



The other side of droughts: wet extremes and topography as buffers of negative drought effects in an Amazonian forest

Erick J. L. Esteban^{1*} , Carolina V. Castilho², Karina L. Melgaço³ and Flávia R. C. Costa^{4*} 

¹Programa de Pós-Graduação em Ciências de Florestas Tropicais, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. Ephigênio Sales 2239, Manaus, AM 69060-20, Brazil; ²EMBRAPA Roraima, Rodovia BR 174, km 8, Distrito Industrial, Boa Vista, RR 69301-970, Brazil; ³School of Geography, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK; ⁴Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. Ephigênio Sales 2239, Manaus, AM 69060-20, Brazil

Summary

Author for correspondence:

Erick J. L. Esteban

Email: elavadoesteban@gmail.com

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- There is a consensus about negative impacts of droughts in Amazonia. Yet, extreme wet episodes, which are becoming as severe and frequent as droughts, are overlooked and their impacts remain poorly understood. Moreover, drought reports are mostly based on forests over a deep water table (DWT), which may be particularly sensitive to dry conditions.
- Based on demographic responses of 30 abundant tree species over the past two decades, in this study we analyzed the impacts of severe droughts but also of concurrent extreme wet periods, and how topographic affiliation (to shallow - SWTs - or deep - DWTs - water tables), together with species functional traits, mediated climate effects on trees.
- Dry and wet extremes decreased growth and increased tree mortality, but interactions of these climatic anomalies had the highest and most positive impact, mitigating the simple negative effects. Despite being more drought-tolerant, species in DWT forests were more negatively affected than hydraulically vulnerable species in SWT forests.
- Interaction of wet–dry extremes and SWT depth modulated tree responses to climate, providing buffers to droughts in Amazonia. As extreme wet periods are projected to increase and at least 36% of the Amazon comprises SWT forests, our results highlight the importance of considering these factors in order to improve our knowledge about forest resilience to climate change.

Introduction

In recent decades there has been an increase in tree mortality in forest ecosystems worldwide (Phillips *et al.*, 2004; Van Mantgem *et al.*, 2009), and this is expected to get worse in the near future. This situation, attributed to observed and projected global environmental changes (especially extreme climatic/weather events such as droughts, heat waves, frosts and floods (Hirabayashi *et al.*, 2008, 2013; IPCC, 2012; Dai, 2013; Cook *et al.*, 2014)), has generated particular concern about the fate of these ecosystems (Friend *et al.*, 2014; Trumbore *et al.*, 2015; McDowell *et al.*, 2018; Gloor, 2019).

Climate-driven forest die-off can rapidly change forests' dynamics, leading to a large-scale alteration of their structure and composition (Allen & Breshears, 1998; Laurance *et al.*, 2004; Bennett *et al.*, 2015; Sande *et al.*, 2016), thus affecting their potential to mitigate the consequences of ongoing climate change, with consequent strong feedbacks to local and global climate. Increased temperature (Allen *et al.*, 2010) and changes in precipitation patterns (Holmgren *et al.*, 2013), coupled with an increased frequency and intensity of drought events (Ciais *et al.*,

2005; Anderegg *et al.*, 2013; Erfanian *et al.*, 2017), have been indicated as the major causes of forest changes, extreme droughts being the focus of most studies of climate-related changes in tropical forest dynamics.

Negative effects of climatic change on forest vegetation dynamics and function, such as decreases in tree growth rates and increases in tree mortality, have already been documented for the largest tropical rainforest, the Amazon (Brienen *et al.*, 2015; Hubau *et al.*, 2020), with consequent compositional changes (Esquivel-Muelbert *et al.*, 2019; Costa *et al.*, 2020). Droughts in 2005, 2009–2010 and 2015–2016 were highlighted as a major cause of large tree mortality, slow growth rates and increased turnover in this ecosystem (Phillips *et al.*, 2009; Gatti *et al.*, 2014; Leitold *et al.*, 2018). Nonetheless, extreme wet periods are also increasing in frequency and intensity over the whole basin (Gloor *et al.*, 2013; Marengo & Espinoza, 2016; Barichivich *et al.*, 2018) and are projected to increase in the future as well (Marengo *et al.*, 2018). For instance, while in the northern Amazon there is an increase of both the frequency of wetter days and amount of rainfall (Espinoza *et al.*, 2019), in the central region around Manaus we observed an increasing precipitation trend of 8.2 mm yr⁻¹ since 1965 (Supporting Information Fig. S1a).

*These authors contributed equally to this work.

Negative effects of extreme wet events have also been reported in Amazonian forests. In 2005, when a major drought struck large areas of the Amazon Basin (Aragão *et al.*, 2007; Marengo *et al.*, 2008), the peak of tree mortality in the central region actually occurred before the intense dry period, when strong squall lines caused windthrows (Negrón-Juarez *et al.*, 2010). In 2013–2014, when a severe period of rainfall generated unexpected floods in the southwestern portions of the Amazon (Espinoza *et al.*, 2014), Moser *et al.* (2019) assigned this event as the cause of massive tree mortality and compositional shifts of floodplain forests. Therefore, wet extremes can be as big a source of Amazonian forest disturbance as droughts.

Yet, such negative effects of droughts and wet events on forests may be counterbalanced when both rainfall extremes occur in sequence. In a ‘wet then dry’ sequence (high rainfall period occurring before the drought), there will be ample soil water recharge that can provide water during the drought, buffering its effects. Together with high radiation loads that characterize dry periods, this soil water availability may also enable trees to photosynthesize more (Huete *et al.*, 2006; Restrepo-Coupe *et al.*, 2013; Saleska *et al.*, 2016). On the other hand, in a ‘dry then wet’ sequence (high rainfall period occurring after a drought), the ample water supply could enable surviving trees to recover from drought-related xylem damage (e.g. through faster growth). Nevertheless, the potential interaction between these increasingly frequent climate events and how this could modify the effect of such extremes on tree growth and mortality in upland terra-firme forests of the Amazon have not yet been evaluated.

Soil water availability, which drives the perception of water deficit or excess by plants, is largely controlled by local edaphic and hydrological conditions, the latter largely mediated by topography (e.g. Horton & Hart, 1998; Tromp-van Meerveld & McDonnell, 2006). Within the same macroclimate, plants can be either in direct contact with groundwater (as in the bottomlands and valleys, with wetter soils where there is a shallow water table) or far from this source (as in hillslopes and plateaus), experiencing higher water deficits and being more dependent on rainfall (Hodnett *et al.*, 1997; Jencso *et al.*, 2009; Pacific *et al.*, 2011; Fan *et al.*, 2017). As a result, the spatial variation in soil moisture along topographical gradients may strongly affect key ecosystem processes, such as soil respiration, evapotranspiration or tree growth (Mackay *et al.*, 2002; Eberbach & Burrows, 2006; Riveros-Iregui & McGlynn, 2009; Pacific *et al.*, 2011; Adams *et al.*, 2014; Berdanier & Clark, 2016). In addition, these hydrological environments imposed by local topography act as a filter of plant composition and traits (Ackerly, 2003; Schiatti *et al.*, 2014; Cosme *et al.*, 2017; Oliveira *et al.*, 2019; Fontes *et al.*, 2020), and have been observed to largely influence how forests experience severe climate conditions, mitigating or intensifying their impacts (e.g. Itoh *et al.* (2012) in a Bornean forest; Zuleta *et al.* (2017) in an Amazon forest; Hawthorne & Miniati (2018) in a USA forest). Thus, interactions between topographically controlled soil-water conditions, climate-driven external factors and the plant trait composition selected along local hydrological gradients should be expected to modulate tree responses to climate variability. Understanding the variation of drought

responses as a function of water table depth gradients is important, given that forests over a SWT are widely different from those over a deep water table (DWT), being characterized by higher turnover rates (i.e. more dynamic forests), owing to the combination of acquisitive species traits (Cosme *et al.*, 2017; Fontes *et al.*, 2020), shallow roots (Fan *et al.*, 2017) and soil instability (Ferry *et al.*, 2010; Cintra *et al.*, 2013), and that the majority of plots in Amazonian monitoring networks, from which most of our knowledge derives to date, is located in DWT forests, even though almost 40% of the Amazon forests have SWTs (with depths < 5 m; Fan & Miguez-Macho, 2010).

Moreover, multi-decadal observed increases in Amazonian tree mortality rates have also been associated with a consistent increase in air temperature (Brienen *et al.*, 2015). Rising temperature, and the resulting increase of vapor pressure deficit (VPD) (Trenberth *et al.*, 2014), can induce elevated tree mortality through hydraulic failure, as a consequence of greater evaporative demand (McDowell & Allen, 2015), or increasing respiratory carbon costs and/or greater stomatal closure, both exacerbating carbon starvation (Clark *et al.*, 2010; Galbraith *et al.*, 2010). Owing to the changing climate, global temperature will continue to rise and this situation is expected to expose forests, especially moist tropical ecosystems, to an unprecedented temperature regime (Allen *et al.*, 2010; Diffenbaugh & Charland, 2016). Therefore, as highlighted earlier for both types of rainfall anomaly (severe wet and drought periods), the constant increases in air temperature should also be critically evaluated to better understand how climate change affects Amazonian forests.

Here we analyze how extreme climate conditions (severe drought and wet periods and increased temperature), local topographic affiliation (from SWT to DWT) and species-level plant functional traits are related to diameter growth and mortality rates of 30 abundant tree species along the last two decades in a central Amazonian terra-firme forest. The main objective of this study was to examine isolated and interaction effects of positive and negative rainfall anomalies over tree demographic rates, and to investigate whether local topography and species life-history strategies mediate these tree responses to climate.

We hypothesized: that extreme climate conditions, represented by positive and negative rainfall anomalies, will negatively affect trees, leading to lower diameter growth and greater mortality rates; that when both extreme drought and wetness periods take place within the same census interval, extreme wetness will buffer the negative impacts of drought on trees; that species functional traits are important mediators of tree responses to climate anomalies; and that local soil hydrological conditions may counteract the climate effects expected based only on the traits, allowing more sensitive plants to not be negatively affected if associated with a lower-risk hydrological environment.

Materials and Methods

Study site and climate

This research was carried out in a terra-firme tropical rainforest in Reserva Florestal Ducke (RFD), located 26 km

northwest of Manaus (02°55'S, 59°58'W) in the central region of the Amazon basin. The vegetation of the RFD is old-growth evergreen forest, with high diversity of tree species and a closed canopy of 30–37 m, with emergent trees reaching 45 m (Guillaumet, 1987). The topography is well dissected, with elevation varying from 40 to 140 m above sea level (Ribeiro *et al.*, 1999). Soil characteristics are related to topography in a hydroedaphic gradient, representing a continuum of clayey latosols on the ridges until sandy podzols in the valleys (Chauvel *et al.*, 1987). Soils are acidic, and poor in phosphorus and exchangeable cations, while often high in aluminum (Chauvel *et al.*, 1987). The RFD experience an 'Am' tropical climate according to Köppen–Geiger classification, with dry and rainy seasons governed by monsoons (Peel *et al.*, 2007). Over the past 51 years (1966–2016), the mean (\pm SD) annual rainfall at the RFD was 2572 ± 351 mm, with an increasing precipitation trend of 8.2 mm yr^{-1} since 1966 (Fig. S1a). The driest month in this long-term local climate record was August, with a historical mean rainfall of 98.8 ± 49.1 mm and temperature of $26 \pm 1^\circ\text{C}$. The wettest month was April, with a mean \pm SD rainfall of 331.4 ± 88.8 mm and temperature of $25.2 \pm 0.9^\circ\text{C}$ (Fig. S2). This forest is representative of the climate, soils and groundwater depth and behavior of *c.* 30% of Amazonia (based on maps from Fan & Miguez-Macho, 2010; Quesada *et al.*, 2011; Miguez-Macho & Fan, 2012a,b; Restrepo-Coupe *et al.*, 2013; Malhi *et al.*, 2015; Esquivel-Muelbert *et al.*, 2019).

Climate anomalies

To represent not only the frequency but also the intensity of rainfall anomalies, here we established indices based on cumulative water deficit (CWD) and excess (CWE) values, using a long-term local climate record (rainfall data from the RFD meteorological station). Both CWD and CWE are metrics that express relevant ecological information about the status of water-related stress for plants, reflecting conditions of deficit and excess of water, respectively. With monthly precipitation records (since 1966) and considering a monthly evapotranspiration rate of 100 mm (as a result of the nearly constant evapotranspiration rate of moist tropical canopies; Shuttleworth, 1988; Rocha *et al.*, 2004), we calculated CWD and CWE values over the past 51 yr, encompassing the census periods from 2001 to 2016. CWD was calculated as in Aragão *et al.* (2007) and CWE as the opposite of CWD. For each month where CWD was reset to zero (no water deficit) the value of CWE was set as the volume of rainfall of that month minus 100 mm (assumed monthly evapotranspiration). The CWE for the next month was then calculated in the same way, and the CWE of previous months was added to that. Whenever CWD reaches positive values (which express a water deficit condition), CWE resets to zero. Several studies demonstrated that runoff contributes < 10% of stream and river discharge in Amazonian forests (reviewed in Miguez-Macho & Fan, 2012a), and in an area close to our study site runoff represented *c.* 3% of total annual rainfall (Lesack, 1993). Thus, as the evapotranspiration is

discounted in the calculation, and water loss as a result of runoff is generally small, most of this rainfall excess (CWE) will recharge the soil and later the groundwater (Tomasella *et al.*, 2008).

Based on this long-term record of CWD and CWE (612 monthly values of both CWD and CWE), we obtained the historical mean and SD of both metrics in order to characterize rainfall anomalies over our study period (2001–2016; Fig. S1). Then, for each census interval, we calculated the water deficit index (WDI) as the sum of monthly CWD values that were > 1 SD of the mean historical CWD (Fig. S3). Monthly CWD values were expressed in terms of SD and we considered only those > 1 in order to ensure that we were really catching severe conditions. Owing to variation in measurement intervals between censuses, we weighted the SD sum by the census interval duration (number of months), in order to have comparable WDI across all intervals. Thus, for each census interval, the WDI was calculated as:

$$\text{WDI} = \sum_{i=1}^n \frac{\text{CWD}_i}{n}; \text{CWD}_i > \text{CWD}_{\text{SD}}$$

where CWD_i is the cumulative water deficit of the month i (expressed in terms of SD, including only those > CWD_{SD}), n is the number of months in the census interval, and CWD_{SD} is the sum of the mean historical CWD with one SD (1966–2016).

Likewise, we calculated the water excess index (WEI) as the sum of monthly CWE values (in SD, and > CWE_{SD}), divided by the number of months in each interval. As it would not be reasonable to calculate cumulative anomalies on temperature among intervals, our metric to evaluate anomalies on this climate factor was established as the mean of all monthly temperature values (MMT) recorded in each interval.

Tree demographic responses

Diameter growth and mortality rates were calculated from data collected on 72 permanent plots (1 ha) systematically distributed over a 10×10 km grid. We selected 30 of the most abundant tree species of the RFD, representing 17.5% of all individuals and 15.2% of the basal area of plots. Half of these are among the most abundant trees in the whole Amazon (the hyperdominants of ter Steege *et al.*, 2013), and 20 of them are within the 100 most abundant species of the Manaus region (Table S1). Thus, despite the extreme diversity of this forest (1176 tree species registered to the Reserve, > 200 species ha^{-1} ; Ribeiro *et al.*, 1999; Hopkins, 2005), our selected 30 species fulfilled the criteria of having a large enough sample (≥ 40 individual trees in each census) for calculation of vital rates and local measurements of traits. Only three of these species had between 23 and 29 individuals in one of the censuses. Both diameter growth and mortality rates of each species were determined based on all individual trees with > 1 cm of diameter at breast height (dbh) registered in each census, from 2001 to 2016. The number of plots evaluated in each census varies from all the 72 (three censuses) to 15 (one census), and measurement intervals from 2 to 7 years.

Stem diameter growth rate (in mm yr^{-1}) for each individual tree in an interval was calculated as in Sheil *et al.* (1995):

$$\frac{(\text{dbh}_f - \text{dbh}_i)}{t}$$

where dbh_f and dbh_i are tree dbh at the final and initial measurements, respectively, and t is the interval between measurements in years. Thus, tree growth rates (GRs) for a species was established as the mean of stem diameter growth rates of all individuals in that interval.

Mortality rates (MR, in $\% \text{ yr}^{-1}$) were calculated as:

$$\frac{[\log(N_i) - \log(N_s)]}{t}$$

where N_i and N_s are the numbers of individuals at the first and last measurements, respectively, without recruits. To reduce the bias associated with measurement intervals variation, we used the general correction proposed by Lewis *et al.* (2004).

Topographic affiliation

To quantify the affiliation of each species to the topographic gradient, we weighted the height above nearest drainage of the plots (HAND (in m); information from Schiatti *et al.*, 2014) by the species abundance in each plot and divided by the species abundance in all plots. We used HAND because it is a descriptor of the drainage potential of any point in the terrain surface, strongly associated with the water-table depth (see Rennó *et al.*, 2008), and the most robust available topographic metric of soil-water gradients relevant for plants (Schiatti *et al.*, 2014). Thus, the topographic affiliation of a species is calculated as:

$$\sum_{i=1}^n \frac{\text{HAND}_i \times \text{AB}_i}{\text{AB}_t}$$

where HAND_i is the HAND value for plot i , AB_i is the species abundance in plot i , and AB_t the total abundance of the species across all plots of the RFD.

Species functional traits

We selected seven functional traits collected from 2014 to 2016 in 21 plots of the RFD: leaf area (LA, cm^2), specific leaf area (SLA, $\text{m}^2 \text{ kg}^{-1}$) and leaf dry matter content (LDMC, mg g^{-1}) as key leaf traits; wood density (WD, g cm^{-3}), wood dry matter content (WDMC, mg g^{-1}) and xylem proportion (XP) as key wood traits; and leaf area per sapwood area ($A_1 : A_2$) representing the investment in photosynthetic area per area supplied by xylem. Individual traits were measured from branches taken as much as possible from the most illuminated side of the crown, and avoiding visually unhealthy leaves or those with epiphylls. Leaves were counted for a 40-cm-long branch piece, the best two leaves were taken for fresh and dry weights and LA, a 4–5 cm terminal piece of the branch was taken for fresh and dry weights

and volume, and a small 1 cm branch piece next to the first was taken for macroanatomical measurements. Leaves were scanned for their area, weighed for fresh mass, and dried for 48 h at 60°C for dry mass. Petioles and rachises were not included in the leaf weights or area. LA was obtained as the mean area of the two selected leaves. SLA, the leaf area per unit leaf dry mass, which indicates the biomass efficiency of leaf display at the leaf level, was calculated by pooling the two leaves per branch and dividing their leaf area by their dry mass. LDMC was calculated as the dry mass over the fresh mass of this tissue and indicates toughness and leaf construction cost. Branch pieces were weighed, and volume was determined with the water displacement method, without bark, and dried at 105°C for 3–4 d for dry mass. WD was calculated as branch-wood dry mass over branch fresh volume and WDMC as the dry mass divided by the fresh mass of that tissue. XP, the proportion of the total basal area of the branch occupied by xylem tissue, was calculated from its diameter, taken directly from the branch piece with a caliper under a stereomicroscope.

The species trait values were obtained as the mean of all values collected on individual trees of each species. We only included species having at least five individuals with measurements of traits, as this number is often recommended for a representative mean trait value (Pérez-Harguindeguy *et al.*, 2013).

Statistical analysis

All statistical analyses and visualizations were performed in the R statistical environment (R Core Team., 2018). To understand the impact of extreme climate conditions (WDI, WEI and MMT) and how topographic affiliation and functional traits were related to growth (GR) and mortality responses (MR) of our 30 selected tree species over the past two decades, we fitted two independent series of mixed models, in which GR and MR were the response variables for each series ($n = 180$, 30 species \times six census intervals). Climate anomalies, species traits and topographic affiliation were fixed effects, and species identity was set as a random effect. As GR values showed normal distribution, models for this demographic rate were directly fitted as linear mixed models (LMMs). MR values, in contrast, were best fitted by zero-adjusted gamma (ZAGA) distribution. Therefore, for correcting nonnormality in MR, we first extracted the residuals of the null model fitted with a ZAGA family distribution, with the package *GAMLSS* (Rigby & Stasinopoulos, 2005), and then used residuals as the response variable in LMM series. Before analysis, all independent variables were standardized, whereby each cell was subtracted from the variable mean and then divided by its SD, allowing comparisons of the standardized regression coefficients and effect sizes of the independent variables. Thus, running models with all combinations of independent variables and considering possible interactions between them, we selected the best-supported models in each series based on Akaike's information criterion (Burnham & Anderson, 1998). All models were run using the package *NLME* (Pinheiro *et al.*, 2019) and pseudo- R^2 for fixed and random effects calculated with *MuMIn* (Barton, 2018).

Results

Extreme climate conditions reduced tree growth and survival

Over the study period (2001–2016), which covered major droughts in 2009–2010 and 2015–2016 and also extreme wet periods in 2005, 2011 and 2013–2014 (Fig. 1), both positive and negative rainfall anomalies had significant negative effects on tree demographic rates, while temperature anomalies were not included in any of the best models for these responses (Tables S2, S3). This means that, across the 30 abundant tree species studied here, a greater frequency and/or intensity of severe droughts or wet periods (expressed as higher values of WDI and WEI, respectively) led to lower diameter growth and higher mortality rates. Extreme drought and wet periods reduced diameter growth rates up to 11% and 42% and increased mortality by 88% and 146%, respectively, when compared with rates recorded in census intervals with the lowest WDI and WEI values (Fig. S4).

Interaction between rainfall anomalies had the highest impact on tree responses

Notwithstanding isolated negative effects, the interaction between periods of water excess and water deficit results in a positive impact on demographic tree responses and had the larger effect size of all terms included in the best models to explain both diameter growth and mortality rates (Fig. 2). Thus, when, during a time interval, water deficit periods are neither followed nor

preceded by periods of water excess (WEI = 0), or the accumulation of water is not large enough, there is reduction in diameter growth and increase in mortality rates according to the severity (frequency and intensity) of droughts (Fig. 3, red lines). However, if any period of extreme wetness occurs along the same census interval as drought, an increase in drought severity (higher WDI) will not be reflected in lower growth or higher mortality (Fig. 3, blue lines). Examining Fig. 1, such a buffer effect of wet extremes over droughts happened four times across our study interval, all in the ‘wet then drought’ sequence: in 2005 (third census interval), 2006 and 2008 (fourth census interval) and 2009 (fifth interval).

Topographic affiliation and wood density modulated tree responses to climate

We found that topographic affiliation of tree species had important interaction effects with periods of water deficit, being a modulator of drought impact on tree demographic responses. Species associated with SWTs do not show decreased growth or increased mortality as drought becomes more severe (Fig. 4, light blue lines), while those associated with DWTs had decreased growth and increased mortality (Fig. 4, brown lines). Once the effects of climate anomalies are controlled for, mortality rates actually tend to be higher in species associated with SWTs (see Fig. S5), which means that during droughts, the ordinary pattern of tree mortality along the topographic gradient is reversed.

Species wood density was the only trait with a significant effect on tree demographic responses, denser woods being

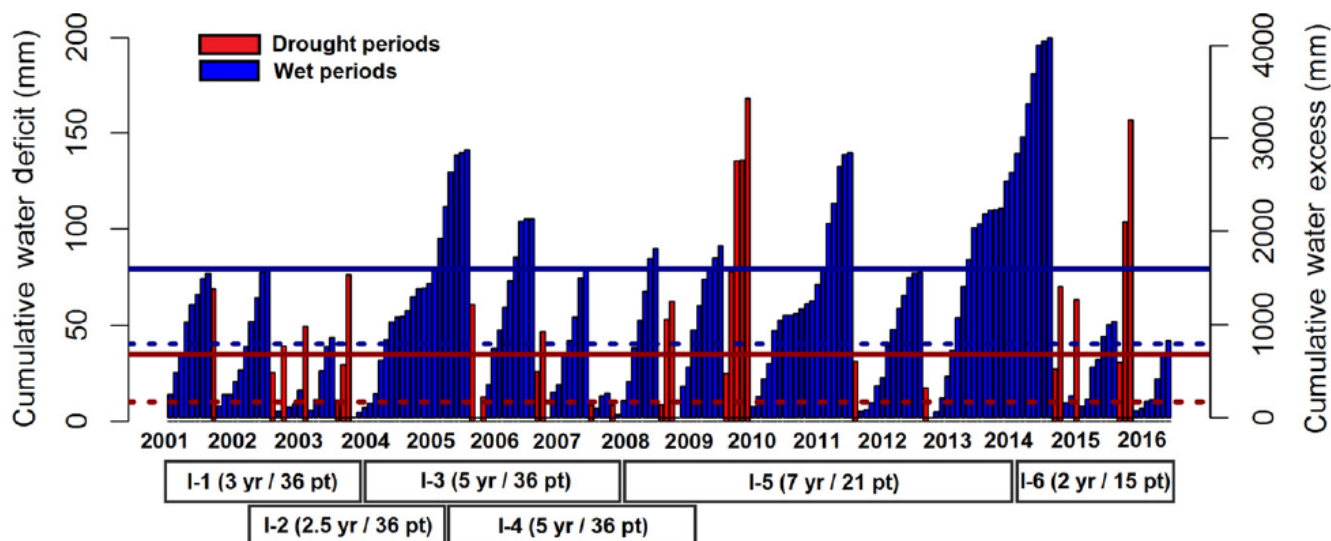


Fig. 1 Cumulative water deficit (CWD) and cumulative water excess (CWE) from 2001 to 2016 for the Reserva Florestal Ducke, central Amazon. Each sequence of colored bars represents a period of water deficit (red bars, scale on the left) or water excess (blue bars, scale on the right) conditions during the study interval. Red and blue dashed lines mark the historical mean and solid lines the threshold for water anomalies (i.e. cumulative value > 1 SD from the historical mean), based on both monthly cumulative water deficit (CWD) and excess (CWE) metrics over a 51 yr period (1966–2016; see Supporting Information Fig. S1). Horizontal bars in the bottom indicate the duration of census intervals (I) and the number of plots included. A set of 36 plots measured in I-1 were remeasured in I-3, and another set of 36 plots measured in I-2 were remeasured in I-4. Plots measured in I-5 and I-6 are a subsample of those measured in previous intervals. This figure highlights: major drought periods in 2009–2010 and 2015–2016 and major wet periods in 2005, 2011 and 2014; and four episodes (2005, 2006, 2008 and 2009) of droughts preceded by wet extremes, leading to the positive interaction effect on tree demographic rates.

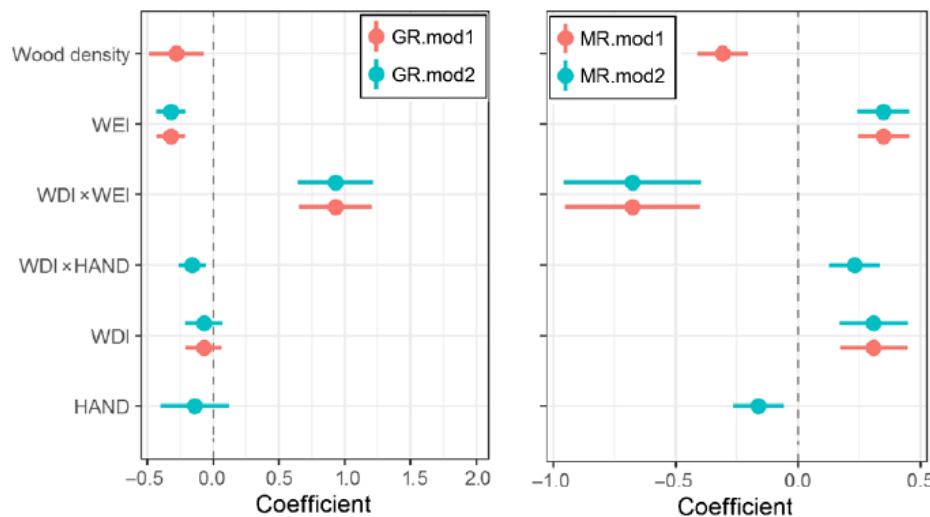


Fig. 2 Best predictors of Amazonian tree demographic responses to extreme climate events. Standardized coefficient values (effect sizes) of predictors included in the best models for tree diameter growth (GR models 1 and 2) and mortality (MR models 1 and 2). For all independent variables, the effect size (solid dot, with 95% confidence interval in solid lines) was obtained from the best-supported models in each series of models to analyze demographic rates (more details in Supporting Information Tables S2, S3). WDI, water deficit index; WEI, water excess index; HAND, height above nearest drainage; × refers to interaction between variables.

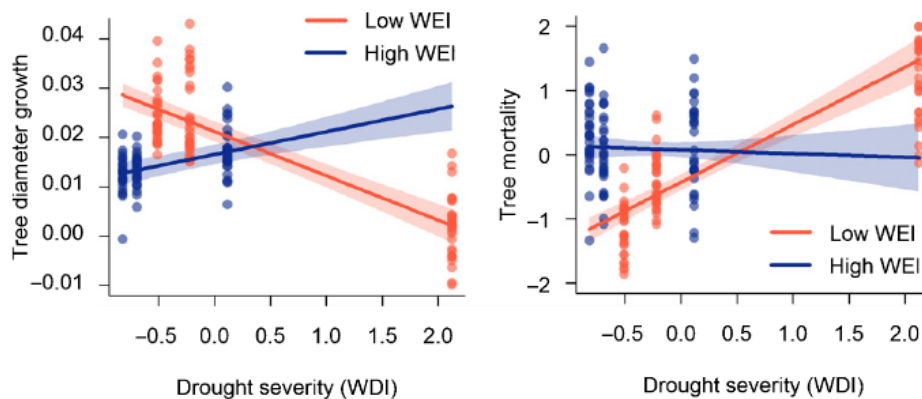


Fig. 3 Extreme wet periods as buffers of negative drought effects on tree demographic responses. Partial relationships between rainfall anomalies and demographic rates, showing significant interactions between the severity of water deficit (WDI) and the severity of water excess (WEI) on tree diameter growth (left) and tree mortality (right). If wet periods are not severe enough to reflect extreme wet conditions over the same time interval as droughts (WEI values from 0.03 to 0.18), there is a reduction of growth and increase in mortality with drought severity (red solid lines, with red shading displaying 95% confidence intervals). When such extreme wet periods (WEI values from 0.34 to 0.60) occur before droughts, an increase in the severity of droughts will not be reflected in lower growth or higher mortality (blue solid lines, with blue shading displaying 95% confidence intervals).

associated with lower diameter growth but also higher survivorship over time (Figs. 2, S6). As expected, this relationship reflects the classical growth–survival tradeoff in plant life strategies. Yet, we also observed that wood density was related to the species topographic affiliation (Fig. S7), lighter woods being mostly found in SWT forests while denser woods are more common in DWT forests.

Discussion

The long-term monitoring of a central Amazonian forest covering droughts but also wet extremes (Fig. 1) has revealed negative effects of both extreme rainfall anomalies on tree growth and survival, but also that, contrary to literature-based expectations, periods of extreme wetness were as important, and even stronger,

determinants of forest dynamics than droughts in central Amazonia (Fig. 2). Notwithstanding negative isolated effects, the interaction of both rainfall anomalies had the highest impact on tree responses, this actually being positive (Fig. 3). We also detected that the topographically defined hydrological environments modulated drought effects (Fig. 4), so that forests over SWTs function as hydrological refugia. Wood density, despite being lower in SWT forests (Fig. S7), does not make plants associated with this environment necessarily more vulnerable to droughts, as they are protected by the hydrology itself.

Extreme drought conditions can cause water stress in plants, reducing forest productivity (Ciais *et al.*, 2005; Yue *et al.*, 2017), or as reported in most studies of drought effects on forests, inducing widespread tree mortality (Allen *et al.*, 2010; Anderegg *et al.*, 2013). This drought-related mortality can be driven through

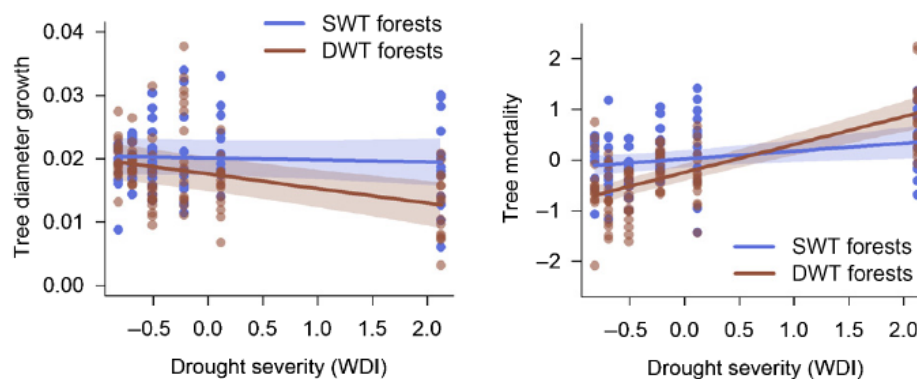


Fig. 4 Topography as buffer of negative drought effects on tree demographic responses. Partial relationships between periods of water deficit, topography and demographic rates, showing significant interactions between the severity of drought (water deficit index, WDI) and the topographic affiliation of the species (to forests over deep or shallow water tables) on tree diameter growth (left) and tree mortality (right). Species associated with shallow water tables (SWTs, with height above nearest drainage (HAND) values from 9.2 to 20 m) do not show decreased growth or increases in mortality as drought becomes more severe (light blue solid lines, with light blue shading displaying 95% confidence intervals (CIs)). Species associated with deep water tables (DWTs, with HAND values from 21 to 33 m), though, present large decreases in growth and increases in mortality as drought severity increases (brown solid lines, with brown shading displaying 95% CIs).

various mechanisms, mainly hydraulic failure, carbon starvation or increased vulnerability to pests (McDowell *et al.*, 2008). On the other hand, the negative impacts of very wet periods on tree demographic rates may have either a physiological or a mechanical cause. Physiologically, a larger amount of time under waterlogged conditions, and thus hypoxia or anoxia, can be detrimental to tree growth and potentially end up increasing mortality (Parent *et al.*, 2008). Nonetheless, waterlogging may only affect SWT forests, while in this study growth reduction and mortality increment were observed on tree species across the full topographic gradient. Thus, more plausible explanations for this forest-wide effect of wet extremes on trees are that it is mainly physiological for tree growth, as a long duration of wet periods is related to increased cloud cover, which in turn leads to increased limitation on light for photosynthesis (Graham *et al.*, 2003); and it is primarily mechanical for tree mortality, through the increased occurrence of windstorms, which accompany episodes of heavy rainfall and have been reported as an important disturbance factor to the Amazon (Espírito-Santo *et al.*, 2010; Chambers *et al.*, 2013; Marra *et al.*, 2014, 2018; Negrón-Juárez *et al.*, 2018). Peaks of tree mortality have been observed to occur more frequently in rainy periods (Fontes *et al.*, 2018; Aleixo *et al.*, 2019), suggesting that certain Amazonian forests can be highly vulnerable to extreme wet periods, as reported in large-scale (Negrón-Juárez *et al.*, 2017, 2018) and long-term assessments (Aleixo *et al.*, 2019).

Still, beyond these relevant negative isolated effects, we found that the highest relative contribution in all the best models to explain tree growth and mortality was given by the interaction of both extreme rainfall-related climate anomalies, which actually resulted in higher tree growth and lower tree mortality than when these anomalies occurred alone (Fig. 3). This counterbalance effect observed when extreme wet and drought conditions occurred during the same census period suggests the role of a key component of water dynamics that probably drives this interaction: the groundwater.

More than 30% of the freshwater on Earth is held as groundwater (Shiklomanov, 1993). This component, though, is extremely complicated to study. Thus, the groundwater dynamics and its role in forest hydrological processes (particularly the potential influence in forest responses to actual and future climate change scenarios) are still poorly understood. Across Amazonia, groundwater plays an important role in the seasonal hydrological cycle behavior: during wet periods, it stores a large part of the water excess (when rainfall is greater than evapotranspiration), being able to feed and maintain surface water bodies during the following dry periods (Lesack, 1993; Miguez-Macho & Fan, 2012b). Nonetheless, once it is a limited source, large reductions in rainfall during severe droughts could lead to a substantial decrease in groundwater storage, which in turn could drastically affect the whole system. Therefore, the mechanism by which the groundwater system is presumably driving the interactions between extreme wet and drought periods, leading to a buffering of the negative impacts over tree growth and mortality rates, would be the groundwater memory effect.

In a very similar system to the one studied here, Tomasella *et al.* (2008) observed that the effect of periods with rainfall anomalies over the groundwater levels strongly persist beyond the year during which the anomaly occurred, suggesting the existence of a strong memory effect of local-scale groundwater systems in Amazonia. This mechanism was later confirmed at regional and basin scales as well, through modeling studies that coupled both surface and groundwater dynamics (Fan & Miguez-Macho, 2010; Miguez-Macho & Fan, 2012b), or by monitoring changes with satellite-based measurements of phreatic levels (Pfeffer *et al.*, 2014). An implication of this hydrological memory is that previous rainfall periods recharging soil-water storage can establish soil moisture conditions with sufficient water availability for plants to maintain their processes (as evapotranspiration) during moderate dry conditions (Negrón-Juárez *et al.*, 2007) or even during severe droughts (Broedel *et al.*, 2017). This argument is reinforced by the fact that hydrology studies in Amazonia indicate that surface

runoff is generally very small (Lesack, 1993; Cuartas, 2008; review in Miguez-Macho & Fan, 2012a), and thus most of the rainfall (*c.* 90%) is incorporated into the soil and recharges the groundwater. At the same time, the vertical drainage along the soil profile until it reaches the water table is very slow (Hodnett *et al.*, 1997; Tomasella *et al.*, 2008; Rodrigues, 2019), meaning that this water is not lost to the streams and rivers via horizontal drainage for a considerably long time, consequently being available for plants.

Our empirical observations (Fig. 1) suggest that the combination of drought and wet extremes generally occurs in a 'wet then dry' sequence (in 2005, 2006, 2008 and 2009), and a short interval between the peak of both extreme events (up to 5 months, as in 2009–2010) may be needed for the occurrence of the positive effect on the vegetation. Results also suggest that the water excess anomaly does not have to be as extreme as the drought anomaly to function as a buffer. Thus, based on all these factors, we argue that 'wet then dry' sequences (*i.e.* a lasting recharge of soil moisture as a consequence of precedent extreme wetness periods) coupled with the memory effect of the whole groundwater system are the most plausible explanation for why wet extremes acted as buffers of negative drought impacts on tree demographic rates.

We also showed that species associated with SWT forests were significantly less affected by severe drought periods than those associated with deeper ones. SWT forests tend to have higher tree mortality in nonextreme climate conditions (Fig. S5; see also Ferry *et al.*, 2010; Toledo *et al.*, 2016), probably as a result of the dominance of faster-growing species (Cosme *et al.*, 2017; Schmitt *et al.*, 2020) with lower biomechanical stability (Van Gelder *et al.*, 2006) and the instability of seasonally waterlogged soils (Hough, 1957). Tree hydraulic resistance is also lower in SWT forests (Oliveira *et al.*, 2019). Notwithstanding that, tree species in these environments actually suffered less than those in DWT forests during extreme drought conditions (as in 2015–16). These differences in tree responses along the hydrological gradient must be linked to the buffering capacity of the SWT levels on lowlands, which may function in drought conditions as hydrological refugia, that is, locations on the landscape that support populations of a species while the surrounding climatic conditions become unsuitable for that species (McLaughlin *et al.*, 2017; Sousa *et al.*, 2020). In valleys, the water table level is shallow and can supply moisture to roots year-round, even in drought years (Hodnett *et al.*, 1997; Cuartas, 2008). Therefore, although severe dry periods are usually characterized by lower rainfall and higher VPD, soil moisture could only be significantly lower at upper topographic positions, meaning that topography modulates vegetation responses to drought (Hawthorne & Miniati, 2018). Moreover, the water table level is dephased from the rainfall, such that the lowest level does not occur at the peak of the dry season but actually a few months later or at the beginning of the wet season (Tomasella *et al.*, 2008), when rains rewet the surface soil. Thus, tree species associated with SWTs may rarely, if ever, experience hydrological droughts.

In addition, soil properties (mainly soil texture) can largely determine the final soil water profile through regulation of

rainfall infiltration and groundwater capillary rise (Fan *et al.*, 2017). The specific combination of soil texture and water table depths along the studied topographic gradient (Chauvel *et al.*, 1987), and most of the terrains derived from Guiana and Brazilian shields (Sombroek, 2000), creates favorable conditions for the memory effect and protection against drought. In DWT forests, the prevalence of fine-textured (clayey) soils, with greater water retention and slower infiltration, enhances the groundwater memory effect in these rainfall-dependent forests, ensuring that water from a preceding high-rainfall period is available for plants during severe droughts (Fig. 3). In SWT forests, despite the prevalence of sandy soils that can worsen drought impacts (through fast infiltration rates and low soil water retention), the close contact with the water table counteracts this tendency towards water loss, allowing trees to cope with droughts (Fig. 4).

Species-specific WD, a key trait in plant ecological strategies, hydraulic safety, mechanical stiffness and overall tree performance (Van Gelder *et al.*, 2006; Chao *et al.*, 2008), was the only functional trait with significant effect on tree demographic responses. As expected, denser wood was associated with lower diameter growth and mortality rates (Fig. S6), reflecting the classical growth–survival tradeoff of plant life strategies. But beyond that, species WD was strongly associated with the hydrological environment, being higher in species affiliated to deeper water tables (Fig. S7). This result, in agreement with previous studies (*e.g.* Cosme *et al.*, 2017; Fontes *et al.*, 2020), highlights the role of topographically defined hydrological conditions as environmental filters of species' taxonomic and functional composition of Amazonian forests, with consequences for forest dynamics. Species with low WD should be those most negatively affected by droughts, as shown elsewhere (Aleixo *et al.*, 2019). However, their association with SWT forests counteracts the negative drought effects, which reinforces the importance of SWTs as buffers to drought.

The implications of these patterns for the future composition of the forest would depend on the dominant type of climatic change. While a potential future increase in the frequency and intensity of wet anomalies could reinforce the filtering of fast-growing species in SWT forests (generating even more dynamic forests), increased dry anomalies could push the forest in the reverse direction (decreased contribution of acquisitive species), if the decrease in precipitation were strong enough to actually cause water table levels to drop significantly in the valleys. Conversely, as forests over DWTs are characterized predominantly by more conservative trees, rooted on deep and stable soils, the opposite patterns described for SWT forests can be expected.

Conclusion

Climate change is critically impacting ecosystems worldwide, mainly through increased variability in the hydrological cycle. Amazonia, the major tropical rainforest, has been the scenario of several climate extremes (Marengo & Espinoza, 2016) and it is expected to get worse over this century (Marengo *et al.*, 2018). Droughts have received particular attention, being highlighted as the major driver of negative impacts in this region. However, we

have shown here that extreme wet events and local topography are modulators of droughts in a central Amazonian forest, providing buffers that counteract its negative effects on tree demographic rates.

The existence of these insurance effects in regions with large areas of SWTs, or with a trend for increasing wet anomalies alongside the dry anomalies, means that previous projections of drought impacts may be overestimated. At least 36% of the forests in Amazonia lie over SWTs (Fan & Miguez-Macho, 2010). Moreover, there has been a significant rainfall increase over the past four decades in most of the northern Peruvian and Brazilian regions, and there are projected increases in both the frequency and extent of extreme wet periods for the coming decades (Gloor *et al.*, 2013; Duffy *et al.*, 2015; Espinoza *et al.*, 2019). This study, the first to our knowledge showing buffers of drought effects on Amazonian tree species along a high range of hydrological and topographic conditions (also see Sousa *et al.*, 2020 for a region dominated by SWT forests), highlights the importance of considering both extreme wetness episodes and hydro-topographic influences when evaluating drought impacts. These have relevant consequences for understanding and predicting the impact of current and future climate: first, the groundwater memory effect can potentially rescue Amazon forests from extreme dry conditions when droughts are preceded by extreme wet periods; second, the large portion covered by SWT forests indicates large potential hydrological refugia. None of these mechanisms is properly acknowledged in models describing or predicting the Amazon's vulnerability to climate change and may also have been omitted in the majority of Amazonian drought reports.



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Author contributions

EJLE and FRCC conceived the study. FRCC, CVC and KLM conducted field work and collected the data. EJLE analyzed the data and wrote the first draft of the manuscript. All authors contributed to manuscript drafts and gave final approval for publication. EJLE and FRCC contributed equally to this work.

ORCID

Flávia R. C. Costa  <https://orcid.org/0000-0002-9600-4625>
Erick J. L. Esteban  <https://orcid.org/0000-0001-9751-745X>

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Annual trend and monthly anomalies of rainfall in a central Amazon forest along the last five decades.

Fig. S2 Historical data of monthly precipitation values for the Ducke Reserve.

Fig. S3 Graphical representation of how the water deficit index (WDI) is calculated based on the cumulative water deficit (CWD) values.

Fig. S4 Negative effects of rainfall anomalies on tree demographic rates.

Fig. S5 Influence of topographic affiliation on tree demographic rates.

Fig. S6 Influence of wood density on tree demographic rates.

Fig. S7 Wood density is associated with hydrological environments generated by topography.

Table S1 Selected tree species.

Table S2 Predictors of Amazonian tree diameter growth in response to climate anomalies.

Table S3 Predictors of Amazonian tree mortality in response to climate anomalies.

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