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Water table depth modulates productivity and biomass across Amazonian forests

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4
5
6 **Title:** Water-table depth modulates productivity and biomass across Amazonian forests

7
8 **Abstract**

9 **Aim** Water availability is the major driver of tropical-forest structure and dynamics.
10 While most research has focused on the impacts of climatic water availability, remarkably
11 little is known about the influence of water-table depth and excess soil water on forest
12 processes. Nevertheless, since plants take-up water from the soil, the impacts of climatic
13 water supply on plants are likely to be modulated by soil water, through groundwater.

14 **Location** Lowland Amazonian forests

15 **Time period** 1971 to 2019

16 **Methods** We use 344 long-term inventory plots distributed across Amazonia to analyse
17 the effects of long-term climatic and edaphic water supply on forest functioning. We
18 modelled forest structure and dynamics as a function of climatic, soil-water, and edaphic
19 properties.

20 **Results** Water supplied by both climate and soils affect forest structure and dynamics, but
21 in different ways. Forests with shallow water table (depth <5 m) had 18% less above-
22 ground-woody productivity and 23% less biomass stock than deep-water-table forests,
23 while forests in drier climates (maximum cumulative water deficit < -160 mm) had 21%
24 less productivity and 24% less biomass than those in wetter climates. Productivity was
25 affected by interactions between climatic water deficit and water-table depth, in which in
26 drier climates, shallow-water-table forests had lower productivity than deep-water-table
27 forests, with this difference decreasing in wet climates.

28 **Main conclusions** We show that the two opposites of "water availability" (excess and
29 deficit) decrease productivity in *terra-firme* forests. The landscape-scale patterns of
30 Amazonian forest structure and dynamics are affected by water table and its interactions
31 with climatic conditions. Our study disentangles the relative contribution of those,
32 improving understanding of tropical-ecosystem functioning and responses to climate
33 change.

34 **Keywords:** groundwater, tropical ecology, seasonality, forest dynamics, above-ground
35 biomass, carbon

36
37 **Introduction**

38 Tropical forests hold a disproportionate share of the Earth's biodiversity and
39 carbon stocks, providing environmental services of global importance through
40 hydrological and carbon cycles (Fauset et al., 2015; Fearnside, 2008; Pokhrel et al.,
41 2014; ter Steege et al., 2013). Amazonia represents the largest of all tropical forests, and
42 plays a fundamental role as a long-term carbon sink, mostly due to the carbon
43 accumulated in woody plants (Pan et al., 2011; Phillips & Brien, 2017). Therefore
44 there is great interest in understanding underlying controls on biomass productivity and

45 dynamics of the Amazonian forests, and how climate change is and will affect them
46 (Llopart et al., 2018; Malhi et al., 2009; Zhao & Running, 2010). Amazonian climates
47 are naturally characterized by spatial and temporal variability in the distribution of
48 rainfall, and recently both droughts and floods have become more frequent, probably
49 driven by anthropogenic climate change (Gloor *et al.*, 2013, 2015; Marengo &
50 Espinoza, 2016). In this context, it is essential to understand the impact of water
51 availability on forest functioning. While this has been studied from the perspective of
52 changes in precipitation seasonality and climatic water deficits (e.g., Phillips *et al.*,
53 2009; Toledo *et al.*, 2011b; Álvarez-Dávila *et al.*, 2017) there has been much less
54 attention paid to the role of water availability in the soil, as regulated by groundwater
55 (but see Nobre *et al.*, 2011; Ivanov *et al.*, 2012; Esteban *et al.*, 2020; Chitra-Tarak *et al.*,
56 2021) and no account of how groundwater affects forest productivity and biomass based
57 on ground measurements currently exists.

58 Water is essential to life and, together with temperature, a key determinant of
59 global patterns of plant distribution and productivity (Ellison et al., 2017; Law et al.,
60 2002; Webb et al., 1978; Whittaker, 1975). Although variation in precipitation is
61 associated with large-scale variation in forest structure and dynamics, soil-water
62 availability to plants is the result of the fine-scale interplay of precipitation and terrain
63 properties at landscape scales. The major landscape factors affecting the redistribution
64 of water entering the system as rainfall are topography and soil texture (Fan, 2015; Fan
65 & Miguez-Macho, 2011; Moeslund et al., 2013). Topography affects the water flow to
66 groundwater, and groundwater movement to lower gravitational positions (lower
67 relative elevation in the landscape) creates gradients of increasing water availability
68 from uplands towards valleys (Fan, 2015; Nobre et al., 2011; Rennó et al., 2008). The
69 retention of water depends on soil texture, decreasing with soil particle size, so that it is
70 greater in clays than in sands (Costa et al., 2013; Hillel, 1998; Parahyba et al., 2019).
71 The dynamics of water drainage and retention in the soil supply the groundwater,
72 influencing seasonal and interannual fluctuations in the water table (Hodnett et al.,
73 1997; Miguez-Macho & Fan, 2012), and also affects soil-water conditions in the rooting
74 zone.

75 Water-table depth (WTD) can be used as a proxy for the accessibility of
76 groundwater to plants, mediated by root depth, which in turn is highly constrained by
77 WTD (Fan et al., 2017), together with soil density (Emilio et al., 2013; Quesada et al.,
78 2012). In *terra-firme* forests, at low topographic positions, roots are in direct contact
79 with the superficial water tables or capillary fringe year-round and during the wet
80 season, but roots become progressively decoupled from the groundwater with increasing
81 ground elevation relative to the local water-table (Fan, 2015; Fan et al., 2017). During
82 normal dry seasons, the water-table level drops and the soil surface becomes drier, but
83 the intensity of this effect depends not simply on climate but also on the soil retention
84 properties and subsidy of groundwater flowing from higher topographic positions
85 (Tanco & Kruse, 2001; Tomasella *et al.*, 2008). Understanding this process is especially
86 important because a considerable portion (~ 50%) of Amazonian forest have a relatively
87 superficial water table of 5m depth or less (Costa et al., 2022; Fan & Miguez-Macho,
88 2010).

89 Therefore, water-table depth is expected to play a key role in the regional
90 patterns of plant growth and mortality (Costa *et al.*, 2022). Easier access to groundwater
91 in shallow-water-table forests can be expected to reduce the effects of precipitation
92 water deficit during the dry season, thus promoting greater productivity in these
93 environments than in sites in the same climatic condition, where the water table is deep.
94 However, excess water in shallow-water-table conditions during the wet season leads to
95 anoxic stress, which may result in reduced plant growth. Water excess inhibits oxygen
96 flow to the roots and limits plant growth, since alternative anaerobic routes of energy
97 production are much less efficient than aerobic respiration (Gibbs & Greenway, 2003;
98 Parolin, 2012). Thus, conditions adequate for growth may become limited to a short
99 window of time, limiting the potential for biomass accumulation. Additionally, to avoid
100 anoxic conditions, tree roots are typically superficial in shallow-water-table
101 environments (Canadell *et al.*, 1996; Fan *et al.*, 2017; Jackson *et al.*, 1996). The
102 resulting poor anchorage, in combination with the loose aggregation of soil particles in
103 waterlogged conditions, increases the risk of treefall (Gale & Barfod, 1999; Gale &
104 Hall, 2001; Ferry *et al.*, 2010). Together, these constraints lead to the expectation that
105 where water tables are shallow, low soil oxygen will lead to low biomass productivity,
106 and weak root anchorage will lead to higher mortality rates. While some local studies
107 have documented these patterns, major uncertainties remain, in part because forests with
108 shallow water tables tend to be understudied, but also because in some local contexts
109 shallow-water-table forests may not have lower biomass productivity than nearby deep-
110 water-table forests under the same climatic conditions (Damasco *et al.*, 2013; Grogan &
111 Galvão, 2006).

112 In summary, it is clear that availability of soil water for plants depends on more
113 than precipitation. Although soil moisture is difficult to measure and characterize over
114 the relevant scales of individual trees and plots across the Amazon, some key
115 determinants of the local hydrological conditions in non-flooded upland forests -
116 precipitation, water-table depth and soil texture (Fan *et al.*, 2017; Freeze & Cherry,
117 1979; Zipper *et al.*, 2015) can be estimated. The effects of those hydrological
118 components on plant responses are not expected to be simple linear additive
119 combinations, but rather complex interactions, as different combinations may give rise
120 to water deficit, excess of water or mesic conditions.

121 Here, we use a unique, extensive long-term forest-monitoring dataset across
122 Amazonia, resulting from the efforts of hundreds of researchers and field assistants
123 (ForestPlots.net *et al.*, 2021), to address two central questions: (1) How does the
124 structure and dynamics of Amazonian forests vary with water-table depth and the long-
125 term average climatic water deficit?, and (2) How does water-table depth interact with
126 climatic water deficit and soil properties to influence Amazonian forest structure and
127 dynamics? There are reasons to expect that above-ground-biomass productivity and
128 above-ground-biomass stock are lower, and mortality higher, with both water deficit
129 and excess. Considering the challenges imposed on plant growth by saturated soils, we
130 predict that the combination of a wet climate and a shallow water table leads to the
131 lowest productivity and highest mortality, while shallow water table within a dry
132 climate mitigates the climatic water deficit, allowing higher productivity than in deep-

133 water-table settings. Soil texture is expected to further modulate those responses, as
134 soils with low-water-retention capacity could reverse the positive interaction of shallow
135 water tables and dry climates.

136

137 **Materials and methods**

138 **Vegetation data**

139 To address our questions, we analyzed plot-level data from long-term ground-
140 based monitoring of Amazon forests, using available records from intact old-growth
141 forests in lowland (125 ± 115 m altitude) Amazonia that are not seasonally or permanently
142 flooded, i.e. *terra-firme* forests. We used data from 344 plots monitoring Amazon
143 vegetation from the RAINFOR and PPBio networks (Lopez-Gonzalez et al., 2011;
144 Magnusson et al., 2013) (see Table S1 for plot details). Only plots with two or more
145 censuses were included in this study. The vegetation monitoring followed standardized
146 measurement protocols. In RAINFOR plots, all trees and palms with a diameter (D) at
147 1.3 m (or above buttress) ≥ 10 cm were tagged and measured (196 plots in this dataset)
148 (Phillips et al., 2010). In PPBio plots all stems with $D \geq 30$ cm are sampled in the full 1
149 ha per plot, stems with $10 \text{ cm} \leq D < 30 \text{ cm}$ were measured in a subplot of 0.5 ha per plot
150 (148 plots in this dataset) (Magnusson et al., 2005). Field data were accessed via
151 ForestPlots.net database (Lopez-Gonzalez et al., 2011), and subject to strict quality
152 control to identify possible measurement or annotation errors, as described in Brien et
153 al. (2015).

154 To evaluate the forest structure and dynamics, we estimated the plot-based above-
155 ground biomass stock (AGB) and above-ground woody productivity (AGWP) of trees
156 and palms per hectare, in each plot. AGB was calculated for each census (Mg ha^{-1}), and
157 AGWP for each census interval ($\text{Mg ha}^{-1} \text{ yr}^{-1}$), and then a time-weighted mean was taken
158 to give one value per plot. Tree biomass was estimated based on the diameter (D), wood
159 density (ρ) and height (H), using the pantropical equation developed by Chave et al.
160 (2014):

$$161 \text{AGB}_{\text{trees}} = 0.0673 \times (\rho D^2 H)^{0.976}$$

162 Species wood density was obtained from the global wood-density database (Chave
163 et al., 2009; Zanne et al., 2009). A 3-parameter regional height-diameter Weibull equation
164 was adjusted using the BiomasaFP R package (Lopez-Gonzalez et al., 2015) to estimate
165 heights.

166 The biomass of palms (Arecaceae family) was calculated from the allometric
167 equation developed by Goodman et al. (2013), based on diameter (D):

$$168 \ln(\text{AGB}_{\text{palm}}) = -3.3488 + 2.7483 \cdot \ln(D)$$

169 Palm trees were excluded from the productivity calculations as variations in
170 diameter are closely related to fluctuation in water content, and most growth of palm trees
171 occurs through increases in height (Tomlinson, 1990; Stahl et al., 2010).

172 AGWP was calculated from the sum of biomass growth of surviving trees and
173 trees that recruited. Biomass-productivity estimates are affected by several factors,
174 including census length, unobserved growth, recruitment, and mortality within each
175 census interval; we corrected these using the method proposed by Talbot et al., (2014).

176 To assess biomass mortality, we first of all estimated the above-ground woody
177 loss over time, in units of $\text{Mg hr}^{-1} \text{ yr}^{-1}$. We also estimated the biomass mortality rate, as
178 $\text{AGB}_{\text{mortality}}/\text{AGB}$, in units of $\text{hr}^{-1} \text{ yr}^{-1}$. This standardization was performed in order to be
179 able to compare the proportional rate of biomass loss among plots with different standing
180 biomass stock. So here, this estimated was referred as biomass mortality rate.

181 Stem mortality, measured as mean annual mortality rate (λ) was calculated as:

182 $\lambda = \frac{[\ln(N_0) - \ln(N_s)]}{t}$, where N_0 and N_s are the number of stems counted of the initial
183 population, and the number of stems surviving to time t , respectively (Sheil *et al.*, 1995).

184 Annual recruitment rates (μ) were calculated as:

185 $\mu = [\ln(N_f/N_s)]/t$, where N_f is the final number of stems, N_s is the original number of
186 stems surviving to final inventory and t is the number of years between inventories.

187 Mortality and recruitment rates were calculated for each census interval ($\% \text{ yr}^{-1}$), and
188 then a time-weighted mean based on the census-interval lengths was taken to give one
189 value per plot. With these results we calculated the stem turnover rate, defined as the
190 mean of recruitment and mortality (Phillips *et al.*, 1994). The length of the census
191 intervals can affect rate estimates, with long intervals between censuses more likely to
192 underestimate rates due to unobserved mortality and recruitment (Lewis *et al.*, 2004).
193 To account for potential impacts of varying census intervals on the rate estimates, we
194 applied the correction factor proposed by Lewis *et al.* (2004).

195

196 **Environmental data**

197 We modelled forest structure and dynamics as a function of climatic, soil-water,
198 and edaphic properties. Maximum cumulative water deficit (MCWD) was used as an
199 inverse proxy to the climatic water supply, water-table depth (WTD) was used as a proxy
200 for local soil-water supply, and soil texture was used as a proxy for soil-water-retention
201 capacity. Maximum temperature and soil fertility were also included in the multiple
202 models in order to control for their known effects on Amazon ecosystem functions (Baker
203 *et al.*, 2003; Malhi *et al.*, 2004; Quesada *et al.*, 2012; Sullivan *et al.*, 2020), thus making
204 it possible to assess the role of hydrological variables, our focus in this manuscript, more
205 clearly.

206 MCWD was calculated based on the long-term average of annual MCWD of each
207 plot, from 1970 to 2019, thus reflecting the climatic conditions experienced by each plot
208 over time and corresponding to the time window of our dataset. MCWD corresponded to
209 the maximum value of the monthly accumulated climatic water deficit reached in each
210 location, i.e., the difference between precipitation and evapotranspiration within each
211 hydrological year (Esquivel-Muelbert *et al.*, 2019). This metric represents the sum of
212 water-deficit values over consecutive months when evapotranspiration is greater than
213 precipitation (Aragão *et al.*, 2007). Precipitation data were extracted from the
214 TerraClimate data set (Abatzoglou *et al.*, 2018), at $\sim 4 \text{ km}$ (1/24th degree) spatial
215 resolution from 1971 to 2019. Monthly evapotranspiration was assumed as fixed at 100
216 mm month^{-1} , considering that Amazonian forest canopies have a nearly constant
217 evapotranspiration rate (Shuttleworth, 1988; Rocha *et al.*, 2004).

218 Water-table depth was extracted from a map developed for the entire Amazon
219 (Fan et al., 2013; Fan & Miguez-Macho, 2010), at ~270 m spatial resolution, based on
220 model simulation constrained by over 1,000,000 direct well measurements from
221 government archives and publications. Water-table depth values were extracted for the
222 geographic coordinates for each plot and did not involve interpolation of values of the
223 surrounding pixels to avoid degrading the already coarse resolution of the WTD data.
224 Clay-content data were obtained from the SoilGrids database, at 250 m resolution (Hengl
225 *et al.*, 2017). As a proxy for soil fertility, we used the soil concentration of exchangeable
226 base cations (Ca + Mg + K), extracted from the Amazon-wide model of Zuquim et al.
227 (2019), since this is the best continuous layer of soil fertility available for the entire study
228 area. SoilGrids has a layer of cation exchange capacity (CEC) (Hengl *et al.*, 2017), but
229 the correlation of measured cations and the mapped CEC has been shown to be low, as
230 CEC includes the concentration of aluminium, which is not a nutrient (Moulatlet *et al.*,
231 2017). Although phosphorus has been indicated as the most limiting nutrient to the growth
232 of tropical forests, this variable is not available for all plots or as a continuous estimated
233 layer. However, the availability of exchangeable cations tends to be correlated well to the
234 amount of phosphorus (Quesada *et al.*, 2010, 2012) and also predicts forest growth well
235 (Quesada *et al.*, 2012). We estimated long-term maximum temperature, using a dataset
236 from TerraClimate, at ~4 km (1/24th degree) spatial resolution from 1971 to 2019.

237

238 **Data analyses**

239 To achieve our goal of understanding the hydrological effects on forest
240 functioning, we used a spatial analysis of the influence of our proxies on the water
241 conditions of each site (water-table depth, MCWD and soil texture), including their
242 potential interactions, on the metrics of forest structure and dynamics (biomass stock,
243 productivity and mortality; stem mortality, recruitment and turnover). To test these
244 effects, we ran multiple linear models considering in addition to hydrological variables
245 (MCWD, WTD and soil texture), soil fertility and air temperature, since they are
246 recognized as important determinants of structure and dynamics of Amazon forests. Our
247 models included interactions because we expected the effect of water-table depth on the
248 forest dynamics to depend on the levels of water-deficit (MCWD) and soil texture (Table
249 S2). Before running the models, we tested for multicollinearity among predictors. The
250 Variance Inflation Factors (VIF) were estimated and only low multicollinearity was
251 detected (VIF < 5, Table S3). To detect if spatial aggregation of plots (which could induce
252 autocorrelation) interfered in our results, we ran generalized linear mixed models
253 (GLMM) with and without a random factor representing the clusters of plots within 50
254 km of each other, checked the model summaries and compared their Akaike's information
255 criterion (Table S4). Adding the random factor improved the models (smaller AIC
256 values), but did not qualitatively change the results, so we present here the models without
257 the random factor.

258 We weighted the plots in regression analyses when testing the effects of the
259 environmental predictors on forest dynamics and structure according to the plot size and
260 monitoring time, as larger plots and those monitored for longer periods are expected to
261 provide better estimates of local, long-term forest properties. To achieve this, following

262 Lewis *et al.* (2009) we plotted the residuals from linear models against plot area and
263 monitoring period, and selected the root transformations of plot area and monitoring
264 period that removed the nonlinear patterns in the residuals when applied as a weight.
265 These empirically-determined weights were: AGWP, $\text{Area}^{1/2}$; AGB, $\text{Area}^{1/3}$; AGB
266 mortality, $\text{Area}^{1/2} + \text{Monitoring length}^{1/4} - 1$; Mortality rate, $\text{Area}^{1/2} + \text{Monitoring length}^{1/3}$
267 $- 1$; Recruitment rate, $\text{Area}^{1/5}$; Stem turnover, $\text{Area}^{1/3} + \text{Monitoring length}^{1/4} - 1$.

268 In order to investigate in more detail the relationships between the response
269 variables (AGB, AGWP, etc) and hydrological variables, we used loess (locally-
270 weighted) regressions. We used partial-dependence plots to visualize the shape of the
271 relationships between response and predictor variables. To visualize interactions, climate
272 and soil texture were divided in three classes based on the standard deviation around the
273 mean of each of these variables.

274 To describe the climate and water-table effects, we used the following data
275 subdivisions of WTD and MCWD, made to provide an idea of the variation in forest
276 structure and dynamics among the extremes of these gradients. We recognize that in
277 nature the forest response is not abrupt or categorized, and the continuous responses are
278 shown in the regression models. Shallower and deeper water-tables were defined using a
279 5-m depth threshold. We chose this division because groundwater $\leq 5\text{m}$ depth is where
280 most roots are potentially in direct contact with the groundwater or the capillary fringe
281 (Fan & Miguez-Macho, 2010; Fan *et al.*, 2017). We also ran boosted regression trees for
282 the relationship between WTD and all response variables (Fig. S1) to check if this value
283 was supported by the data. Wet (MCWD > -160 mm) and dry (MCWD < -160 mm)
284 forests were divided based on the MCWD average in our data set (see the histograms in
285 Fig. S2). To test whether there was a significant statistical difference in forest structure
286 and dynamics between the shallow and deep-water table subgroups, or dry and wet
287 climates, we used unpaired *Welch two-sample t-tests* for unequal sized samples.

288 All analyses were conducted in R version 3.6.1 software. We used the *BiomasaFP*
289 R package (Lopez-Gonzalez *et al.* 2015) to calculate AGB, AGWP and AGB mortality.
290 Multicollinearity was tested using the package *performance* (Lüdtke *et al.*, 2021);
291 LOESS regressions were calculated with package *ggplot2* (Wickham, 2011); multiple
292 linear regressions with package *car* (Fox *et al.*, 2018); the interaction plots with the
293 package *interactions* (Bauer & Curran, 2005); and boosted regression trees with the
294 packages *rpart* (Milborrow, 2019) and *gmb* (Greenwell *et al.*, 2019).

295

296 **Results**

297

298 *How does the structure and dynamics of Amazonian forest vary with the water-table*
299 *depth and climatic water deficit?*

300 Based on the simple relationships between WTD and forest dynamics and
301 biomass, shallower water tables (depth < 5 m) on average decreased the forest biomass
302 productivity ($t = -5.62$; $df = 342$; $p < 0.01$) and biomass stocks ($t = -6.28$; $df = 342$; $p <$
303 0.01) of Amazon forests (Figures 1a and 1b, respectively). Shallower-water-table forests
304 had on average 18% lower biomass productivity ($4.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and 23% lower
305 biomass stock (234.6 Mg ha^{-1}) than those on deeper water tables ($5.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and

306 306.9 Mg ha⁻¹, respectively). Also, based on the simple relationships between MCWD
307 and forest dynamics and biomass, climatically drier sites (MCWD < -160 mm) had 21%
308 lower biomass productivity (4.5 Mg ha⁻¹ yr⁻¹; t = -7.67; df = 342; p < 0.01) and 24%
309 lower biomass stock (240.2 Mg ha⁻¹; t = -7.01; df = 342; p < 0.01) than those in wetter
310 climates (5.7 Mg ha⁻¹ yr⁻¹, 314.3 Mg ha⁻¹) (Figures 2a and 2b, respectively). Thus, the
311 negative direct effects of climatic-water deficit (MCWD) were only slightly stronger
312 than the negative effects of excess soil water associated with shallow water tables.

313 Stem mortality rate (2.6% yr⁻¹, Fig. 1c; t = 3.40; df = 342; p < 0.01) and stem
314 turnover (2.4% yr⁻¹, Fig. 1d; t = 3.62; df = 342; p < 0.01) were higher in shallower-
315 water-table forests than in those with deeper water tables (2.1% yr⁻¹ and 2.0 % yr⁻¹,
316 respectively). Conversely, stem mortality rate (2.8% yr⁻¹; t = 7.21; df = 342; p < 0.01),
317 recruitment rate (2.3% yr⁻¹; t = 3.62; df = 342; p < 0.01) and stem turnover (2.5% yr⁻¹; t
318 = 6.24; df = 342; p < 0.01) were higher in drier than in wet climates (1.9% yr⁻¹, 1.8% yr⁻¹
319 and 1.9% yr⁻¹, respectively) (Figures 2d, 2e and 2f).

320 The greatest biomass stocks were found in the eastern and northeastern portions
321 of the Amazon, which combine, on average, intermediate MCWD, deep water-table and
322 clayey soils (Figures 3c, 3e and 3a, respectively). Biomass productivity was higher in
323 the western portion of the basin and on the Guiana shield, associated with wetter
324 climates (Fig. 3f). Within the Guiana shield, higher productivity was associated with
325 deep water tables (Fig. 3d). Beyond these trends already captured by regression
326 analyses, the maps depict the large local variation (i.e., within sites) of biomass stock
327 and productivity, largely due to intra-site (between plot) variation in topography and
328 consequently in WTD.

329

330 *How does water-table depth interact with climatic-water deficit and soil texture to*
331 *influence Amazonian forest biomass?*

332 A significant interaction between WTD and MCWD was detected only for
333 AGWP. The best model (Table S2) fit of the interaction divides MCWD data into three
334 groups, based on the standard deviation around the mean, following a gradient from
335 wetter (blue line) to drier climates (red line). Shallow-water-table forests had lower
336 AGWP than deeper-water-table forests when under drier climates, with this difference
337 decreasing in wet climates (Fig. 4). The very low biomass productivity of some plots (<
338 2 Mg ha⁻¹ yr⁻¹) is related to the vegetation structure, as in these sites most trees are very
339 thin and therefore have lower productivity. However, the removal of these plots from
340 the analysis does not change the productivity pattern found for the Amazon basin in
341 relation to the interaction between water table depth and climate (Fig. S4).

342 Despite the average negative effect of shallow water table on forest productivity
343 within dry climates, the more complex interactions between soil texture, MCWD and
344 water-table depth indicate a contribution of soil drainage to forest functioning (Fig. 5).
345 These interactions pointed that forest productivity was lower in shallower-water-table
346 conditions within dry climates when the soil is less clayey, as compared to deeper-
347 water-table conditions under the same climate (red line, Fig. 5a). However, when the
348 soil was more clayey dry-climate forests with shallower water table had greater
349 productivity than their climatic equivalents on deeper water tables (red line, Fig. 5c).

350 However, we have a data gap covering the variation of climate, water table and soil
351 texture that limit the interpretation of this result.

352 The variation in AGB, mortality and turnover rates was related to the interaction
353 between MCWD and clay content, with less-clayey and climatically drier sites having
354 lower AGB, whereas mortality and turnover are higher in those sites (Fig. S3).

355
356 *The effects of other factors*

357 The well-known effects of soil fertility on forest dynamics were detected in the
358 multiple linear models. Above-ground woody productivity and biomass mortality rate
359 increased with soil fertility (Table S2). Soil fertility also affects mortality, recruitment
360 rates and stem turnover, which were higher on more fertile soils (Table S2). The effects
361 of maximum temperature in the multiple-regression models were detected only for
362 biomass stock, with sites with higher maximum temperature having lower biomass
363 stock (Table S2).

364
365 **Discussion**

366 Our study demonstrates for the first time the large-scale effects of water-table
367 depth on the structure and dynamics of the Amazon forests, based on a unique
368 combination of ground-plot data and water-table-depth modelling. Amazon forests with
369 shallower water tables had, on average, lower biomass productivity, lower biomass
370 stock, higher stem mortality and higher turnover. Amazon forests with drier climates
371 had, on average, lower biomass productivity, lower biomass stock, higher stem
372 mortality and higher turnover. This indicates that an excess of water, as well as a deficit,
373 has a detrimental effect on forest functioning.

374 Our results show that the landscape-scale patterns of Amazonian forest structure
375 and dynamics are affected by groundwater and its interaction with climatic conditions.
376 Therefore, WTD is an especially important environmental variable to be considered in
377 modelling the effects of climate change on vegetation (Fan et al., 2013; Fan & Miguez-
378 Macho, 2011; Roebroek et al., 2020; Taylor et al., 2013).

379
380 *Effects of water-table depth and the long-term average climatic water deficit on the*
381 *structure and dynamics of Amazon forests*

382 We hypothesized that shallow water tables impose constraints on plant through
383 excess soil water and consequent oxygen limitation. Our results support this hypothesis
384 since, in average, sites with shallow water table tended to have lower biomass
385 productivity (Fig. 1a). However, there is a high data variability, in which some sites,
386 despite the restriction of excess soil water, have high biomass productivity. Therefore, it
387 is important to understand the possible mechanisms related to the two extremes of low
388 and high biomass productivity in shallow water table. To understand the lower
389 productivity, we must review the response of soils and plants to waterlogging, the
390 condition prevailing to various degrees – seasonal to permanent - in many of the
391 shallow-water-table sites. When soils are waterlogged, most of the soil spaces are
392 occupied with water, and the metabolism of roots and microorganisms quickly
393 consumes the available oxygen and produces carbon dioxide. As oxygen is depleted,

394 roots and aerobic microorganisms lose most of their capacity to produce energy through
395 aerobic respiration (Gibbs & Greenway, 2003). In this case, the major pathway to
396 energy production is alcoholic fermentation, which has a much lower yield (2 mols ATP
397 per glyucose molecule) than respiration (36 ATP), and thus severely limits plant growth
398 (Setter & Belford, 1990; Kreuzwieser & Rennenberg, 2014). Low oxygen levels also
399 reduce root permeability (North et al., 2004; Vandeleur et al., 2005), generating a
400 cascade of responses that reduce stomatal conductance and thus limit photosynthesis
401 (Lopez & Kursar, 1999, 2003; Parent et al., 2008; Pezeshki, 2001). Low photosynthetic
402 activity and consequent low growth is well documented in periodically flooded forests
403 (Parolin, 2000; Waldhoff et al., 1998), although this a more extreme condition than the
404 soil waterlogging examined here. Given the various deleterious effects of excess water
405 on plant metabolism and physiology, most tree growth occurs during the windows when
406 water-table levels decrease and anoxia is relieved, mostly in the dry season. Such
407 growth windows have been described in flooded areas, where the largest diameter
408 growth occurs in the non-flooded period (Schöngart et al., 2002; 2004). Therefore, the
409 period of environmental conditions suitable for growth is shorter in shallow water table,
410 and therefore, on average, biomass productivity is lower in these locations than in deep
411 water table. Despite the anoxic conditions, high biomass productivity observed in some
412 plots with shallow water table may be related to the functional traits of plants
413 evolutionarily established in these environments. Shallow water tables filters trees with
414 lower wood density (Kraft *et al.*, 2008; Ferry *et al.*, 2010; Cosme *et al.*, 2017), higher
415 specific leaf area (SLA), xylem with wider vessels and larger sapwood area (Cosme *et*
416 *al.*, 2017), these acquisitive strategy together translate into fast-growing plants,
417 therefore, greater biomass accumulation. Therefore, even in shallow water tables, some
418 plants are able to adapt to excess water conditions and show their greatest growth
419 potential.

420 For vegetation dynamics, we recorded higher mortality and stem turnover in
421 shallow-water-table sites, as we had hypothesized. Poorly drained sites have higher
422 mortality rates due to weak plant anchorage caused by the groundwater layer that
423 prevents deep root growth, and this is also generally associated with loose soil texture
424 (Gale & Barfod, 1999; Toledo et al., 2011). This low adherence to the soil increases the
425 tree's susceptibility to uprooting (Madelaine *et al.*, 2007). Forests with waterlogged soils
426 have higher proportions of uprooting as the tree mode of death, whereas forests on well-
427 drained soils have higher proportions of trees dying standing (Gale & Hall, 2001). The
428 effects of excess water on forest structure and dynamics are well described in the
429 literature for floodplain forests (Simone et al., 2003; Godoy et al., 1999; Parolin et al.,
430 2004; Piedade et al., 2013; Schöngart et al., 2004), but little is known about the effects
431 of shallow-water-tables on *terra-firme* forests. In local studies, paired comparisons of
432 shallow and deep water tables within the same wet macroclimate have shown similar
433 patterns of lower biomass productivity and basal area (Castilho et al., 2006; Castilho et
434 al., 2010; Ferry et al., 2010), higher tree mortality (Ferry et al., 2010; Toledo et al.,
435 2011) and recruitment rates (Ferry *et al.*, 2010) in seasonally waterlogged shallower-
436 water-table forests than on deeper-water-table hilltops, as we now find here to occur at
437 an Amazon-wide scale. In a global analysis, based on remote sensing data, water-table

Commented [TRdS1]: I decided to keep this part of the discussion, because despite having high productivity values in shallow water table, on average the productivity is lower in shallow water table, compared to deep water table.

438 depth was associated with forest productivity, stimulating or hindering vegetation
439 growth depending on climate (Roebroek *et al.*, 2020), and our large-scale on-the-ground
440 assessment of this effect supports those results for the Amazonian forests, but here with
441 above-ground wood productivity data.

442

443 *Interactions among water-table depth, climatic water deficit and soil properties*
444 *influence Amazon-forest structure and function*

445 Our results also agree with a well-described average effect of increasing climate
446 seasonality lowering productivity and biomass stock, and increasing stem turnover
447 (Álvarez-Dávila *et al.*, 2017; Malhi *et al.*, 2004, 2006; Saatchi *et al.*, 2007; Vilanova *et al.*,
448 2018). The effects of soil fertility were in line with those described in the literature,
449 in which forest dynamics and especially above-ground woody productivity were greater
450 on more fertile soils (Baker *et al.*, 2003; Malhi *et al.*, 2004; Quesada *et al.*, 2012; Banin
451 *et al.*, 2014; Esquivel-Muelbert *et al.*, 2020). However, neither soil properties, nor
452 climatic or groundwater conditions alone fully explain the distribution of biomass and
453 vegetation growth in our study or worldwide (Baraloto *et al.*, 2011; Quesada *et al.*,
454 2012; Fan, 2015).

455 We hypothesized that an interaction of these factors would provide a better
456 description of the vegetation patterns, with drier regions with shallow water table
457 having higher biomass productivity, while in wetter climates shallow water tables
458 would result in excess water, however, that is not what we found. The combination of
459 shallow water table and dry climate provided lower biomass productivity. A probable
460 explanation for this is the temporal fluctuation of the water table, and this is a limitation
461 of our data, as we only have the static values of this variable. Seasonal and interannual
462 water table fluctuation can be a key factor in understanding vegetation responses to
463 climatic variations (Costa *et al.*, 2022). Water-table depth fluctuates more in drier
464 climates (Míguez-Macho & Fan, 2012; Costa *et al.*, 2022). In the case of our results, it
465 may be that in a dry climate and shallow water table plants are exposed to stresses of
466 both water deficit in the dry season and water excess in the wet season, giving rise to
467 the worst scenario for plant growth. In the wet season the rise in the water table
468 promotes stress due to excess water that limits the plants growth. In the dry season, the
469 water table level drops, and due to the shallow root system characteristic of these
470 environments, plants cannot access the groundwater and go through the stress of lack of
471 water, also limiting the biomass accumulation. Contrary to our general hypothesis, the
472 limitation of biomass productivity given by the combination of wet climate and shallow
473 water table occurred only where the water table is very shallow. This may be because
474 where the water table is very shallow, plants have functional traits of faster growth, but
475 there is a soil anoxic condition that limits this. As this stress condition alleviates a little,
476 the plants can fully develop their fast-growing evolutionary characteristics.

477 Moreover, a full accounting of the factors affecting soil moisture requires
478 consideration of soil properties, especially soil texture (Richter & Babbar, 1991;
479 Quesada *et al.*, 2012). In general, the ecological effects of the soil water regime will
480 depend on the degree of soil saturation in the wet months, the degree and frequency of
481 water deficit periods, the water-holding capacity of the soil, and the root distribution in

482 the soil (Franco & Dezzeo, 1994). By having higher aggregation particles, clayey soils
483 have better water-holding capacity (Richter & Babbar, 1991), therefore, clay soils
484 should increase the time interval between precipitation inputs and groundwater
485 recharge, while predominantly sandy soils should have faster groundwater level
486 responses to precipitation. Our results indicate a possible contribution of clayey texture
487 in increasing productivity in dry climates with shallow water table (Fig. 5 C), however,
488 we have a lack of data in these environmental conditions that limits this statement. The
489 inclusion of plots that fill this gradient of climate and soil texture can help to elucidate
490 the vegetation responses.

491

492 *Limitations of this study*

493 While this and other work points to a key role for water-table depth and
494 consequent soil hydrology in shaping the structure and composition of tropical forests
495 (e.g. Damasco et al., 2013; Jirka et al., 2007; Moulatlet et al., 2014; Schietti et al.,
496 2013; Sousa et al., 2020; and see a review in Costa et al. 2022), precise measurement of
497 water-table depth and its fluctuation is still limited due to the challenge of installation of
498 equipment and periodic monitoring in the field. The clear alternative for large-scale
499 analytical studies like these is to use water-table-depth models, such as the Fan et al.
500 (2013) model used here. These, however, come with limitations as they condense the
501 full micro-spatial variation of hydrology in a relatively coarse spatial resolution, here of
502 ~ 270 m. A further difficulty in assessing hydrology for forest-dynamics studies is that
503 vegetation-monitoring plots may not be designed to detect variation in hydrological
504 environments, such that varying hydrological conditions may occur within the same plot
505 (see Magnusson et al., 2005 for a design that minimizes this problem). These
506 imprecisions probably limit our capacity to detect the local effects of water-table depth
507 on forest functioning, so that effects in nature may eventually prove to be even stronger
508 than shown here.

509 Also, while we could account for the major trends, there was large variation in
510 biomass-productivity, and some shallow-water-table plots had high biomass
511 productivity ($> 5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Such unexpected variation suggests we have still not
512 accounted for all the key variables and processes, with additional variation related to
513 species composition and functional traits being obvious candidates. Species
514 composition and dominant functional traits differ across the hydrological environments
515 within the same climate (Schietti *et al.*, 2013; Cosme *et al.*, 2017), but it is not known
516 whether they are filtered similarly across soil hydrology under different macroclimates,
517 or soil vs. macroclimate interactions that could potentially change the responses of
518 shallow-water-table forests under different climates. This is an important subject to
519 address in future studies because it could suggest ways to mitigate carbon losses.

520

521 *Final considerations*

522 The Amazon hydrological cycle is already changing due to climate change and
523 these are projected to intensify in the future (Gloor *et al.*, 2015). To predict ecological
524 impacts and mitigate their effects on the Amazon forests, it is essential to assess the
525 functioning and ecology of forests at the ecosystem level. Improved understanding of

526 the effects of local hydrology on forest functioning is also key to plan the conservation
527 and management on the scales at which landscapes are normally exploited. Our results
528 indicate the need to protect some critical environments with shallow-water-table forests
529 as buffers against the negative effects of climate change. They also provide indications
530 of critical missing factors when modelling the biomass dynamics of Amazonia.

531 By analyzing long-term forest monitoring records from across the 6 million km²
532 expanse of lowland Amazonia, we find a significant, large-scale control of forest
533 structure and dynamics by water-table depth. Both water excess and water deficit hinder
534 vegetation development. Above-ground productivity is suppressed, tree mortality
535 increased and thus biomass stocks reduced in shallow-water-table forests. These key
536 effects of water-table depth are often absent (Malhi et al., 2015, 2006; Saatchi et al.,
537 2007), but must be considered in global environmental modelling to better understand
538 the relative contribution of environmental drivers to Amazon forest structure and
539 dynamics, and the ecosystem functions they provide.

540

541 **Data Availability Statement**

542 Data available from the Dryad Digital Repository: XXXXX (XXX et al., 2021)

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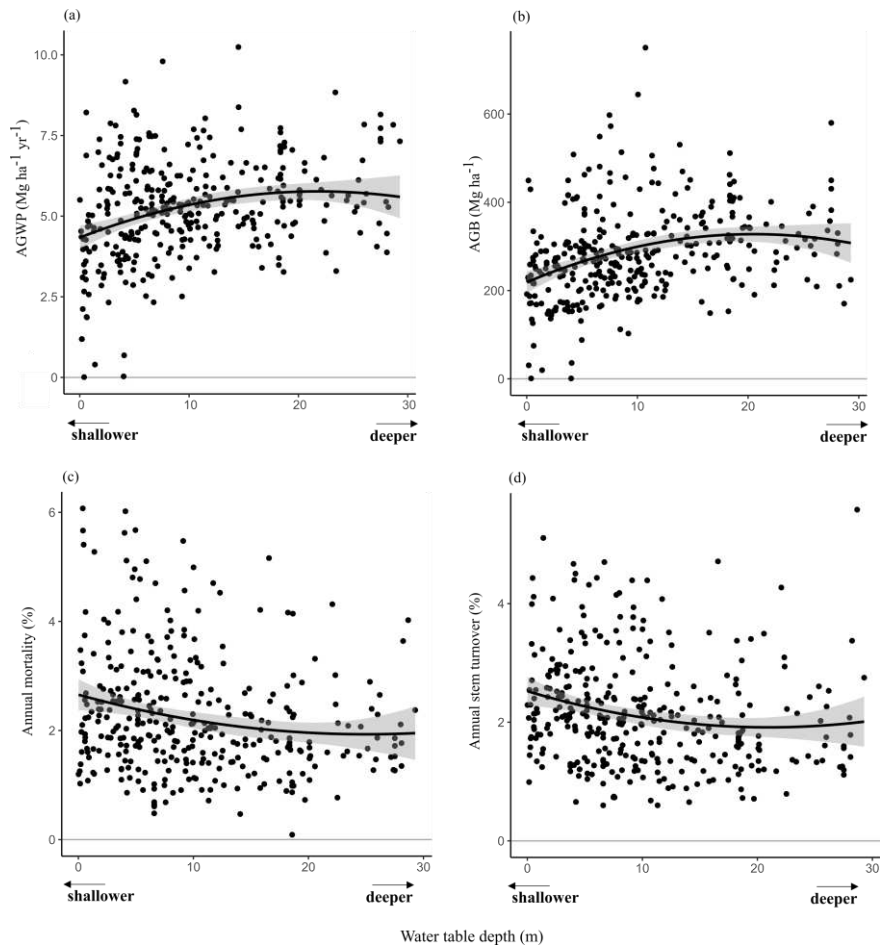


Figure 1. Impact of water-table depth on (A) biomass productivity; (B) biomass stock; (C) mortality rate; and (D) stem turnover in Amazonian forests. LOESS regression was used to adjust the relationships between the response variables and WTD. The shaded region shows the confidence interval of the regression.

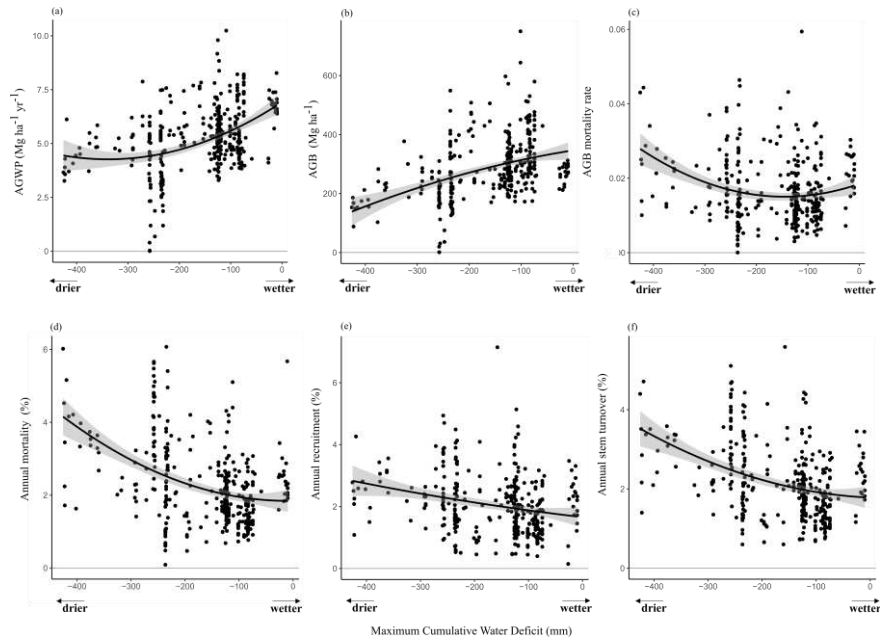


Figure 2. Impact of the maximum cumulative water deficit on (A) biomass productivity; (B) biomass stock; (C) biomass mortality rate; (D) mortality rate; (E) recruitment rate; and (F) stem turnover in Amazonian forests. LOESS regression was used to adjust the relationships between the response variables and MCWD. The shaded region shows the confidence interval of the regression.

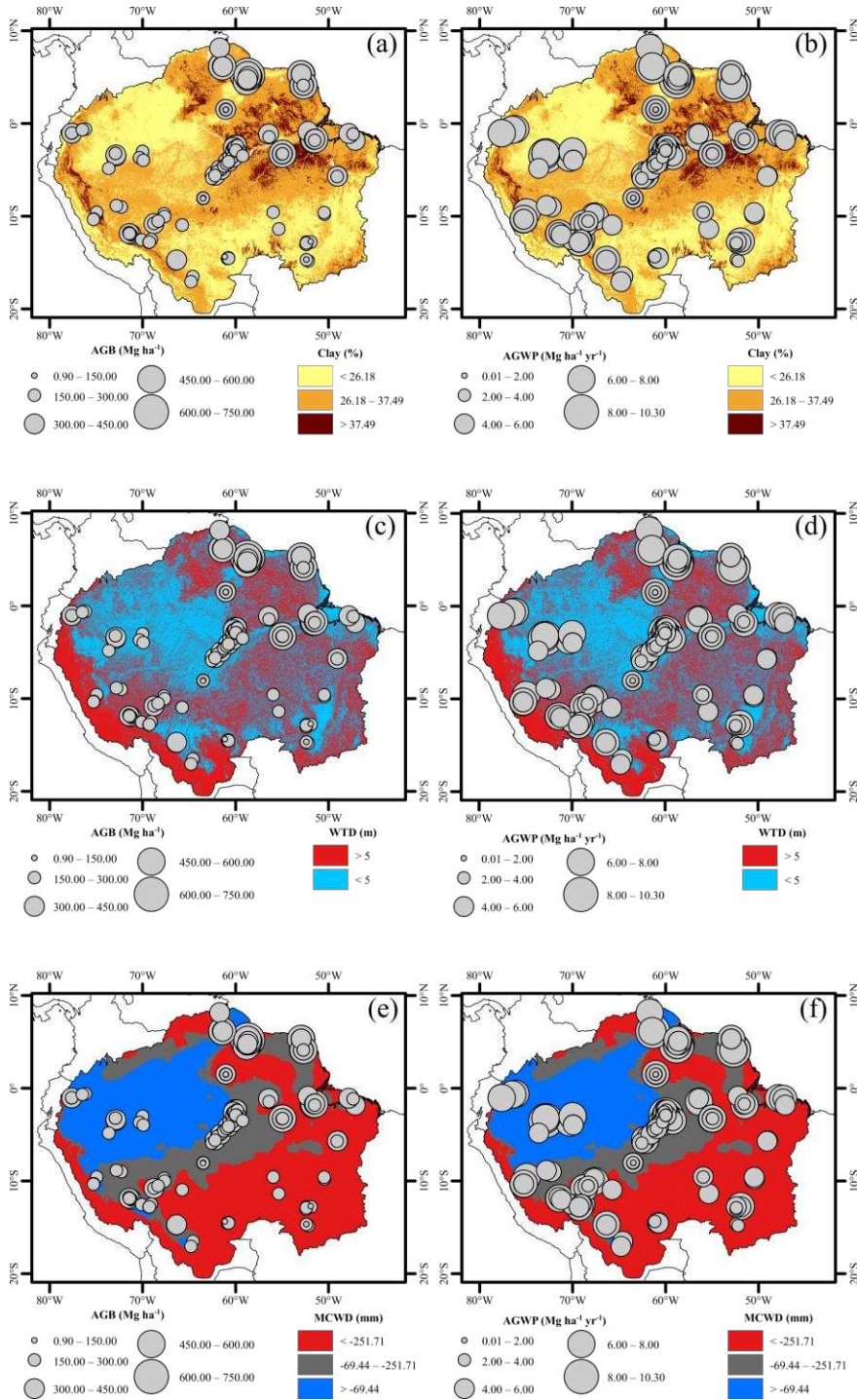


Figure 3. Spatial variation in forest biomass and productivity across Amazonia. Plots a and b display these metrics against a background of clay content; c and d the WTD background; and e and f the MCWD background. The clay content and MCWD classes were defined based on the standard deviation around the mean of each of these variables, shallow and deep-water tables follow the definitions of Fan & Miguez-Macho (2010). These classes are the same those used in Figures 4 and 5. Gray dots represent plots with size proportional to the biomass stock or productivity.

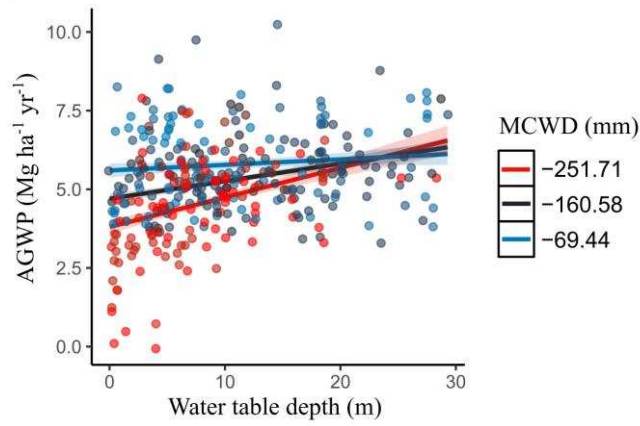


Figure 4. Partial-dependence plot of the interaction between MCWD and water-table depth on biomass productivity. In order to visualize interactions, climate was divided in three classes based on the standard deviation around the mean. Red colour is for plots with MCWD values less than one standard deviation below the mean; black is for plots with MCWD values within one standard deviation of the mean; and blue is for plots with MCWD values greater than one standard deviation above the mean. Shaded regions represent confidence intervals.

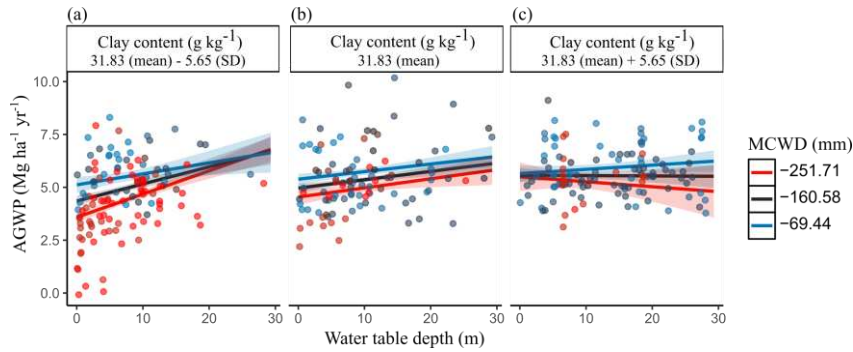


Figure 5. Partial-dependence plots derived from multiple-regression models investigating the effects of interactions among clay content, water-table depth and MCWD on biomass productivity in Amazonian forests. (a) Partial plots of the interaction in less clayey soil; (b) Partial effect of the interaction in moderately clayey soil; and (c) Partial effect of the interaction in more clayey soil. In order to visualize interactions, climate and soil texture were divided in three classes based on the standard deviation around the mean. Red colour is for plots with MCWD values less than one standard deviation below the mean; black is for plots with MCWD values within one standard deviation of the mean; and blue is for plots with MCWD values greater than one standard deviation above the mean. Shaded regions represent confidence intervals.

