

Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics

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Abstract

45
46 Drought-induced wildfires have increased in frequency and extent over the tropics. Yet, the
47 long-term (> 10 years) responses of Amazonian lowland forests to fire disturbance are poorly
48 known. To understand post-fire forest biomass dynamics, and to assess the time required for
49 fire-affected forests to recover to pre-disturbance levels, we combined 16 single with 182
50 multiple forest census into a unique large-scale and long-term dataset across the Brazilian
51 Amazonia. We quantified biomass, mortality and wood productivity of burned plots along a
52 chronosequence of up to 31 years post-fire and compared to surrounding unburned plots
53 measured simultaneously. Stem mortality and growth were assessed among functional groups.
54 At the plot level, we found that fire affected forests have biomass levels $24.8 \pm 6.9\%$ below the
55 biomass value of unburned control plots after 31 years. This lower biomass state results from
56 the elevated levels of biomass loss through mortality, which is not sufficiently compensated for
57 by wood productivity (incremental growth + recruitment). At the stem level, we found major
58 changes in mortality and growth rates up to 11 years post-fire. The post-fire stem mortality rates
59 exceeded unburned controls plots by 680% (i.e. >40cm DBH; 5-8 years since last fire) and
60 315% (i.e. >0.7 g cm⁻³ WD; 0.75-4 years since last fire). Our findings indicate that wildfires in
61 humid tropical forests can significantly reduce forest biomass for decades by enhancing
62 mortality rates of all trees, including large and high wood density trees, which store the largest
63 amount of biomass in old-growth forests. This assessment of stem dynamics, therefore,
64 demonstrate that wildfires slow down or stall the post-fire recovery of Amazonian forests.

65
66 **Key-words:** post-fire dynamics, stem mortality, wood productivity, long-term recovery, fire
67 disturbance, drought

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1. Introduction

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87 The successful reduction of the deforestation rate in the Brazilian Amazon between 2004-2017
88 has not been sufficient to reduce disturbance in the remaining forests[1]. Recent studies
89 demonstrate that human-induced disturbances (e.g. wildfires and selective logging) can halve
90 the conservation value and significantly decrease the carbon stocks of remaining Amazonian
91 forests[2–4]. Moreover, Amazonian forests affected by wildfires are estimated to contribute on
92 average with $31 \pm 21\%$ of the gross emission values from deforestation, with contributions
93 beyond 50% during drought years [5]. Yet, there is a critical knowledge gap regarding the long-
94 term recovery of carbon stocks in forests affected by anthropogenic disturbances such as fire
95 [2,3,6].

96 Humid tropical forests are not a fire-adapted ecosystem [7,8]. Previous studies suggested that
97 wildfires in the Amazon basin have been rare since the start of the Holocene, with fire-return
98 intervals exceeding centuries or millennia [8,9]. However, over the past three to four decades
99 wildfires have become increasingly prevalent across humid tropical forests, including
100 Amazonia [10]. These tropical fires generally require an anthropogenic source to ignite, which
101 generally comes from agricultural practices [11]. The likelihood of wildfires occurrence is also
102 increased by forest disturbance, such as selective logging [12], and by deforestation that
103 exposes remaining forests to edge effects [13] and reduces rainfall [14,15]. In addition,
104 wildfires can be greatly exacerbated by extreme drought events [5,12,16–19]. For example,
105 during the 2015 El Niño-induced extreme drought 799,293 km² of the Brazilian Amazon
106 experienced positive active fire anomalies[5]. Given that extreme droughts are predicted to
107 occur at greater frequency in the Amazon Basin [20], wildfires are likely to become even more
108 pervasive[21].

109 These wildfires have a major impact on forest carbon stocks, accounting for the mortality of up
110 to 36% of tree stems and 67% of the biomass loss in central Amazonian forests three years after
111 fires [22,23]. Fire-affected forests consequently become a global important carbon source:
112 based on the 2010 fire season, it was estimated that 27,555 km² of old-growth forests burned in
113 the whole Brazilian Legal Amazon, contributing to 14.8Tg of C emissions to the atmosphere
114 from direct combustion of organic material [19]. Immediately combustible carbon stocks – such
115 as leaf litter and fine woody debris – make up only a very small proportion of forests
116 aboveground carbon stock [2] and most emissions are committed (0.001 to 0.165 Pg of C), as
117 they are likely to occur years after wildfires as a result of vegetation mortality and its subsequent
118 decomposition[16].

119 Despite the growing prevalence and importance of wildfires in humid tropical forests, our
120 knowledge of their ecological consequences is constrained by the lack of data in three key areas.
121 First, the longer-term effects of wildfires on forest biomass is not known as most studies to date
122 have focussed on relatively short-term responses of vegetation to fire [24–27]. For example, a
123 pan-tropical assessment suggests there is no recovery of forest carbon stocks within at least five
124 years [28], while a study on flooded Amazonian forests highlight the potential for fires to
125 impede forest succession in the first 15 years after fire [29]. Second, most assessments are one
126 off inventories, meaning ecological processes and stem dynamics in fire-affected forests are
127 very poorly understood. Extensive field assessments in undisturbed Amazonian forests show
128 the importance of repeat surveys, which have enabled researchers to link the spatial variation
129 of forest biomass to stem dynamics such as mortality and recruitment [30,31]. Finally, there is
130 no data linking post-fire long-term forest dynamics with functional traits. Plant traits such as
131 bark thickness and wood density provide important insights into post-fire changes and the
132 susceptibility of forest ecosystems [32–36], especially as they are directly related to carbon
133 storage function [37]. Recently, an assessment of the impacts of fire and other forest
134 disturbances has shown that wood density remains below baseline conditions for at least 25
135 years following disturbance, indicating a slow recovery or impeded succession [38]. Longer
136 term assessments of forest dynamics could provide additional insights into the successional
137 trajectories of burned forests, and their ability to recompose carbon stocks.

138 We address these knowledge gaps by using a unique large-scale and long-term assessment of
139 forest dynamics, which is based on a set of chronosequences and re-census data from burned
140 and unburned forests in five distinct regions of the Brazilian Amazon. We ask two main
141 research questions:

142 i) What are the longer-term effects of wildfires on forest biomass (i.e. up to 31 years after
143 the fires)? We address this question by comparing, at the plot-level, the total aboveground
144 biomass, and forest dynamics represented by mortality and wood productivity, between
145 burned and unburned forests. The balance between tree mortality and productivity defines
146 the ability of these fire-affected forests to recover to pre-disturbance carbon levels and offset
147 carbon emissions.

148 ii) How do wildfires affect forest growth, recruitment and mortality at stem-level, and what
149 insights do key structural traits such as wood density and stem size (Diameter at Breast
150 Height) provide into the mechanisms underpinning the changes in biomass? We focus on
151 wood density and size because both are important predictors of short-term fire-induced

152 mortality [32,33] and both are linked to stem growth rates and carbon storage in undisturbed
153 forests [39,40]. We divided stems into three classes of wood density and size to examine
154 the changes in the probability density functions of growth, recruitment and mortality over
155 time since fire degradation.

156 Finally, we combine results from both questions to discuss to what extent Amazon forests are
157 recovering from fires.

158 **2. Materials and Methods**

159 *2.1 Experimental design for field data collection*

160 We used tree inventory data collected as part of the Fire-Associated Transient Emissions in
161 Amazonia (FATE) network. Since 2009, the FATE network has been monitoring permanent
162 forest plots established in burned forests with different times since wildfire occurrence. Here,
163 we collected and analysed field data from 64 permanent plots across Amazonia, from which we
164 revisited and re-measured 55 All plots are located on old growth non-flooded forests (*Terra*
165 *Firme*) with 269.3 m median distance from the edge. We examined the terrain elevation and
166 slope within 100 m buffer of each plot using a high resolution (12.5m) digital elevation model
167 (ALOS PALSAR RTC). There is very small slope across the plots (range: 2.8° – 9.4°). Plots
168 ranged from 0.25 to 1 ha. From a total of 64 plots, 29 are in unburned and 35 plots are in burned
169 forests (supplementary material table S1).

170 We selected burned forest sites based on the inspection of Landsat images (1984-2016)
171 followed by on-the-ground field confirmation. When we did not find evidence of fire in the
172 satellite image for a specific site, but there was charcoal in the ground, we assumed the fire
173 event occurred at the time of the earliest image (i.e. 1984). Because of the high intensity of the
174 1982-83 El Niño event, when 3.6 million ha were burned in East Kalimantan [41], it is likely
175 that several forested areas elsewhere were affected by wildfires during this period. To enable
176 pairwise comparisons between burned and unburned control sites, both were selected to avoid
177 other anthropogenic disturbances such as selective logging. The unburned control plots,
178 moreover, were carefully chosen to encompass a similar range and heterogeneity of both soils
179 and topography as the burned sites. Independent proxies of fire intensity, such as char height,
180 are not available for plots assessed a long time after fires when many of the affected trees will
181 have died and decomposed. Without this additional information, we assume that all plots were
182 subjected to low intensity understorey wildfires that are the norm in previously undisturbed
183 forests.

186 Our 31 years chronosequence dataset captures the effect of wildfires driven by El Niño events
187 and North tropical Atlantic warming since the 1980s. The distribution of the FATE plots reflects
188 the spatial occurrence of these major wildfire events (e.g. figure 1a) and accessibility. In order
189 to link drought intensity over the last 40 years with wildfire extent, we used re-analysis derived
190 data to calculate Maximum Climatological Water Deficit (MCWD) and satellite derived
191 products of burned area (please see detailed methods in supplementary material method S.1).
192 The data extracted from each plot location, along the burned area and MCWD time series,
193 shows the association between MCWD and burned area at all plots region (figure1b). Figure
194 1b also demonstrates when each site was sampled relative to the last fire event.

195 *2.3 Field inventory and total aboveground biomass*

196 The inventory was conducted following the RAINFOR network protocol for the establishment
197 of permanent sample plots [42]. We estimated aboveground biomass (AGB) of 9,836 live trees,
198 palms and lianas with diameter at breast height (DBH) ≥ 10 cm. For both burned and unburned
199 forests, total aboveground biomass (TAGB) represent the sum of all trees, palms and lianas
200 AGB, and was estimated using a specific allometric equation for each group, following [37] for
201 trees, [43] for palms, and [44] for lianas. The AGB estimates for palms and lianas were based
202 solely on their diameter, whilst for trees DBH and specific wood density values were used as
203 input variables. We used the global wood density database [45,46] to match specific wood
204 density to each species. For individuals not identified to the species level (~5%), we used the
205 mean value for the species belonging to that genus. Similarly, we used the mean specific wood
206 density of the family for trees not identified at the genus level [30]. When an accurate
207 identification was not achieved, the plot mean specific wood density was used.

208 *2.4 Plot-level assessment of long-term effects of wildfires on forest biomass*

209 *2.4.1 Quantification of plot-level forest dynamics*

210 To understand the response of old growth forests to wildfires, we evaluated the long-term shifts
211 in forest dynamics at the plot-level. We quantified for all burned and unburned plots the net
212 biomass change (Net TAGB), which is a function of wood productivity (Wp) and mortality (M)
213 of all stems in the plot (Equation 1).

$$214 \quad \text{Net TAGB} = \Sigma Wp - \Sigma M \quad (2.1)$$

215 The term ΣM corresponds to plot mortality ($\text{Mg ha}^{-1} \text{y}^{-1}$), which was calculated as the amount

216 of the biomass of all stems recorded as dead within a given census interval. The term ΣW_p
217 corresponds to the sum of the values of W_p for all measured stems in the plot and can be
218 decomposed as (Equation 2).

$$219 \quad \Sigma W_p = \Sigma \text{Recruits} + \Sigma \text{Growth} \quad (2.2)$$

220 W_p ($\text{Mg ha}^{-1} \text{ y}^{-1}$) was calculated as the sum of the biomass of stems that recruited during each
221 census interval ($\Sigma \text{Recruits}$) and the sum of the growth in biomass of each stem present in the
222 plot (ΣGrowth) during this same census interval.

223 Because census interval varied among plots, rates were weighted by the census interval length.
224 In order to account for trees that both recruited and died during the census interval and also to
225 correct for tree growth prior their death, M and W_p values were corrected at a tree-by-tree basis,
226 following methods of [47].

227 *2.4.2 Quantification of differences between burned and unburned forests*

228 To assess if TAGB and dynamics from burned forests recovered to pre-disturbance levels, we
229 quantified the percent of difference between burned and unburned forests. For TAGB and each
230 dynamic parameter, the proportional difference between each burned plot and the mean of
231 unburned plots, was calculated as described below (Equation 3):

$$232 \quad \% \Delta X = \frac{(X_{BU(i)} - X_{UB(\text{mean})})}{X_{UB(\text{mean})}} \cdot 100 \quad (2.3)$$

233 where X represents the variable of interest (TAGB, M , W_p , and Net TAGB), $BU_{(i)}$ is each of
234 the burned plots, and $UB_{(\text{mean})}$ is the local mean of all unburned plots sampled in the same region
235 at the same time as the burned plots. The error is presented as standard error of the mean (SE).

236 *2.4.3 Long-term trajectories of burned forests TAGB and dynamics*

237 We used Generalized additive mixed models (GAMM) to assess the trajectories of TAGB,
238 mortality, W_p and Net TAGB over the time since last fire chronosequence. We used each
239 individual plot measured repeatedly as a random effect. To assess the direction of the difference
240 (%) in each variable in relation to the control-unburned forests, we used the local polynomial
241 regression fit (LOESS), choosing the span values based on the minimum residual standard error
242 obtained. All statistical analyses were performed in R 3.3.3 using *gamm4[X]* R and *lme4[X]*
243 packages.

244 *2.5 Stem-level assessment of growth, recruitment and mortality*

245 To explore the structural and successional mechanisms driving the long-term changes on TAGB
246 of burned forests, we assessed the empirical probability density function of stem mortality rate
247 and stem growth in three DBH (cm) classes: 10.0 to 19.9, 20 to 39.9 and >40.0; and three
248 specific wood density (g cm^{-3}) classes: 0.1 to 0.49, 0.5 to 0.69 and > 0.7 for both burned and
249 unburned plots. Including all plots from all regions, we divided the dataset into four categories
250 considering the years since last fire (YSLF): 0.75-4; 5-8; 9-11; 12-31 years. For each plot we
251 calculated stem mortality as the exponential mortality coefficient ($\%y^{-1}$) [48], mean stem
252 growth as the annual mean growth (cm y^{-1}) of all living individuals, and stem recruitment as
253 the percentage rate of stems recruited relative to live stems in each census ($\%y^{-1}$). Stem
254 mortality and stem growth from each plot were stratified by classes of diameter, wood density
255 and YSLF. Stem recruitment by plot was stratified by YSLF class, but we only used a grouping
256 based on wood density class, as all recruitment falls into the smallest DBH class. The
257 probability density functions of the unburned and burned plots were compared using the
258 Wilcoxon test for two samples.

259 **3. Results**

260 *3.1 The long-term effects of wildfires on forest biomass at plot-level*

261 During the monitoring period, the biomass of unburned forest plots remained generally
262 unchanged, with exception of forest plots from southeast and east Amazonia that have
263 experienced high mortality in the drought years of 2015 ($15.2 \text{ Mg ha}^{-1} \text{ y}^{-1}$; $n=4$) and 2016 (9.9
264 $\text{Mg ha}^{-1} \text{ y}^{-1}$; $n=20$) respectively (supplementary material, table S2). In contrast, the biomass of
265 burned forest plots changed greatly with time since fire (table 1). Immediate fire effects on
266 TAGB were smaller, with reduction of $-2.1 \pm 3.9\%$ up to four years post-fire. From 5-8 years
267 since fire, we found a much greater difference in TAGB, with reduction of $-22.1 \pm 2.9\%$ in
268 burned plots compared to unburned controls. The significantly lower biomass persisted up to
269 31 years post-fire, when burned plots remained $24.8 \pm 6.9\%$ below the baseline value of the
270 control plots (figures 2a, 2e).

271 The reduction in TAGB observed in burned forests reflect the imbalance between wood
272 productivity and mortality. Although post-fire mortality declined during the first eight years of
273 the chronosequence (figure 2b), its negative influence on burned forests biomass is evident
274 (figure 2a). The maximum difference in mortality between unburned and burned forests was at

275 4 years post-fire ($247.4\% \pm 135.6$, table 1), with higher mortality values for burned forests.
276 There was no difference in mortality between burned and unburned forests from 8 until 31 years
277 (figure 2f). Wood productivity in burned forests followed a linear decline along the
278 chronosequence (figure 2c). However, when compared to unburned forests, Wp rates in burned
279 forests remained higher and the difference increased to its maximum value ($30\% \pm 7.8$, table 1)
280 until 8 years post-fire. The difference in Wp between burned and unburned forests then
281 decreased and remained in a near-steady state until 31 years post-fire (figure 2g). Moreover,
282 Net TAGB in burned forests increased during the first 8 years shifting from a strong negative
283 sign (source) to a neutral state (figure 2d). Compared to unburned forests, Net TAGB rates in
284 burned forests was lower but increased until 6 years of the chronosequence, and then remained
285 steady and equivalent to unburned forests levels (figure 2h).

286 3.2. *Uncertainties*

287 Across pools, the largest uncertainties (table 1) are associated with mortality, due to the large
288 influence exerted by the death of a single large tree. Temporally, and for all variables, there
289 were large uncertainties from 16 to 27 years after fire, where data was lacking (Figures 2a-2h).
290 It is reassuring that the trajectories predicted along the chronosequence using the GAMM model
291 and LOESS fit agree. All GAMM fitted models intercept and smooth component (YSLF) are
292 statistically significant (table 2). While all models are significant (supplementary material,
293 figure S1), residual variability may be associated to the “random” deviations from the predicted
294 values that are not due to plots’ specificities and/or YSLF, suggesting possible association with
295 fire intensity and environment conditions. Accordingly, the large TAGB and mortality
296 variability observed across the plots explains the higher Std. Error found in the intercept and
297 slope of TAGB and mortality models. The fitted model’s effective degrees of freedom values
298 consistently show that burned forests TAGB, mortality and Net TAGB response to time is non-
299 linear, while Wp is linear. For Wp the effective degrees of freedom is equal to 1 meaning
300 linearity for Wp in relation to time.

301 3.3 *Mortality, recruitment and growth rates at stem-level*

302 Wildfires had persistent effects on burned forest dynamics at stem-level: from a total of 48
303 comparisons between burned and unburned forests of stem mortality and growth, 16 were
304 significant ($p < 0.05$), and another five were marginally significant at $p < 0.10$ (figure 3 and 4).
305 These significant results were distributed across all classes of time since last fire disturbance,

306 and all classes of tree size and wood density.

307 Stem mortality was skewed towards zero, but still higher in burned forests when compared to
308 unburned forests. The significantly higher stem mortality was observed across all tree size and
309 wood density classes – but not in all YSLF categories (figure 3a, 4a). The largest stem mortality
310 differences between burned and unburned forests were observed at 0.75-4 YSF. On average
311 22.8 ± 2.4 % of trees from small classes of size (i.e. 10-19.9 cm DBH) and 23.8 ± 5.0 % of trees
312 with the lightest wood density (i.e. 0.1-0.49 g cm⁻³) died during 0.75-4 YSLF – these mortality
313 rates were 341% and 239% higher than the equivalent size and wood density classes in
314 unburned controls. However, the larger size stems (i.e. >40cm DBH; 5-8 YSLF) and higher
315 wood density classes (i.e. >0.7 g cm⁻³; 0.75-4 YSLF) were also significantly affected in burned
316 forest, being 680% and 315% higher than unburned controls, respectively. Between 9-11 years
317 since the wildfires, small size stems (i.e. 10-19.9 cm DBH) and stems from small (i.e. 0.1-0.49
318 g cm⁻³) and medium (i.e. 0.5-0.69 g cm⁻³) classes of wood density experienced significant higher
319 mortality in burned forests – these mortality rates were 74%, 173% and 69% higher than
320 unburned controls, respectively.

321 Stem growth followed a normal distribution, and the mean values of burned forests were
322 generally higher than those in unburned forests (figure 3b, 4b). The greatest difference in stem
323 growth was observed in the small and medium size classes: when compared to unburned
324 controls, mean stem growth was 94.1 and 96.6% higher in burned forests for small size class in
325 the 5-8 and 9-11 YSLF categories, respectively, and 54.2% and 27.0% higher in burned forests
326 for the medium size classes at 5-8 and 9-11 YSLF categories, respectively. Similarly, for the
327 class of low wood density, mean stem growth was 121.1% and 62.1% higher in burned forests
328 than in unburned forests in the 5-8 and 9-11 YSLF categories, respectively. For medium wood
329 density stems, mean stem growth was 50.0% higher in burned forests than in unburned forests
330 at the 9-11 YSLF category. Finally, for high wood density stems, growth was 24.0% and 26.0%
331 higher in burned forests than in unburned forests at 5-8 and 9-11 YSF, respectively.

332 Stem recruitment was skewed towards zero (supplementary material, figure S2). Overall, mean
333 stem recruitment values were generally higher in burned than unburned forests up to 12 years
334 since last fire (supplementary material, figure S3). There were no significant differences
335 between recruitment in burned and unburned forests when separated by wood density classes.

336 **4. Discussion**

337 We provide one of the longest post-fire chronosequence assessments of fire-affected
338 Amazonian forests, analysing the most extensive dataset to date. Our findings reveal that burned
339 Amazonian forests persist in a reduced biomass state for at least 31 years since last fire, at which
340 point they store approximately 25% less above-ground biomass than equivalent unburned
341 forests. This decrease in biomass is driven by increases in mortality that are not fully
342 compensated for by the relatively small changes in recruitment and growth rates (table 1). The
343 high mortality in burned forests was not exclusively limited to small diameter and light wood
344 trees, but also includes the large-stemmed and hardwood trees which contribute most to the
345 carbon stock [30,49,50]. In contrast, the positive post-fire growth response was predominantly
346 associated with small-medium sized trees and lighter or intermediate classes of wood density -
347 groups that contribute relatively little to overall above-ground carbon stocks. We examine in
348 more detail these findings to understand how the post-fire changes in dynamics rates influence
349 forest biomass in the long-term, and how this is underpinned by mortality, recruitment and
350 growth among functional groups. Finally, we discuss the prospects of long-term slow recovery
351 of Amazonian fire-affected forests and the future of tropical humid forests under the risk of
352 wildfires.

353 *4.1 Post-fire changes in forest dynamics and consequences for the long-term recovery of*
354 *biomass stocks*

355 Our data show that long-term reduction on TAGB after fire is persistent, but the uncertainties
356 inherent in space-for-time comparisons and delayed mortality of large trees mean it only
357 became fully evident after five years of the fire events. After the initial fire-induced mortality,
358 wood productivity rates in burned forests were higher than unburned controls probably because
359 of the increase in light and nutrients availability to the remaining survivors' trees. However,
360 this initial short-term increase in wood productivity (plot level biomass gain) does not exceed
361 mortality (plot level biomass loss), and is insufficient to counteract the total biomass losses
362 through mortality along the whole chronosequence. Previous studies have raised the question
363 of whether enhanced forest growth, promoted by low-intensity fires, offsets carbon emissions
364 due to post-fire tree mortality [51]. Our assessment refutes that: although burned forests were
365 no longer a net carbon source six years after fires, the lack of biomass accumulation from 6-31
366 years shows they will not recover to pre-fire conditions on decadal time-scales. Our findings
367 also emphasize the importance of longer-term and larger-scale studies to monitor carbon
368 dynamics in burned forests, which are particularly important for incorporating the variation of
369 mortality and growth rates in C emission models for the growing extent of fire-affected tropical

370 forests.

371 *4.2 Post-fire mortality among functional groups with high contribution to biomass stocks*

372 Wildfires affected the stem mortality rates of small-medium sized trees and all wood density
373 classes in the first YSLF category (0.75-4) of the chronosequence. An initial increase in the
374 mortality of high wood density trees (315%) compared to unburned forests, combined with a
375 late increase in the mortality of large-sized trees (680%), has important impacts upon overall
376 aboveground biomass loss. A burned forest that lost its large-size (figure 3a) and high-wood
377 density stems (figure 4a) will inevitably store less biomass than it did prior to disturbance
378 (figures 2a, 2e). As well as corroborating previous studies on the late increase in mortality of
379 large trees [23], we also show for the first time that this process can continue for up to eight
380 years after fire – suggesting that almost all previous studies will have underestimated total
381 biomass loss from fires.

382 Although previous findings show tree mortality decreased as a function of increasing wood
383 density [33], we show that all wood density classes are at risk of fire-induced mortality,
384 especially in the first 4 years after the burn. It is important to note, our results do not show
385 higher susceptibility of high wood density trees compared to lower wood density trees to post-
386 fire mortality, instead we show higher stem mortality of high wood density trees in burned
387 forests compared to unburned controls. One explanation for this high post-fire mortality across
388 wood density classes reflects the fact that the full range of wood densities can be found in the
389 small (i.e. 10.0-19.9 cm DBH) and medium (i.e. 20.0 – 39.9 cm DBH) size classes, which are
390 the fire-susceptible groups. Smaller trees are shown to have thinner bark, which in turn are at
391 more risk of heat stress and fire-induced mortality [11,32].

392 *4.3 Post-fire stem growth and recruitment*

393 The significant loss of large size and emergent trees is likely to have triggered the increase in
394 the growth of light-dependent and fast-growing species. As expected, this increase in wood
395 productivity is associated with the stem growth responses of small and medium size trees from
396 all wood density classes, and to a lesser extent to stem recruitment. Although light availability
397 is expected to also benefit new recruits [52], stem recruitment is less evident and not
398 significantly higher than undisturbed in each individual wood density class. However, an
399 ongoing successional process may be occurring within burned forests, as components of wood

400 productivity (recruitment + growth) was higher compared to unburned (supplementary material,
401 table S3, figure S3). Our results suggest that pioneer species are colonizing and growing after
402 fire, maintaining a natural forest succession process after disturbance. For instance, the late
403 stem mortality of small trees (i.e. 10-19.9 cm DBH; 9-11 YSLF) and stem growth at mid-long
404 term (i.e. 5-8 and 9-11 YSLF) observed, supports the expected post-disturbance forest
405 succession. However, it is expected that recruitment of old growth species is limited after fire
406 disturbance which negatively affects the forest's ability to recover to its pre-disturbance
407 functional state [29,53]. Consequently, fire disturbances are likely to shift forest composition
408 and dynamics for much longer than 30 years.

409 *4.4 Prospects for forest recovery beyond the time-scale of our data*

410 Although our data extend to 31 years post-fire, there are reasons to expect slow recovery for
411 many decades beyond this time-frame. First, the Net TAGB in burned forests was close to
412 unburned forests equilibrium in the long-term of the chronosequence, and did not provide any
413 signs of continued recovery. For the recovery to occur gains would need to surpass loss during
414 this stage. Second, the fires killed many large-size and high-wood density trees, which will take
415 the longest to recover; perhaps unsurprisingly we also found that their re-establishment will
416 take longer than 31 years, and many could take centuries to recover, given the large trees age
417 (200 to 1,400 yr) in undisturbed Amazonian forests [54]. However, other unassessed factors
418 could be important and are worthy of further investigation. For example, the destruction of the
419 seedbank by fire and a low seedling survival may act to limit stem recruitment, as previously
420 found in Amazonian flooded forest affected by fire in long-term [29]. In addition, remaining
421 seeds from shade-tolerant species have lower chances to germinate in larger canopy gaps [55].
422 Finally, the reduced biomass stock may result from the dominance of early successional species
423 inhibiting emergent and shade-tolerant species on decadal time scales [52].

424 *4.5 Post-fire forest recovery limitations and the future of tropical humid forests under the risk* 425 *of wildfires*

426 Forest disturbance from fires may interact with a changing climate. For example, burned forests
427 have a more open canopy which allows the entrance of solar radiation. The increasing
428 temperature in the interior of burned forests results in the increase of vapour pressure deficit
429 and evapotranspiration, further exacerbating soil drying [7,56]. At the same time, the Amazon
430 has seen an increase in drought conditions, limiting water availability [57] and potentially

431 limiting the recruitment of trees [58]. Although Amazonian forests seem to be resilient to dry
432 conditions, it is likely that water limitation can limit their recovery from fire-disturbances
433 [57,59]. Whether post-fire succession is permanently arrested or is just occurring at a very slow
434 rate is difficult to ascertain based on the temporal scale of our dataset. As we only assessed
435 individuals ≥ 10 cm DBH within 31 years of since the last fires, we are unlikely to detect longer
436 term recovery or the reestablishment of slow growing (high wood density) species. Although,
437 assessments of saplings and seed bank on disturbed Amazonian forests indicates a slowdown
438 or stalled forest recovery [29,38]. Nonetheless, it is notable that the stabilisation of recovery
439 after wildfires is in marked contrast to the consistent increases in forest biomass observed in
440 the first decades after disturbance in selectively logged or secondary forests [60–62].

441 Nonetheless, considering the increase in frequency and intensity of extreme events, such as the
442 2015/2016 El Niño, associated with increasing fire incidence [5], our findings highlight the
443 urgent need to avoid fires in humid tropical forests. Our study, provide the largest ground-based
444 assessment on patterns of post-fire forest recovery, which is particularly important considering
445 the role of the Amazon in the global carbon cycle. Moreover, in our effort to cover the
446 heterogeneity of once-burned forests subjected to similar fire intensities, our estimates describe
447 a general response of Amazonian old growth *Terra Firme* forests to fire disturbance. However,
448 it is important to state that in our study we investigated the effect of a single fire event on forest
449 dynamics and biomass stocks through time. Recurrent fires are still somewhat rare in the
450 Amazon – in 2010, they only accounted for 16% of all wildfires [63]. However, recurrent fires
451 are likely to be increasingly prevalent across the Amazon, given the synergies between a drier
452 and hotter climate, the pervasive use of fire in agriculture [64], and the human-induced
453 disturbances such as selective logging that turn forests more vulnerable to fires due to changes
454 in the microclimate [2,11]. The combination of these factors will also affect the ability of forests
455 to recovery from fire disturbance.

456 **Data accessibility**

457 All relevant data are within the paper and its Supporting Information files.

458

459 **Authors' contribution**

460 L.E.O.C.A conceived the study. L.E.O.C.A., J.B. and L.O.A. designed the study. C.S., A.L.,
461 M.S, B.C. processed the data. C.S. performed the analyses with support from L.E.O.C.A.,
462 F.D.E.S. and J.B. C.S., L.E.O.C.A., I.B., H.X., E.B., P.G., M.S., B.C., L.K., A.L. carried out

463 the FATE field data collection. C.S., L.E.O.C.A and J.B. wrote the paper with contributions
464 from all co-authors.

465

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490

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680 FIGURES CAPTIONS

681

682 **Figure 1. Tree inventory plots and overlap of Maximum Cumulative Water Deficit**

683 **(MCWD) and Burned area (BA) anomalies (sd) over Brazilian Amazon region.**

684 **MCWD was derived from ERA-Interim and BA derived from MODIS (detailed**

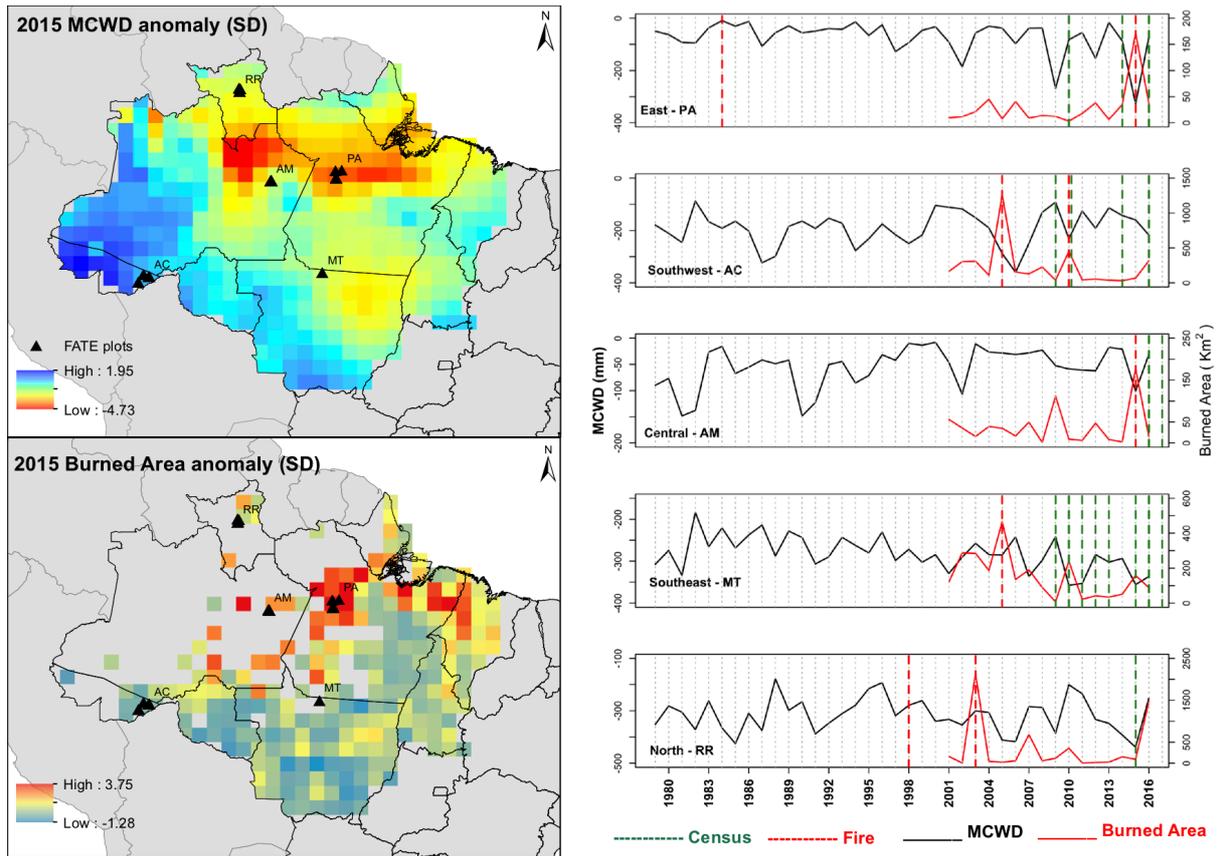
685 **methods in method S.1). Left panel: MCWD red values representing extreme**

686 **drought, or negative anomalies (sd) in relation to 1979-2016 period; BA red values**

687 **representing extreme large affected areas, or positive anomalies (sd) in relation to**

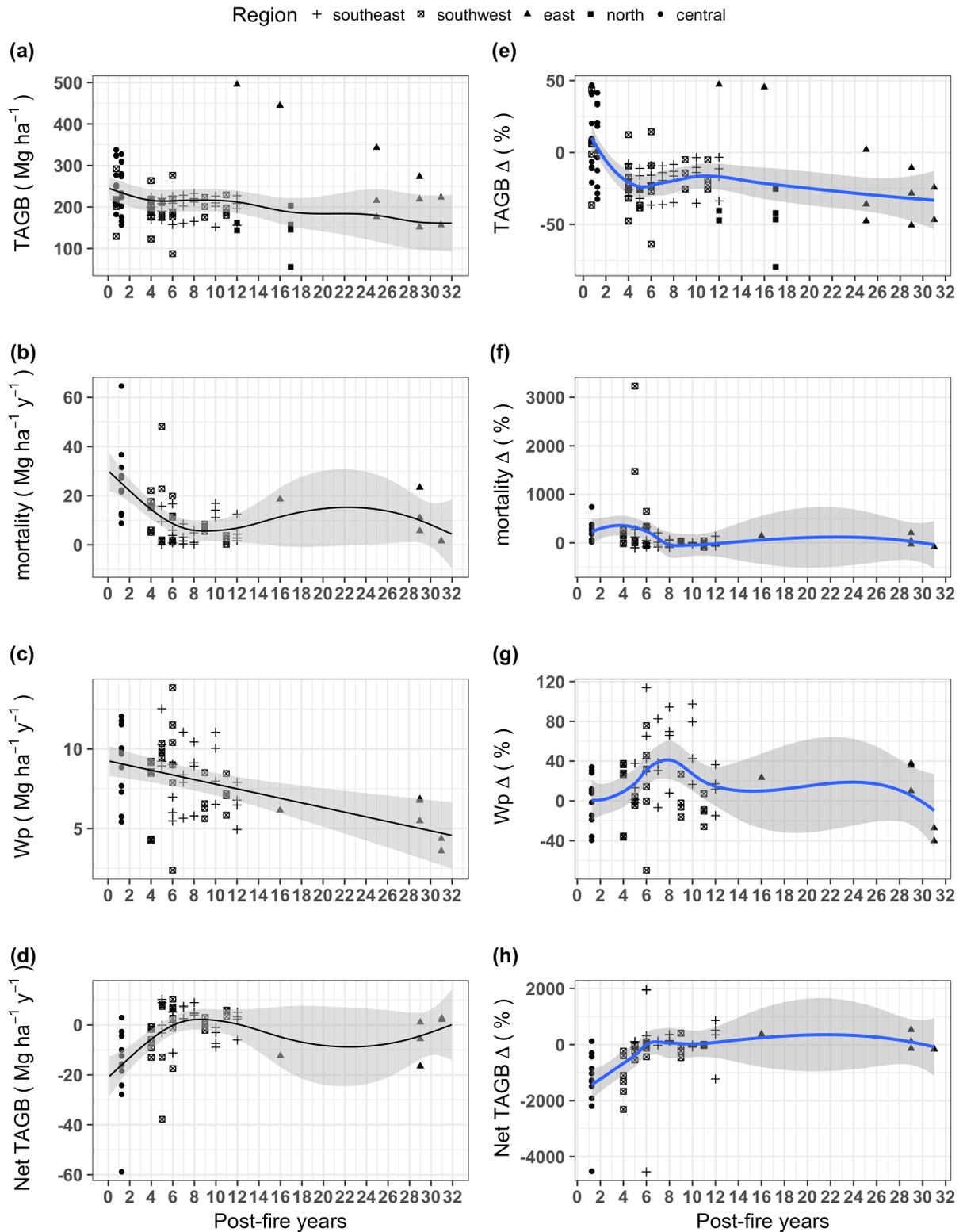
688 **2001-2016 period. Right panel: MCWD and BA variation over time extracted from**

689 **each plots region, year of the tree inventory and year of fire.**



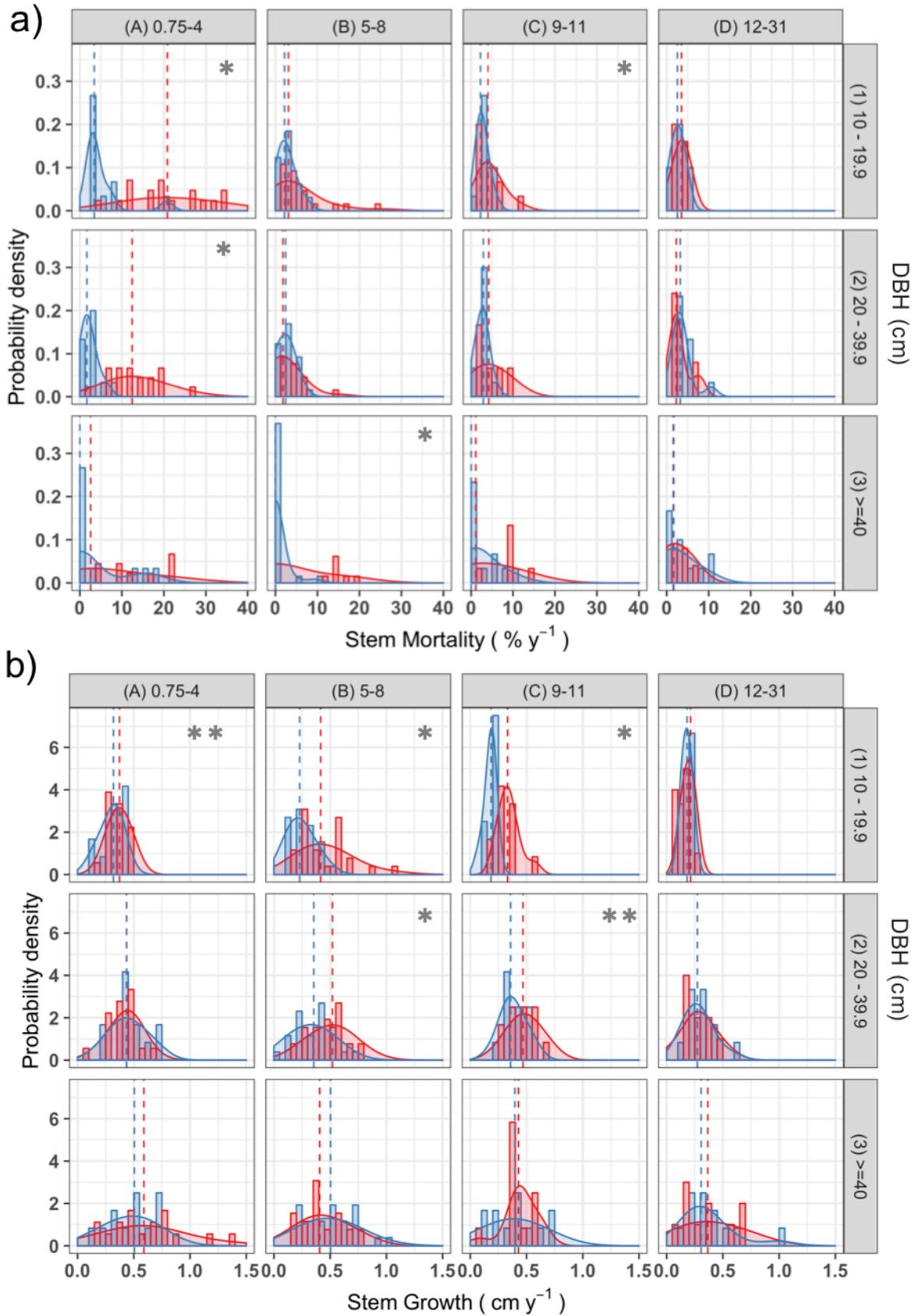
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Figure 2. GAMM fitted models of burned forests pathways by dependent variables: (a) Total Aboveground Biomass (TAGB), (b) Mortality, (c) Wood productivity (Wp) and (d) Net TAGB; and LOESS fit for percent difference of each variable in relation to unburned forest (e-h).



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Figure 3. Probability density function of: a) Stem Mortality (%y⁻¹) and, b) Stem Growth (cm y⁻¹) by Size classes (DBH: 10.0-19.9; 29.9-39.9; >40.0 cm) in lines and years since last fire (YSLF) classes (0.75-4; 5-8; 9-11; 12-31 years) in columns. Dashed lines represent median, red colour for burned and blue for unburned forests. Significance of Wilcoxon text is represented by: * p<0.05 and ** p<0.10.

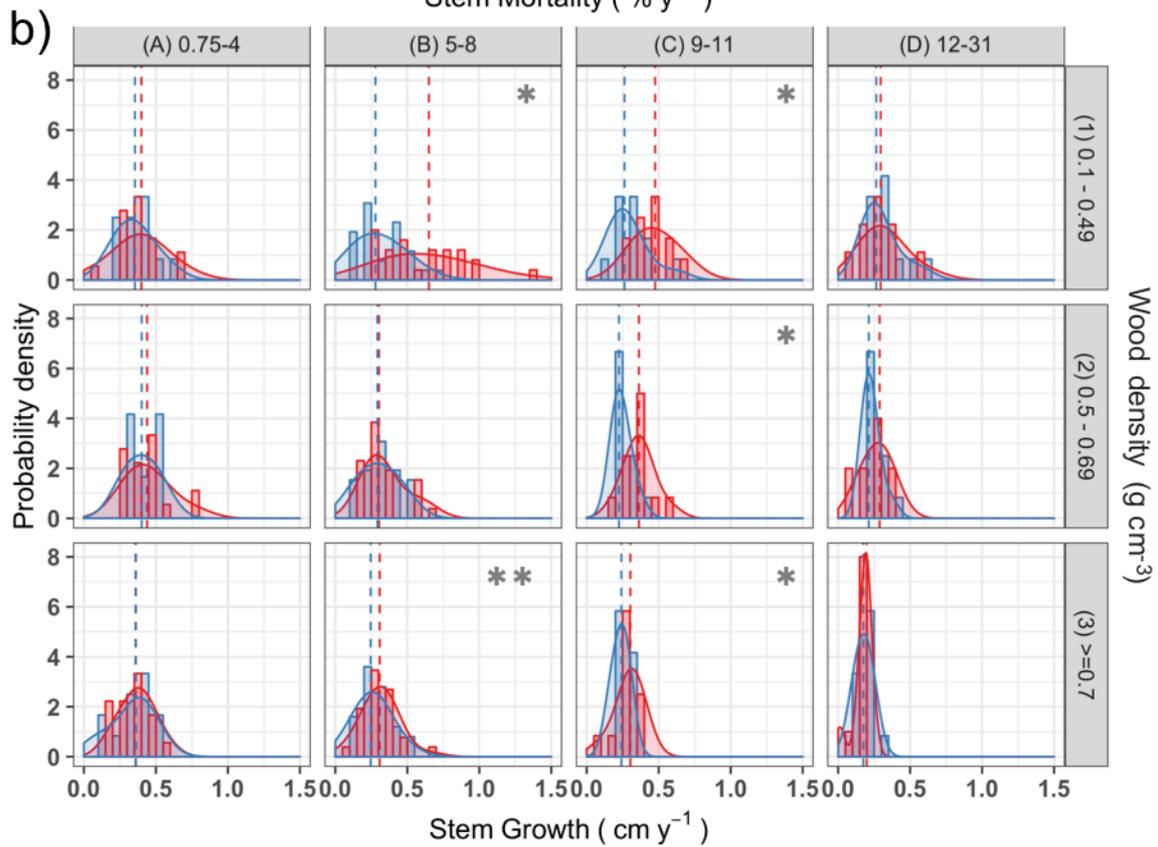
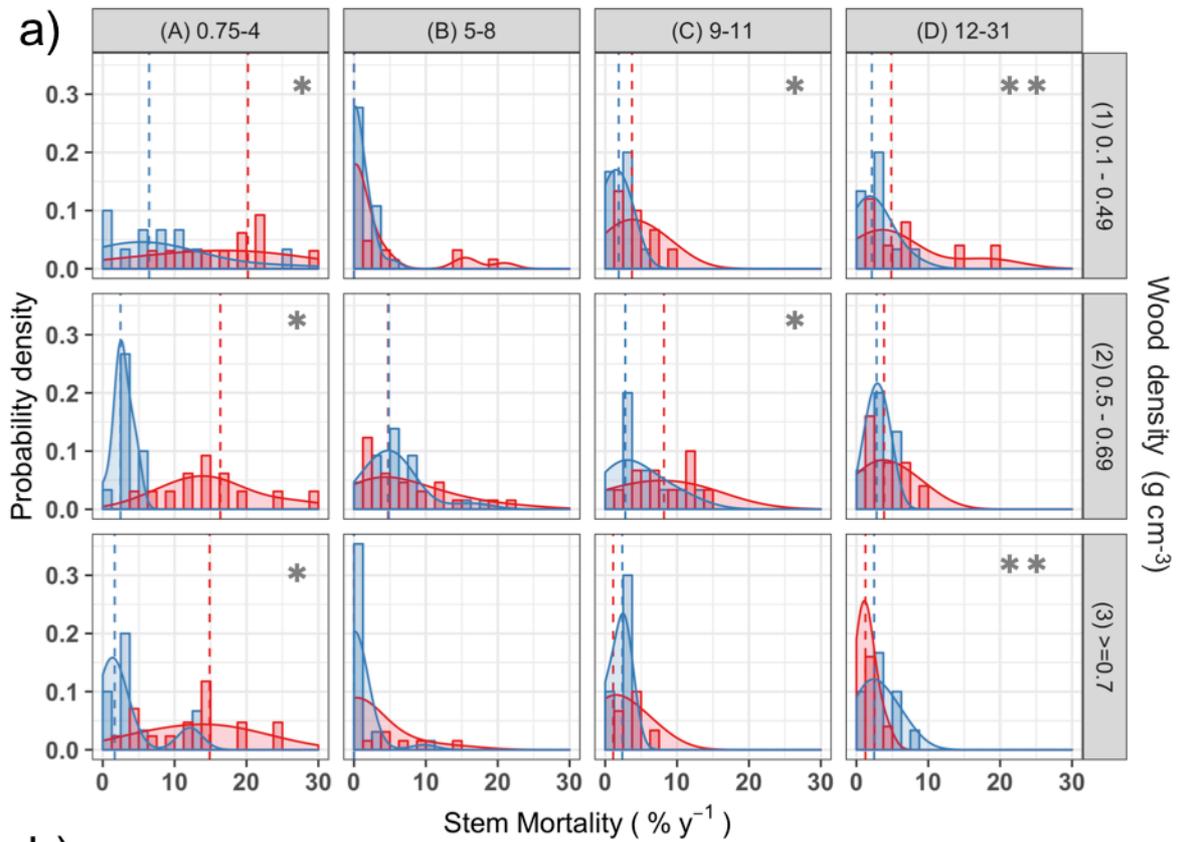


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Figure 4. Probability density function classes of a) Stem Mortality in (%y⁻¹) and, b) Stem Growth (cm y⁻¹) by Wood Density (WD: 0.1- 0.49; 0.5-0.69; > 0.7 g cm⁻³) in lines and years since last fire (YSLF) classes (0.75-4; 5-8; 9-11; 12-31 years) in columns. Dashed

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lines represent median, red colour for burned and blue for unburned forests.
Significance of Wilcoxon text is represented by: * $p < 0.05$ and ** $p < 0.10$.



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TABLES

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Table 1. Mean difference in % (\pm SE) between each burned plot and unburned mean values of TAGB, mortality, wood productivity (increment and recruitment values in table S3, supplementary material) and Net TAGB.

YSLF categories	Census year	TAGB Stock		TAGB Dynamics			
		TAGB $\Delta\%$	N	Mortality $\Delta\%$	Wood productivity $\Delta\%$	Net TAGB $\Delta\%$	N
(0.75 to 4)	2009; 2011; 2014; 2015; 2016	-2.1(3.9)	42	199.2 (43.5)	4.0(6.9)	-1308.4 (263.1)	17
(5 to 8)	2010; 2011; 2012; 2013; 2016	-22.1(2.9)	26	247.4 (135.6)	30.0(7.8)	-26.8 (212.1)	26
(9 to 11)	2014; 2015; 2016	-17.1(2.9)	12	-8.6 (10.8)	16.7(11.2)	-45.5 (57.2)	12
(12 to 31)	2010; 2014; 2016; 2017	-24.8(6.9)	20	20.7 (33.7)	8.9(8.7)	105.0 (183.3)	10

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Table 2. GAMM models output by fixed term for intercept and the smooth term YSLF.

		TAGB	Mortality	Wp	Net TAGB
Intercept	Estimate	216.2	11.4	8.1	-3.3
	Std. Error	12.5	1.2	0.3	1.3
	Std. dev.	72.8	0	1.3	0
	Pr(> t)	<2e-16	2.71E-13	<2e-16	0.01
Smooth term (YSLF)	Estimate	-34.2	-21.4	-1.0	19.7
	Std. Error	17.9	9.6	0.3	9.7
	Std. dev.	102.7	22.5	0	22.6
	edf*	5.2	3.5	1	3.5
	p-value	0.000463	2.05E-05	0.00064	0.000119

Residuals	Std. dev.	12.3	9.9	1.8	10.2
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724 * effective degrees of freedom

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