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The other side of tropical forest drought: do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought?

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Contents

Summary	1	V. Agenda: revealing the role of water table depth variation in tropical forest climate response	14
I. Introduction	2	VI. Conclusions	16
II. The importance of water table depth spatial patterns and dynamics to the Amazon forest	6	Acknowledgements	16
III. Current evidence for contrasting structure and function of shallow water-table depth forests	9	References	17
IV. Conceptual framework to account for soil water regimes in forest climate responses	11		

Summary

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Tropical forest function is of global significance to climate change responses, and critically determined by water availability patterns. Groundwater is tightly related to soil water through the water table depth (WT), but historically neglected in ecological studies. Shallow WT forests (WT < 5 m) are underrepresented in forest research networks and absent in eddy flux measurements, although they represent c. 50% of the Amazon and are expected to respond differently to global-change-related droughts. We review WT patterns and consequences for plants, emerging results, and advance a conceptual model integrating environment and trait distributions to predict climate change effects. Shallow WT forests have a distinct species composition, with more resource-acquisitive and hydrologically vulnerable trees, shorter canopies and lower biomass than deep WT forests. During 'normal' climatic years, shallow WT forests have higher mortality and lower productivity than deep WT forests, but during moderate droughts mortality is buffered and productivity increases. However, during severe drought, shallow WT forests may be more sensitive due to shallow roots and drought-intolerant traits. Our evidence supports the hypothesis of neglected shallow WT forests being resilient to moderate drought, challenging the prevailing view of widespread negative effects of climate change on Amazonian forests that ignores WT gradients, but predicts they could collapse under very strong droughts.

Resumo

O funcionamento da floresta tropical é de importância global para as respostas às mudanças climáticas e é criticamente determinado pelos padrões de disponibilidade de água. A água subterrânea está intimamente relacionada à água do solo através da profundidade do lençol freático, que tem sido historicamente negligenciado em estudos ecológicos. Florestas com lençol freático raso (<5 m) estão sub-representadas nas redes de pesquisa florestal e ausentes nas medições de fluxo de gases, embora representem ~50% da Amazônia e devam responder de forma diferente às secas relacionadas às mudanças globais. Aqui revisamos os padrões de profundidade do lençol freático e suas consequências para plantas, resultados emergentes, e avançamos em um modelo conceitual que integra o ambiente e as distribuições de características funcionais para prever os efeitos das mudanças climáticas. As florestas com lençol freático raso têm uma composição de espécies distinta, com árvores mais aquisitivas na obtenção de recursos e hidrológicamente vulneráveis, dosséis mais baixos e menor biomassa do que as florestas com lençol freático profundo. Durante os anos climáticos 'normais', as florestas com lençol freático raso têm maior mortalidade e menor produtividade do que as florestas com lençol freático profundo, mas durante secas moderadas, a mortalidade é amortecida e a produtividade aumenta. No entanto, durante secas severas, as florestas com lençol freático raso podem ser mais sensíveis devido às raízes superficiais e características funcionais de intolerância à seca. Nossas evidências apoiam a hipótese de que as florestas com lençol freático raso, historicamente negligenciadas, sejam resilientes à seca moderada, desafiando a visão predominante dos efeitos negativos generalizados da mudança climática nas florestas amazônicas que ignora gradientes de profundidade do lençol freático, mas prevê que elas podem entrar em colapso sob secas muito fortes.

Resumen

La función de los bosques tropicales es de importancia mundial para las respuestas al cambio climático y está críticamente determinada por los patrones de disponibilidad de agua. El agua subterránea está estrechamente relacionada con el agua del suelo a través de la profundidad del nivel freático (NF), pero históricamente se ha negligenciado en los estudios ecológicos. Los bosques con NF poco profundos (NF < 5 m) están subrepresentados en las redes de investigación forestal y ausentes en las mediciones de flujo de gases, aunque representan ~50% de la Amazonía y se espera que respondan de manera diferente a las sequías relacionadas con el cambio climático global. Aquí revisamos los patrones de NF y las consecuencias para las plantas, los resultados emergentes y avanzamos en un modelo conceptual que integra distribuciones ambientales y de rasgos funcionales para predecir los efectos del cambio climático. Los bosques con NF poco profundos tienen una composición de especies distinta, con árboles más adquisitivos en la obtención de recursos e hidrológicamente más vulnerables, dosel más bajo y menor biomasa que los bosques de NF profundo. Durante los años climáticos 'normales', los bosques con NF poco profundos tienen una mayor mortalidad y menor productividad que los bosques con NF profundos, pero durante sequías moderadas la mortalidad se amortigua y la productividad aumenta. Sin embargo, durante una sequía severa, los bosques de NF poco profundos pueden ser más sensibles debido a raíces poco profundas y rasgos de intolerancia a la sequía. Nuestra evidencia apoya la hipótesis de que los bosques de NF poco profundos, mayoritariamente desconsiderados, son resistentes a sequías moderadas, desafiando la visión predominante de impactos negativos generalizados del cambio climático en los bosques amazónicos, que ignora los gradientes de NF, pero predice que podrían colapsar bajo sequías muy fuertes.

I. Introduction

Water availability to plants is an important driver of plant ecology, from species distribution to ecosystem functioning (Whittaker, 1975; Silvertown *et al.*, 2015). Changing water availability and limitation is central to the global response of vegetation to climate change (Guan *et al.*, 2015). During some large-scale climate anomalies rainfall is reduced and tropical forest function can shift from ameliorating global warming to contributing to it; for

example, during the strong El Niño of 2015 to 2016 tropical forests released a net 2.5 ± 0.34 gigatons of carbon into the atmosphere (Liu *et al.*, 2017). Droughts linked to climate change can also kill tropical trees and cause large carbon emissions, enhancing climate warming in a dangerous feedback (Allen *et al.*, 2015; Brienen *et al.*, 2015). However, the long-term resilience (or sensitivity) of tropical forest to droughts is poorly resolved for forecasting (Friedlingstein *et al.*, 2014). Global vegetation simulation models predict a wide gamut of tropical forest responses to climate change ranging from

forest collapse to robust resilience (IPCC, 2013; Friedlingstein *et al.*, 2014; Negrón-Juárez *et al.*, 2015). Furthermore, these large-scale models neglect hydrologic variation, even in recent models accounting for climate and landscape heterogeneity in soils and land use (Levine *et al.*, 2015; Longo *et al.*, 2018; but see Fang *et al.*, 2017), which contributes to uncertainty (Chitra-Tarak *et al.*, 2018). Resolving this uncertainty is a pressing challenge that requires an integrative ecological Earth System approach to better link aboveground and belowground forest processes, including all factors determining soil water availability and variation.

Uncertainty in forest sensitivity to drought undermines our ability to predict tropical forest climate feedbacks to global warming (Allen *et al.*, 2015; McDowell *et al.*, 2018). Because of the importance of soil water, a bias in field research to well drained and deep water table sites that tend to be more drought-sensitive significantly exacerbates this uncertainty (Fig. 1a). Plant soil water availability is a critical determinant of ecosystem structure and function resulting from the interplay of water input (via precipitation), water loss (via evapotranspiration and drainage), and water retention (affected by soil

characteristics and topography), particularly groundwater storage (Fig. 1b). Thus, the interaction of precipitation, topography, soil properties and groundwater, gives rise to the local soil water availability, which is reflected in the water table depth (WT) (Davie, 2008; Marklund, 2009). Sites with high water drainage potential, with deep water tables (high-grounds or plateaus, Table 1), are more directly linked to climatic fluctuations, since roots are decoupled from the water table, sites in intermediate topographic positions, at toe slopes or river terraces, are relatively well-drained but access moisture via proximity to groundwater, while in sites with low drainage potential and thus shallow WT (low-grounds or valleys), tree roots may be in direct contact with the water table or the capillary fringe (Fan *et al.*, 2017). Thus, deep WT forests that rely on precipitation inputs, are expected to be more hydrologically exposed to drought, and may in effect be more drought-sensitive than those over shallow WT with access to groundwater (Table 1). Drought tolerant functional traits, in contrast, are expected to be more frequent over deep rather than shallow WT because of drought exposure, and this trait distribution may reverse the drought

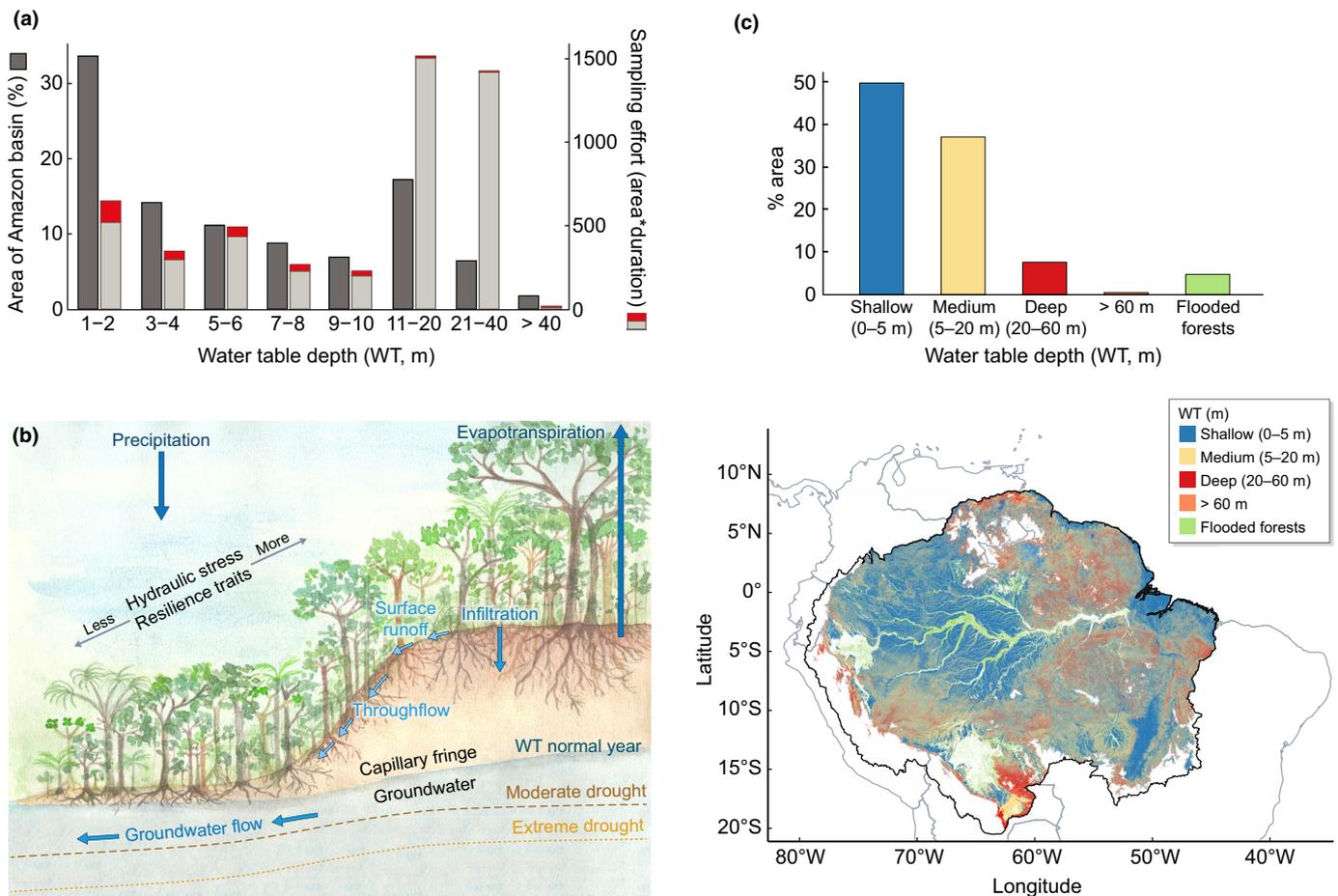


Fig. 1 Water table depth (WT) in perspective. (a) The disproportional plot sampling effort across WTs (black bars showing percent Amazon basin in WT categories from Fan & Miguez-Macho (2010) WT product, gray and red bars showing sampling effort from forest plots). Sampling effort was calculated as plot size (in hectares) \times census duration (in years). Gray bars indicate sampling effort of plots analyzed by Brienen *et al.* (2015) (319 plots), red bars indicate sampling effort of a new network of 86 PPBio plots (Supporting Information Table S1). (b) The components of the water cycle creating variability in local hydrological conditions across topography and the expected behavior of WT across drought scenarios. (c) The distribution of WT across the Amazon (map) and the percent of Amazon basin area (bar chart) in five WT classes (redrawn from model output from Fan & Miguez-Macho (2010)). WT classes: shallow (< 5 m, blue, 49.9%), medium (5–20 m, yellow, 37.2%), deep (21–60 m, red, 7.7%), > 60 m (orange, 0.5%), and floodplain forests (green, 4.8%).

Table 1 Definitions of important terms.

Term/concept	Definition	Citation
Ancient shield land-formation	Geological formations of mostly Proterozoic origin, comprising the Guiana and Brazilian shields, where the long history of erosion has left a dominant topography of rolling to hilly dissected lands and rounded hills with convex slopes	Sombroek (2000) Gómez <i>et al.</i> (2019)
Anoxia	Complete absence of oxygen in the rooting zone	
Capillary fringe	The zone above the water table where the groundwater seeps up by tension (capillary force) and fills pores. The thickness of the capillary fringe depends on the soil texture, from a few centimeters in sandy soils to several meters in clayey soils	Berkowitz <i>et al.</i> (2004) Lohman (1972)
Ecosystem functional response	In the context of hydrological regimes, this is a curve giving the expected value at the ecosystem level of some function such as tree growth over variation in soil hydrological states	For related concepts see Díaz & Cabido (1997); Savage <i>et al.</i> (2007); Enquist <i>et al.</i> (2015)
Groundwater	Water in the subsurface that fully saturates the pores or cracks in soils and geological formations (aquifer)	Freeze & Cherry (1979)
Growth window	Period favorable for plant growth (as defined by a proportion of the annual peak growth). Mesic, predominantly aseasonal Amazon forests may have a full year growth window, while in waterlogged forest growth mostly occurs in the period with drier aerated mesic soil conditions. In high-ground highly seasonal forest, the growth window occurs in the wet season when water is sufficiently available. Similar to the familiar 'growth season' concept, but more appropriate for tropical forests where established climatological seasons, when present, may not directly correspond to tree growth windows because of hydrological factors	This study
Inundated (flooded) soil	To avoid confusion with waterlogged soils, we distinguish inundated soil as when water saturates the soil and exceeds the soil surface; present in seasonally flooded forest types such as várzea and igapó	This study
High-grounds vs low-grounds	High-grounds are the upper parts of the topographic profiles (catenas) where the soil is well drained and the groundwater flow is divergent ('hilltops' or 'plateaus'), while low-grounds are the regions where the groundwater flow is typically convergent (e.g. 'valleys'). High-grounds have deeper water table depth (WT) and low-grounds shallower WT	Miguez-Macho & Fan (2012a)
Hypoxia	Oxygen depletion caused by soil water saturation in the rooting zone	
Moderate and severe drought	In this article we define moderate droughts as those that do not cause a reduction of soil water availability in shallow water table forests, and that do not decrease the water table level below the reach of roots. Severe droughts, in contrast, result in water tables out of the reach of roots	This study
Oases vs hydrological refugia	Oases are zones of the landscape with high water availability (mesic environments) generated by groundwater convergence that result in shallow water tables, having little dependence on climate processes, where plants can develop and persist despite a predominantly dry climate. Hydrological refugia are shallow water table zones of the landscape that behave as oases when there is atmospheric water scarcity (droughts). These zones are relatively buffered from climate change droughts	Fan (2015) McLaughlin <i>et al.</i> (2017)
Shallow vs intermediate vs deep WT	WT < 5 m, where most roots are potentially in direct contact with the groundwater or the capillary fringe, is considered shallow. Depending on soil properties, WT up to 10 m may still be accessed seasonally by roots, while WT > 20 m is most likely out of reach for roots and is here considered deep. Thus, WT 5–20 m is intermediate, and WT > 20 m is considered deep	Fan <i>et al.</i> (2017)
Shallow WT vs inundated forests (also referred as flooded or floodplain forests, encompassing 'várzea' and 'igapó' types)	Shallow WT appear in low topographic positions, mostly due to groundwater convergence from higher positions. Shallow WT may also arise if an impermeable soil layer blocks water drainage to the saturated zone, creating perched water tables (when the water table is above the regional level). Shallow water table conditions are distinct from inundated conditions created by regular seasonal floods (flood pulse) in floodplains adjacent to many large and intermediate sized Amazon rivers, where flood pulse amplitudes range from 2 to 15 m. Acknowledging that floodplain forests experience shallow WT conditions during a portion of the low-river level season, and may represent an extreme 'end member' of soil water regime variation, we restrict our definition of shallow WT forests to regions that do not regularly experience flooding. Hence, we classify seasonally flooded floodplain forests as a type of wetland (as per Hess <i>et al.</i> , 2015), comprising 5% of the Amazon (Fig. 1a,c), and not as shallow WT forest	Junk <i>et al.</i> (2014) Fan (2015) Freeze & Cherry (1979)

Table 1 (Continued)

Term/concept	Definition	Citation
Soil water (hydrological) regime	The long-term soil water content means and variation. It summarizes the seasonal and interannual patterns of the amount of water in the soil layer at a site, which is critically determined by rainfall inputs and groundwater, mediated by soil characteristics and landform/topographic factors. The soil water regime encompasses water deficit to water excess conditions, and is an essential component of the environment impacting plant functional assembly and responses	This study; for similar definition of 'rainfall regime' see Longo <i>et al.</i> (2018)
Unsaturated zone	Also called the <i>zone of aeration</i> or <i>vadose zone</i> , this is the nonsaturated part of the subsurface between the land surface and the water table.	Freeze & Cherry (1979)
Waterlogged soil	Here we define waterlogged soil as when water saturates the soil, but does not exceed the soil surface as a water column, although it creates root hypoxic to anoxic conditions stressful for plants. These soils can be recognized by distinctive gray horizons that result from reduction–oxidation processes	This study
Water table	The continuous surface separating the saturated (groundwater) and unsaturated zones, at which the atmospheric pressure equals the water pressure	Marklund (2009)
Water table depth (WT)	The annual average vertical distance from land surface to the surface of the groundwater (saturated zone)	Fan <i>et al.</i> (2013, 2017)
Water table depth (WT) fluctuation	The variation in WT that occurs in a particular location through time, a dimension of soil water regime variation. WT variation can be measured by the difference between the minimum and maximum WTs along the hydrological year (intra-annual or seasonal variation) or among years. The water table level rises due to increased groundwater storage when the rate of recharge exceeds the rate of discharge and declines when these conditions are reversed	Marklund (2009)
Young Fluvio-lacustrine land-formation	Neogene-Quaternary geological formation that comprises large lowland areas of rivers and lake sediment deposits in the western and central Amazon basin	Sombroek (2000)

responses of shallow vs deep WT forests when droughts become stronger. Intermediate WT forests experience mesic conditions most of the time, but may face strong drought impacts if traits more closely resemble shallow WT forests, though the latter currently lacks documentation. Nevertheless, WT variation is absent from most studies of drought effects and global vegetation models, despite recognition and ongoing progress by the ecohydrology community (reviewed in Fan *et al.*, 2019; see also Roebroek *et al.*, 2020; Tai *et al.*, 2020). We explore the significance of WT variation here, considering both direct effects of soil water on plant performance and of long-term soil water regime variation on community-scale physiological drought (and waterlogging) tolerance.

Soil moisture is a central determinant of plant function, and WT an effective indirect indicator of soil water conditions where groundwater plays significant roles. Despite the potentially critical contribution of WT to forest function and the fact that shallow water tables make up a large proportion of the Amazon (Fig. 1a,c), the majority of studies in forest ecology and ecosystem function focus on the climatic drivers of tree responses, while tending to overlook local soil water dynamics. In the Amazon basin, and in many tropical forests around the world, the soil water table plays a large role determining plant water availability and forest evapotranspiration (Miguez-Macho & Fan, 2012a). Published estimates of the area of the Amazon basin comprising shallow water tables (< 5 m) range from 36% to 60% (Fan & Miguez-Macho, 2010; Miguez-Macho & Fan, 2012b, respectively), depending on the model used to force the WT simulation (CLM and HTESEL, respectively). Our reanalysis of WT products by Fan & Miguez-Macho (2010) and Fan *et al.* (2013) gives values between 47% and 64%, for which variation is due to the spatial resolution of the WT product, Amazon boundary, and whether wetland areas are

included or not in the shallow WT group (Supporting Information Table S1; for WT classes presented in Fig. 1(a,c) we utilize the WT estimates of Fan & Miguez-Macho (2010) and consider seasonally flooded forest a separate wetland type, distinct from shallow WT forest; see Table 1). Yet forests over shallow water tables are strongly underrepresented in long-term forest monitoring efforts (Fig. 1a). Neglecting WT variation may explain controversial debates about the resilience of tropical forests to drought, and the Amazon in particular, with remote sensing studies (covering all forest types) showing resilience (e.g. Brando *et al.*, 2010; Guan *et al.*, 2015), and forest inventory plots (mostly focused on deep WT) showing vulnerability to drought (e.g. Phillips *et al.*, 2010; Brienen *et al.*, 2015). We propose that the typically understudied shallow WT forests are more resilient to drought than other forests, and generally represent hydrologic refugia from drought (*sensu* McLaughlin *et al.*, 2017), due to critical differences in underlying soil water regimes (Fig. 1b).

In this article we review what is known about WT variation in the Amazon (Section II), its effects on forest traits, structure and dynamics (Section III), and propose a new conceptual framework and hypotheses linking WT, climate, and trait ecology to better predict forest responses to increasing drought and changing soil hydrological regimes (Section IV). Throughout this review we focus on comparisons among deep and shallow extremes of the WT gradient, with less data available to evaluate intermediate WT positions; however, we consider the full continuous gradient of hydrological conditions in our conceptual treatment.

Our hypothesis (Section IV) recognizes that climate interacts with topography in its effects on soil water availability and thus on vegetation response (Fan *et al.*, 2019; Roebroek *et al.*, 2020). In mesic to drier climates, shallow water tables supply water that

enhances productivity. However, within large expanses of the Amazon with moist to very wet climates, shallow water tables create anoxic conditions, limiting plant function and development. The relief of these conditions as WT levels decrease in moderate droughts should be beneficial, extending the plant growth window when soils are moist but not anoxic (Section III). Soil water regimes in the long-term also critically impact community functional composition, which mediates responses to soil water extremes. Evolutionary adaptation and ecological community assembly, including environmental filtering, will assort plant functional responses to match soil hydrological regime variation to a certain degree (Silvertown *et al.*, 2015). There is evidence (Section III), that trees in wet forests with shallow WT have hydraulic systems less resilient to water stress. In these conditions, even where moderate dry seasons are typical, we expect relatively little selection for water stress and drought resistance traits. Shallow WT forests are also characterized by shallow root systems, an adaptation to the negative effects of soil anoxia (Section III); together, these traits should make shallow WT forest highly sensitive to hydraulic failure under very strong drought, decreasing growth and threatening high tree mortality. We hypothesize that the response of the Amazon region as a whole to climate change, and its future contribution to the exacerbation or mitigation of warming, will critically depend on the differential sensitivities of shallow vs deep WT forest to changes in soil water availability (Fig. 2). We predict that through intermediate warming and drying of the Amazon, shallow WT forest resilience will ameliorate carbon losses, potentially synergizing with biomass enhancing CO₂ fertilization to better allow the region's forests to act as carbon sinks (Lloyd & Farquhar, 2008; but see Fleischer *et al.*, 2019). However, we predict strong sensitivity of shallow WT forests to more severe (and frequent) droughts, contributing to a potential tipping point-type collapse of future forest and carbon sink integrity (Fig. 2). We elaborate on this continuum of responses from positive to negative and the long-term trajectory of the Amazon climate function in Section IV.

In our final main section (Section V) we advance an agenda to rapidly improve understanding of soil hydrological regime mediation of tropical forest climate responses and feedback. We highlight crucial data network needs and opportunities spanning field-to-remote sources and physiological to demographic processes, essential to understand the future of the Amazon and other tropical forests.

II. The importance of water table depth spatial patterns and dynamics to the Amazon forest

Groundwater is a critical source of water for plants when the soil is not recharged by precipitation inputs. Consistent with this, plant rooting depth worldwide is more closely coupled to WT than to any other soil or climatic variable (Fan *et al.*, 2017). However, water table levels (see Table 1) vary over time, and thus plant access to this resource may not be continuous. The depth of the water table and its temporal fluctuation, both seasonally and inter-annually, may be key to understanding the responses of vegetation to climate variations. The WT varies from < 1 to 40–65 m across the Amazon basin (Miguez-Macho & Fan, 2012a; CPRM, 2021). Considering the geographical estimate of WT from the data-constrained groundwater simulation model of Fan & Miguez-Macho (2010), we find that 50% of the Amazon area has shallow water tables, an additional 37% medium WTs (5–20 m), 8% deep WTs (> 20 m), and 5% are seasonally flooded forests (Fig. 1a,c; and see Methods S1; Notes S1; Table S1; Figs S1, S2, where we also consider coverages in just *terra firme* areas, excluding seasonally flooded forest as wetland). Furthermore, during the late wet season, 48% of the Amazon basin can experience very shallow WTs (< 2 m; Miguez-Macho & Fan, 2012b). Forests over shallow water tables are thus an important, yet undersampled and underaccounted, Amazon forest type (Fig. 1a; Methods S1; Table S2).

Groundwater plays a key role in the hydrological cycle (Fig. 1b), storing water from precipitation, supplying water to

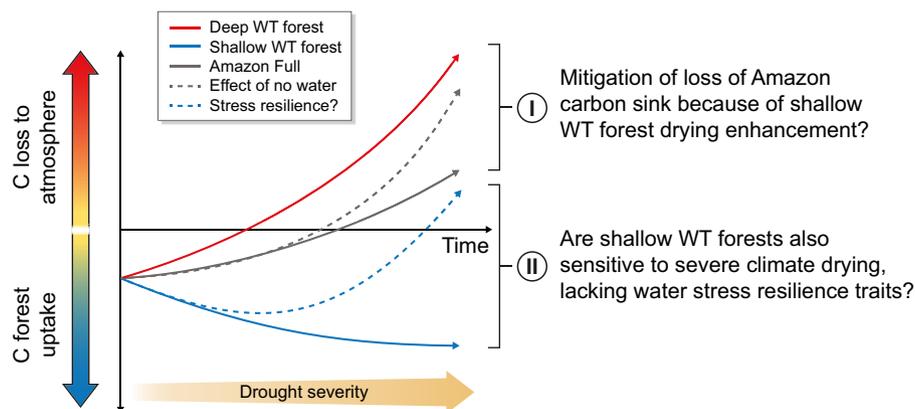


Fig. 2 Hypothesized significance of water table depth (WT) to long-term climate change impacts. We hypothesize that deep WT forests are sensitive to drought (c. two-fifths of the basin, red curve), which causes a decrease in the Amazon carbon sink as climate change intensifies drought impacts. Shallow WT forests, in contrast, may act as hydrologic refugia, benefitting from drought-enhanced longer growing seasons free from waterlogging, enhancing carbon sinks in half of the basin (solid blue curve). The net impact (shown in 'I') is a mitigation of carbon loss (solid black curve, weighted mean of blue and red curves). Shallow WT forests also have superficial root systems, and may lack drought resilience traits, such that severe drought could pass a threshold causing severe carbon loss (shown in 'II', and by dashed lines). Carbon sink reductions could eventually surpass those in deep WT forests with shallow WT forest contributing to an Amazon tipping point.

rivers and lakes, and supporting portions of ecosystem evapotranspiration. In a forested drainage basin, the portion of water from precipitation that is not intercepted by vegetation and evaporated from wet surfaces, flows across the land surface and seeps through unsaturated soil layers until it reaches the groundwater (runoff in Amazon forests is small; Lesack, 1993; Hodnett *et al.*, 1997; Grogan & Galvão, 2006). The regional climate determines recharge, and together with soil properties (primarily texture) regulates infiltration. However, it is the local topography that controls water drainage, and ‘this is why the water table depth (WT) reflects local topography as much as or more than regional climate’ (Fan *et al.*, 2017). Thus, the main factors controlling WT and its seasonal fluctuation – which we argue is the central feature of the Amazon soil hydrological regime – are the regional precipitation regime, topographic heterogeneity and soil properties (Miguez-Macho & Fan, 2012b; Fang *et al.*, 2017). In the subsections that follow we briefly detail the most important features impacting WT, the spectrum of soil hydrological regimes of the basin, and the associated physical and physiological consequences for plants.

1. Spatial and temporal variation – water table depth interactions with climate, geomorphology and soils

Amazonia is made up of two major land formations (Gomez *et al.*, 2019; Fig. 3a) that affect the properties of shallow water table environments. The first comprises young (Neogene-Quaternary) interfluvial/fluviolacustrine deposits in the western to central portion of the basin, where the shallow water table environment covers large mostly undissected lowland areas (Fig. 3a). The second land formation is composed of highly weathered sediments, characteristic of older rolling and deeply incised terrain that developed on Guianan and Brazilian crystalline shield blocks, found in eastern, northern and southern portions of the Amazon. This formation also includes the eastern sedimentary uplands along the Amazon River, characterized by an alternation of flat and undulating terrains derived from crystalline shield materials (Alter do Chão formation; Sombroek, 2000). In these old dissected land formations, forests over shallow water tables are mostly confined to the margins of streams and river valleys in the bottom of topographic profiles, and are thus less extensive, more dissected and spatially heterogeneous than those in the young terrains of the western-central Amazonian lowlands. The ‘plateaus’ and ‘valleys’ of these dissected formations correspond with broader definitions we adopt here from Miguez-Macho & Fan (2012a) of deep WT ‘high-grounds’ vs shallow WT ‘low-grounds’, respectively (Table 1). These contrasting land-formations determine the extent of shallow WT terrains, and affect the maximum depths and fluctuation of water levels over the seasonal cycle, together with climate and soil properties (Miguez-Macho & Fan, 2012b).

Local climatology, geology and geomorphology, and soil properties affect the processes of the water cycle, and determine patterns of variation in WT at sites (Fig. 3; data from literature and from the new network of PPBIO plots, see Methods S2; Table S3). In the old-dissected land formations, the seasonal fluctuation of WT levels in low-grounds is strongly bounded by site climatology

(Fig. 3c), and tends to be very small (0.5–1.5 m) in less seasonal climates (1–3 dry season months), but increases with seasonality (2.5–4 m where there are up to 6 months with less than 100 mm of precipitation yr^{-1}). These patterns are driven by water recharge and depletion dynamics associated with local-scale topographic variation under the local precipitation regime; here storage in high-grounds can buffer variation in WT in the low-grounds (Tomasella *et al.*, 2008). However, younger and flatter formations with less high-ground water storage, may experience much higher seasonal variation in WT (up to 8 m) with the amplitude less coupled to local climate seasonality (Fig. 3c). As a direct consequence of the flat topography, precipitation falling directly over these plains quickly raises the water table levels (Fig. 3e), while local groundwater influx from convergence is limited due to the distant location of highlands in these landscapes. These contrasts are consistent with the observed higher variation in WT levels in landscapes with lower topographic variation, especially in sites experiencing higher climatic water deficits (Fig. 3c,d). In flatter land formations the absence of storage in high-grounds may also decrease the time-lag between precipitation inputs and the rise of WT levels. In topographically varied formations, the peak of the water table level occurs at the beginning of the dry season, lagging precipitation as water travels slowly from high-land storage (Tomasella *et al.*, 2008), while in landscapes dominated by flat terrains this dephasing between precipitation and WT appears smaller (Fig. 3e).

The topographical control on seasonal fluctuations in water table levels (Tomasella *et al.*, 2008; Fang *et al.*, 2017) may be modulated by physical properties of the unsaturated zone such as soil permeability and water retention capacity. Clayey soils should increase the time lag between precipitation inputs and water table level responses to precipitation (though we note that macropores from biological activities provide flow paths that increase water infiltration and flow velocity independent of matrix porosity; Beven & Germann, 1982). Furthermore, alternation of textures along the soil profile may change water retention and the height of the capillary fringe in complex ways that should be accounted for in modeling the impacts of WT on soil water, necessitating more detailed soil data inputs. Impeding layers such as hardpans can also modify the expected relationship between topography and WT, creating ‘perched’ water tables, when a zone of saturated soil is formed in the unsaturated soil layer, above the groundwater table, potentially creating ‘unexpected’ waterlogged conditions and soil water regimes for plants.

2. Physical and physiological consequences for plants

Water table depth critically modifies the availability of water over the soil profile during dry periods (in contrast to rainy periods when infiltration plays a large role). Within depths of *c.* 5 m, the water table or the capillary fringe above it may directly supply water to the rooting zone, with the exact extent of capillary water uprise depending on soil texture, from less than a meter for sands to several meters in clay rich soils (Aubertin *et al.*, 2003; Babu, 2011). This direct influence of the water table on the rooting zone impacts plants and ecosystems. On the one hand, shallow WT increases

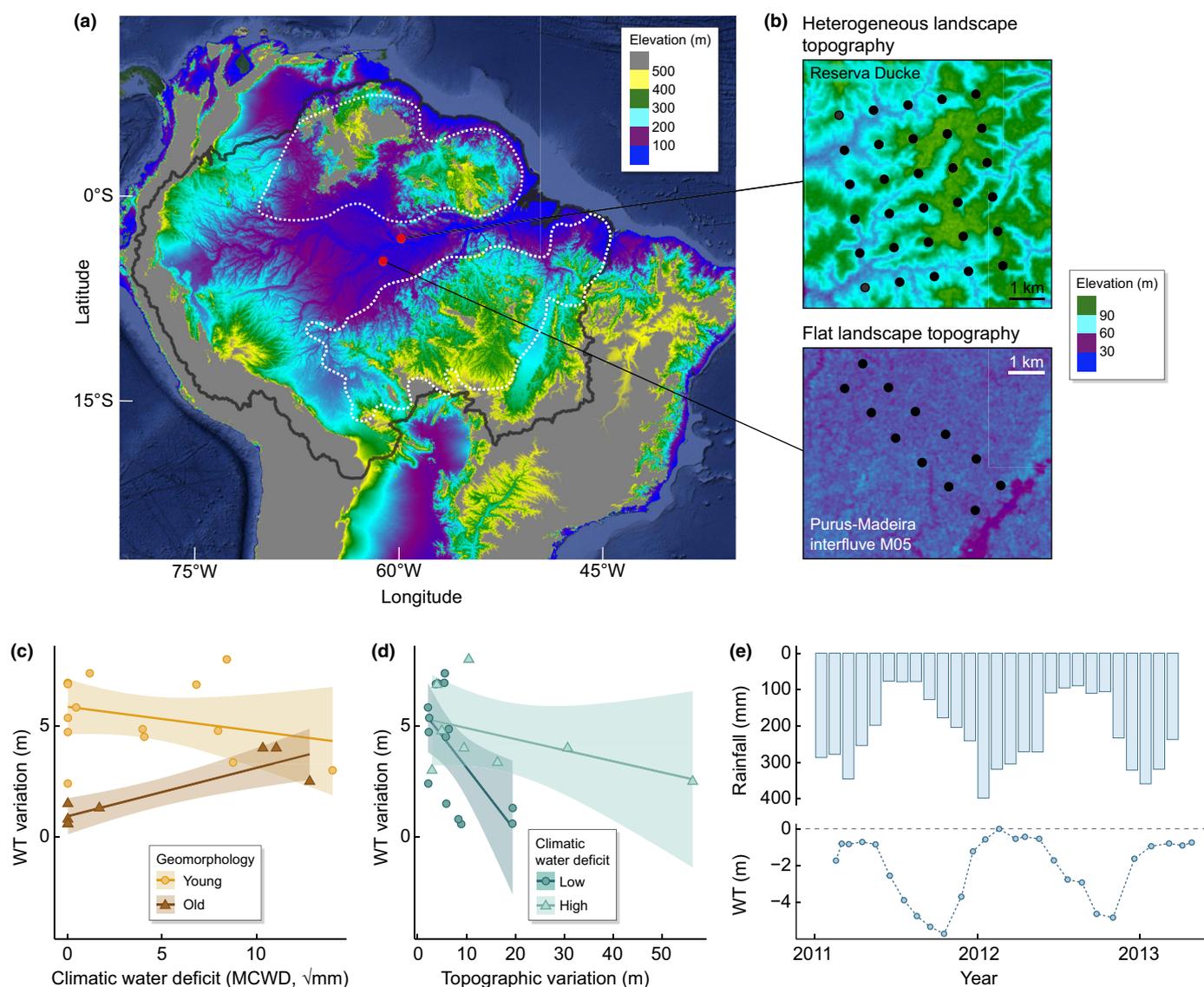


Fig. 3 Spatial and temporal patterns of water table depth (WT) in the Amazon. (a) Shallow WT are widespread in the geologically young terrains along the western to central corridor, while the distribution is fine grained within the old-weathered geologies dominating the northern and southern regions (outlined by dashed white lines). (b) Insets provide a zoom with examples of these conditions at our study sites (Reserva Ducke – upper, M05 site of the Purus-Madeira interfluvium – lower, points indicate vegetation plots). (c) The amplitude of seasonal WT variation increases with maximum cumulative water deficit (MCWD) in old terrains, but is always large in young terrains (95% confidence interval in the shaded area). (d) The amplitude of seasonal WT variation is higher in landscapes with low topographic variation, especially if climate water deficit is low. High MCWD is associated with lower variation but also deeper WT (95% confidence interval in the shaded area). (e) The seasonality of WT fluctuation in a shallow WT site with young geology (Purus Madeira interfluvium M02 site) closely follows precipitation, without the lag described for sites on old geologies.

water availability relative to deep WT areas within the same climatic zone, especially during the dry season, which contributes importantly to evapotranspiration (Miguez-Macho & Fan, 2012b). On the other hand, shallow WT under moist to wet climates impedes soil drainage and may create waterlogged and low oxygen conditions for plant roots, at least seasonally (Fan *et al.*, 2017).

The hypoxic to anoxic conditions of waterlogged soils (Table 1) have a negative impact on root physiology and function (Parent *et al.*, 2008), preventing tree roots from growing deep into the soil profile (Fan *et al.*, 2017). As oxygen is depleted, roots lose aerobic respiration capacity (Gibbs & Greenway, 2003), switching mostly to alcoholic fermentation for energy production, which has a much

lower yield (two adenosine triphosphate (ATP) per glucose molecule) than respiration (36 ATP), severely limiting plant growth (Parent *et al.*, 2008; Kreuzwieser & Gessler, 2010). Low oxygen levels also reduce root permeability, probably due to inhibition of aquaporins (North *et al.*, 2004; Vandeleur *et al.*, 2005), generating a cascade of responses that reduce stomatal conductance and limit photosynthesis (Lopez & Kursar, 1999, 2003; Pezeshki, 2001; Parent *et al.*, 2008). Morphological adaptations to waterlogging (e.g. adventitious roots, aerenchyma, barriers to oxygen loss and lenticels) in plants associated with shallow WT forests are not yet known, but can be expected given their frequent occurrence in wetland plants (Kozłowski, 1997).

Their effectiveness in counterbalancing anoxia depends however on plant size, physical resistances to transport and metabolic rates, as well as environmental properties (Jackson & Armstrong, 1999), such that plants may tolerate anoxia but still have limited growth. At the other extreme, soil profiles with a deep source of water, develop a highly negative water potential during drought that jeopardizes plant hydrologic function, with risks of conductance-damaging embolisms (McDowell, 2011), favoring xylem resilience or drought-deciduous strategies (Oliveira *et al.*, 2021).

Soil waterlogging, and thus low oxygen, creates reducing conditions that affect the availability of several plant nutrients (Ponnamperuma, 1972). Among major nutrients, nitrogen availability is reduced due to lower mineralization or nitrification rates, and higher denitrification rates (Ponnamperuma, 1972; Luizão *et al.*, 2004). Alternating wetting and drying of the soil increases the denitrification loss (Ponnamperuma, 1972). However, phosphorus may become more available within waterlogged soils as ferric phosphates are converted into more soluble ferrous compounds and due to the increased effective diffusion coefficient of phosphorus in water (Patrick & Mahapatra, 1968). Reduced mineral availability, reduced root:shoot ratios and impaired root uptake capacity in waterlogged soils may negatively affect the mineral nutrition of plants, but this response is highly variable among species (Rubio *et al.*, 1997; Kreuzwieser & Gessler, 2010). Very adapted species may increase uptake capacity, compensating for decreased root:shoot biomass (Rubio *et al.*, 1997). Mycorrhizal associations established before waterlogging can be maintained even during long periods of oxygen depletion, and may benefit tree species forming these associations, particularly with arbuscular fungi, in shallow WT forest (Kreuzwieser & Gessler, 2010).

Beyond the effects of shallow WT on water availability and chemistry, there are also impacts on root anchoring. The capacity of the soil to resist torsional forces such as those imposed on roots when trees are subjected to lateral forces from wind, floods, or other trees falling, decreases with increasing soil-moisture content (Hough, 1957). Shallow rooting depths of trees in waterlogged soils also decrease the stability of root anchorage and increase the likelihood of uprooting (Fraser, 1962). Therefore, forests on shallow water tables are expected to be more dynamic, suffering more uprooting during windstorms (Gale & Hall, 2001; Toledo *et al.*, 2016).

III. Current evidence for contrasting structure and function of shallow water-table depth forests

1. Shallow water table depth forest function under historical environmental regimes

Shallow water tables often create either permanent or seasonal waterlogging of the soil under the predominantly moist to wet Amazonian climates, resulting in hypoxic or anoxic conditions and unstable root anchorage that are sub-optimal for plant development. At the same time, shallow WTs create wetter soils during most or all of the year, depending on the major land formation and climate (Section II), providing advantageous growth conditions at least during the dry season. This set of variably favorable and

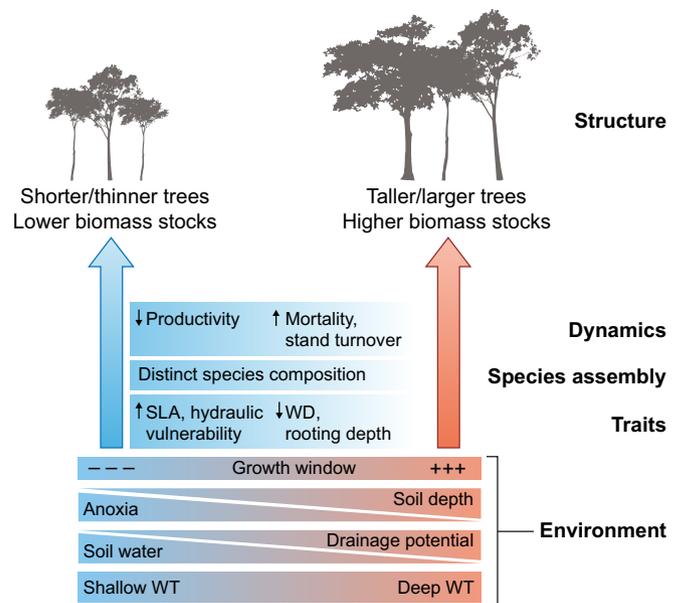


Fig. 4 The effects water table depth (WT) on forest function in 'normal' historical years (average climatic conditions). We summarize the understanding of how WT affects soil conditions, and the direct and indirect (through traits selection) effects of these on forest dynamics and structure, and the contrast to the deep WT forests. As in the article, the focus is on the climatically moist to wet forests dominant in the Amazon.

unfavorable conditions affects all aspects of shallow WT forest organization, from functional traits and species assembly, to forest dynamics and structure (Fig. 4). Conversely, in the drier end of the hydrological gradient, the best conditions for growth will be during the rainy season. Thus, climate seasonality may create an alternation of periods of limitation of soil water or oxygen and periods favorable for growth, determining the growth window.

Shallow WT conditions under moist to wet tropical climates select for lower wood density trees (Kraft *et al.*, 2008; Ferry *et al.*, 2010; Toledo *et al.*, 2016; Cosme *et al.*, 2017; Fontes *et al.*, 2020), and related xylem traits – wider vessels, larger sapwood area (Cosme *et al.*, 2017), higher vulnerability to embolism (Oliveira *et al.*, 2019; Fontes *et al.*, 2020; Garcia *et al.*, 2021), higher specific leaf area (SLA) (Cosme *et al.*, 2017; Fontes *et al.*, 2020) and other acquisitive leaf traits (Schmitt *et al.*, 2020). Shallow rooting depths are also associated with shallow water tables (Fan *et al.*, 2017). Trees less adapted to water stress – common in shallow WT forest – may also have a lower capacity to produce soluble sugars (a component of nonstructural carbohydrates) during droughts, potentially reducing the resilience of hydraulic function (Signori-Müller *et al.*, 2021). Leaf phenology – abscission, flushing, and maturation – patterns are also important drivers of tropical forest function (Wu *et al.*, 2016) that differ along WT gradients, from a predominance of deciduous species, with leaf abscission and flush aligned with the flood pulse in flooded forests (Parolin *et al.*, 2002), to a predominance of evergreen to brevideciduous species flushing in the dry season in deep WT forests (Lopes *et al.*, 2016), but have not yet been addressed in shallow WT forests.

This trait selection is likely the basis of community dynamics and assembly processes, including species filtering in more extreme dry

or waterlogged conditions, leading to striking compositional differences in tree (Lieberman *et al.*, 1985; Péllissier *et al.*, 2002; Valencia *et al.*, 2004; Jirka *et al.*, 2007; Schietti *et al.*, 2014), palm (Jirka *et al.*, 2007; Costa *et al.*, 2009), liana (Schietti *et al.*, 2014) and herbaceous (Drucker *et al.*, 2008; Moulatlet *et al.*, 2014) plant communities over WT gradients.

Trait differences contribute to different demographic dynamics in WT contrasts. The shallow WT forests trait differences highlighted earlier, particularly low tree wood densities – typically associated with shorter life-times and lower resistance to disturbances (Chave *et al.*, 2009) – and poorly anchored shallow root systems, help explain observations of higher mortality rates (Ferry *et al.*, 2010; Toledo *et al.*, 2013, 2016; Sousa *et al.*, 2020) and the formation of larger gaps (Goulamoussène *et al.*, 2017) in these environments. Higher mortality rates give rise to more dynamic and younger forests, with higher biomass turnover rates than deep WT forests (Cintra *et al.*, 2013; Vilanova *et al.*, 2018). At the same time, some traits selected for in these forests (higher SLA, higher vessel diameter) – typically aligned with faster resource acquisition and growth (Wright *et al.*, 2004) – do not translate into higher biomass productivity under average climatic conditions within the year, nor across years. Available evidence, instead, suggests that tropical forest productivity is lower in extreme shallow WT environments (de Castilho *et al.*, 2010; Ferry *et al.*, 2010) while increasing with water availability in well drained sites (Rowland *et al.*, 2014). The low wood densities may contribute to lower biomass, while anoxic conditions that favor the low efficiency fermentative pathway shorten growth windows and limit shallow WT forest biomass productivity (Parent *et al.*, 2008). The suppressive effect of anoxia and hypoxia on growth is well known for seasonally flooded igapó and várzea forest ecosystems (Parolin, 2000; Lopez & Kursar, 2003), where tree growth rates are concentrated in a low-water season growth window (Schongart *et al.*, 2002). Poor mineral nutrition can also contribute to the lower biomass production in waterlogged soils (Kreuzwieser & Gessler, 2010). Also, counterintuitively, elevated mortality rates do not give rise to higher coarse woody debris (CWD, or necromass) stocks than in deep WT forests (Martins *et al.*, 2014; Silva *et al.*, 2016). The lower average individual tree mass (Schietti *et al.*, 2016) may hasten decomposition and reduce necromass stocks.

The combination of lower wood density, higher mortality rates, and lower productivity than in deep WT forest gives rise to forests that are shorter (Coomes & Grubb, 1996; Jirka *et al.*, 2007), with smaller diameter trees (Sabatier *et al.*, 1997; Allié *et al.*, 2015; Schietti *et al.*, 2016), and that generally have lower aboveground biomass (Bongers *et al.*, 1985; Coomes & Grubb, 1996; Sabatier *et al.*, 1997; Valencia *et al.*, 2004; de Castilho *et al.*, 2006; Jirka *et al.*, 2007; Ferry *et al.*, 2010; Vilanova *et al.*, 2018). However, total stand biomass is not always less in shallow WT forest, particularly in climatically drier regions (Grogan & Galvão, 2006; Damasco *et al.*, 2013; Schietti *et al.*, 2016; Guimarães *et al.*, 2021). In drier regions shallow WT may act as oases, providing moisture during the dry season but never reaching anoxic states; in these cases, the average effect on plant production across normal years is positive. Investigating global patterns of forest growth with a

MODIS satellite proxy (fraction of absorbed solar radiation) over WT and precipitation/climate-driven hydrological variation, Roebroek *et al.* (2020) find that the influence of WT on forest growth varies over climate and the landscape. In the Amazon WT appeared to control growth, with decreasing WT – along with increasing precipitation – contributing to anoxic stress limitation in many areas, and to convergence-driven increases in growth in valleys in other areas.

2. Shallow water table depth forest function under moderate drought conditions

Although forests with shallow water tables under moist to wet climates may face limitations to growth in average years, in drought years the period of waterlogging is shortened, reducing exposure to stressful anoxic conditions. Reducing the anoxic period while maintaining moist soils likely provides an increased growth window that can benefit trees in shallow WT forest, resulting in higher growth and lower mortality rates. Some of these effects have been recorded in our focal study sites (Fig. 5). Drought mortality appears buffered: trees and palms did not experience increased mortality during the 2015–2016 drought, compared to previous years, in a region dominated by shallow water tables over young central Amazonian land formations (Sousa *et al.*, 2020) (Fig. 5a,b). At the same time, recruitment rates increased, which may indicate increased growth. Investigating droughts from 2001 to 2016, valley (shallow WT) tree mortality was lower with increasing drought intensity, compared with deep WT plateaus in the older geomorphology north of Manaus (Esteban *et al.*, 2021) (Fig. 5c). In this case, drought did not increase stem growth in shallow WT forest, but buffered growth and drought-induced mortality, which were both impacted in deep WT forest. Buffering effects of shallow water tables were also observed on a monthly basis during the 2015–2016 drought, when strong growth reductions impacted especially the larger trees on plateaus with deep water tables, but not those on shallow WT forest (Ramirez-Mendez, 2018). Similar responses were observed in seasonally flooded forests, where El Niño events leading to a longer duration of the terrestrial phase were associated with higher stem growth (Schongart *et al.*, 2004).

Remote sensing is a critical source of inference on Amazon forest drought responses; however, the few studies that consider vegetation responses to soil water variation over WT differences do not investigate drought response specifically (Guan *et al.*, 2015; Roebroek *et al.*, 2020; Tai *et al.*, 2020). Enhanced vegetation index (EVI) – linked with canopy photosynthetic architecture – has been shown to increase overall with drought (Huete *et al.*, 2006; Brando *et al.*, 2010; Wu *et al.*, 2016), the phenomenon of drought ‘greenup’. During the 2005 El Niño Amazon drought, strong EVI greenup occurred in the shallow WT regions in the southwestern Amazon, including in the Purus-Madeira interfluvium south of Manaus (Samanta *et al.*, 2010). Furthermore, 2005 drought regions that displayed the opposite pattern of EVI decrease (‘browndown’), included higher elevation deeper WT areas on the west-southwest edge of the Amazon. These patterns appear broadly consistent with vegetation response to regular variation in WT in these regions (Roebroek *et al.*, 2020), and with the expectations of

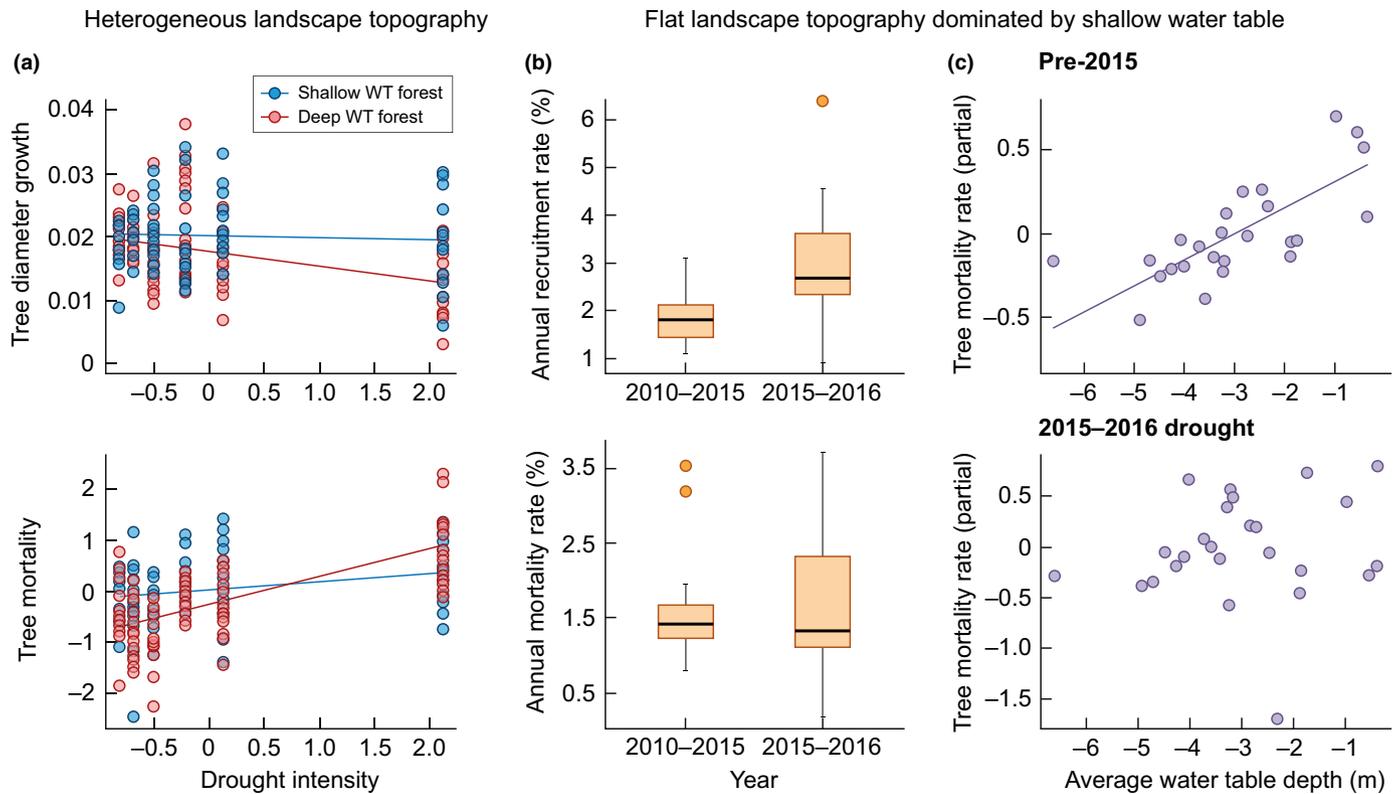


Fig. 5 The effects of water table depth (WT) on forest function in drought years. (a) The buffering effects of shallow as compared to deep water tables on tree growth and mortality, as drought intensity increased along the 2000–2016 period, within a landscape with high topographic variation (plots of partial effects from interaction models redrawn from Esteban *et al.* (2021), blue line shows the nonsignificant slope for shallow WT, in contrast to the trend in deep WT, red line). (b) The average positive effects of shallow WT on tree recruitment (upper plot) in the 2015–2016 drought, with no effect on mortality (lower plot), in a flat landscape dominated by shallow WT (redrawn from Sousa *et al.* (2020), horizontal bars show the averages and points outside bars are outliers). (c) The negative effects of shallow WT in ‘normal’ years (pre-2015) on mortality, but the suppression of this effect in a drought year (from Sousa *et al.*, 2020).

our WT hydrological hypothesis for moderate drought response. We expect remotely detected metrics of vegetation function will contribute significantly to increase the geographical coverage of the understanding of WT-dependent drought responses.

Hydraulic failure under water stress can kill trees and the degree of resilience to water stress is impacted by the adaptive traits of the tree (Maherali *et al.*, 2004). As reviewed in the previous section, trees in shallow WT forests have lower resistance to embolism (Oliveira *et al.*, 2019; Fontes *et al.*, 2020), which should lead to higher mortality under drought, but the opposite has been observed under moderate drought (Esteban *et al.*, 2021). Moreover, tree species with high embolism vulnerability were more likely to die from droughts in deep WT forests than in shallow WT forests (Córdoba, 2018).

In contrast to moderate drought, relatively little is known about the impacts of severe droughts (Table 1) in shallow WT forest. Broadly, more intense tropical droughts lead to higher increases in post-drought tree mortality, and contribute to shifting forests in the Amazon from being carbon sinks to carbon sources (Phillips *et al.*, 2010; Brienen *et al.*, 2015). In contrast to the buffering of drought mortality observed by (Estebán *et al.*, 2021), severe drought strongly increased tree mortality rates (243% increase over average) in shallow WT forest relative to deeper WT forests on plateaus and slopes (*c.* 60% increase) in the wet Colombian Amazon (Zuleta *et al.*, 2017). Floodplain forests may offer further clues to shallow WT

forest responses if they represent an ‘endmember’ periodically waterlogged forest state that suffers severe drought impacts during strong droughts. Both drought and fire – which is promoted by and often co-occurs with drought – have been shown to drive catastrophic tree and biomass losses, closed-to-open canopy transitions, and conversion to a savanna-like state, particularly in low fertility slow growing igapó inundated forest (Almeida *et al.*, 2016; Flores *et al.*, 2017). In sum, neither plant traits nor forest hydrology alone can predict the fate of tropical trees and ecosystem function under drought; instead, an interplay of plant traits, hydrology, climate and environmental variation appears to be at work.

IV. Conceptual framework to account for soil water regimes in forest climate responses

To predict tropical forest responses to current moderate and future severe climate drying scenarios we must understand how hydrologic regimes (Table 1), and tree functional composition together influence forest responses to drought (Fu *et al.*, 2013; Gloor *et al.*, 2013). To predict changing forest ecosystem function, we present a site-level framework that depends on long-term site conditions. This framework first addresses how the long-term hydrological regime impacts ecosystem functional response to soil water variation via effects on community functional composition (Section III); it then asks how a new hydrologic regime imposed

by climate change interacts with this site template to alter function. Considering drought and waterlogging stress limitations in this framework introduces nonlinear responses to drying regime shifts that can be both positive and negative, as we have hypothesized for shallow WT forest. To fully account for the future trajectory of the Amazon (Fig. 2), we cover the widest possible spectrum of current hydrological regimes, ecosystem functional responses, and future regime shifts, which includes transient or regional wetting (even while drying is the dominant trend; Spracklen & Garcia-Carreras, 2015; Khanna *et al.*, 2017). The spatio-temporal hydrological regime can be conceptualized as the soil water conditions that result from the combination of precipitation and groundwater inputs (increasing with shallower WT), such that combinations in space and time leading to mesic conditions increase productivity, while deviations from these decrease productivity (Fig. 6; Roebroek *et al.*, 2020).

Vegetation–environment relationships are linked to tree species' demographic performances over environmental gradients. We expect demographic-linked growth potential curves and other functional responses of tree species to display peaks of optimal performance over the range of possible hydrological states because of fundamental physiological trade-offs that limit performance in one environment vs another (Lambers *et al.*, 2008). For example, a species with very low resistance to embolism may perform well in shallow WT but poorly in the deep WT forest where water stress is common. Scaling up, plant functional composition determines ecosystem function over environmental gradients and environmental change (Savage *et al.*, 2007; Suding *et al.*, 2008; Lavorel, 2013; Violle *et al.*, 2014; Enquist *et al.*, 2015). Applying this to our framework, we expect ecosystem functional responses (Table 1) over soil hydrological variation (Fig. 7a–c) to reflect the local long-term hydrological regime, with a larger dominance of species whose optimal responses are within frequent conditions of the local

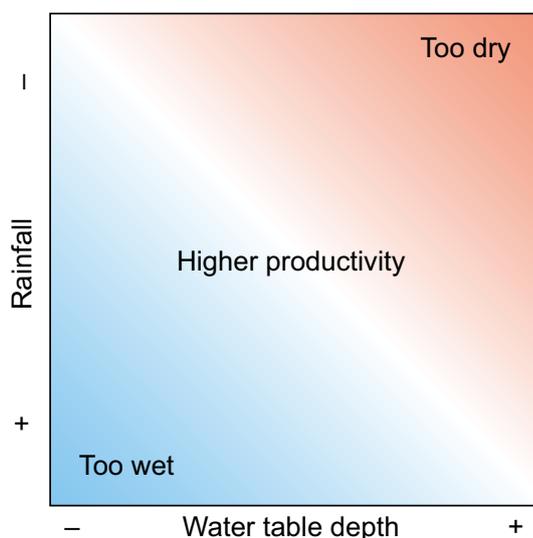


Fig. 6 Illustrating the broad role of rainfall and water table depths (WTs) in jointly influencing hydrological conditions, leading to a gradient from too wet hypoxic to anoxic conditions up to too dry water stress and water limitation conditions for trees. The highest potential productivity conditions fall between these extremes in mesic conditions.

regime (e.g. Longo *et al.*, 2018). The simplest hypothesis to connect the ecosystem functional response to the hydrological regime is a proportional response to the frequency of the soil water condition (e.g. compare solid black and red curves in Fig. 7a–c): under a soil water condition representative of 10% of site variation, tree growth would be proportionally less than in a condition representative of 25%, or 50% of the variation, and so on. When the regime changes because of climate change, it is this ecosystem functional response curve that predicts the ecosystem function change. For instance, if dry seasons intensify at a mesic site, the system will spend more time in a low moisture state with lower productivity, lowering the annual biomass productivity.

This scaled response hypothesis, however, risks overlooking the role of physiological stress limitation (Section II; Fig. 7), and potential limitations of the hydrological regime control over community functional assembly (Vellend, 2010; Lin *et al.*, 2011). There are consistently favorable soil conditions for plant growth – mesic aerated conditions with abundant moisture – and consistently detrimental conditions related to chronic stress – water and oxygen limitation in dry and waterlogged conditions, respectively (Section II). How will the stress limitation of plant function influence the link between the soil hydrological regime and the ecosystem functional response of a site? The impact of soil oxygen deficit on the one side and soil water deficit on the other side suggests that when one of these conditions is the most common state of the site, the maximal potential ecosystem function will be shifted away from these extremes towards less stressful conditions (see Enquist *et al.*, 2015). This predicts the enhancement of production when drying makes permanent and seasonally waterlogged areas more mesic, likely under climate change, and when wetting reduces water stress in dry deep WT forest (Fig. 7a,c). While wetting is less likely under global warming, it may occur as a regional or transient change over a range of forest WT driven by increasing climate variability, deforestation and other factors (Kundzewicz *et al.*, 2014; Spracklen & Garcia-Carreras, 2015; Khanna *et al.*, 2017).

Focusing on biomass production, consider a typically waterlogged site that is drying: initially, production will be enhanced as stress is reduced, but as drying continues, enhancement will diminish, and when a severity threshold is exceeded, production will begin to (nonlinearly) decrease. In this scenario, drier soil water regimes that exceed the region of waterlogging stress reduction (moving right on the blue curve in Fig. 7d), will increasingly represent environmental conditions for which the community is not adapted – shallow WT lack drought tolerance – and production will decrease rapidly relative to the pre-shift environment. In other cases, when a forest is mesic and functional optima and environmental regime variation align, we expect that regime shifts – either drying or wetting – decrease production (green curve, Fig. 7d). Likewise, when water deficit limited sites get drier, or water excess limited sites get wetter, production will decrease. Overall, the production response, either enhancement or reduction, depends on (1) the historical environment and its influence on the ecosystem functional response, on (2) how far climate change has shifted the regime, and (3) on whether it has shifted towards or away from more stressful soil water conditions (Fig. 7d,f).

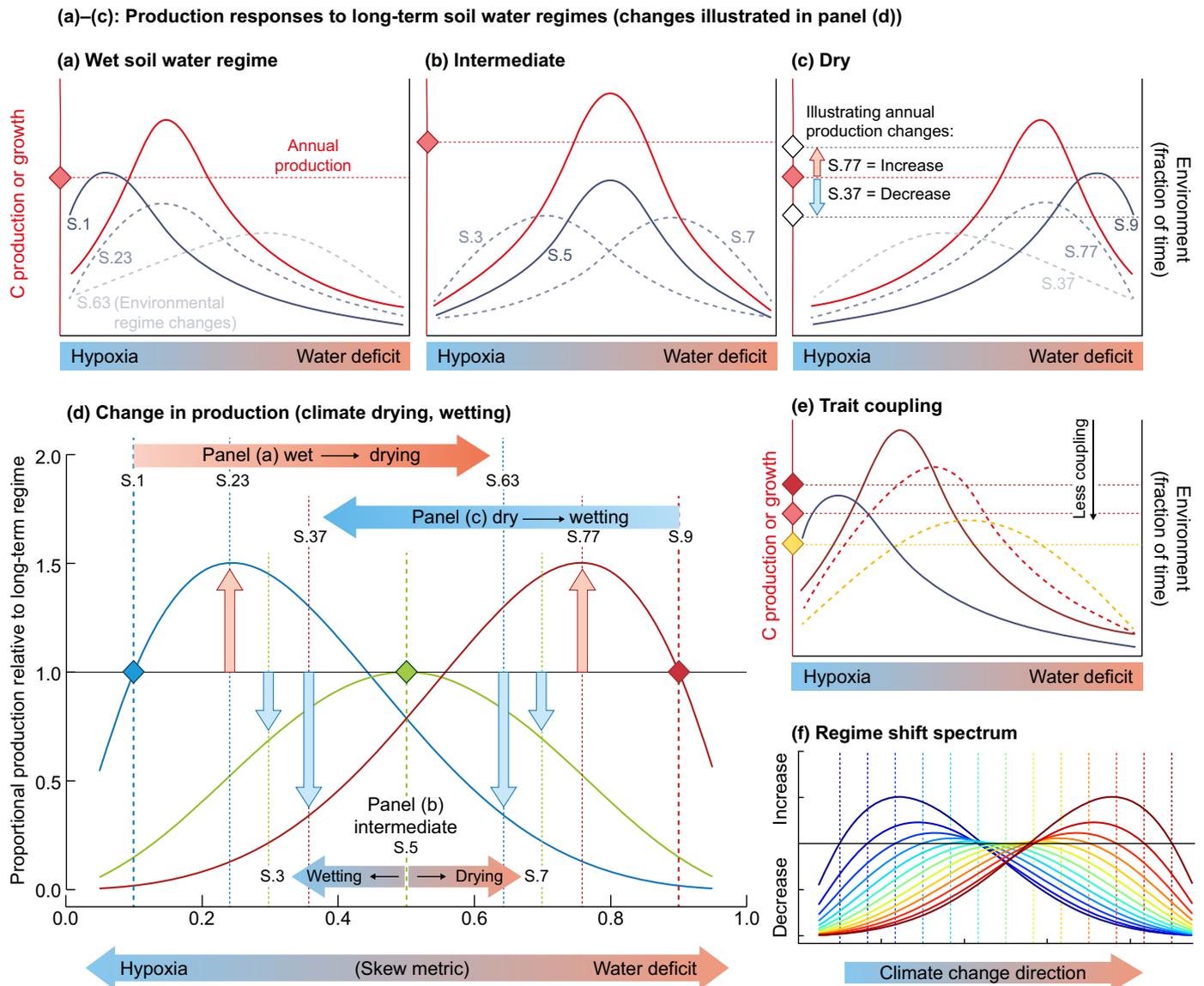


Fig. 7 Predictive framework for the role of long-term hydrologic regime coupling in short-term ecosystem function responses to soil water changes from droughts (drying) to waterlogging (wetting). Panels depict either site-level production responses to variation in soil water conditions, from soil water excess (hypoxia) to deficit (a–c, e), or change in annual production due to shifting soil water regimes caused by climate change (d, f), with drying and wetting both considered. (a–c) Ecosystem functional responses (here production) are shown as solid red curves while the hydrological regime is depicted by the long-term distribution of soil water states (x-axis) as solid dark gray curves. Panels (a–c) capture wet, intermediate and dry hydrological regimes respectively – note the coupling between regime curves and production responses, with production optima offsets caused by stress limitation at extremes (a and c). Red diamond symbols and dashed lines on vertical production axes are annual averages (sum of production values times regime normalized frequencies). Gray dashed curves indicate possible specific future environmental regime shift scenarios, and are labeled with scenario skew number, for example, ‘S.1’ (e.g. ‘Skew = 0.1’ in a gamma distribution) for connection to (d). In both (a) and (c) depicted regime shifts increase and then decrease production with increasing change, depicted with open diamonds in (c) (detailed in (d)). Panel (d) answers ‘what happens to annual production under a full range of possible climate-induced regime shifts?’ for each regime in (a–c). On the y-axis we plot annual production change (proportional) from the current regime condition. For each curve, excepting the point at which relative production is one (highlighted with vertical dashed lines), the x-axis represents regime shifts, conceptualized as changing gamma distribution skew (in nature regimes could change in more complex ways). Skewness ranges from zero to one: very skewed wet-hypoxic to very skewed dry-water stressed regime. (Skewness values are shown in (a–c) and marked by vertical dashed lines and labeled in (d)). Vertical arrows highlight scenario proportional production impacts with production enhancement (red, up) and degradation of production (blue, down) occurring with increasing regime change in stressful regimes ((a) and (c); dark blue and red curves respectively) while the mesic intermediate site (green curve) is only degraded by shifts. (e) Highlights the importance of the coupling of the ecosystem functional response (color curves) with the local environmental regime (dark gray curve). Three different coupling scenarios show decreasing coupling (skew) of the production response curve – going from high to low with dark red, red, yellow curves – because of different ecological or biogeographical conditions impacting community functional traits and annual production (diamonds). Coupling would also impact responses to shifts. (f) A companion to (d) illustrating the wide spectrum of starting regimes (vertical dashed lines) and positive and negative shift responses (curves) encompassed by our conceptual model. The arrow highlights the climate change mean expectation (move along curves from x-intercept to the right for predicted responses).

For the sake of simplicity, and to allow a graphical representation of our hypothesis, we have eschewed thus far additional factors that could make the response patterns depicted on Fig. 7 more complex. Among these are the effects of biogeographical contexts on trait assortment vs trait plasticity, variation in timing and duration of droughts in interaction with WT and biological properties of trees that may feedback to climate and WT, and other environmental factors that may interact with WT via trait assortment, such as soil fertility. We discuss these factors in the next sections and indicate the need for data and additional conceptual development to address questions concerning these more complex scenarios.

V. Agenda: revealing the role of water table depth variation in tropical forest climate response

1. Advancing hypotheses linking hydrological regimes and forest climate responses

The water table is a critical component of the hydrological regime influencing the ecology of tropical forests. Unanswered questions, however, limit predictive understanding and forecasting of tropical forest responses to changing climate and hydrological regimes:

- (1) When, where, and how does production enhancement occur under shifting environmental regimes? Although we have shown growing evidence suggesting that shallow WT forests are not disadvantaged by all drying, understanding of the constraints to and extent of the positive effects of droughts is still highly limited.
- (2) At some range of drying, is tree growth and tree loss more vulnerable in shallow than deep WT forest because these forests lack water stress resilience traits? Will this contribute to tropical forest change tipping points? Are such negative responses already occurring?
- (3) What is the full range of forest functional responses to drying or wetting across the WT gradient? Climate change will enhance extremes and variability, and projecting all consequences requires understanding the full range of responses.
- (4) How do long-term hydrological regimes shape ecosystem functional responses to drought conditions, and abnormal water-logging? While vegetation–environment relationships are an established driver of responses to environmental changes (Lambers *et al.*, 2008; Diaz *et al.*, 2013), little quantitative information along hydrological regime variation is available. Currently more is known about typically drier deep WT and typically wetter shallow WT forests; what are the functional responses in forests with highly variable WTs (within or between years), or at intermediate WT positions?
- (5) Do community, evolutionary, and biogeographic processes impact the coupling between ecosystem functional responses and long-term hydrological regimes? Does variation in coupling lead to site or regional differences in responses to regime shifts under climate change?
- (6) How will the nonlinear mechanisms that determine tree mortality and growth responses to drought affect ecosystem-level patterns over the WT gradient?
- (7) Increasing atmospheric CO₂ concentrations caused by human activities can allow stomata to open less, boosting the water-use

efficiency of production. How will this effect impact soil moisture responses over WT gradients? How do soil hydrological regimes interact with other environmental factors, especially soil fertility, to impact functional responses to the environment and climate change linked drought responses? Will shallow WT plants be able to take advantage of elevated atmospheric CO₂ if phosphorus is limited?

(8) Can the conceptual framework developed above to explore these questions predict forest responses in the Amazon and elsewhere after being fit to field and remotely sensed data? Can it also be adapted to accommodate the important complexities raised in the questions earlier?

Better understanding the role of biodiversity in ecosystem function – specifically functional diversity linked to hydrological stress responses – is central to our agenda. We hypothesize that the degree of coupling between ecosystem functional response and hydrological regime varies because of ecological and biogeographical factors (Question 5). The role of variability, not just the mean hydrological regime likely plays a central role. For instance, in extremely stressful regimes with little variation, strong selection for tolerance traits may significantly constrain functional response optima to a narrow hydrological range, representing tight community trait coupling to the environmental regime. However, fluctuation dependent community processes can maintain species with a broad range of performance optima when sufficient environmental variation occurs (Chesson, 2003; Johnson *et al.*, 2017), such that forests with a long-term history of high hydrological variation, including differences at multiple timescales, would contain a wider range of plant functional responses. In this case, intermediate WT forest may be expected to contain the highest range of functional types if variation allows species more suited to shallow and deep WT to persist. High variation in hydrological regimes in space can have a similar effect. Consider the fine-grained hillslope-valley topography characteristic of the Guiana and Brazilian Shields; here dispersal may decrease the dominance of functional types in adjacent shallow and deep WT environments. Testing the importance of WT and its variation in time and in space for ecosystem responses over WT gradients may reveal the importance of these poorly understood community mechanisms in tropical forest. Functional plasticity and other forms of intra-specific variation such as local adaptation also likely enhance the match between function and the local regime (Schmitt *et al.*, 2020; Garcia *et al.*, 2021). Larger-scale evolutionary and biogeographic processes impact functional biodiversity as well (Esquivel-Muelbert *et al.*, 2017; Dick & Pennington, 2019). In sum, differing degrees of trait–environment coupling may shape direct responses to hydrological conditions and annual-scale responses of net ecosystem function to regime shifts (Fig. 7e).

The interaction of climate patterns, the WT gradient and biological properties whose responses may feedback to affect climate have the potential to create more complex responses than those depicted in our conceptual framework. A growing literature on mechanisms and drivers of tree demographic responses to drought – including how lethal droughts are – has identified condition-dependent nonlinear factors that could alter responses over WT gradients (Allen *et al.*, 2015; McDowell *et al.*, 2018). These factors

include how droughts alter vapor pressure deficits and water stress; the prevalence of nonstructural carbohydrate storage, on which trees may rely on during droughts or in recovery; and we suggest leaf phenological strategies – including drought deciduousness – which may critically alter the impacts of droughts depending on when they occur during the phenophase. These factors could all differ over WT gradients. Higher evapotranspiration and latent heat fluxes in shallow WT forest could result in cooler droughts there, while ecological dynamics likely assort carbon storage and phenological strategies over hydrological gradients (Poorter & Kitajima, 2007; Signori-Müller *et al.*, 2021). Stomatal regulation can also impact drought effects and feedbacks according to WT. A strong impact could arise if stomatal regulation strategies – isohydric vs anisohydric – (1) determine water use efficiency changes under increasing CO₂ (Domec *et al.*, 2017), and (2) if the prevalence of these strategies changes with community functional assortment over WT gradients (see Oliveira *et al.*, 2019; Oliveira *et al.*, 2021). Such a difference could have far-flung impacts for the significance of WT variation on recharge, runoff, and atmospheric hydrological cycling under anthropogenic CO₂ levels (Berry *et al.*, 2010). Tree size can also mediate responses to variability over WT gradients, since larger trees have deeper water access but more hydraulically stress-vulnerable traits (Brum *et al.*, 2019). It follows that forest size and stand structure differences over WT gradients can influence climate change responses (Schietti *et al.*, 2016).

Another expected interaction is between WT gradients and soil fertility. High fertility sites may select faster growing less drought tolerant species, but little quantitative information is available to address this question and assess possible interacting impacts of WT variation (Oliveira *et al.*, 2021). At the same time, higher soil fertility may improve stomatal regulation, thus spatial variation of soil fertility across the Amazon – especially of phosphorus, may also affect how CO₂ fertilization will impact water use efficiency across the WT gradient (Fleischer *et al.*, 2019).

All of these controls on ecosystem response should be addressed to predict the role of shallow WT in the sensitivity of the Amazon to climate change (Fig. 2).

2. Critical data and networks needed

Data are critically needed to evaluate forest responses to the hydrological regime variation, and regime shifts. ‘Ground measurements’ are essential in Ecology, and historically, shallow WT sites have been underrepresented. Recent efforts discussed earlier have begun to significantly correct this and reveal the effects of shallow WT from normal to drought years. Many of these new insights emerged from a sampling network specifically designed to control soil hydrological conditions within vegetation monitoring plots, while capturing hydrological variation across the landscape among plots (Magnusson *et al.*, 2005; Methods S1). Soil hydrology is controlled by setting a network of 1 ha plots along elevation isolines. Sites contain plots separated by 1 km spanning at least 5 km of linear distance, typically allowing within-site pairing of deep and shallow WT conditions. Replicating across sites allows local hydrological variation to be compared across climates and soil types (e.g. Schietti *et al.*, 2016; Sousa *et al.*, 2020). Nevertheless,

there is an urgent need to expand this hydrologically-designed network, especially to the western and southern Amazon, to allow paired WT comparisons within regions of similar geomorphological history and macroclimates. This will pave the way for correct representation and parametrization of hydrological responses in large-scale models.

Reliable data is also critically needed to better understand the roles of WT and its variability in soil moisture dynamics. *In situ* monitoring of water table levels has been limited to a few sites, mostly in the old and well dissected land formations of the Guiana and Brazilian shields (Miguez-Macho & Fan, 2012a), and has only recently expanded to include young land formations in the Purus-Madeira Interfluvium (Sousa *et al.*, 2020) and Viruá National Park (Damasco *et al.*, 2013). The majority of long-term (> 4 yr) WT monitoring is restricted to urban sites (e.g. CPRM, 2021), and we are unaware of long-term monitoring in forest sites. These data are critical to inform models of WT (e.g. Fan *et al.*, 2013) and its seasonal fluctuation (Miguez-Macho & Fan, 2012a,b), and must be stratified across land formations and forest types. Long-term seasonal or continuous monitoring of WT, rainfall, and soil moisture profiles across these gradients is needed to fully understand and model hydrological regimes. Satellite derived rainfall, evapotranspiration, and groundwater estimates can inform landscape understanding (Guan *et al.*, 2015; Roebroek *et al.*, 2020), but only properly stratified field data can validate estimation.

Hydrologically-designed plot networks should measure pools and fluxes of woody biomass and functional composition dynamics to investigate responses to changing soil hydrological regimes. Such efforts require the tracking of individual trees in repeated demographic surveying (Magnusson *et al.*, 2005; Malhi *et al.*, 2009). Additional direct information on the response of canopy photosynthesis is also needed; eddy covariance measurements of carbon, water, and energy fluxes are invaluable tools in ecosystem ecology and forest-atmosphere interactions (Malhi *et al.*, 2021). These measurements, necessitating tall above-canopy towers and significant infrastructure and investment, can be complemented with above-canopy observation platforms including multispectral cameras, phenocams, and solar induced fluorescence spectrometers (Lopes *et al.*, 2016; Gonçalves *et al.*, 2020). These complementary measurements directly link to satellite observations of the same type, and have revealed that leaf phenological dynamics controls seasonal canopy photosynthesis differences (Wu *et al.*, 2016; Gonçalves *et al.*, 2020). Our group is currently adding multiple canopy towers with multispectral monitoring to shallow WT sites near Manaus (Brazil) to address this data gap and link with broader tower networks. Finally, tree size and canopy environment variation in heterogeneous forest canopies must be accounted for to understand size structured hydrological responses (Brum *et al.*, 2019), which can be addressed with LiDAR (light detection and ranging) data and forest microenvironmental modeling from ground, air, and now space (Schietti *et al.*, 2016; Tang & Dubayah, 2017; Smith *et al.*, 2019; Dubayah *et al.*, 2020).

Among key plant traits mediating the responses of plants to hydrological gradients and climate change, functional rooting depth (where roots actively absorb water), continues to be a

significant knowledge gap. Despite significant progress made by Fan *et al.* (2017) in demonstrating the WT controls on rooting depth, site level studies remain scarce; rooting depths and architectures within tree communities appear diverse, indicating the potential for varied responses to soil moisture and WT variation (Chitra-Tarak *et al.*, 2018; Brum *et al.*, 2019). Moreover, the capacity of roots to follow the water table as it moves down is virtually unknown; although root growth is stimulated by soil humidity (e.g. Yavitt & Wright, 2001; Lane & Ridge, 2008), at present it is not possible to disentangle root growth plasticity from changes in the depth of water uptake by preexisting roots in response to changes in the soil water profile (Stahl *et al.*, 2013; Pivovarovff *et al.*, 2021). Understanding hydraulic traits – including rooting depth – variation within WT conditions and climates, along with their intra-specific variation and acclimation potential, may be essential to model the evolution of communities under shifting hydrological regimes, the resilience of ecosystem function and the vulnerability of biodiversity (Moran *et al.*, 2016).

VI. Conclusions

Although tropical forests may be perceived as environments continuously favorable for growth, geographical and temporal variation frequently encompasses too wet and too dry soil conditions, with major consequences for forest processes and function. WTs are a central component of this variation, profoundly constraining rooting and soil moisture availability. In tropical forest regions critical to global climatic stability, such as the Amazon, vast regions of shallow WTs where soil conditions are too wet represent an understudied potential fulcrum of alterations to global carbon, water, and energy fluxes that could play an unforeseen role in global climate change. On the positive side, these regions are candidates for enhancing global resilience. Our review highlights the resilience or even enhancement of productivity in these regions during some droughts. On the negative side, shallow water table forests lack plant traits to persist in severe water stress conditions, such that tipping point drought severity thresholds may lead to exceptionally strong ecological collapse. In this case, these shallow water table regions could form a much larger ‘Achilles Heel of the Amazon’ than was initially envisioned for seasonally inundated forests highly sensitive to fire and drought (Flores *et al.*, 2017). It is essential to now understand if, when, and for how long, regions like the shallow water table Amazon forests will serve as climate change refugia of ecosystem function and biodiversity, and under what conditions will they fall over the precipice leading to forest die-off and collapse of climate services. Significant new data streams and model development and evaluation are needed. It is also essential to evaluate hydrological interactions with forest conversion, forest fires, and savannization that are rapidly reducing global ecosystem service capacity and imperiling tropical forest peoples and biodiversity (Stark *et al.*, 2020; Walker, 2021).

Our predictive conceptual framework and research agenda aim for rapid resolution of the importance of shallow WT forests to global ecosystem services. We offer a new way to frame the prediction of changes in plant stress by climate change centered on

how plant functional responses have been shaped by environmental history. Quantifying and addressing this connection offers a bridge between physiological, community and ecosystem scales and emphasizes the importance of historical patterns of climate/environmental variation on present day responses to new regimes. To understand the role of shallow water table forests in climate response, and to aid climate, biodiversity, and conservation action plans, the data gaps must be addressed on the ground. Otherwise, remote inference will be stretched too far, with poorly constrained approaches risking spurious conclusions that could obscure mechanisms essential to predict nonlinear forest responses under future conditions.

An implication of the patterns and hypotheses described here is the need to prioritize shallow water table forest conservation that ensures the full landscape protection of groundwater and its supplies. Conservation can provide short- to mid-term hydrological refugia for biodiversity and ecosystem services, and protect from threats such as fire over long-term climate drying. Amazon soil fertility has a strong geographical pattern (increasing to the west), which in interaction with WT may generate large-scale aggregation in drought responses, and if so, also needs to be taken into account in conservation planning. The future of the Amazon and other tropical forests may be more fine-grained than appreciated because of the role of water table variation, and this heterogeneity must be accounted for in efforts to protect and understand tropical forest ecosystem services.

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Author contributions

FRCC, SCS and JS contributed symmetrically and are co-lead (first) authors of this manuscript. MNS performed the geospatial

analyses and graphing of WTs, sampling effort, and elevations, in addition to contributing to the writing and intellectual development of the manuscript.

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Data availability

All data is included in the Supporting Information.

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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 Distribution of water table depths (WTs) across the Amazon redrawn using low resolution WT product, exploring different sources of variation in % WT estimates.

Fig. S2 Distribution of water table depths (WTs) across the Amazon redrawn using high resolution WT product, exploring different sources of variation in % WT estimates.

Methods S1 Methods used to calculate water table depth distribution and sampling effort across the Amazon (Fig. 1 of main text), and the new PPBio plot network.

Methods S2 Methods used to explore spatial and temporal patterns of shallow water table variation in the Amazon (Fig. 3 of main text).

Notes S1 Major sources of variation in estimates of Amazonian water table depth distribution.

Table S1 Estimates of water table depth (WT) frequencies across the Amazon for different mapping scenarios and WT products.

Table S2 List of new PPBio plots included in the water table depth vs sampling effort analysis (Fig. 1 of main text).

Table S3 List of sites included in the analyses of spatial and temporal patterns of water table depth in the Amazon (Fig. 3 of main text) with key environmental variables.

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