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RESEARCH ARTICLE

# Water table depth modulates productivity and biomass across Amazonian forests

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## Abstract

**Aim:** Water availability is the major driver of tropical forest structure and dynamics. Most research has focused on the impacts of climatic water availability, whereas remarkably little is known about the influence of water table depth and excess soil water on forest processes. Nevertheless, given that plants take up water from the soil, the impacts of climatic water supply on plants are likely to be modulated by soil water conditions.

**Location:** Lowland Amazonian forests.

**Time period:** 1971–2019.

**Methods:** We used 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 precipitation and groundwater affects forest structure and dynamics, but in different ways. Forests with a shallow water table (depth < 5 m) had 18% less above-ground woody productivity and 23% less biomass stock than forests with a deep water table. 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 the interaction between climatic water deficit and water table depth. On average, in drier climates the forests with a shallow water table had lower productivity than those with a deep water table, with this difference decreasing within wet climates, where lower productivity was confined to a very shallow water table.

**Main conclusions:** We show that the two extremes of water availability (excess and deficit) both reduce productivity in Amazon upland (*terra-firme*) forests. Biomass and productivity across Amazonia respond not simply to regional climate, but rather to its interaction with water table conditions, exhibiting high local differentiation. Our study disentangles the relative contribution of those factors, helping to improve understanding of the functioning of tropical ecosystems and how they are likely to respond to climate change.

**KEYWORDS**
above-ground biomass, carbon, forest dynamics, groundwater, seasonality, tropical ecology

## 1 | INTRODUCTION

Tropical forests hold a disproportionate share of the Earth's biodiversity and carbon stocks, providing environmental services of global importance through their 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 owing to the carbon accumulated in woody plants (Pan et al., 2011; Phillips & Brienen, 2017). Therefore, there is great interest in understanding the underlying controls on biomass productivity and dynamics of the Amazonian forests and how climate change is affecting them and will continue to do so (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. Although this has been studied from the perspective of changes in precipitation seasonality and climatic water deficits (e.g., Álvarez-Dávila et al., 2017; Phillips et al., 2009; Toledo, Poorter, et al., 2011), there has been much less attention paid to the role of water availability in the soil, as regulated by groundwater (but see Chitra-Tarak et al., 2021; Esteban et al., 2020; Ivanov et al., 2012; Nobre et al., 2011), and no account of how groundwater affects forest productivity and biomass measured on the ground 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 (da 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 affect 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 is highly constrained by WTD (Fan et al., 2017), and soil density (Quesada et al., 2012). In Amazon non-flooded (*terra-firme*) forests, at low topographic positions the roots are in direct contact with the superficial water tables or capillary fringe year-round or 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 (*c.* 50%) of the Amazonian forest has a relatively superficial water table of 5 m depth or less (Costa et al., 2022; Fan & Miguez-Macho, 2010).

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 forests with a shallow water table is likely to reduce the effects of precipitation water deficit during the dry season, hence promoting greater productivity in these environments than in sites in the same climate where the water table is deep. However, excess water in shallow water table conditions during the wet season leads to anoxic stress, which can result in reduced plant growth. Water excess inhibits oxygen flow to the roots and limits plant growth, because alternative anaerobic routes of energy production are much less efficient than aerobic respiration (Gibbs & Greenway, 2003; Parolin, 2012). Thus, optimal conditions for growth might be restricted 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 (Ferry et al., 2010; Gale & Barfod, 1999; Gale & Hall, 2001). Together, these constraints lead to the expectation that where water tables are shallow, low soil oxygen will lead to low productivity, and weak root anchorage will lead to higher mortality rates and reduced stand biomass. Although 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 forests with shallow water tables might not have lower biomass productivity than nearby forests with deep water tables in the same climatic conditions (Damasco et al., 2013; Grogan & Galvão, 2006).

In summary, the impacts of water on forests depend on much more than simply how much rain falls. 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, WTD 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 and additive effects, but rather involve complex interactions, because different combinations can 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 working for decades (ForestPlots.net et al., 2021), to address two central questions: (1) how do the structure and dynamics of Amazonian forests vary with WTD and the long-term average climatic water deficit?; and (2) how does WTD 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, both with water deficit and with water 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, whereas a 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 modulate those responses further, because soils with low water-retention capacity could reverse the positive interaction of shallow water tables and dry climates.

## 2 | MATERIALS AND METHODS

### 2.1 | Vegetation data

To address our questions, we analysed 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 a.s.l.) Amazonia that are not seasonally or permanently flooded (i.e., *terra-firme* forests). We used data from 344 plots monitoring Amazon vegetation from the Red Amazónica de Inventarios Forestales (RAINFOR) and Programa de Pesquisa em Biodiversidade (PPBio) networks (Lopez-Gonzalez et al., 2011; Magnusson et al., 2013; for plot details, see Supporting Information Table S1). 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) ≥ 10 cm were tagged and measured (196 plots in this dataset) (Phillips et al., 2009). In PPBio plots, all stems with $D \geq 30$ cm are sampled in the full 1 ha per plot; stems with 10 cm ≤ $D < 30$ cm were measured in a subplot of 0.5 ha per plot (148 plots in this dataset) (Magnusson et al., 2005). Field data were curated and accessed via the ForestPlots.net database (Lopez-Gonzalez et al., 2011) and subject to strict quality control to identify possible measurement or annotation errors, as described by 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. The AGB was calculated for each census (in megagrams per hectare) and AGWP for each census interval (in megagrams per hectare per year), then a time-weighted mean was taken to give one value per plot. Tree biomass was estimated based on the diameter ($D$), wood density ($\rho$) and height ($H$), using the pantropical equation developed by Chave et al. (2014):

$$\mathrm{AGB}_{\mathrm{trees}} = 0.0673 \times \left(\rho D^2 H\right)^{0.976}.$$

Species wood density was obtained from the global wood-density database (Chave et al., 2009; Zanne et al., 2009). A three-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 ($D$):

$$\ln\left(\mathrm{AGB}_{\mathrm{palm}}\right) = 3.3488 + 2.7483 \ln(D).$$

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

The AGWP was calculated from the sum of biomass growth of surviving trees and trees that recruited. Estimates of biomass productivity are affected by several factors, including census duration, 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 estimated the above-ground woody loss over time, in units of megagrams per hectare per year. We also estimated the "biomass mortality rate", as $\mathrm{AGB}_{\mathrm{mortality}}/\mathrm{AGB}$, in units of hectares per year. This standardization was performed in order to be able to compare the proportional rate of biomass loss among plots with different standing biomass stock.

We also calculated stem mortality, measured as mean annual mortality rate ($\lambda$) as:

$$\lambda = \frac{\left[\ln\left(N_0\right) - \ln\left(N_s\right)\right]}{t},$$

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). For each site, we also calculated annual recruitment rates ($\mu$) as:

$$\mu = \left[\ln\left(N_f / N_s\right)\right] / t,$$

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 (as a percentage per year), and then a time-weighted mean based on the census-interval lengths was taken to give one value per plot. With these results, we derived 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 being more likely to underestimate rates owing 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).

### 2.2 | 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 for the climatic water supply, WTD as a proxy for local soil-water supply, and soil texture 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.

We calculated MCWD based on the long-term average of the annual MCWD of each plot, from 1971 to 2019, thus reflecting the climatic conditions experienced by each plot over time and corresponding to the time window of our dataset. The 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 dataset (Abatzoglou et al., 2018), at *c.* 4 km (1/24th degree) spatial resolution, from 1971 to 2019. Monthly evapotranspiration was assumed to be fixed at 100 mm/month, considering that Amazonian forest canopies have a nearly constant evapotranspiration rate (Rocha et al., 2004; Shuttleworth, 1988).

Water table depth was extracted from a map developed for the entire Amazon (Fan et al., 2013; Fan & Miguez-Macho, 2010), at *c.* 270 m spatial resolution, based on model simulation constrained by >1,000,000 direct well measurements from government archives and publications. We extracted WTD values for the geographical coordinates for each plot and did not interpolate 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), because 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, because CEC includes the concentration of aluminium, which is not a nutrient (Moulatlet et al., 2017). Although phosphorus is widely considered to be a key limiting nutrient for growth in tropical forests, this variable was not available for all plots or as a continuous estimated layer. However, the availability of exchangeable cations tends to be correlated well with 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 *c.* 4 km (1/24th degree) spatial resolution from 1971 to 2019.

## 2.3 | 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 for the water conditions of each site (WTD, 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, because they are recognized as important determinants of structure and dynamics of Amazon forests. Our models included interactions because we expected the effect of WTD on the forest dynamics to depend on the levels of water deficit (MCWD) and soil texture (Supporting Information Table S2). Before running the models, we tested for multicollinearity among predictors. The variance inflation factors (VIFs) were estimated, and only low multicollinearity was detected ($\text{VIF} < 5$; Supporting Information Table S3). To detect whether spatial aggregation of plots (which could induce autocorrelation) interfered with our results, we ran generalized linear mixed models (GLMMs), 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 information criterion (AIC) values (Supporting Information Table S4). Adding the random factor improved the models (smaller AIC values), but did not change the results qualitatively, hence 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, because 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 we 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 as follows: 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$^{1/5}$; and 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 locally estimated scatterplot smoothing (LOESS) 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 into 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 depth threshold of 5 m. We chose this division because groundwater ≤5 m in depth is where most roots are potentially in direct contact with the groundwater or the capillary fringe (Fan et al., 2017; Fan & Miguez-Macho, 2010). We also ran boosted regression trees for the relationship between WTD and all response variables (Supporting Information Figure S1) to check whether this value was supported by the data. Wet ($\text{MCWD} > -160$ mm) and dry ($\text{MCWD} < -160$ mm) forests were divided based on the MCWD average in our dataset (see the histograms in Supporting Information Figure S2). To test whether there was a significant statistical difference in forest structure and dynamics between the shallow and deep water table subgroups or between dry and wet climates, we used Welch's unpaired two-sample *t*-tests for samples of unequal size.

All analyses were conducted in R v.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 the package *ggplot2* (Wickham, 2011); multiple linear regressions with the package *car* (Fox et al., 2019); the interaction plots with the package *interactions* (Bauer & Curran, 2005); and boosted regression trees with the packages *rpart* (Milborrow, 2016) and *gmb* (De'ath et al, 2006).

## 3 | RESULTS

### 3.1 | How do the structure and dynamics of Amazonian forests 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 ($t = -5.62$; d.f. = 342; $p < .01$) and biomass stocks ($t = -6.28$; d.f. = 342; $p < .01$) of Amazon forests (Figure 1a,b, respectively). Shallower water table forests had, on average, 18% lower biomass productivity (4.5 Mg/ha/year) and 23% lower biomass stock (234.6 Mg/ha) than those on deeper water tables (5.5 Mg/ha/year and 306.9 Mg/ha, 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/year; $t = -7.67$; d.f. = 342; $p < .01$) and 24% lower biomass stock (240.2 Mg/ha; $t = -7.01$; d.f. = 342; $p < .01$) than those in wetter climates (5.7 Mg/ha/year and 314.3 Mg/ha; Figure 2a,b, 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%/year; Figure 1c; $t = 3.40$; d.f. = 342; $p < .01$) and stem turnover (2.4%/year; Figure 1d; $t = 3.62$; d.f. = 342; $p < .01$) were higher in shallower water table forests than in those with deeper water tables (2.1%/year and 2.0%/year, respectively). Conversely, stem mortality rate (2.8%/year; $t = 7.21$; d.f. = 342; $p < .01$), recruitment rate (2.3%/year; $t = 3.62$; d.f. = 342; $p < .01$) and stem turnover (2.5%/year; $t = 6.24$; d.f. = 342; $p < .01$) were higher in drier than in wet climates (1.9%/year, 1.8%/year and 1.9%/year, respectively; Figure 2d–f).

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 (Figure 3a,c,e). Biomass productivity was higher in the western portion of the basin and on the Guiana shield, associated with wetter climates (Figure 3f). Within the Guiana shield, higher productivity was associated with deep water tables and clayey soils (Figure 3b, d). 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 attributable to intra-site (between-plot) variation in topography, and consequently, in WTD.

### 3.2 | 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 (Supporting Information 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 in drier climates, with this difference decreasing in wet climates (Figure 4). The very low biomass productivity of some plots (<2 Mg/ha/year) is related to vegetation structure, because in these sites most trees are very thin and therefore have lower productivity. Additional analysis showed that excluding these plots did not change the Amazon-wide pattern of the interactive effects of WTD and climate on productivity (Supporting Information Figure S3 ).

Despite the average negative effect of a shallow water table on forest productivity within dry climates, the more complex interactions between soil texture, MCWD and WTD suggest a contribution of soil drainage to forest functioning (Figure 5). These interactions show that forest productivity was lower in shallower water table conditions in dry climates when the soil was less clayey, in comparison to deeper water table conditions in the same climate (red line, Figure 5a). However, when the soil was more clayey, dry-climate forests with a shallower water table had greater productivity than their climatic equivalents on deeper water tables (red line, Figure 5c). The data coverage of some combinations of climate, water table and soil texture were low (especially for clayey soils in dry climates and with a shallow water table), which might limit the interpretation of this result. We also note some nonlinear trends in wet climates and sandier soils, where AGWP was low where the water table was very shallow (<2 m) but increased to reach a peak in the range of 2–8 m depth (Figure 5a).

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 were higher in those sites (Supporting Information Figure S4).

### 3.3 | 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 (Supporting Information Table S2). Soil fertility also affected mortality, recruitment rates and stem turnover, which were higher on

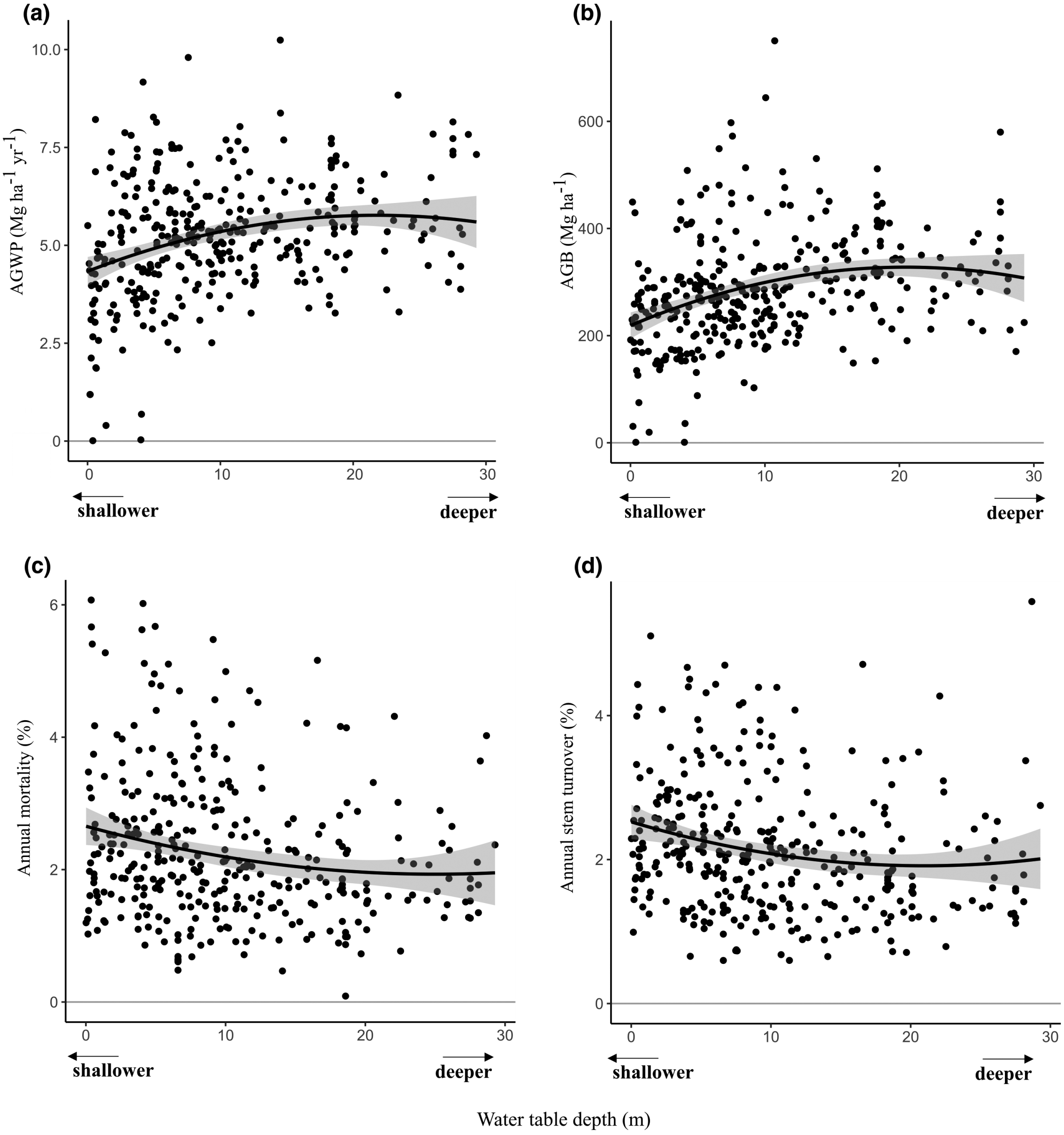

FIGURE 1 Impact of water table depth on (a) biomass productivity (AGWP); (b) biomass stock (AGB); (c) annual mortality rate; and (d) annual stem turnover in Amazonian forests. Locally estimated scatterplot smoothing (LOESS) regression was used to adjust the relationships between the response variables and water table depth. The shaded region shows the confidence interval of the regression.

more fertile soils (Supporting Information 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 (Supporting Information Table S2).

## 4 | DISCUSSION

Our study demonstrates, for the first time, the large-scale effects of WTD on the structure and dynamics of the Amazon forests, based on a unique combination of ground-plot data and WTD 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, in addition to 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).

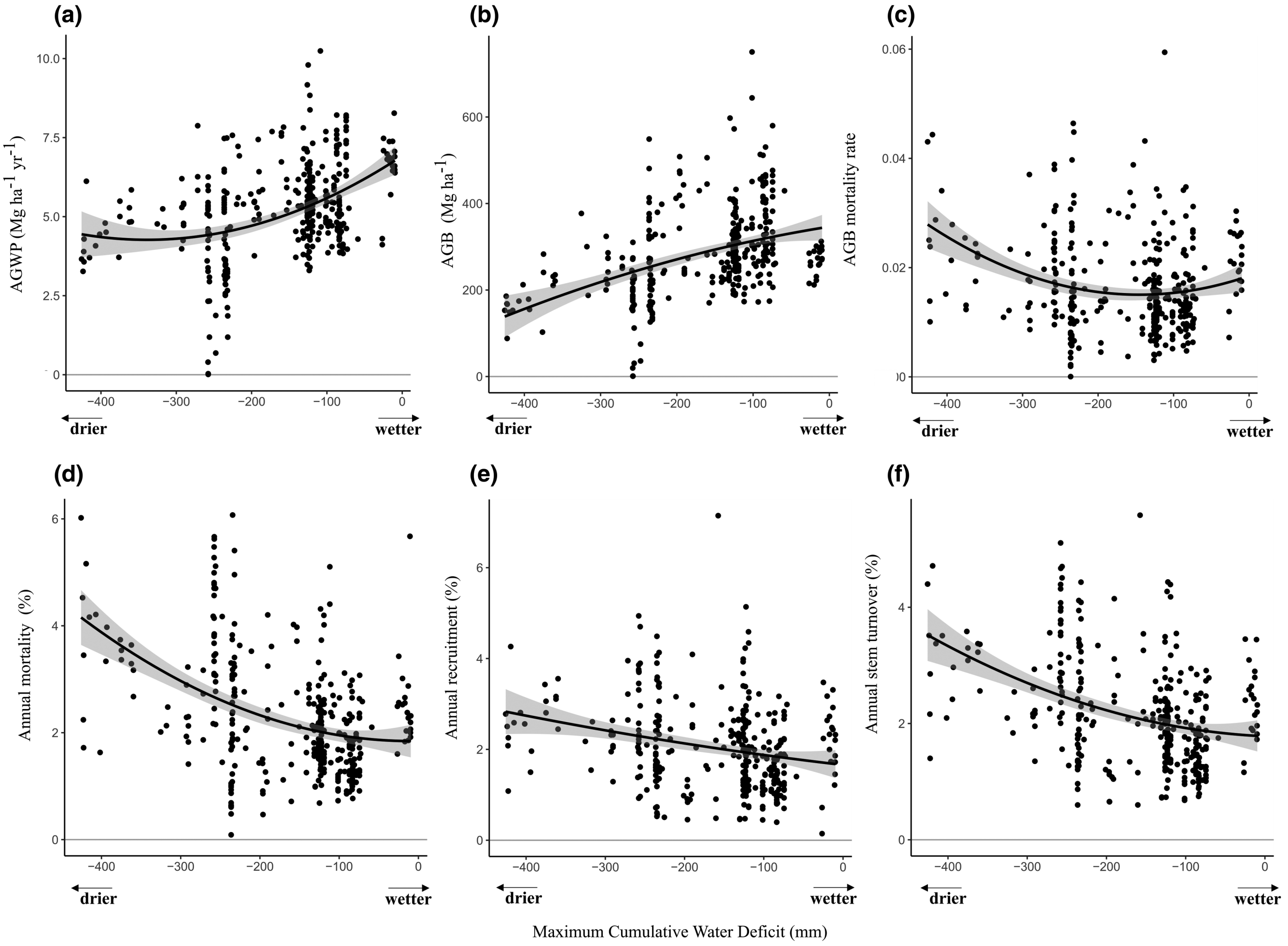

FIGURE 2 Impact of the maximum cumulative water deficit on: (a) biomass productivity (AGWP); (b) biomass stock (AGB); (c) biomass mortality rate (AGB mortality rate); (d) annual mortality rate; (e) annual recruitment rate; and (f) annual stem turnover in Amazonian forests. Locally estimated scatterplot smoothing (LOESS) regression was used to adjust the relationships between the response variables and maximum cumulative water deficit (MCWD). The shaded region shows the confidence interval of the regression.

### 4.1 | 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 development in the generally wet climates of Amazonia, through excess soil water and consequent oxygen limitation. Our results support this hypothesis because, on average, sites with a shallow water table tended to have lower biomass productivity (Figure 1a). However, there was high variability in AGWP, with some sites having high biomass productivity despite the shallow water table. Therefore, it is important to explore the mechanisms that might lead to the two extremes of low and high biomass productivity in shallow water tables. To help in understanding 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 provides a much lower yield (two adenosine triphosphate (ATP) per glycose molecule) than respiration (36 ATP), and thus severely limits plant growth (Kreuzwieser & Rennenberg, 2014; Setter & Belford, 1990). 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 are 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

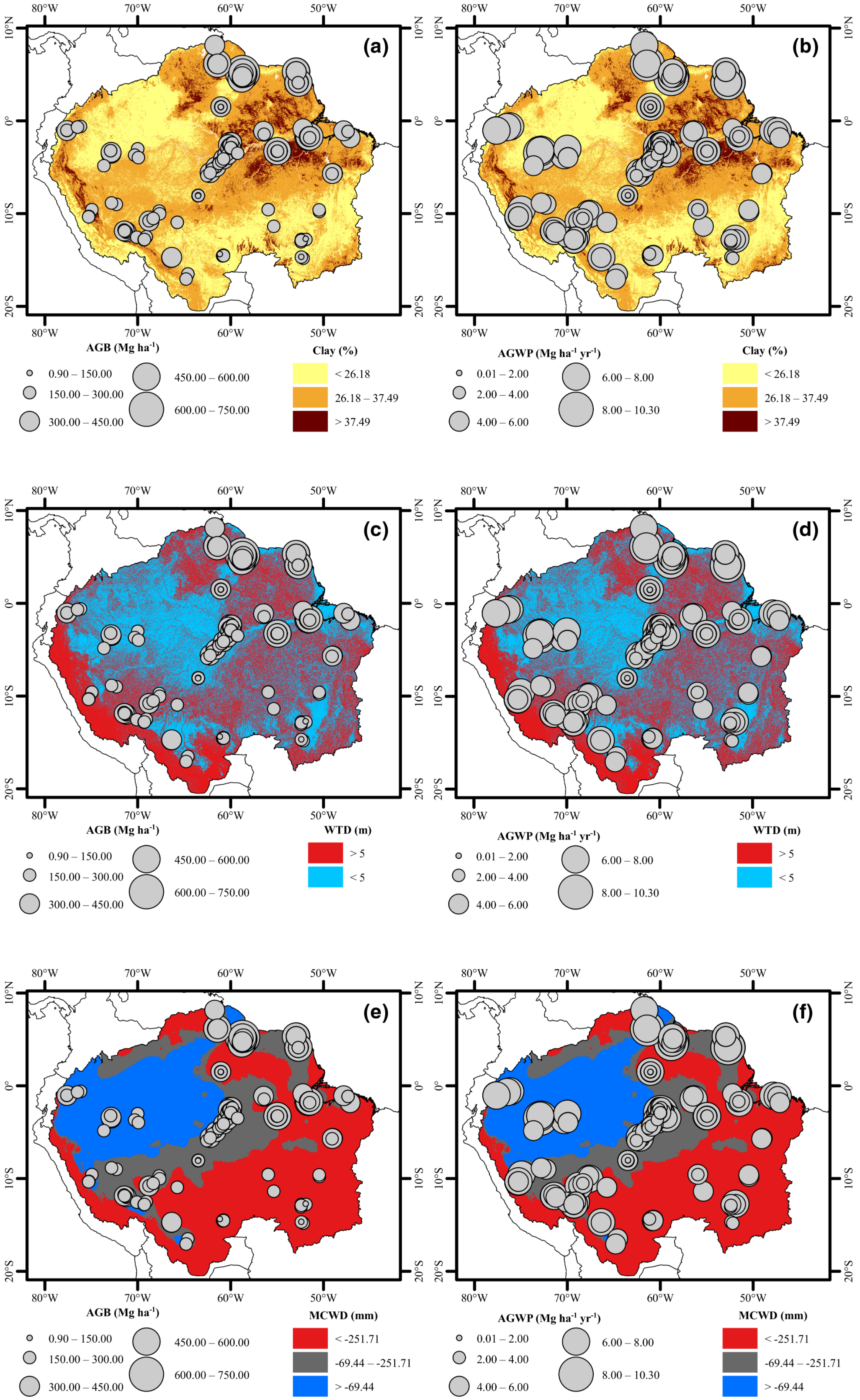

**FIGURE 3** Spatial variation in forest biomass and productivity across Amazonia. (a,b) These metrics are displayed against a background of clay content. (c,d) These metrics are displayed against a background of the water table depth (WTD). (e,f) These metrics are displayed against a background of maximum cumulative water deficit (MCWD). 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 by Fan and Miguez-Macho (2010). These classes are the same as those used in Figures 4 and 5. Grey dots represent plots with size proportional to the biomass stock or productivity.

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 with environmental conditions suitable for growth is shorter in a shallow water table, and therefore, on average, biomass productivity is lower in these locations than in a deep water table (but see next section, because these patterns change when combined with climate).

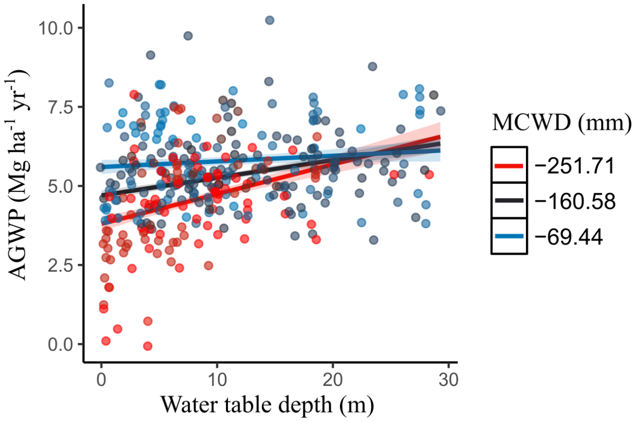

FIGURE 4 Partial-dependence plot of the interaction between maximum cumulative water deficit (MCWD) and water table depth on biomass productivity. In order to visualize interactions, climate was divided into three classes based on the standard deviation around the mean. Red is used for plots with MCWD 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.

For vegetation dynamics, we found higher mortality and stem turnover in shallow water table sites, as we had hypothesized. Poorly drained sites have higher mortality rates owing 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, Magnusson, et al., 2011). This low adherence to the soil increases the susceptibility of trees 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 that die standing (Gale & Hall, 2001). The effects of excess water on forest structure and dynamics are well described in the literature for floodplain forests (Godoy et al., 1999; Parolin et al., 2004; Piedade et al., 2013; Schöngart et al., 2004; Simone et al., 2003), 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, 2010; Ferry et al., 2010) with higher tree mortality (Ferry et al., 2010; Toledo, Magnusson, et al., 2011) and recruitment rates (Ferry et al., 2010) in seasonally waterlogged forests with a shallower water table 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, WTD 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

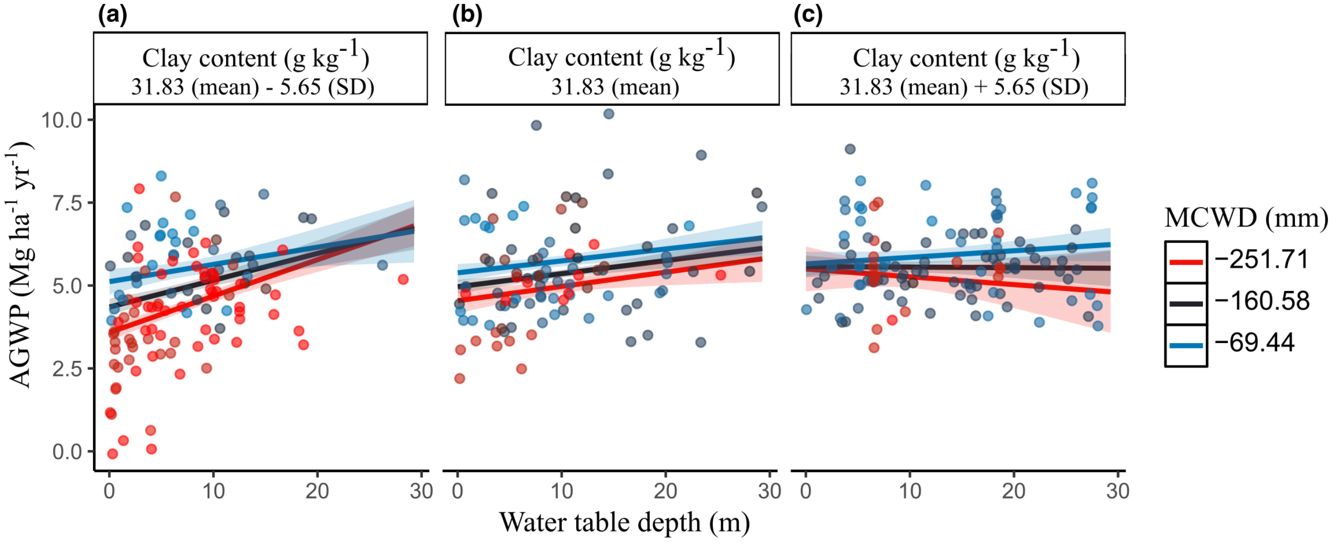

FIGURE 5 Partial-dependence plots derived from multiple-regression models investigating the effects of interactions among clay content, water table depth and maximum cumulative water deficit (MCWD) on biomass productivity in Amazonian forests. (a) Partial plots of the interaction in less clayey soil. (b) Partial effect of the interaction in moderately clayey soil. (c) Partial effect of the interaction in more clayey soil. In order to visualize interactions, climate and soil texture were divided into three classes based on the standard deviation around the mean. Red is used 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.

effect supports those results for the Amazonian forests, but here with above-ground wood productivity data.

### 4.2 | 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 in 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 are 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; Banin et al., 2014; Esquivel-Muelbert et al., 2020; Malhi et al., 2004; Quesada et al., 2012). However, neither soil properties nor climatic or groundwater conditions alone fully explain the distribution of biomass and vegetation growth in our study or world-wide (Baraloto et al., 2011; Fan, 2015; Quesada et al., 2012).

We hypothesized that an interaction of these factors would provide a better description of the vegetation patterns, with drier regions with a shallow water table having higher biomass productivity, whereas in wetter climates shallow water tables would result in excess water and lower productivity; however, this is not what we found. The combination of a shallow water table and dry climate resulted in lower biomass productivity. This outcome might result from an aspect of the water availability that was not accounted in this study: the temporal fluctuation of the water table. The available WTD product gives what is expected to be the average WTD of each pixel, but there might be varying degrees of temporal fluctuation modulated by climatic, topographic and geomorphological conditions (Costa et al., 2022). In drier climates, the seasonal fluctuation of the water table tends to be higher (Costa et al., 2022; Miguez-Macho & Fan, 2012), hence plants might be 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 growth. In the wet season, the rise in the water table might lead to anoxic stress. In the dry season, when the water table level drops, the shallow plant root systems characteristic of these environments might not access the groundwater and might go through water deficit stress, also limiting the biomass accumulation.

Also 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 was very shallow (<2 m deep), which is where most fine roots tend to be (Jackson et al., 1996). This seems to restrict the pure anoxic limitation of productivity to a smaller range of very wet conditions than our hypotheses predicted. Still in wet climates, we see high biomass production in the intermediate shallow water table (2–5 m; Figure 5a) that might be a consequence of an interaction of the tree functional traits typically selected in wet environments [lower wood density, higher xylem vessel diameter and higher specific leaf area (reviewed by Costa et al., 2022), aligned with faster resource acquisition and growth] and the potentially moist, instead of anoxic conditions, during a large period of the year. The number of plots within each combination of climate, water table and soil conditions was relatively low here, and there is a clear need for more work to improve the evaluation of these potential nonlinearities in the response of forest productivity to the determinants of water availability.

A full accounting of the factors affecting soil moisture also requires consideration of soil properties, especially soil texture (Quesada et al., 2012; Richter & Babbar, 1991). 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, whereas predominantly sandy soils should have faster groundwater level responses to precipitation. Our results suggest a contribution of clayey texture in increasing productivity in dry climates with a shallow water table (Figure 5c). However, here too the dataset lacks complete coverage of the relevant environmental combinations, limiting our conclusions.

### 4.3 | Limitations of this study

Although this and other work points to a key role for WTD 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 by Costa et al., 2022), precise measurement of WTD and its fluctuation is still limited, owing to the challenge of installation of equipment and periodic monitoring in the field. The alternative for large-scale analytical studies like these is to use WTD models, such as the model of Fan et al. (2013) used here. These, however, come with limitations because they condense the full microspatial variation of hydrology at a relatively coarse spatial resolution (here *c*. 270 m). A further difficulty is that vegetation-monitoring plots might not be designed to detect variation in hydrological environments, such that varying hydrological conditions might occur within the same plot (for a design that minimizes this problem, see Magnusson et al., 2005). These imprecisions probably limit our capacity to detect the local effects of WTD on forest functioning, meaning that effects in nature might eventually prove to be even stronger than shown here.

Also, although 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/year). Such unexpected variation suggests that 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

(Cosme et al., 2017; Schietti et al., 2013), but it is not known whether they are similarly filtered across soil hydrology in different macroclimates, or whether soil-macroclimate interactions that could potentially change the responses of shallow water table forests. This is an important subject to address in future studies because it could suggest ways to mitigate carbon losses.

### 4.4 | Final considerations

The Amazon hydrological cycle is already changing because of climate change, and this is 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 planning 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 analysing 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 WTD. Both water excess and water deficit hinder vegetation development. Above-ground productivity is suppressed, tree mortality increased and thus biomass stocks are reduced in shallow water table forests. These key effects of WTD have typically been neglected in large-scale studies (e.g., Malhi et al., 2006, 2015; Saatchi et al., 2007), but must be considered in global environmental modelling to gain a better understanding of the relative contribution of the key drivers of Amazon forest structure and dynamics and the ecosystem functions they provide.

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## CONFLICT OF INTEREST

None declared.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in ForestPlots.net data package at http://doi.org/10.5521/forestplots.net/2022_2

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