

Water table depth modulates productivity and biomass across Amazonian forests

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DOI:

<https://doi.org/10.1111/geb.13531>

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Document Version

Peer reviewed version

Citation for published version (Harvard):

De Sousa, TR, Schietti, J, Esquivel-Muelbert, A, Phillips, OL, Costa, FRC & Ribeiro, I 2022, 'Water table depth modulates productivity and biomass across Amazonian forests', *Global Ecology and Biogeography*, vol. 31, no. 8, pp. 1571-1588. <https://doi.org/10.1111/geb.13531>

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1 **Title:** Water table depth modulates productivity and biomass across Amazonian forests

2
3 **Abstract**

4 **Aim** Water availability is the major driver of tropical forest structure and dynamics. While
5 most research has focused on the impacts of climatic water availability, remarkably little
6 is known about the influence of water table depth and excess soil water on forest
7 processes. Nevertheless, since plants take-up water from the soil, the impacts of climatic
8 water supply on plants are likely to be modulated by soil water conditions.

9 **Location** Lowland Amazonian forests

10 **Time period** 1971 to 2019

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

15 **Results** Water supplied by both precipitation and groundwater affect forest structure and
16 dynamics, but in different ways. Forests with shallow water table (depth < 5 m) had 18%
17 less above-ground-woody productivity and 23% less biomass stock than deep water table,
18 while forests in drier climates (maximum cumulative water deficit < -160 mm) had 21%
19 less productivity and 24% less biomass than those in wetter climates. Productivity was
20 affected by the interaction between climatic water deficit and water table depth: on
21 average, in drier climates shallow water table forests had lower productivity than deep
22 water table forests, with this difference decreasing within wet climates where lower
23 productivity is confined to very shallow water table.

24 **Main conclusions** We show that the two opposites of "water availability" (excess and
25 deficit) both reduce productivity in Amazon upland (*terra-firme*) forests. Biomass and
26 productivity across Amazonia respond not simply to regional climate but rather to its
27 interaction with highly locally differentiated water table conditions. Our study
28 disentangles the relative contribution of those factors, helping to improve understanding
29 of tropical-ecosystem functioning and how they are likely to respond to climate change.

30
31 **Keywords:** groundwater, tropical ecology, seasonality, forest dynamics, above-ground
32 biomass, carbon

33
34 **Introduction**

35 Tropical forests hold a disproportionate share of the Earth's biodiversity and
36 carbon stocks, providing environmental services of global importance through their
37 hydrological and carbon cycles (Fauset et al., 2015; Fearnside, 2008; Pokhrel et al.,
38 2014; ter Steege et al., 2013). Amazonia represents the largest of all tropical forests, and
39 plays a fundamental role as a long-term carbon sink, mostly due to the carbon
40 accumulated in woody plants (Pan et al., 2011; Phillips & Brien, 2017). Therefore
41 there is great interest in understanding underlying controls on biomass productivity and
42 dynamics of the Amazonian forests, and how climate change is and will affect them
43 (Llopart et al., 2018; Malhi et al., 2009; Zhao & Running, 2010). Amazonian climates
44 are naturally characterized by spatial and temporal variability in the distribution of

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

55 Water is essential to life and, together with temperature, a key determinant of
56 global patterns of plant distribution and productivity (Ellison *et al.*, 2017; Law *et al.*,
57 2002; Webb *et al.*, 1978; Whittaker, 1975). Although variation in precipitation is
58 associated with large-scale variation in forest structure and dynamics, soil-water
59 availability to plants is the result of the fine-scale interplay of precipitation and terrain
60 properties at landscape scales. The major landscape factors affecting the redistribution
61 of water entering the system as rainfall are topography and soil texture (Fan, 2015; Fan
62 & Miguez-Macho, 2011; Moeslund *et al.*, 2013). Topography affects the water flow to
63 groundwater, and groundwater movement to lower gravitational positions (lower
64 relative elevation in the landscape) creates gradients of increasing water availability
65 from uplands towards valleys (Fan, 2015; Nobre *et al.*, 2011; Rennó *et al.*, 2008). The
66 retention of water depends on soil texture, decreasing with soil particle size, so that it is
67 greater in clays than in sands (Costa *et al.*, 2013; Hillel, 1998; Parahyba *et al.*, 2019).
68 The dynamics of water drainage and retention in the soil supply the groundwater,
69 influencing seasonal and interannual fluctuations in the water table (Hodnett *et al.*,
70 1997; Miguez-Macho & Fan, 2012), and also affects soil-water conditions in the rooting
71 zone.

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

86 Water table depth is expected to play a key role in the regional patterns of plant
87 growth and mortality (Costa *et al.*, 2022). Easier access to groundwater in shallow water
88 table forests is likely to reduce the effects of precipitation water deficit during the dry

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

108 In summary, the impacts of water on forests depend on much more than simply
109 how much rain falls. Although soil moisture is difficult to measure and characterize
110 over the relevant scales of individual trees and plots across the Amazon, some key
111 determinants of the local hydrological conditions in non-flooded upland forests -
112 precipitation, water table depth and soil texture (Fan et al., 2017; Freeze & Cherry,
113 1979; Zipper et al., 2015) - can be estimated. The effects of those hydrological
114 components on plant responses are not expected to be simple linear and additive effects,
115 but rather involve complex interactions, as different combinations may give rise to
116 water deficit, excess of water or mesic conditions.

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

132

133 **Materials and methods**

134 **Vegetation data**

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

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

157
$$\text{AGB}_{\text{trees}} = 0.0673 \times (\rho D^2 H)^{0.976}$$

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

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

164
$$\ln(\text{AGB}_{\text{palm}}) = -3.3488 + 2.7483 \cdot \ln(D)$$

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

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

172 To assess biomass mortality, we first estimated the above-ground woody loss over
173 time, in units of $\text{Mg hr}^{-1} \text{ yr}^{-1}$. We also estimated the ‘biomass mortality rate’, as
174 $\text{AGB}_{\text{mortality}}/\text{AGB}$, in units of $\text{hr}^{-1} \text{ yr}^{-1}$. This standardization was performed in order to be

175 able to compare the proportional rate of biomass loss among plots with different standing
176 biomass stock.

177 We also calculated stem mortality, measured as mean annual mortality rate (λ) as:

178 $\lambda = \frac{[\ln(N_0) - \ln(N_s)]}{t}$, where N_0 and N_s are the number of stems counted of the initial

179 population, and the number of stems surviving to time t , respectively (Sheil *et al.*, 1995).

180 For each site we also calculated annual recruitment rates (μ) as:

181 $\mu = [\ln(N_f/N_s)]/t$, where N_f is the final number of stems, N_s is the original number of
182 stems surviving to final inventory and t is the number of years between inventories.

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

191

192 **Environmental data**

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

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

214 Water table depth was extracted from a map developed for the entire Amazon (Fan
215 *et al.*, 2013; Fan & Miguez-Macho, 2010), at ~270 m spatial resolution, based on model
216 simulation constrained by over 1,000,000 direct well measurements from government
217 archives and publications. We extracted water table depth values for the geographic

218 coordinates for each plot and did not interpolate values of the surrounding pixels to avoid
219 degrading the already coarse resolution of the WTD data. Clay-content data were obtained
220 from the SoilGrids database, at 250 m resolution (Hengl *et al.*, 2017). As a proxy for soil
221 fertility, we used the soil concentration of exchangeable base cations (Ca + Mg + K),
222 extracted from the Amazon-wide model of Zuquim *et al.* (2019), since this is the best
223 continuous layer of soil fertility available for the entire study area. SoilGrids has a layer
224 of cation exchange capacity (CEC) (Hengl *et al.*, 2017), but the correlation of measured
225 cations and the mapped CEC has been shown to be low, as CEC includes the
226 concentration of aluminium, which is not a nutrient (Moulatlet *et al.*, 2017). Although
227 phosphorus is widely considered as a key limiting nutrient for growth in tropical forests,
228 this variable is not available for all plots or as a continuous estimated layer. However, the
229 availability of exchangeable cations tends to be correlated well to the amount of
230 phosphorus (Quesada *et al.*, 2010, 2012) and also predicts forest growth well (Quesada *et al.*,
231 2012). We estimated long-term maximum temperature, using a dataset from
232 TerraClimate, at ~4 km (1/24th degree) spatial resolution from 1971 to 2019.

233

234 **Data analyses**

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

254 We weighted the plots in regression analyses when testing the effects of the
255 environmental predictors on forest dynamics and structure according to the plot size and
256 monitoring time, as larger plots and those monitored for longer periods are expected to
257 provide better estimates of local, long-term forest properties. To achieve this, following
258 Lewis *et al.* (2009), we plotted the residuals from linear models against plot area and
259 monitoring period, and selected the root transformations of plot area and monitoring
260 period that removed the nonlinear patterns in the residuals when applied as a weight.
261 These empirically-determined weights were: AGWP, $\text{Area}^{1/2}$; AGB, $\text{Area}^{1/3}$; AGB

262 mortality, $\text{Area}^{1/2} + \text{Monitoring length}^{1/4} - 1$; Mortality rate, $\text{Area}^{1/2} + \text{Monitoring length}^{1/3}$
263 $- 1$; Recruitment rate, $\text{Area}^{1/5}$; Stem turnover, $\text{Area}^{1/3} + \text{Monitoring length}^{1/4} - 1$.

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

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

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

291

292 **Results**

293

294 *How does the structure and dynamics of Amazonian forest vary with the water table*
295 *depth and climatic water deficit?*

296 Based on the simple relationships between WTD and forest dynamics and
297 biomass, shallower water tables (depth < 5 m) on average decreased the forest biomass
298 productivity ($t = -5.62$; $df = 342$; $p < 0.01$) and biomass stocks ($t = -6.28$; $df = 342$; $p <$
299 0.01) of Amazon forests (Figures 1a and 1b, respectively). Shallower water table forests
300 had on average 18% lower biomass productivity ($4.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and 23% lower
301 biomass stock (234.6 Mg ha^{-1}) than those on deeper water tables ($5.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and
302 306.9 Mg ha^{-1} , respectively). Also, based on the simple relationships between MCWD
303 and forest dynamics and biomass, climatically drier sites (MCWD < -160 mm) had 21%
304 lower biomass productivity ($4.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; $t = -7.67$; $df = 342$; $p < 0.01$) and 24%
305 lower biomass stock (240.2 Mg ha^{-1} ; $t = -7.01$; $df = 342$; $p < 0.01$) than those in wetter

306 climates ($5.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, 314.3 Mg ha^{-1}) (Figures 2a and 2b, respectively). Thus, the
307 negative direct effects of climatic-water deficit (MCWD) were only slightly stronger
308 than the negative effects of excess soil water associated with shallow water tables.

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

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

325

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

328 A significant interaction between WTD and MCWD was detected only for
329 AGWP. The best model (Table S2) fit of the interaction divides MCWD data into three
330 groups, based on the standard deviation around the mean, following a gradient from
331 wetter (blue line) to drier climates (red line). Shallow water table forests had lower
332 AGWP than deeper water table forests when under drier climates, with this difference
333 decreasing in wet climates (Fig. 4). The very low biomass productivity of some plots ($<$
334 $2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) is related to vegetation structure, as in these sites most trees are very thin
335 and therefore have lower productivity. Additional analysis showed that excluding these
336 plots does not change the Amazon-wide pattern of the interactive effects of water table
337 depth and climate in productivity (Fig. S4).

338 Despite the average negative effect of shallow water table on forest productivity
339 within dry climates, the more complex interactions between soil texture, MCWD and
340 water table depth suggest a contribution of soil drainage to forest functioning (Fig. 5).
341 These interactions show that forest productivity was lower in shallower water table
342 conditions in dry climates when the soil is less clayey, as compared to deeper water
343 table conditions in the same climate (red line, Fig. 5a). However, when the soil was
344 more clayey dry-climate forests with shallower water table had greater productivity than
345 their climatic equivalents on deeper water tables (red line, Fig. 5c). The data coverage
346 of some combinations of climate, water table and soil texture were low (especially
347 clayey soils under dry climates and shallow water table), what may limit the
348 interpretation of this result. We also note some non-linear trends in wet climates and

349 sandier soils, where AGWP is low where the water table is very shallow (< 2 m) but
350 increases to reach a peak in the range of 2 to 8 m depth (Fig. 5a).

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

354

355 *The effects of other factors*

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

363

364 **Discussion**

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

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

378

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

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

393 dioxide. As oxygen is depleted, roots and aerobic microorganisms lose most of their
394 capacity to produce energy through aerobic respiration (Gibbs & Greenway, 2003). In
395 this case, the major pathway to energy production is alcoholic fermentation, which has a
396 much lower yield (2 mols ATP per glucose molecule) than respiration (36 ATP), and
397 thus severely limits plant growth (Setter & Belford, 1990; Kreuzwieser & Rennenberg,
398 2014). Low oxygen levels also reduce root permeability (North et al., 2004; Vandeleur
399 et al., 2005), generating a cascade of responses that reduce stomatal conductance and
400 thus limit photosynthesis (Lopez & Kursar, 1999, 2003; Parent et al., 2008; Pezeshki,
401 2001). Low photosynthetic activity and consequent low growth is well documented in
402 periodically flooded forests (Parolin, 2000; Waldhoff et al., 1998), although this a more
403 extreme condition than the soil waterlogging examined here. Given the various
404 deleterious effects of excess water on plant metabolism and physiology, most tree
405 growth occurs during the windows when water table levels decrease and anoxia is
406 relieved, mostly in the dry season. Such growth windows have been described in
407 flooded areas, where the largest diameter growth occurs in the non-flooded period
408 (Schöngart et al., 2002; 2004). Therefore, the period with environmental conditions
409 suitable for growth is shorter in shallow water table, and therefore, on average, biomass
410 productivity is lower in these locations than in deep water table (but, see next section,
411 these patterns change when combined with climate).

412 For vegetation dynamics, we found higher mortality and stem turnover in
413 shallow water table sites, as we had hypothesized. Poorly drained sites have higher
414 mortality rates due to weak plant anchorage caused by the groundwater layer that
415 prevents deep root growth, and this is also generally associated with loose soil texture
416 (Gale & Barfod, 1999; Toledo et al., 2011). This low adherence to the soil increases the
417 tree's susceptibility to uprooting (Madelaine *et al.*, 2007). Forests with waterlogged soils
418 have higher proportions of uprooting as the tree mode of death, whereas forests on well-
419 drained soils have higher proportions of trees dying standing (Gale & Hall, 2001). The
420 effects of excess water on forest structure and dynamics are well described in the
421 literature for floodplain forests (Simone et al., 2003; Godoy et al., 1999; Parolin et al.,
422 2004; Piedade et al., 2013; Schöngart et al., 2004), but little is known about the effects
423 of shallow water tables on *terra-firme* forests. In local studies, paired comparisons of
424 shallow and deep water tables within the same wet macroclimate have shown similar
425 patterns of lower biomass productivity and basal area (Castilho et al., 2006; Castilho et
426 al., 2010; Ferry et al., 2010), higher tree mortality (Ferry et al., 2010; Toledo et al.,
427 2011) and recruitment rates (Ferry *et al.*, 2010) in seasonally waterlogged shallower
428 water table forests than on deeper water table hilltops, as we now find here to occur at
429 an Amazon-wide scale. In a global analysis, based on remote sensing data, water table
430 depth was associated with forest productivity, stimulating or hindering vegetation
431 growth depending on climate (Roebroek *et al.*, 2020), and our large-scale on-the-ground
432 assessment of this effect supports those results for the Amazonian forests, but here with
433 above-ground wood productivity data.

434

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

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

447 We hypothesized that an interaction of these factors would provide a better
448 description of the vegetation patterns, with drier regions with shallow water table
449 having higher biomass productivity, while in wetter climates shallow water tables
450 would result in excess water and lower productivity, however, this is not what we
451 found. The combination of shallow water table and dry climate resulted in lower
452 biomass productivity. This outcome may result from an aspect of the water availability
453 that was not accounted in this study - the temporal fluctuation of the water table. The
454 available WTD product gives what is expected to be the average water table depth of
455 each pixel, but there may be varying degrees of temporal fluctuation modulated by
456 climate, topographic and geomorphological conditions (Costa *et al.* 2022). In the drier
457 climates, the seasonal fluctuation of the water table tends to be higher (Miguez-Macho
458 & Fan, 2012; Costa *et al.* 2022), so plants may be exposed to stresses of both water
459 deficit in the dry season and water excess in the wet season, giving rise to the worst
460 scenario for growth. In the wet season the rise in the water table may lead to anoxic
461 stress. In the dry season, when the water table level drops, the shallow plant root
462 systems characteristic of these environments may not access the groundwater and go
463 through water deficit stress, also limiting the biomass accumulation.

464 Also contrary to our general hypothesis, the limitation of biomass productivity
465 given by the combination of wet climate and shallow water table occurred only where
466 the water table is very shallow (< 2 m deep), which is where most fine roots tend to be
467 (Jackson *et al.*, 1996). This seems to restrict the pure anoxic limitation of productivity to
468 a smaller range of very wet conditions than previously hypothesized here. Still under
469 wet climates, we see high biomass production in the intermediate shallow water table
470 (2-5 m, Fig. 5a) that may be a consequence of an interaction of the tree functional traits
471 typically selected under wet environments (lower wood density, higher xylem vessel
472 diameter and higher specific leaf area, review in Costa *et al.* 2022, aligned with faster
473 resource acquisition and growth) and the potentially moist, instead of anoxic conditions,
474 during a large period of the year. The number of plots within each combination of
475 climate, water table and soil conditions is relatively low here, and there is a clear need
476 for more work to improve the evaluation of these potential non-linearities in the
477 response of forest productivity to the determinants of water availability.

478 A full accounting of the factors affecting soil moisture also requires consideration
479 of soil properties, especially soil texture (Richter & Babbar, 1991; Quesada *et al.*,
480 2012). In general, the ecological effects of the soil water regime will depend on the

481 degree of soil saturation in the wet months, the degree and frequency of water deficit
482 periods, the water-holding capacity of the soil, and the root distribution in the soil
483 (Franco & Dezzio, 1994). By having higher aggregation particles, clayey soils have
484 better water-holding capacity (Richter & Babbar, 1991), therefore, clay soils should
485 increase the time interval between precipitation inputs and groundwater recharge, while
486 predominantly sandy soils should have faster groundwater level responses to
487 precipitation. Our results suggest a contribution of clayey texture in increasing
488 productivity in dry climates with shallow water table (Fig. 5 C). However, here too the
489 dataset lacks complete coverage of the relevant environmental combinations, limiting
490 our conclusions.

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 alternative for large-scale analytical
499 studies like these is to use water table depth models, such as the Fan et al. (2013) model
500 used here. These, however, come with limitations as they condense the full micro-
501 spatial variation of hydrology in a relatively coarse spatial resolution (here ~ 270 m). A
502 further difficulty is that vegetation-monitoring plots may not be designed to detect
503 variation in hydrological environments, such that varying hydrological conditions may
504 occur within the same plot (see Magnusson et al., 2005 for a design that minimizes this
505 problem). These imprecisions probably limit our capacity to detect the local effects of
506 water table depth on forest functioning, so that effects in nature may eventually prove to
507 be even stronger than shown here.

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

519

520 *Final considerations*

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

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

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

539

540 **Data Availability Statement**

541 Data for the analyses are available as a ForestPlots.net data package at
542 http://doi.org/10.5521/forestplots.net/2022_2

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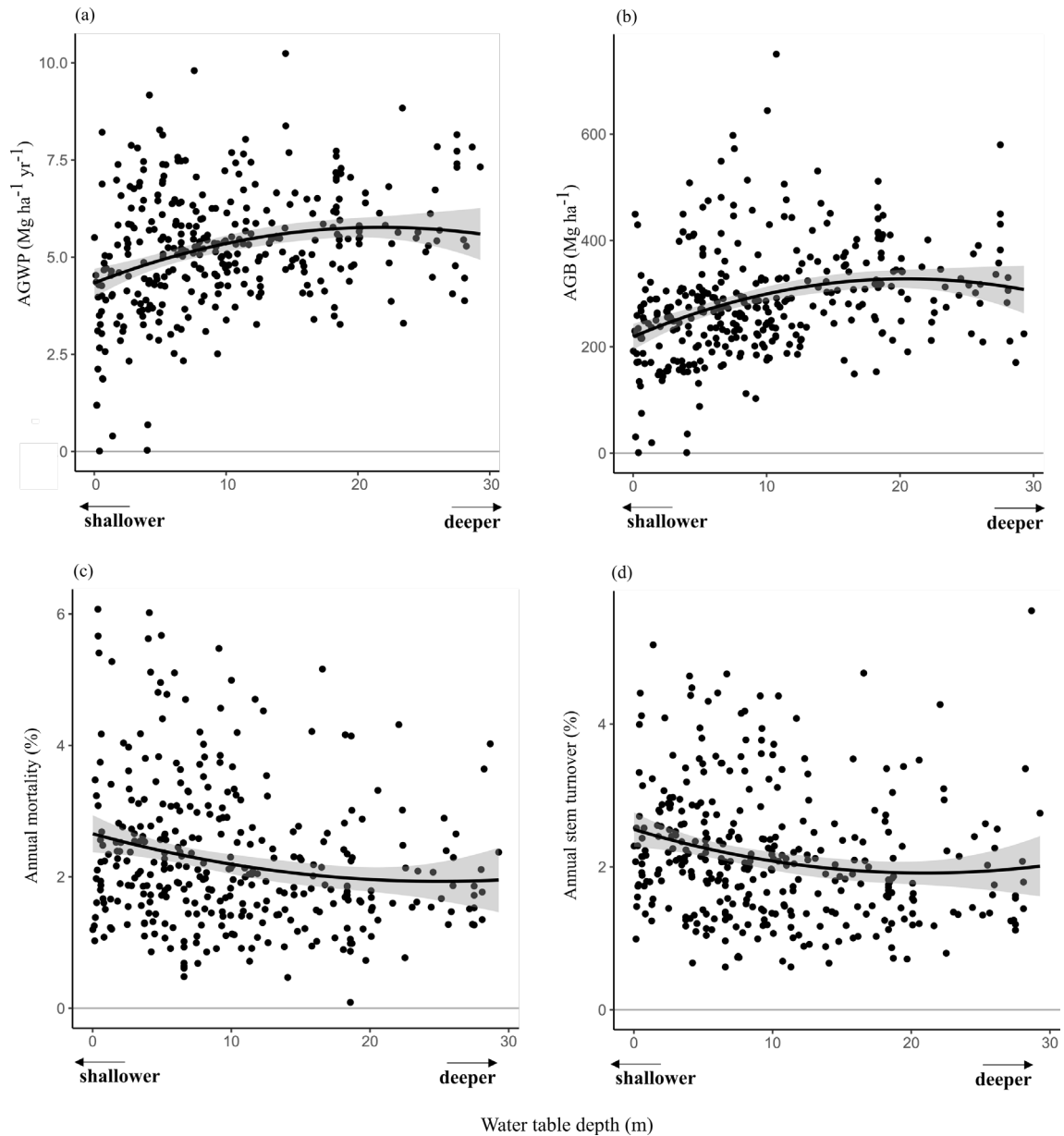


Figure 1. Impact of water table depth on (A) biomass productivity; (B) biomass stock; (C) mortality rate; and (D) stem turnover in Amazonian forests. LOESS regression was used to adjust the relationships between the response variables and WTD. The shaded region shows the confidence interval of the regression.

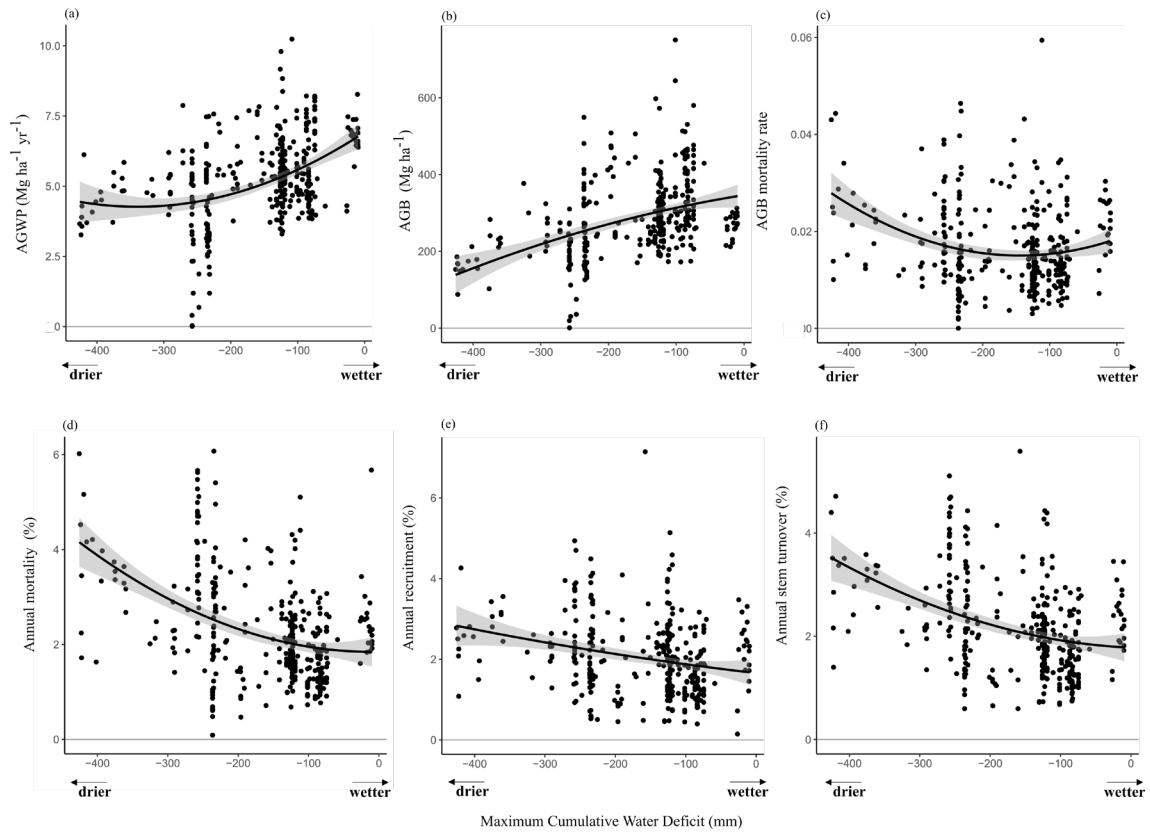


Figure 2. Impact of the maximum cumulative water deficit on (A) biomass productivity; (B) biomass stock; (C) biomass mortality rate; (D) mortality rate; (E) recruitment rate; and (F) stem turnover in Amazonian forests. LOESS regression was used to adjust the relationships between the response variables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

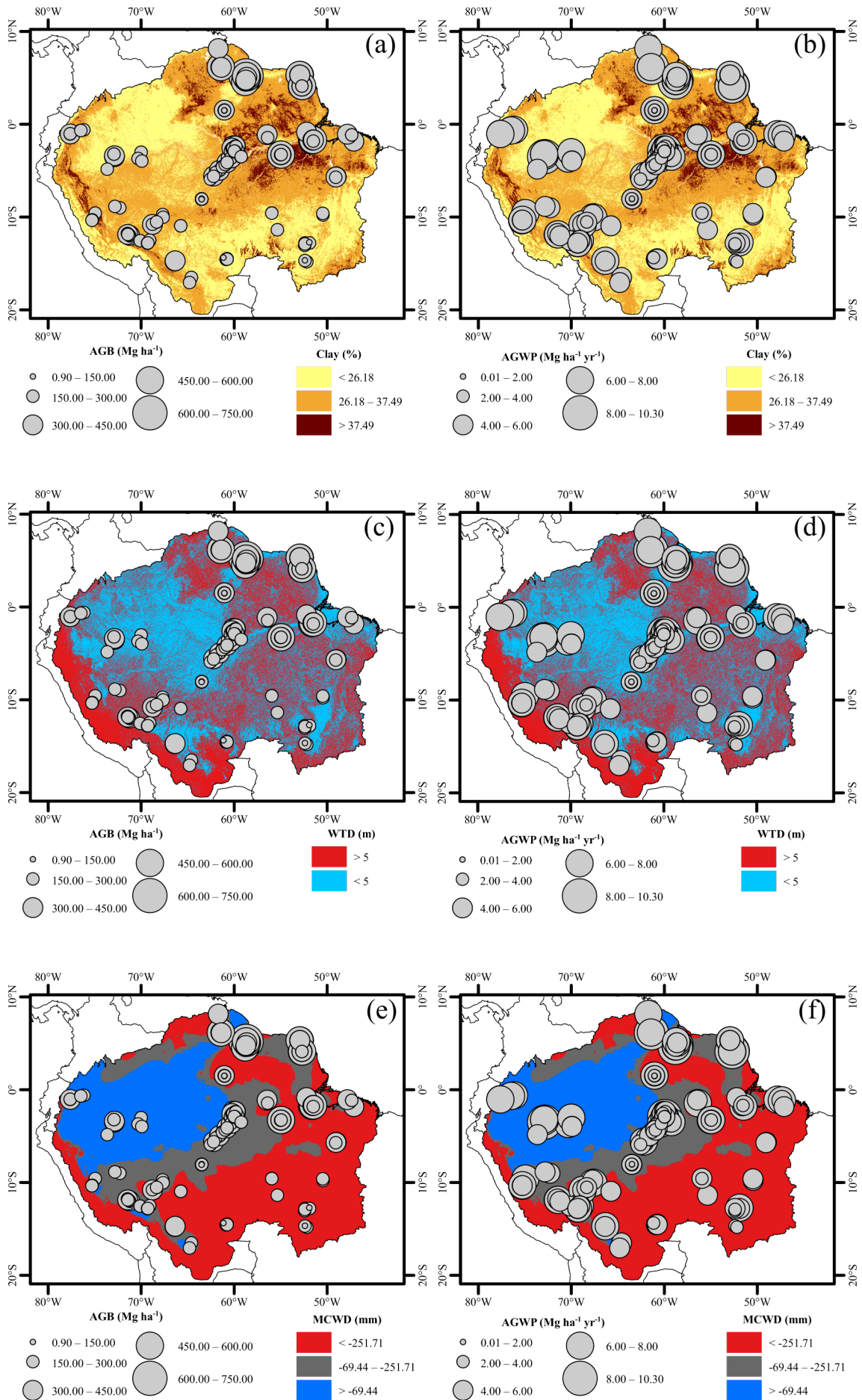


Figure 3. Spatial variation in forest biomass and productivity across Amazonia. Plots a and b display these metrics against a background of clay content; c and d the WTD background; and e and f the MCWD background. The clay content and MCWD classes were defined based on the standard deviation around 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.

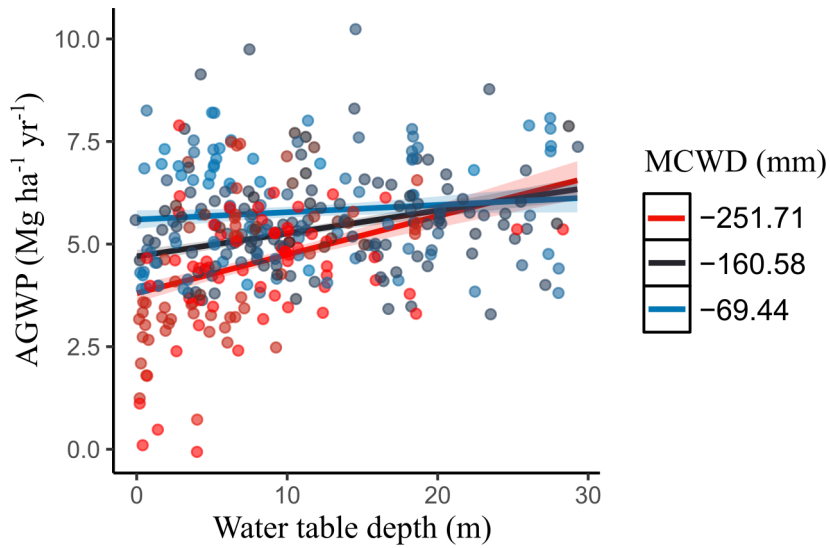


Figure 4. Partial-dependence plot of the interaction between MCWD and water table depth on biomass productivity. In order to visualize interactions, climate was divided in three classes based on the standard deviation around the mean. Red colour is for plots with MCWD values less than one standard deviation 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.

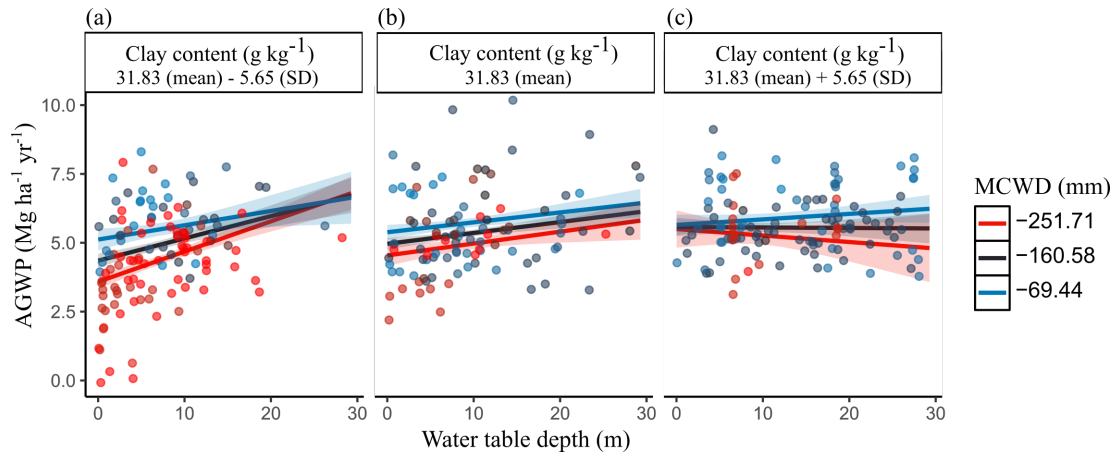


Figure 5. Partial-dependence plots derived from multiple-regression models investigating the effects of interactions among clay content, water table depth and MCWD on biomass productivity in Amazonian forests. (a) Partial plots of the interaction in less clayey soil; (b) Partial effect of the interaction 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.

