181 registered in the plots had their height measured. For those stems that did not had their
182 height measured, we used species-level means, either the site-level mean height for the
183 most abundant species (*Lepidocaryum tenue* and *Oenocarpus bataua*) or the overall

184 mean height for remaining species. We disregarded changes in palm height over time
185 and used the height measurements from 2015 for all censuses (2010, 2015 and 2016).
186 Our evaluation of changes in the palm biomass stock is based on only on the population
187 changes, i.e. recruitment and mortality. We assumed zero stem diameter growth, as
188 palm diametric variations are mostly governed by fluctuations in water content (Stahl et
189 al., 2010). We note that palm growth occurs via increasing height, with the addition of
190 new metamers (Tomlinson, 1990), so quantifying biomass increases in individual palms
191 requires repeated height measurements which were not possible here.

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

$$195 \text{ Tree biomass} = 0.0673 \times (\rho D^2 H)^{0.976}$$

196 Tree height was estimated using D-H allometric equations adjusted for each of
197 the 8 research sites along the transect (Schietti et al., 2016). Species wood density was
198 obtained from the global wood-density data base (Chave et al., 2009; Zanne et al.,
199 2009).

200 Annual mortality rates (λ) were calculated as: $\lambda = [\ln(N_0) - \ln(N_s)]/t$, where N_0
201 and N_s are the number of stems counted of the initial population, and the number of
202 stems surviving to time t, respectively (Sheil, Burslem, & Alder, 1995). Annual
203 recruitment rates (μ) were calculated following Phillips et al (1994) equation: $\mu =$
204 $[\ln(N_f/N_s)]/t$, where N_f is the final number of stems, N_s is the original number of stems
205 surviving to final inventory and t is the number of years between inventories. Mortality
206 and recruitment rates were calculated for the intervals 2010-2015 and for 2015-2016. In
207 this paper stand mortality and stand recruitment were treated as mortality and
208 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 $\lambda_{\text{corr}} = \lambda \times t^{0.08}$, 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.

215 **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 0.25° 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 (Schiatti 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

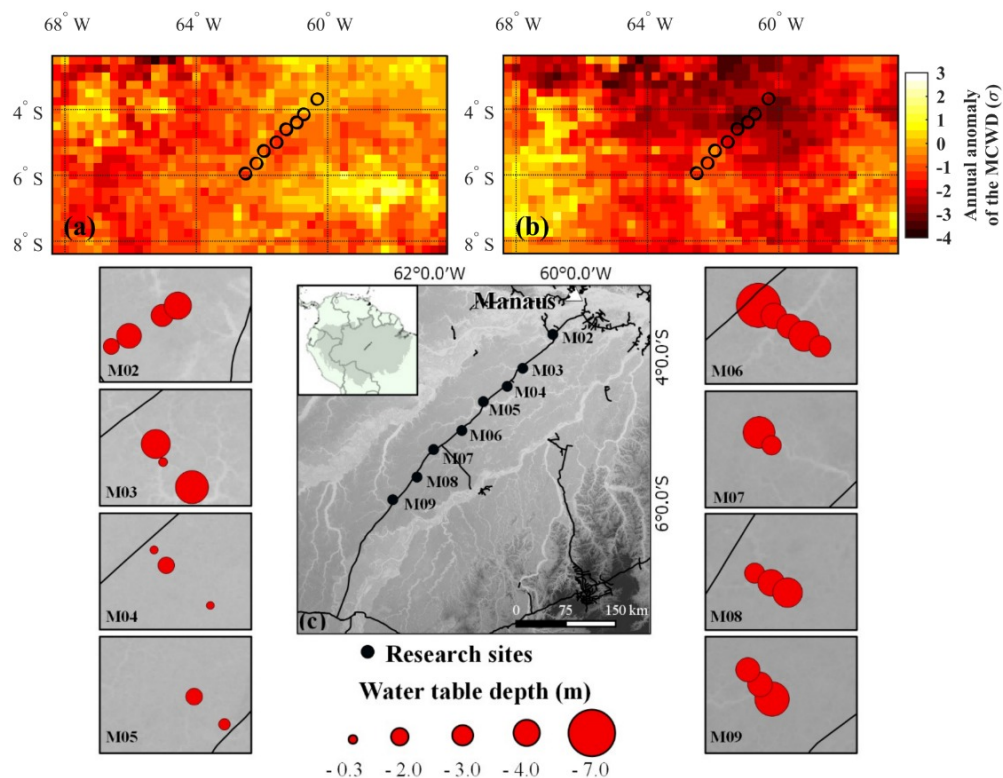
259 years of 2010, 2015 and 2016. To investigate the relationships of palm and tree
260 dynamics with environmental conditions, we used generalized linear mixed models,
261 with package GAMLSS (Stasinopoulos & Rigby, 2007), assuming a Beta distribution
262 for demographic rates. Site was included in 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 *Lepidocaryum 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.

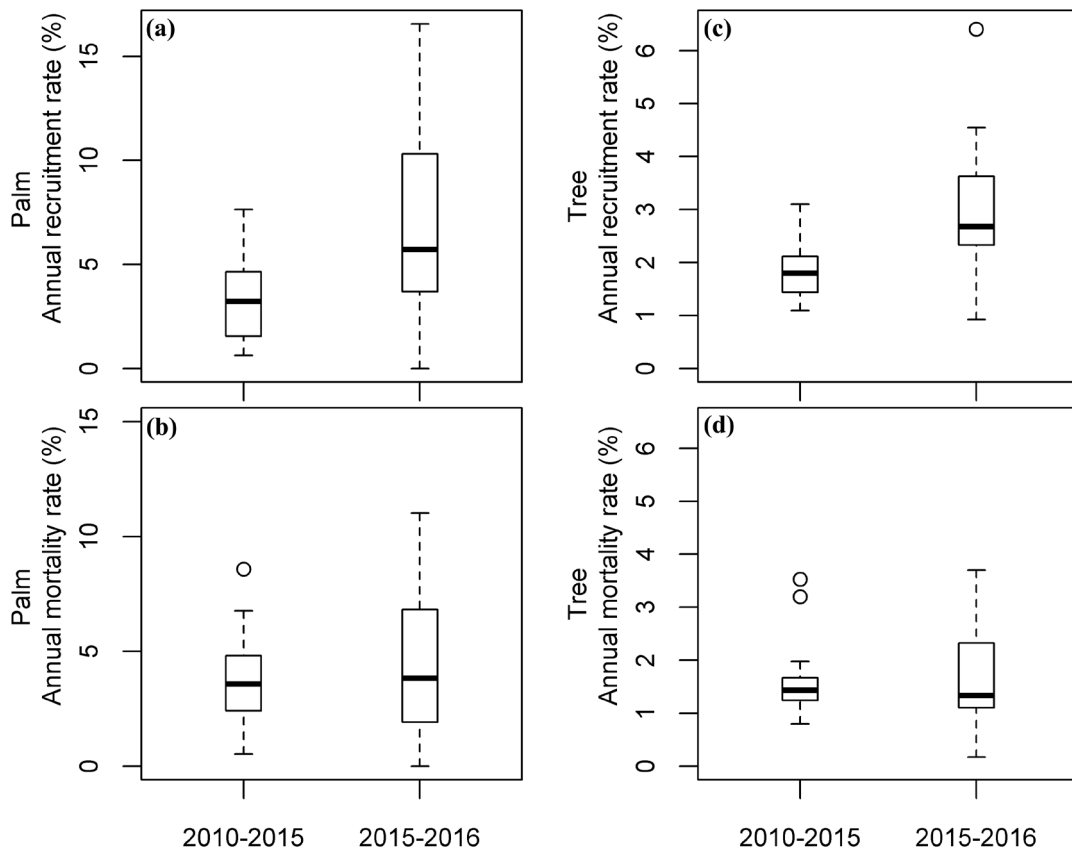


292

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 interfluvium, 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

300 3.30% \pm 1.94 (mean \pm SD) per year in the period 2010 to 2015 and doubled to 6.78% \pm
301 4.40 (mean \pm 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% \pm 0.52 (mean \pm SD) per year from 2010 to 2015, and was 1.5
304 times greater between 2015 and 2016 (2.92% \pm 1.21, mean \pm SD) (Fig. 2c). However,
305 there was no change in annual mortality rates over the same intervals for palms (3.67%
306 \pm 1.93, 2010-2015 and 4.28% \pm 3.69, 2015-2016) or trees (1.56% \pm 0.62, 2010-2015
307 and 1.69% \pm 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 ($1 \text{ cm} \leq \text{dbh} < 10 \text{ cm}$), 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 ($\text{dbh} \geq 30 \text{ cm}$) did not have higher mortality in years of severe
312 drought (Fig. S5).



313

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

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

323 The best model to explain palm mortality rates included the interaction between
 324 cumulative water deficit and average water table depth, and soil physical restriction
 325 index (Table 1). In the interval from 2010 to 2015, sites that experienced less negative
 326 water deficit ($MCWD > -90$ mm) and with shallowest water table (Fig. 3a, grey points
 327 on the right of the dashed line) had higher palm annual mortality rate ($\bar{x} = 4.12\%$). In

328 contrast, forests sites that experienced more negative water deficit (MCWD < -90 mm)
329 and shallowest water table (Fig. 3a, black points on the right dashed line) had lower
330 palm mortality rates ($\bar{x} = 2.36\%$). Palm mortality was also higher in soils with lower
331 physical constraints (Fig. 3b).

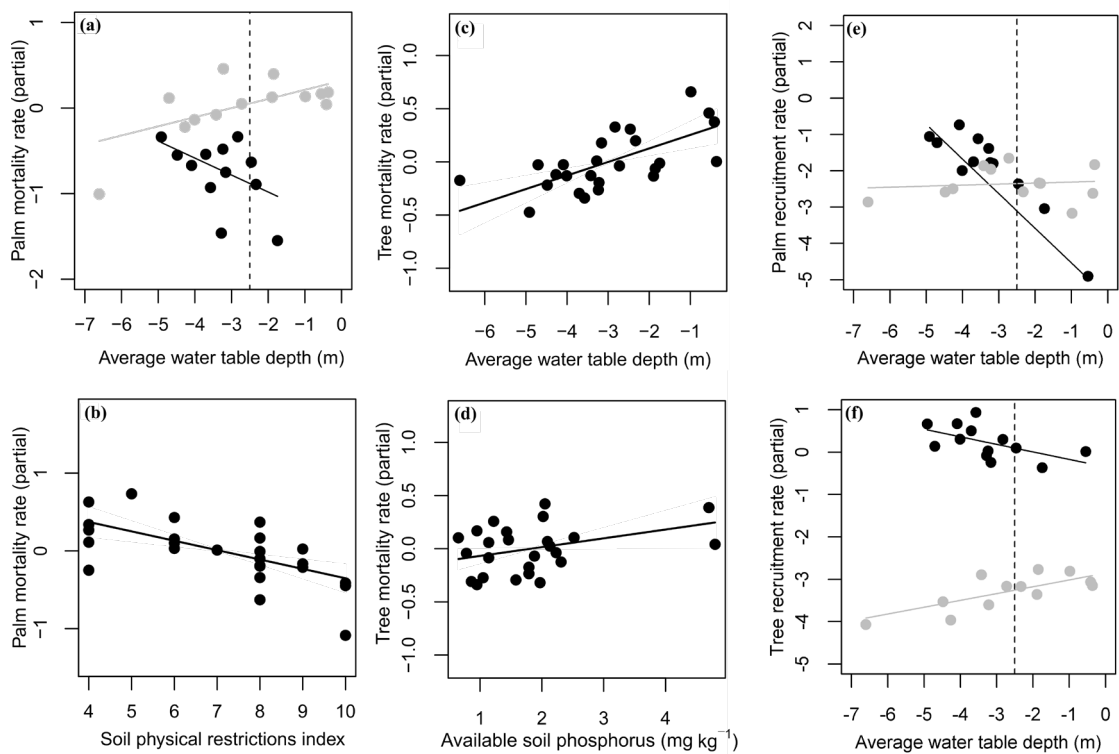
332 The best model for palm recruitment included only hydrological variables, i.e.
333 an interaction between the maximum cumulative water deficit and average water table
334 depth in the interval from 2015 to 2016 (Table 1). On average, during this interval, palm
335 annual recruitment rates did not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

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

352 **TABLE 1.** Statistical summary of the best generalized mixed models to explain the
353 relationship between palm and tree dynamics and environmental variables. Intercept and

354 slopes of each predictor included in the regressions are presented; Δ AIC is the
 355 difference between the model with the lowest AIC and the model chosen.

Models	Predictors	p	Δ AIC	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		

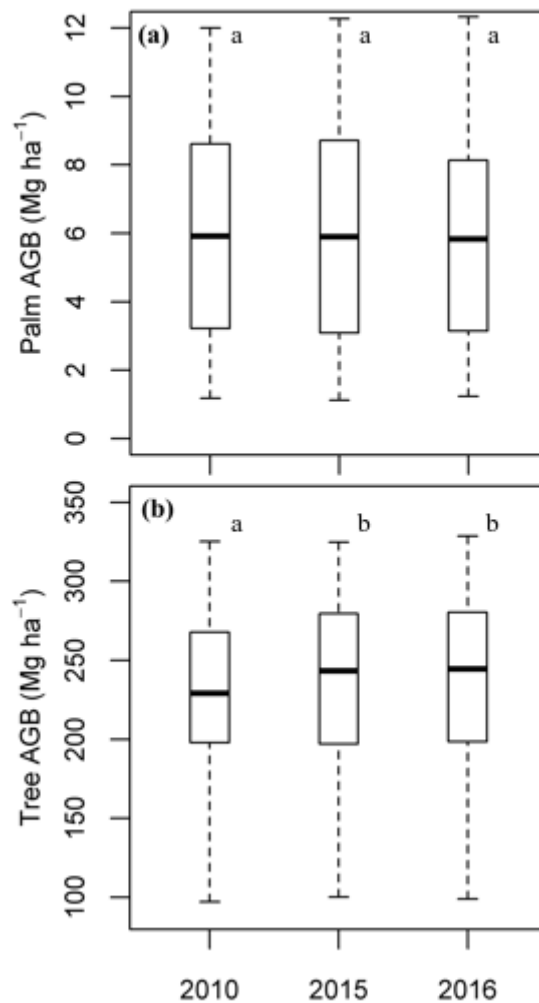


356

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



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

388

389 **Discussion**

390 We analyzed for the first time the effect of droughts of different intensities over
 391 shallow water table Amazonian forests (SWTF). Our results show that palms were no
 392 more vulnerable to extreme droughts than trees in these forests. The strong drought of
 393 2015 did not increase palm or tree mortality rates, but instead, promoted increased
 394 recruitment rates. The drought responses in terms of recruitment and mortality were

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; Schiatti
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 (Augsburger, 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 Lahteenoja 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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528

529 **Data Availability Statement:**

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

531

532 **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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