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

Abstract

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

Location Lowland Amazonian forests

Time period 1971 to 2019

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

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

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

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

Introduction

Tropical forests hold a disproportionate share of the Earth’s biodiversity and carbon stocks, providing environmental services of global importance through hydrological and carbon cycles (Fauset et al., 2015; Fearnside, 2008; Pokhrel et al., 2014; ter Steege et al., 2013). Amazonia represents the largest of all tropical forests, and plays a fundamental role as a long-term carbon sink, mostly due to the carbon accumulated in woody plants (Pan et al., 2011; Phillips & Brienen, 2017). Therefore there is great interest in understanding underlying controls on biomass productivity and dynamics of the Amazonian forests, and how climate change is and will affect them (Llopart et al., 2018; Malhi et al., 2009; Zhao & Running, 2010). Amazonian climates are naturally characterized by spatial and temporal variability in the distribution of rainfall, and recently both droughts and floods have become more frequent, probably driven by anthropogenic climate change (Gloor *et al.*, 2013, 2015; Marengo & Espinoza, 2016). In this context, it is essential to understand the impact of water availability on forest functioning. While this has been studied from the perspective of changes in precipitation seasonality and climatic water deficits (e.g., Phillips *et al.*, 2009; Toledo *et al.*, 2011b; Álvarez-Dávila *et al.*, 2017) there has been much less attention paid to the role of water availability in the soil, as regulated by groundwater (but see Nobre *et al.*, 2011; Ivanov *et al.*, 2012; Esteban *et al.*, 2020; Chitra-Tarak *et al.*, 2021) and no account of how groundwater affects forest productivity and biomass based on ground measurements currently exists.

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

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

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

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

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

Materials and methods

Vegetation data

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

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

$$AGB_{\text{trees}} = 0.0673 \text{ x } (\rho D^2 H)^{0.976}$$

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

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

$$\ln(AGB_{\text{palm}}) = -3.3488 + 2.7483.\ln(D)$$

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

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

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

Stem mortality, measured as mean annual mortality rate (λ) was calculated as: $\lambda = \frac{[ln\ (N_0) - ln(N_s)\ ]}{t}$, where N_0 and N_s are the number of stems counted of the initial population, and the number of stems surviving to time t, respectively (Sheil *et al.*, 1995). Annual recruitment rates (μ) were calculated as:
$\mu = [\ln(N_f / N_s)]/t$, where N_f is the final number of stems, N_s is the original number of stems surviving to final inventory and t is the number of years between inventories. Mortality and recruitment rates were calculated for each census interval (% yr^{-1}), and then a time-weighted mean based on the census-interval lengths was taken to give one value per plot. With these results we calculated the stem turnover rate, defined as the mean of recruitment and mortality (Phillips et al., 1994). The length of the census intervals can affect rate estimates, with long intervals between censuses more likely to underestimate rates due to unobserved mortality and recruitment (Lewis *et al.*, 2004). To account for potential impacts of varying census intervals on the rate estimates, we applied the correction factor proposed by Lewis et al. (2004).

Environmental data

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

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

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

Data analyses

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

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

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

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

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

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

Results

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

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

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

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

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

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

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

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

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

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

The effects of other factors

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

Discussion

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

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

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

We hypothesized that shallow water tables impose constraints on plant through excess soil water and consequent oxygen limitation. Our results support this hypothesis since, in average, sites with shallow water table tended to have lower biomass productivity (Fig. 1a). However, there is a high data variability, in which some sites, despite the restriction of excess soil water, have high biomass productivity. Therefore, it is important to understand the possible mechanisms related to the two extremes of low and high biomass productivity in shallow water table. To understand the lower productivity, we must review the response of soils and plants to waterlogging, the condition prevailing to various degrees – seasonal to permanent - in many of the shallow-water-table sites. When soils are waterlogged, most of the soil spaces are occupied with water, and the metabolism of roots and microorganisms quickly consumes the available oxygen and produces carbon dioxide. As oxygen is depleted, roots and aerobic microorganisms lose most of their capacity to produce energy through aerobic respiration (Gibbs & Greenway, 2003). In this case, the major pathway to energy production is alcoholic fermentation, which has a much lower yield (2 mols ATP per glycose molecule) than respiration (36 ATP), and thus severely limits plant growth (Setter & Belford, 1990; Kreuzwieser & Rennenberg, 2014). Low oxygen levels also reduce root permeability (North et al., 2004; Vandeleur et al., 2005), generating a cascade of responses that reduce stomatal conductance and thus limit photosynthesis (Lopez & Kursar, 1999, 2003; Parent et al., 2008; Pezeshki, 2001). Low photosynthetic activity and consequent low growth is well documented in periodically flooded forests (Parolin, 2000; Waldhoff et al., 1998), although this a more extreme condition than the soil waterlogging examined here. Given the various deleterious effects of excess water on plant metabolism and physiology, most tree growth occurs during the windows when water-table levels decrease and anoxia is relieved, mostly in the dry season. Such growth windows have been described in flooded areas, where the largest diameter growth occurs in the non-flooded period (Schöngart et al., 2002; 2004). Therefore, the period of environmental conditions suitable for growth is shorter in shallow water table, and therefore, on average, biomass productivity is lower in these locations than in deep water table. Despite the anoxic conditions, high biomass productivity observed in some plots with shallow water table may be related to the functional traits of plants evolutionarily established in these environments. Shallow water tables filters trees with lower wood density (Kraft *et al.*, 2008; Ferry *et al.*, 2010; Cosme *et al.*, 2017), higher specific leaf area (SLA), xylem with wider vessels and larger sapwood area (Cosme *et al.*, 2017), these acquisitive strategy together translate into fast-growing plants, therefore, greater biomass accumulation. Therefore, even in shallow water tables, some plants are able to adapt to excess water conditions and show their greatest growth potential.

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.

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

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

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

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

Moreover, a full accounting of the factors affecting soil moisture requires consideration of soil properties, especially soil texture (Richter & Babbar, 1991; Quesada *et al.*, 2012). In general, the ecological effects of the soil water regime will depend on the degree of soil saturation in the wet months, the degree and frequency of water deficit periods, the water-holding capacity of the soil, and the root distribution in the soil (Franco & Dezzeo, 1994). By having higher aggregation particles, clayey soils have better water-holding capacity (Richter & Babbar, 1991), therefore, clay soils should increase the time interval between precipitation inputs and groundwater recharge, while predominantly sandy soils should have faster groundwater level responses to precipitation. Our results indicate a possible contribution of clayey texture in increasing productivity in dry climates with shallow water table (Fig. 5 C), however, we have a lack of data in these environmental conditions that limits this statement. The inclusion of plots that fill this gradient of climate and soil texture can help to elucidate the vegetation responses.

Limitations of this study

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

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

Final considerations

The Amazon hydrological cycle is already changing due to climate change and these are projected to intensify in the future (Gloor *et al.*, 2015). To predict ecological impacts and mitigate their effects on the Amazon forests, it is essential to assess the functioning and ecology of forests at the ecosystem level. Improved understanding of the effects of local hydrology on forest functioning is also key to plan the conservation and management on the scales at which landscapes are normally exploited. Our results indicate the need to protect some critical environments with shallow-water-table forests as buffers against the negative effects of climate change. They also provide indications of critical missing factors when modelling the biomass dynamics of Amazonia.

By analyzing long-term forest monitoring records from across the 6 million km^2 expanse of lowland Amazonia, we find a significant, large-scale control of forest structure and dynamics by water-table depth. Both water excess and water deficit hinder vegetation development. Above-ground productivity is suppressed, tree mortality increased and thus biomass stocks reduced in shallow-water-table forests. These key effects of water-table depth are often absent (Malhi et al., 2015, 2006; Saatchi et al., 2007), but must be considered in global environmental modelling to better understand the relative contribution of environmental drivers to Amazon forest structure and dynamics, and the ecosystem functions they provide.

Data Availability Statement

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

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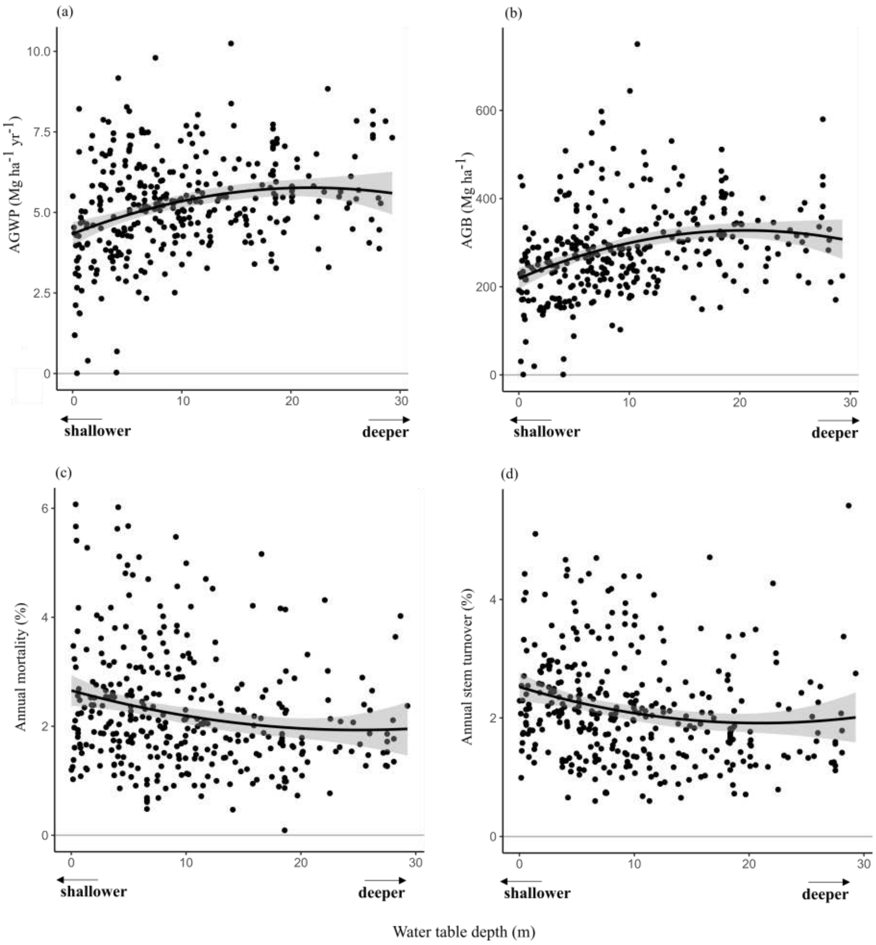


Figure 1. Impact of water-table depth on (A) biomass productivity; (B) biomass stock; (C) mortality rate; and (D) stem turnover in Amazonian forests. LOESS regression was used to adjust the relationships between the response variables and WTD. The shaded region shows the confidence interval of the regression.

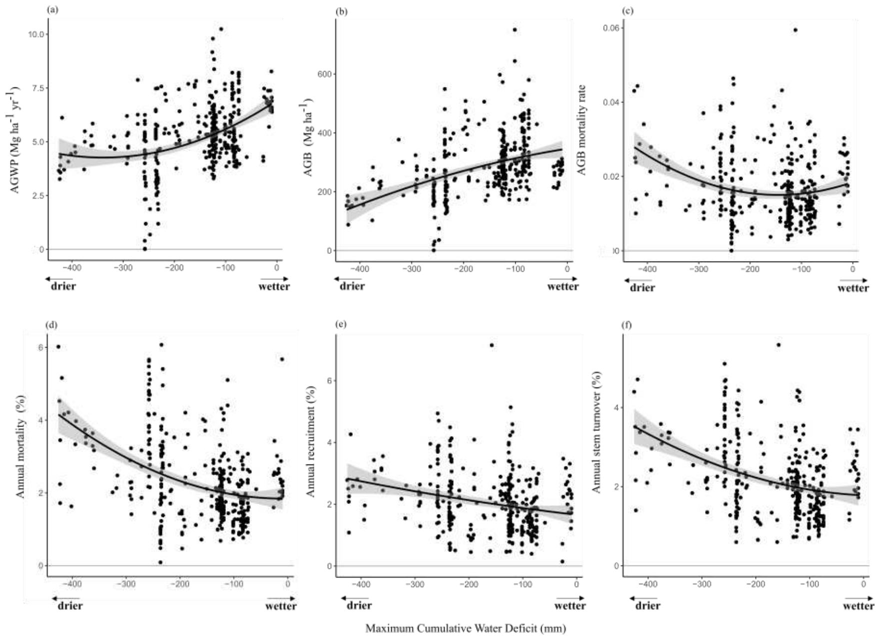
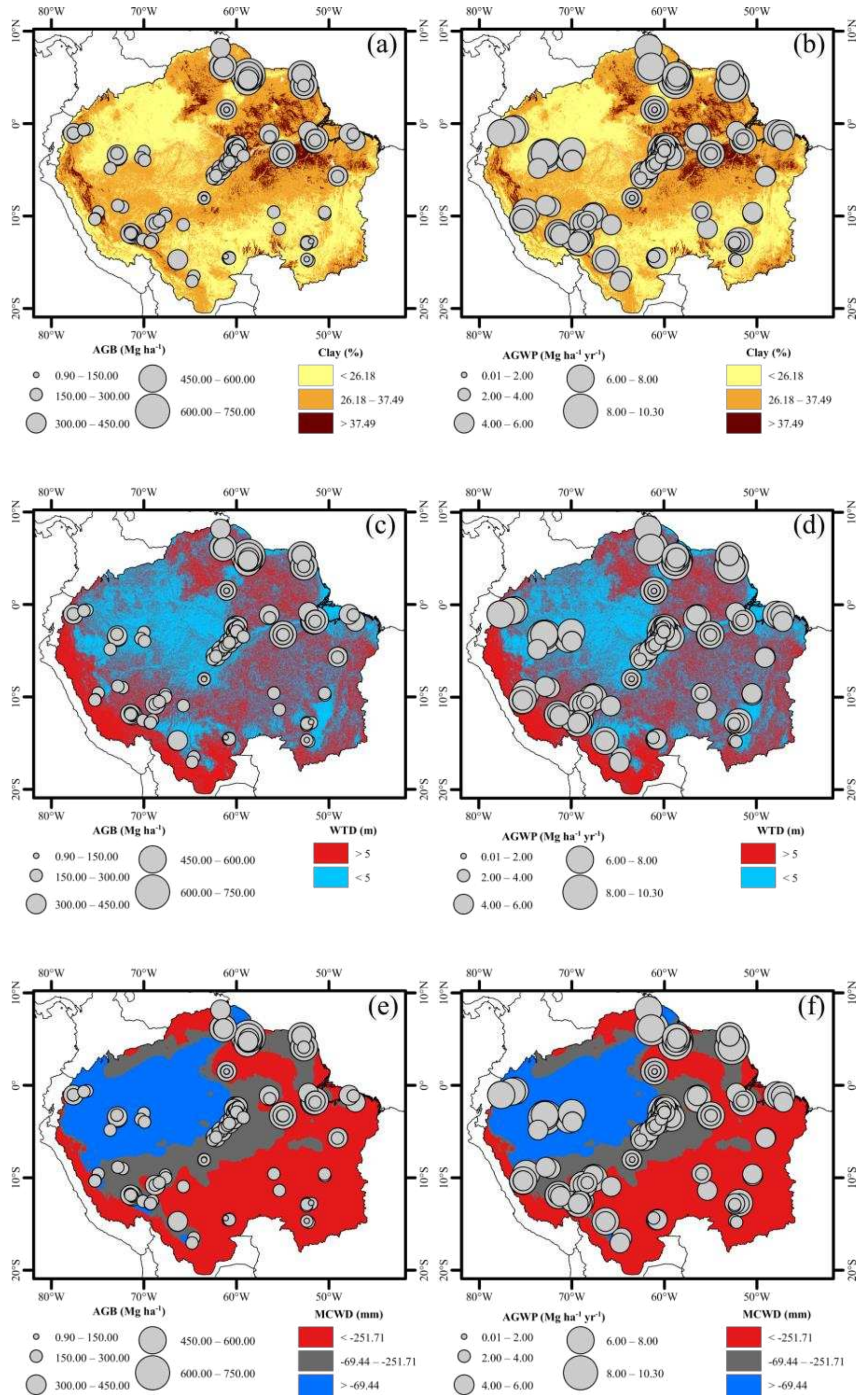


Figure 2. Impact of the maximum cumulative water deficit on (A) biomass productivity; (B) biomass stock; (C) biomass mortality rate; (D) mortality rate; (E) recruitment rate; and (F) stem turnover in Amazonian forests. LOESS regression was used to adjust the relationships between the response variables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



(a)
(b)
(c)
(d)
(e)
(f)
80°W
70°W
60°W
50°W
10°N
0°
10°S
20°S
AGB (Mg ha⁻¹)
0.90 – 150.00
150.00 – 300.00
300.00 – 450.00
450.00 – 600.00
600.00 – 750.00
AGWP (Mg ha⁻¹ yr⁻¹)
0.01 – 2.00
2.00 – 4.00
4.00 – 6.00
6.00 – 8.00
8.00 – 10.30
Clay (%)
< 26.18
26.18 – 37.49
> 37.49
WTD (m)
> 5
< 5
MCWD (mm)
< -251.71
-69.44 – -251.71
> -69.44

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.

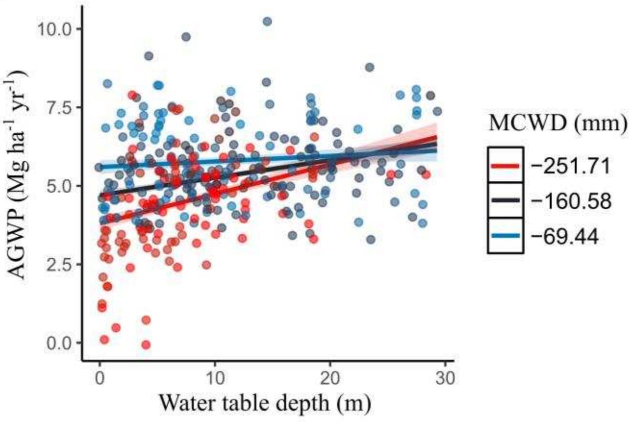


Figure 4. Partial-dependence plot of the interaction between MCWD and water-table depth on biomass productivity. In order to visualize interactions, climate was divided in three classes based on the standard deviation around the mean. Red colour is for plots with MCWD values less than one standard deviation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

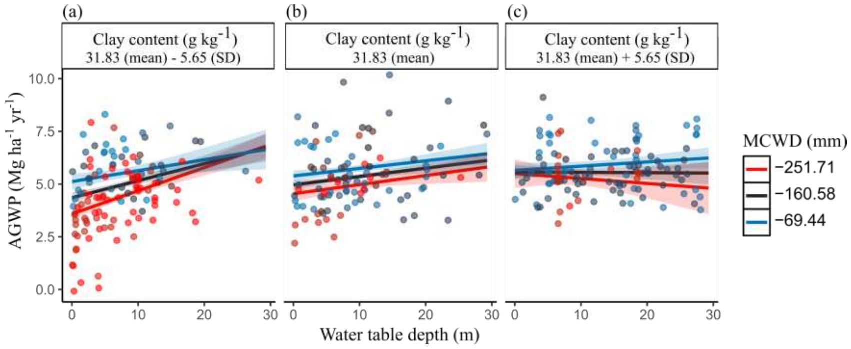


Figure 5. Partial-dependence plots derived from multiple-regression models investigating the effects of interactions among clay content, water-table depth and MCWD on biomass productivity in Amazonian forests. (a) Partial plots of the interaction in less clayey soil; (b) Partial effect of the interaction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