INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA (ECOLOGIA)

PROFUNDIDADE DO LENÇOL FREÁTICO: EFEITOS NA DINÂMICA, ESTRUTURA E RESPOSTA DA FLORESTA ÀS SECAS INTENSAS NA AMAZÔNIA

THAIANE RODRIGUES DE SOUSA

Manaus, Amazonas
Fevereiro, 2022

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Dra. FLÁVIA REGINA CAPELLOTTO COSTA
Dra. Juliana Schietti de Almeida
Dr. Oliver Phillips

Tese apresentada ao programa de Pós-graduação em Biologia (Ecologia) do Instituto Nacional de Pesquisas da Amazônia como requisito final para obtenção do título de Doutor em Biologia (Ecologia).

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Aos 08 dias do mês de Março do ano de 2022, às 13h30min, via videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o Dr. **Jochen Schongart**, do Instituto Nacional de Pesquisas da Amazônia – INPA, a Dra. **Márcia Cristina Marques**, da Universidade Federal do Paraná – UFPR, o Dr. **Paulo Monteiro Brando**, da Universidade da Califórnia, a Dra. **Flávia Machado Durgante**, do Instituto de Tecnologia de Karlsruhe (Karlsruhe Institute of Technology - KIT) e o Dr. **José Júlio deToledo**, da Universidade Federal do Amapá – UNIFAP, tendo como suplentes o Dr. Ingo Wahnfried, da Universidade Federal do Amazonas - UFAM e o Dr. Bruce Walker Nelson, do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência da orientadora, a fim de proceder a arguição pública do trabalho de **TESE DE DOUTORADO** de **THAIANE RODRIGUES DE SOUSA**, intitulado: **"PROFUNDIDADE DO LENÇOL FREÁTICO: EFEITOS NA DINÂMICA, ESTRUTURA E RESPOSTA DA FLORESTA ÀS SECAS INTENSAS NA AMAZÔNIA"**, orientada pela Dra. Flávia Regina Capellotto Costa, do Instituto Nacional de Pesquisas da Amazônia – INPA e Co-orientadora pela Dra. Juliana Schietti de Almeida, da Universidade Federal do Amazonas – UFAM.

Após a exposição, o discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO (A) ☐ REPROVADO (A)

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Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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Sinopse:

Nesta pesquisa foi avaliado o papel da hidrologia local, dada pela profundidade do lençol freático, na estrutura e dinâmica da floresta amazônica, bem como sua importância na mitigação dos efeitos de secas intensas. Foi investigado como a estrutura da floresta amazônica varia de acordo com a profundidade do lençol freático, média histórica de déficit hídrico climático e propriedades do solo, no longo prazo. Além disso, foi avaliado como a profundidade do lençol freático e as propriedades do solo interagem com as secas climatológicas para influenciar a dinâmica de árvores e palmeiras, no período das secas intensas de 2010 e 2015-16.

Palavras-chave: lençol freático, floresta tropical, carbono, dinâmica da floresta, mudanças climáticas.

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amor incondicional em toda minha trajetória.

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Resumo

A disponibilidade de água é um dos principais influenciadores da estrutura, dinâmica e resposta das florestas tropicais a eventos climáticos extremos. No entanto, pouco se sabe sobre a relação entre a disponibilidade de água subterrânea, regulada pela profundidade do lençol freático e o funcionamento da floresta. Nesta tese, visando entender o funcionamento natural da floresta, investiguei como a estrutura da floresta amazônica varia de acordo com a profundidade do lençol freático, média histórica de déficit hídrico climático e propriedades do solo (capítulo 1). Em seguida, busquei compreender o funcionamento da floresta nos anos de secas intensas, portanto investiguei como a profundidade do lençol freático e as propriedades do solo interagem com as secas climatológicas para influenciar a dinâmica de árvores e palmeiras (capítulo 2). A água fornecida tanto pela precipitação quanto pelo solo afetou a estrutura e a dinâmica da floresta amazônica, mas de maneiras diferentes. Florestas com lençol freático superficial (profundidade <5 m) tiveram menor produtividade e estoque de biomassa acima do solo do que aquelas sobre lençol freático profundo. Florestas localizadas em climas mais secos (máximo déficit hídrico acumulado < -160 mm) tiveram também menor produtividade e estoque de biomassa acima do solo do que aquelas localizadas em climas mais úmidos. A produtividade (AGWP) foi afetada pelas interações entre déficit hídrico climático, profundidade do lençol freático e textura do solo. Em climas mais secos, as florestas com lençol freático superficial apresentaram menor AGWP do que as florestas com lençol freático profundo. No entanto, a combinação de lençol freático superficial e solo argiloso reduziu a limitação imposta pelo clima seco à produtividade, enquanto a combinação de lençol freático superficial e solo arenoso ocasionou o oposto. Portanto, neste capítulo 1 separei a contribuição relativa do lençol freático e do clima, melhorando a compreensão do funcionamento das florestas tropicais. Em se tratando de secas intensas, a resposta da floresta tropical às mudanças climáticas é de importância global e é criticamente determinada pelos padrões de disponibilidade de água. Não houve mudança nas taxas de mortalidade de caules e perda de biomassa em resposta à seca nas florestas localizadas sobre lençol freático superficial. Em vez disso, houve um aumento nas taxas de recrutamento em comparação com as taxas no intervalo pré-El-Nino. Além disso, houve um aumento significativo na biomassa das árvores para o período analisado (2010-2016). Portanto, neste capítulo 2 mostrei que as florestas que crescem sobre lençol freático superficial são notavelmente resistentes à seca, aprimorando assim a compreensão dos efeitos integrados da seca, abrangendo clima, hidrologia local e solo, na dinâmica das florestas tropicais.

Abstract

Water availability is one of the main influences on the structure, dynamics and response of tropical forests to extreme events. However, little is known about the relationship between the water availability provided by the groundwater, modulated by depth to the water table, and forest functioning. In this research, aiming to understand the natural forest functioning, I investigated how the structure of the Amazon forest varies according to the water table depth, historical average of climatic water deficit and soil properties (chapter 1). Then, I evaluated forest functioning in years of strong drought, investigating how water table depth and soil properties interact with climatological droughts to influence tree and palm dynamics (chapter 2). Water provided by both precipitation and soil affected the structure and dynamics of the Amazon forest, but in different ways. Forests with shallow water table (depth <5 m) had lower aboveground biomass productivity and aboveground biomass stock than those with deep water table. Forests located in drier climates (maximum cumulative water deficit < -160 mm) also had lower productivity and biomass stocks than those located in wetter climates. Productivity (AGWP) was affected by interactions between climatic water deficit, water table depth and soil texture. In drier climates, shallow water table forests had lower AGWP than deep water table forests. However, the combination of shallow water table and clayey soil reduced the limitation imposed by the dry climate on productivity, while the combination of shallow water table and sandy soil caused the opposite. Therefore, in this first chapter I have separated the relative contribution of water table and climate, improving the understanding of the functioning of tropical ecosystems. When it comes to strong droughts, forest responses to climate change are of global importance and are critically determined by patterns of water availability. There was no change in stem mortality rate and biomass loss in response to drought in forests dominated by shallow water-table. Instead, there was an increase in recruitment rates compared to rates in the pre-El-Niño. In addition, there was a significant increase in tree biomass for the analyzed period (2010-2016). Therefore, in this chapter 2 I have shown that forests that grow on shallow water table are remarkably resistant to drought, thus enhancing our understanding of the integrated effects of drought, encompassing climate, local hydrology and soil, on tropical forest dynamics.

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Table S3. Statistical summary of the generalized mixed models tested to investigate the relationship between palm dynamics and environmental variables.

Table S4. Statistical summary of the generalized mixed models tested to investigate the relationship between tree dynamics and environmental variables.

Introdução geral

As florestas tropicais abrigam enorme biodiversidade de animais e plantas, com um valor intrínseco imensurável (ter Steege et al. 2013, Fearnside 2021). Além disso, prestam serviços ambientais de grande importância para a sociedade, influenciando no ciclo hidrológico e de carbono do planeta (Marengo 2006, Fearnside 2008). Dada sua importância, uma das grandes questões da ecologia de florestas tropicais é entender os fatores ambientais que modulam a estrutura e dinâmica da vegetação para poder entender como responderão às mudanças climáticas globais, incluindo sua resposta a secas intensas (Phillips et al. 2009, Schietti et al. 2013, McDowell et al. 2018, Esquivel-Muelbert et al. 2019). Os gradientes ambientais têm reconhecida importância como determinantes da estrutura e dinâmica da floresta, principalmente a precipitação, por ser um fator essencial para estabelecimento e crescimento da vegetação (Toledo et al. 2011, Wagner et al. 2014). É possível encontrar na literatura diversos estudos mostrando os efeitos do solo, temperatura e clima no funcionamento das florestas tropicais (Quesada et al. 2012, Esquivel-Muelbert et al. 2017, Sullivan et al. 2020), mas pouco se sabe sobre como é esta relação com a hidrologia local regulada pela profundidade do lençol freático.

A água é essencial para a vida e, junto com a temperatura, é determinante para os padrões globais de distribuição e produtividade das plantas (Webb et al. 1978, Law et al. 2002, Ellison et al. 2017). A entrada de água no sistema terrestre é dada pela precipitação, parte desta água será interceptada por troncos e folhas, outra parte será drenada para o solo e depois para a água subterrânea. Quando a água subterrânea está dentro de uma distância vertical acessível para as raízes, ela pode prover uma fonte de água maior do que seria possível apenas via extração do solo. Sendo assim, a profundidade do lençol freático pode ser usada como um *proxy* para a acessibilidade hídrica das plantas (Fan et al. 2017), além de influenciar diretamente no funcionamento da floresta, atuando nos processos fisiológicos e no desenvolvimento das raízes (Nicoll and Ray 1996, Fan and Miguez-Macho 2010). Entender esse processo é especialmente importante porque uma porção considerável (~ 50%) da floresta amazônica tem lençol freático superficial, com profundidade < 5m (Fan and Miguez-Macho 2010, Costa et al. 2022), onde o excesso de água pode representar uma limitação para o crescimento das árvores(Lopez and Kursar 2003, Cintra et al. 2013).

Solos com lençol freático superficial e mal drenados proporcionam, em geral, uma condição estressante para as plantas devido à anoxia (falta de oxigênio), além de serem limitantes no desenvolvimento do sistema radicular, inibindo o crescimento em profundidade das raízes (Canadell et al. 1996, Jackson et al. 1996, Fan et al. 2017), o que possibilita menor ancoragem no solo (Gale and Barfod 1999, de Toledo et al. 2012). No entanto, em cenários de seca moderada, seguindo a definição proposta por Costa *et al.* (2022) em que mesmo com essa alteração climática as raízes das plantas ainda conseguem alcançar a água disponível no lençol freático, o encharcamento do solo tende a diminuir, podendo levar a um aumento da janela de crescimento das árvores, de forma semelhante ao relatado para florestas de várzea (Schöngart et al. 2004, 2005). Isso é o oposto do que é observado em florestas com lençol freático profundo, onde a redução de umidade do solo e acesso à água levam à redução da fotossíntese e da produção primária líquida (p. ex. Zhao and Running 2010, Santos et al. 2018).

Diante do exposto, pode-se esperar que a profundidade do lençol freático desempenhe um papel fundamental nos padrões regionais de crescimento e mortalidade das plantas, sendo necessários estudos para melhor compreensão de como ocorre este processo. O acesso mais fácil a água subterrânea em florestas com lençol freático superficial tem o potencial para reduzir os efeitos do déficit hídrico causado pela diminuição da precipitação durante a estação seca, e promover maior produtividade nesses ambientes do que em locais nas mesmas condições climáticas, mas com lençol freático profundo. No entanto, o excesso de água em condições de lençol freático superficial durante a estação chuvosa pode levar ao estresse por falta de oxigênio para as raízes e, consequentemente, resultar na redução do crescimento das plantas. Assim, as condições adequadas para o crescimento tornam-se restritas a uma curta janela de tempo, potencialmente limitando o acúmulo de biomassa. Além disso, as raízes das árvores são tipicamente rasas em ambientes de lençol freático superficial (Jackson et al. 1996, Fan et al. 2017), sendo assim, a ancoragem pobre resultante aumenta o risco de queda de árvores (Gale and Hall 2001, Ferry et al. 2010). Juntas, essas restrições levam à expectativa de que florestas sobre lençol freático superficial tenham baixa produtividade em biomassa e taxas de mortalidade mais altas.

Em um contexto de mudanças climáticas, estudos têm mostrado que a floresta amazônica apresentou substanciais alterações nas últimas décadas, em que a mortalidade e turnover das árvores tem aumentado e o crescimento reduzido (Malhi and Wright 2004, Brienen et al. 2015, Feldpausch et al. 2016). Estas alterações têm sido atribuídas principalmente à ocorrência de secas intensas ligadas a eventos climáticos como as anomalias positivas de temperatura na superfície do mar no Pacífico Equatorial e no Atlântico Tropical Norte nas últimas décadas (Jiménez-Muñoz et al. 2016, Marengo and Espinoza 2016). Neste cenário, o aumento da mortalidade tem provocado a redução das taxas de absorção de dióxido de carbono e, portanto, impactando no papel da floresta amazônica como sumidouro de carbono da atmosfera (Lewis et al. 2011, Brienen et al. 2015, Baccini et al. 2017). No entanto, a maioria das avaliações dos efeitos da seca não considera as condições hidrológicas do solo e a interação das plantas com o lençol freático e assume a precipitação como única fonte de água para as plantas. Dentre as métricas mais utilizadas para estimar a seca está o máximo déficit hídrico acumulado, calculado através do balanço entre a precipitação e a evapotranspiração, no entanto as fontes hídricas subterrâneas, não estão explicitamente incluídas nestes cálculos.

Portanto, considerando os fatores abordados acima, espero que a profundidade do lençol freático desempenhe um papel fundamental nos padrões regionais de estrutura e dinâmica da vegetação sob condições climáticas “normais” e também sob condições climáticas extremas como durante grandes secas. Além disso, espero que esta fonte de água subterrânea minimize os efeitos das secas intensas para as plantas em regiões com lençol freático superficial, mudando assim as previsões de vulnerabilidade da floresta amazônica à seca.

Visando contribuir para o entendimento do papel do lençol freático na estrutura e dinâmica da floresta amazônica, bem como na mitigação dos efeitos de secas intensas, elaborei os seguintes capítulos desta tese de doutorado. No capítulo 1 da tese, utilizando um extenso conjunto de dados de parcelas permanentes de longo prazo distribuídas pela bacia amazônica, investiguei como a estrutura e dinâmica da floresta amazônica variam de acordo com a profundidade do lençol freático e a média histórica de déficit hídrico climático; e como a profundidade do lençol freático interage com o déficit hídrico climático e as propriedades do solo para influenciar a estrutura e dinâmica da floresta amazônica. Há razões para esperar que a produtividade em biomassa e o estoque de biomassa acima do solo diminuam, e a mortalidade aumente, com déficit e excesso de água no solo. Considerando os desafios impostos ao crescimento das plantas por solos saturados de água, minha previsão é de que a combinação de clima úmido e lençol freático superficial leve à menor produtividade e maior mortalidade, enquanto lençóis freáticos superficiais em climas secos possam mitigar o déficit hídrico climático, permitindo maior produtividade do que em configurações de lençol freático profundo. A textura do solo deve modular ainda mais essas respostas, já que solos com baixa capacidade de retenção de água podem reverter a interação positiva de lençóis freáticos superficiais e climas secos.

No capítulo 2 da tese, usando uma rede de parcelas permanentes localizadas em uma paisagem dominada por lençol freático superficial, o interflúvio Purus-Madeira, e monitoradas durante os anos das secas intensas de 2010 e 2015-16, investiguei como a profundidade do lençol freático e as propriedades do solo interagem com as secas climatológicas para influenciar a dinâmica de árvores e palmeiras; se palmeiras são mais vulneráveis a secas extremas do que as árvores; e qual o impacto das diferentes intensidades de seca climatológica na dinâmica das árvores e palmeiras. É possível que as palmeiras sejam mais sensíveis às secas extremas do que as árvores, dadas suas características anatômicas particulares e sua preferência por ambientes mais úmidos, de modo que a redução da disponibilidade de água em secas extremas aumente suas taxas de mortalidade. Por outro lado, pode haver também uma diminuição no nível do lençol freático e uma consequente redução na condição anóxica estressante do solo e, assim, melhorar as condições de crescimento tanto para as palmeiras quanto para as árvores. Nesse cenário, as plantas se beneficiariam com as secas, sem alterações em sua mortalidade e com aumento nas taxas de recrutamento.

Sendo assim, minha tese teve como objetivo geral determinar o papel da hidrologia local, regulada pela profundidade do lençol freático, na estrutura e dinâmica da floresta amazônica, bem como na mitigação dos efeitos das secas intensas.

Objetivos

Objetivo geral

Esclarecer o papel da hidrologia local, regulada pela profundidade do lençol freático, nos padrões estruturais da floresta amazônica e na mitigação do efeito de secas intensas.

Objetivos específicos

1. Avaliar como a estrutura e dinâmica da floresta amazônica são afetadas pela profundidade do lençol freático e como se dá esse processo quando associado ao déficit hídrico climático histórico e propriedades edáficas.
2. Avaliar como a profundidade do lençol freático em conjunto com as propriedades do solo interage com as secas climatológicas para influenciar a dinâmica da vegetação e se as palmeiras são mais vulneráveis a secas intensas do que árvores.

CAPÍTULO 1

Sousa, T.R. et al., 2022. Water-table depth modulates productivity and biomass across Amazonian forests. *Global Ecology and Biogeography, doi.org/10.1111/geb.13531*

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

Abstract

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

Location Lowland Amazonian forests

Time period 1971 to 2019

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

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

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

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

Introduction

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

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

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

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

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

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

Materials and methods

Vegetation data

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

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

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

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

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

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

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

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

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

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

$\lambda = \frac{[ln\,(N_0) - ln(N_s)\ ]}{t}$, where N_0 and N_s are the number of stems counted of the initial population, and the number of stems surviving to time t, respectively (Sheil *et al.*, 1995). For each site we also calculated annual recruitment rates (μ) as:

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

Environmental data

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

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

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

Data analyses

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

We weighted the plots in regression analyses when testing the effects of the environmental predictors on forest dynamics and structure according to the plot size and monitoring time, as larger plots and those monitored for longer periods are expected to provide better estimates of local, long-term forest properties. To achieve this, following Lewis *et al.* (2009), we plotted the residuals from linear models against plot area and monitoring period, and selected the root transformations of plot area and monitoring period that removed the nonlinear patterns in the residuals when applied as a weight. These empirically-determined weights were: AGWP, Area$^{1/2}$; AGB, Area$^{1/3}$; AGB mortality, Area$^{1/2}$ + Monitoring length$^{1/4}$ -1; Mortality rate, Area$^{1/2}$ + Monitoring length$^{1/3}$ -1; Recruitment rate, Area$^{1/5}$; Stem turnover, Area$^{1/3}$ + Monitoring length$^{1/4}$ -1.

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

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

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

Results

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

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

lower biomass productivity (4.5 Mg ha^{-1} yr^{-1}; t = -7.67; df = 342; p < 0.01) and 24% lower biomass stock (240.2 Mg ha^{-1}; t = -7.01; df = 342; p < 0.01) than those in wetter climates (5.7 Mg ha^{-1} yr^{-1}, 314.3 Mg ha^{-1}) (Figures 2a and 2b, respectively). Thus, the negative direct effects of climatic-water deficit (MCWD) were only slightly stronger than the negative effects of excess soil water associated with shallow water tables.

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

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

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

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

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

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

The effects of other factors

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

Discussion

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

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

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

We hypothesized that shallow water tables impose constraints on plant development under generally wet climates of Amazonia, through excess soil water and consequent oxygen limitation. Our results support this hypothesis since, on average, sites with shallow water table tended to have lower biomass productivity (Fig. 1a). However, there is high variability in AGWP, with some sites having high biomass productivity despite the shallow water table. Therefore, it is important to explore the mechanisms which may lead to the two extremes of low and high biomass productivity in shallow water tables. To help understand the lower productivity, we must review the response of soils and plants to waterlogging, the condition prevailing to various degrees – seasonal to permanent - in many of the shallow water table sites. When soils are waterlogged, most of the soil spaces are occupied with water, and the metabolism of roots and microorganisms quickly consumes the available oxygen and produces carbon dioxide. As oxygen is depleted, roots and aerobic microorganisms lose most of their capacity to produce energy through aerobic respiration (Gibbs & Greenway, 2003). In this case, the major pathway to energy production is alcoholic fermentation, which has a much lower yield (2 mols ATP per glycose molecule) than respiration (36 ATP), and thus severely limits plant growth (Setter & Belford, 1990; Kreuzwieser & Rennenberg, 2014). Low oxygen levels also reduce root permeability (North et al., 2004; Vandeleur et al., 2005), generating a cascade of responses that reduce stomatal conductance and thus limit photosynthesis (Lopez & Kursar, 1999, 2003; Parent et al., 2008; Pezeshki, 2001). Low photosynthetic activity and consequent low growth is well documented in periodically flooded forests (Parolin, 2000; Waldhoff et al., 1998), although this a more extreme condition than the soil waterlogging examined here. Given the various deleterious effects of excess water on plant metabolism and physiology, most tree growth occurs during the windows when water table levels decrease and anoxia is relieved, mostly in the dry season. Such growth windows have been described in flooded areas, where the largest diameter growth occurs in the non-flooded period (Schöngart et al., 2002; 2004). Therefore, the period with environmental conditions suitable for growth is shorter in shallow water table, and therefore, on average, biomass productivity is lower in these locations than in deep water table (but, see next section, these patterns change when combined with climate).

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

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

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

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

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

A full accounting of the factors affecting soil moisture also requires consideration of soil properties, especially soil texture (Richter & Babbar, 1991; Quesada *et al.*, 2012). In general, the ecological effects of the soil water regime will depend on the degree of soil saturation in the wet months, the degree and frequency of water deficit periods, the water-holding capacity of the soil, and the root distribution in the soil (Franco & Dezzeo, 1994). By having higher aggregation particles, clayey soils have better water-holding capacity (Richter & Babbar, 1991), therefore, clay soils should increase the time interval between precipitation inputs and groundwater recharge, while predominantly sandy soils should have faster groundwater level responses to precipitation. Our results suggest a contribution of clayey texture in increasing productivity in dry climates with shallow water table (Fig. 5 C). However, here too the dataset lacks complete coverage of the relevant environmental combinations, limiting our conclusions.

Limitations of this study

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

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

Final considerations

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

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

Data Availability Statement

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

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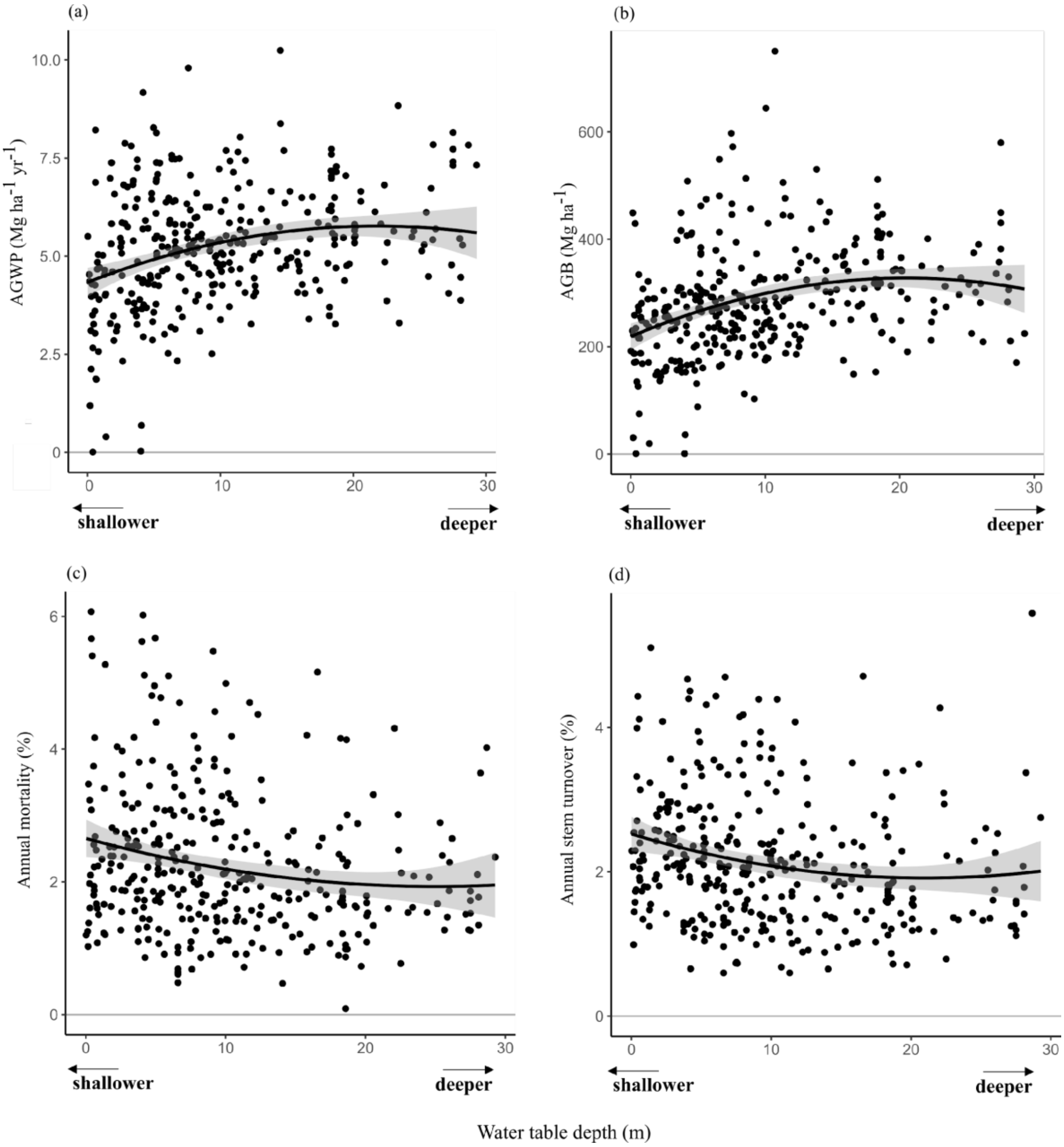

Figure 1. Impact of water-table depth on (A) biomass productivity; (B) biomass stock; (C) mortality rate; and (D) stem turnover in Amazonian forests. LOESS regression was used to adjust the relationships between the response variables and WTD. The shaded region shows the confidence interval of the regression.

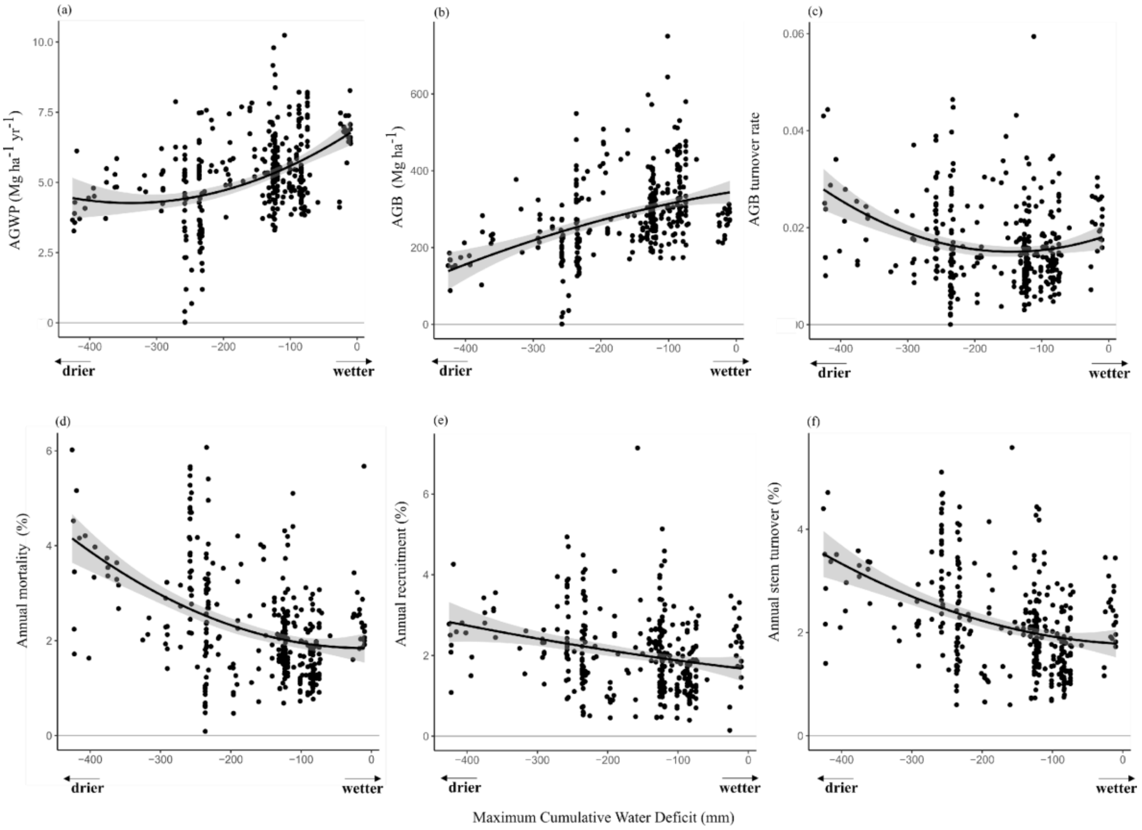

Figure 2. Impact of the maximum cumulative water deficit on (A) biomass productivity; (B) biomass stock; (C) biomass turnover; (D) mortality rate; (E) recruitment rate; and (F) stem turnover in Amazonian forests. LOESS regression was used to adjust the relationships between the response variables and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

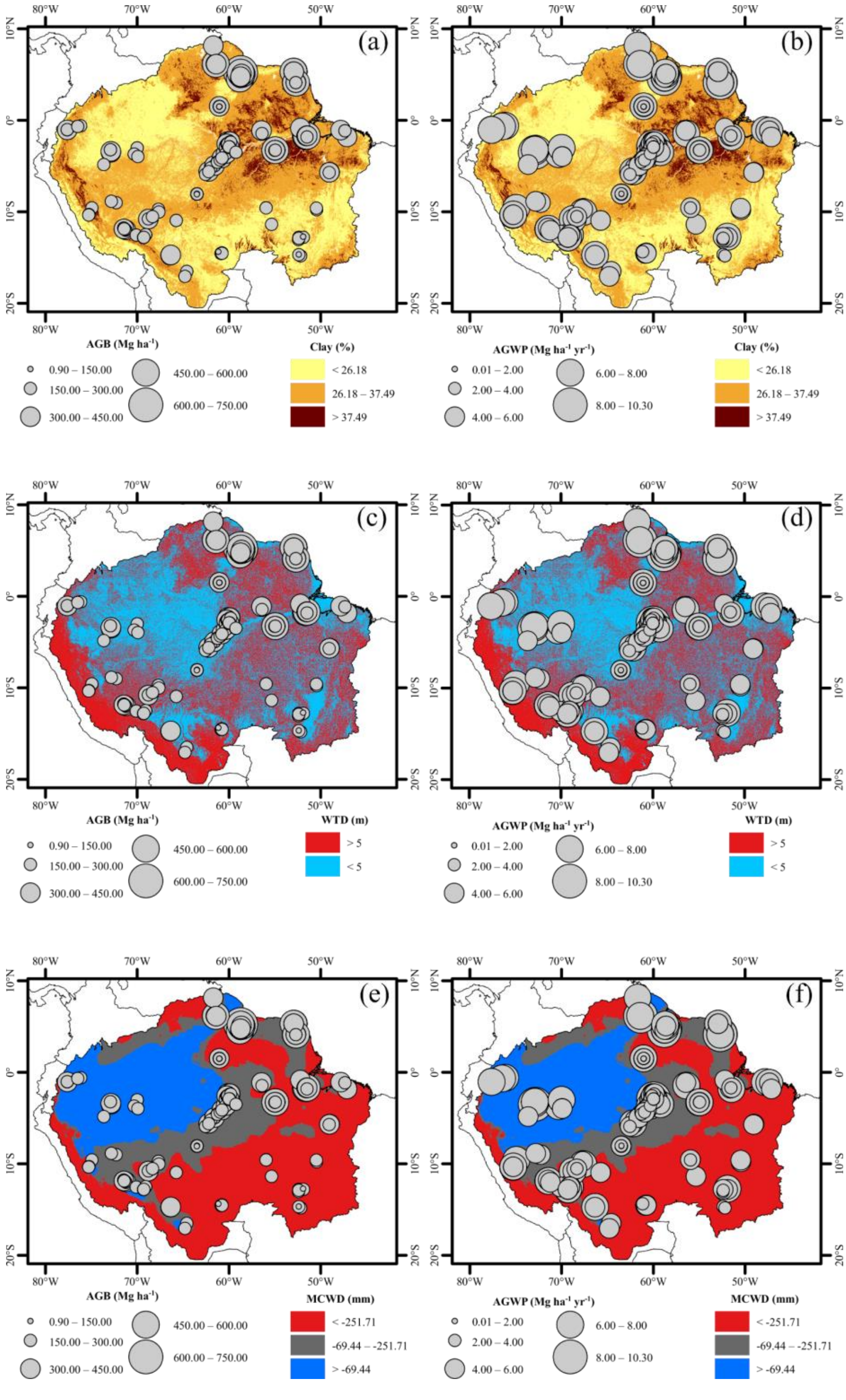

Figure 3. Spatial variation in forest biomass and productivity across Amazonia. Plots a and b display these metrics against a background of clay content; c and d the WTD background; and e and f the MCWD background. The clay content and MCWD classes were defined based on the standard deviation around the mean of each of these variables, shallow and deep water tables follow the definitions of Fan & Miguez-Macho (2010). These classes are the same those used in Figures 4 and 5. Gray dots represent plots with size proportional to the biomass stock or productivity.

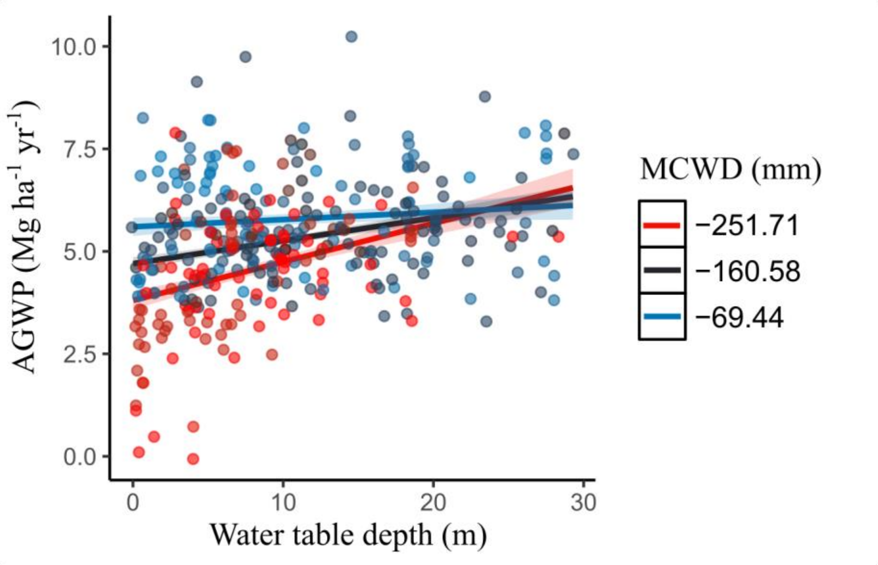

Figure 4. Partial-dependence plot of the interaction between MCWD and water table depth on biomass productivity. In order to visualize interactions, climate was divided in three classes based on the standard deviation around the mean. Red colour is for plots with MCWD values less than one standard deviation below the mean; black is for plots with MCWD values within one standard deviation of the mean; and blue is for plots with MCWD values greater than one standard deviation above the mean. Shaded regions represent confidence intervals.

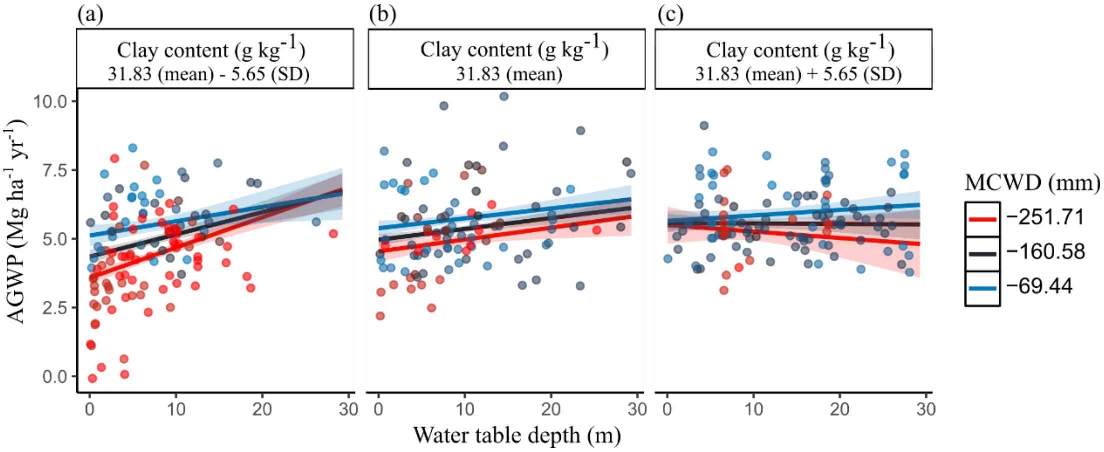

Figure 5. Partial-dependence plots derived from multiple-regression models investigating the effects of interactions among clay content, water table depth and MCWD on biomass productivity in Amazonian forests. (a) Partial plots of the interaction in less clayey soil; (b) Partial effect of the interaction in moderately clayey soil; and (c) Partial effect of the interaction in more clayey soil. In order to visualize interactions, climate and soil texture were divided in three classes based on the standard deviation around the mean. Red colour is for plots with MCWD values less than one standard deviation below the mean; black is for plots with MCWD values within one standard deviation of the mean; and blue is for plots with MCWD values greater than one standard deviation above the mean. Shaded regions represent confidence intervals.

Supporting Information

Table S1. List of permanent Amazon forest monitoring plots used in this study.

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Bolivia	BEE-01	-16.53	-64.58	180	1	4
Bolivia	BEE-05	-16.53	-64.58	180	1	4
Bolivia	CHO-01	-14.39	-61.15	170	1	2
Bolivia	EBB-05	-14.76	-66.34	210	1	2
Bolivia	EBB-09	-14.73	-66.32	220	1	2
Bolivia	HCC-21	-14.53	-60.74	729	1	7
Bolivia	HCC-22	-14.53	-60.73	747	1	7
Bolivia	HCC-23	-14.56	-60.75	809	1	5
Bolivia	HCC-24	-14.57	-60.75	735	1	5
Bolivia	LFB-01	-14.58	-60.83	245	1	8
Bolivia	LFB-02	-14.58	-60.83	227	1	9
Bolivia	RET-05	-10.97	-65.72	160	1	10
Bolivia	RET-06	-10.97	-65.72	160	1	10
Bolivia	RET-08	-10.97	-65.72	160	1	10
Bolivia	RET-09	-10.97	-65.72	160	1	10
Bolivia	SCT-01	-17.09	-64.77	248	1	7
Brazil	ALF-01	-9.6	-55.94	269	1	5
Brazil	ALF-02	-9.58	-55.92	277	1	4
Brazil	BDF-01	-2.34	-60.1	75	2	6
Brazil	BDF-03	-2.42	-59.85	75	1	6
Brazil	BDF-04	-2.43	-59.85	75	1	6
Brazil	BDF-05	-2.43	-59.85	75	1	6
Brazil	BDF-06	-2.41	-59.86	75	3	6
Brazil	BDF-07	-2.4	-59.9	75	1	6
Brazil	BDF-08	-2.4	-59.9	75	1	6
Brazil	BDF-09	-2.4	-59.85	75	1	5
Brazil	BDF-10	-2.39	-59.86	75	2	5
Brazil	BDF-11	-2.38	-59.85	75	3	5
Brazil	BDF-12	-2.39	-59.85	75	2	5
Brazil	BDF-13	-2.4	-59.91	75	9	6
Brazil	BDF-14	-2.36	-59.97	75	1	7
Brazil	BNT-01	-2.64	-60.16	73	1	22
Brazil	BNT-02	-2.64	-60.15	73	1	22
Brazil	BNT-04	-2.63	-60.15	73	1	21

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Brazil	BNT-05	-2.63	-60.17	73	1	5
Brazil	BNT-06	-2.63	-60.17	73	1	5
Brazil	BNT-07	-2.63	-60.17	73	1	5
Brazil	CAX-06	-1.72	-51.46	20	1	6
Brazil	CAX-08	-1.85	-51.47	10	1	8
Brazil	CNA-10	-8.07	-63.49	89	1	2
Brazil	CNA-11	-8.07	-63.48	89	1	2
Brazil	CNA-12	-8.07	-63.47	86	0.992	2
Brazil	CNA-13	-8.07	-63.46	89	0.966	2
Brazil	CNA-14	-8.07	-63.45	75	0.981	2
Brazil	CNA-20	-8.08	-63.49	87	0.99	2
Brazil	CNA-21	-8.08	-63.48	87	0.999	2
Brazil	CNA-22	-8.08	-63.47	87	0.999	2
Brazil	CNA-23	-8.08	-63.46	86	0.989	2
Brazil	CNA-24	-8.08	-63.45	73	0.989	2
Brazil	CNA-30	-8.09	-63.49	86	0.979	2
Brazil	CNA-31	-8.09	-63.48	83	0.951	2
Brazil	CNA-32	-8.09	-63.47	87	0.997	2
Brazil	CNA-33	-8.09	-63.46	78	0.951	2
Brazil	CNA-34	-8.09	-63.45	72	0.967	2
Brazil	CNA-40	-8.1	-63.49	73	0.969	2
Brazil	CNA-41	-8.1	-63.48	83	0.977	2
Brazil	CNA-42	-8.1	-63.47	78	0.98	2
Brazil	CNA-43	-8.1	-63.46	78	0.998	2
Brazil	CNA-44	-8.1	-63.45	73	1	2
Brazil	CNA-50	-8.11	-63.49	84	0.981	2
Brazil	CNA-51	-8.11	-63.48	82	0.995	2
Brazil	CNA-52	-8.11	-63.47	74	0.992	2
Brazil	CNA-53	-8.11	-63.46	67	0.985	2
Brazil	CNA-54	-8.11	-63.45	66	0.976	2
Brazil	CNA-60	-8.12	-63.49	86	0.993	2
Brazil	CNA-61	-8.12	-63.48	83	0.971	2
Brazil	CNA-62	-8.12	-63.47	80	0.996	2
Brazil	CNA-64	-8.12	-63.45	77	0.998	2
Brazil	CPP-01	-1.84	-47.1	73	1	2
Brazil	DOI-01	-10.57	-68.32	203	1	10
Brazil	DOI-02	-10.55	-68.31	203	1	8
Brazil	DUK-10	-2.93	-59.97	85	1	3

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Brazil	DUK-11	-2.93	-59.96	108	1	3
Brazil	DUK-12	-2.92	-59.95	109	1	3
Brazil	DUK-13	-2.92	-59.94	104	1	3
Brazil	DUK-14	-2.92	-59.93	89	1	3
Brazil	DUK-15	-2.92	-59.92	70	1	3
Brazil	DUK-16	-2.92	-59.91	59	1	3
Brazil	DUK-17	-2.92	-59.9	54	1	3
Brazil	DUK-21	-2.94	-59.97	61	1	3
Brazil	DUK-22	-2.94	-59.96	98	1.1	4
Brazil	DUK-23	-2.93	-59.95	75	1	6
Brazil	DUK-24	-2.93	-59.94	81	1.1	3
Brazil	DUK-25	-2.93	-59.93	65	1	3
Brazil	DUK-26	-2.93	-59.92	96	1	3
Brazil	DUK-27	-2.93	-59.91	59	1	3
Brazil	DUK-28	-2.93	-59.9	45	1	3
Brazil	DUK-31	-2.94	-59.96	81	1.1	3
Brazil	DUK-32	-2.94	-59.95	61	1	6
Brazil	DUK-33	-2.94	-59.94	53	1	6
Brazil	DUK-34	-2.94	-59.94	55	1	6
Brazil	DUK-35	-2.94	-59.93	88	1	6
Brazil	DUK-36	-2.94	-59.92	74	1	3
Brazil	DUK-37	-2.94	-59.91	40	1	3
Brazil	DUK-38	-2.94	-59.9	51	1	3
Brazil	DUK-41	-2.95	-59.96	46	1	6
Brazil	DUK-42	-2.95	-59.95	55	1	3
Brazil	DUK-43	-2.95	-59.94	100	1	6
Brazil	DUK-44	-2.95	-59.93	105	1	6
Brazil	DUK-45	-2.95	-59.93	98	1	6
Brazil	DUK-46	-2.95	-59.92	92	1	3
Brazil	DUK-47	-2.95	-59.91	66	1	3
Brazil	DUK-48	-2.95	-59.91	66	1	3
Brazil	DUK-51	-2.96	-59.96	56	1	3
Brazil	DUK-52	-2.96	-59.95	93	1	3
Brazil	DUK-53	-2.96	-59.94	73	1	6
Brazil	DUK-56	-2.96	-59.91	60	1	6
Brazil	DUK-57	-2.95	-59.91	90	1	3
Brazil	DUK-58	-2.95	-59.9	39	1	3
Brazil	DUK-62	-2.97	-59.95	53	1	5

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Brazil	DUK-63	-2.97	-59.94	60	1	6
Brazil	DUK-64	-2.97	-59.93	100	1	3
Brazil	DUK-65	-2.97	-59.92	75	1	3
Brazil	DUK-66	-2.96	-59.91	77	1	3
Brazil	DUK-67	-2.96	-59.9	53	1	3
Brazil	DUK-68	-2.96	-59.9	60	1	3
Brazil	DUK-71	-2.98	-59.96	58	1	5
Brazil	DUK-72	-2.98	-59.95	84	1	5
Brazil	DUK-73	-2.98	-59.94	101	1	3
Brazil	DUK-74	-2.98	-59.93	92	1	6
Brazil	DUK-75	-2.97	-59.92	100	1	3
Brazil	DUK-76	-2.97	-59.91	100	1	3
Brazil	DUK-77	-2.97	-59.9	95	1	3
Brazil	DUK-78	-2.97	-59.89	63	1	3
Brazil	DUK-81	-2.99	-59.96	52	1	6
Brazil	DUK-82	-2.99	-59.95	49	1	5
Brazil	DUK-83	-2.99	-59.94	63	1	3
Brazil	DUK-84	-2.98	-59.93	56	1	3
Brazil	DUK-85	-2.98	-59.92	102	1	3
Brazil	DUK-87	-2.98	-59.9	47	1	3
Brazil	DUK-88	-2.98	-59.89	95	1	3
Brazil	DUK-91	-3	-59.95	60	1	3
Brazil	DUK-92	-3	-59.94	87	1	3
Brazil	DUK-93	-3	-59.94	87	1	3
Brazil	DUK-94	-2.99	-59.93	56	1	3
Brazil	DUK-95	-2.99	-59.92	85	1	3
Brazil	DUK-96	-2.99	-59.91	57	1	3
Brazil	DUK-98	-2.99	-59.89	97	1	3
Brazil	FEC-01	-10.07	-67.62	204	1	5
Brazil	FLO-01	-12.81	-51.85	377	1	5
Brazil	FLO-02	-12.75	-51.88	366	1	4
Brazil	GMT-01	-1.11	-47.8	50	1	3
Brazil	IPM-20	-3.69	-60.33	50	1	3
Brazil	IPM-21	-4.62	-61.24	NA	1	3
Brazil	IPM-22	-3.68	-60.32	44	1	3
Brazil	IPM-25	-3.67	-60.31	44	1	3
Brazil	IPM-26	-4.98	-61.57	61	1	3
Brazil	IPM-27	-4.99	-61.56	50	1	3

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Brazil	IPM-28	-3.67	-60.3	44	1	3
Brazil	IPM-37	-4.16	-60.72	37	1	3
Brazil	IPM-39	-4.14	-60.73	40	1	3
Brazil	IPM-40	-4.15	-60.73	30	1	3
Brazil	IPM-42	-4.38	-60.95	45	1	3
Brazil	IPM-43	-4.38	-60.94	48	1	3
Brazil	IPM-46	-4.4	-60.92	46	1	3
Brazil	IPM-55	-4.6	-61.26	51	1	3
Brazil	IPM-62	-4.99	-61.56	57	1	3
Brazil	IPM-63	-5	-61.55	58	1	3
Brazil	IPM-64	-5	-61.54	59	1	3
Brazil	IPM-79	-5.25	-61.96	62	1	3
Brazil	IPM-80	-5.25	-61.96	63	1	3
Brazil	IPM-86	-5.63	-62.19	69	1	3
Brazil	IPM-87	-5.63	-62.19	65	1	3
Brazil	IPM-88	-5.64	-62.18	70	1	3
Brazil	IPM-98	-5.95	-62.51	69	1	3
Brazil	IPM-99	-5.94	-62.52	70	1	3
Brazil	JAC-01	-2.61	-60.21	73	5	8
Brazil	JAC-02	-2.62	-60.2	73	5	8
Brazil	JRI-01	-0.89	-52.19	150	1	6
Brazil	MRB-01	-5.73	-49.05	90	2	4
Brazil	MRB-02	-5.72	-49.03	90	2	4
Brazil	MRB-03	-5.7	-49	90	2	4
Brazil	MTH-01	-8.88	-72.79	246	1	6
Brazil	NOC-01	-3.52	-59.27	14	0.25	4
Brazil	NOC-02	-3.52	-59.27	14	0.25	4
Brazil	NOC-03	-3.52	-59.27	17	0.25	4
Brazil	NXV-02	-14.7	-52.35	250	0.5	3
Brazil	NXV-06	-14.72	-52.36	346	0.47	6
Brazil	POR-01	-10.82	-68.77	268	1	9
Brazil	POR-02	-10.8	-68.77	268	1	8
Brazil	PPB-01	-1.18	-47.32	50	1	2
Brazil	PPB-02	-1.18	-47.32	50	1	2
Brazil	PPB-03	-1.18	-47.32	50	1	2
Brazil	PTB-01	-1.17	-56.41	180	1	2
Brazil	PTB-02	-1.48	-56.39	40	1	2
Brazil	RBR-01	-5.93	-62.52	NA	1	3

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Brazil	RFH-01	-9.75	-67.67	176	1	6
Brazil	RST-01	-9.04	-72.27	279	1	6
Brazil	SAA-01	-9.79	-50.43	177	1	4
Brazil	SAA-02	-9.64	-50.45	207	1	3
Brazil	SIP-01	-11.41	-55.32	385	0.76	3
Brazil	STO-03	-3.3	-54.96	132	0.25	3
Brazil	STO-05	-3.34	-54.98	170	0.25	3
Brazil	STO-06	-3.34	-54.96	178	0.25	3
Brazil	STO-07	-3.32	-54.96	163	0.25	3
Brazil	TAN-02	-13.08	-52.38	382	1	5
Brazil	TAN-03	-12.83	-52.35	356	1	5
Brazil	TAN-04	-12.92	-52.37	389	1	5
Brazil	TAP-50	-3.31	-54.94	100	0.25	3
Brazil	TAP-51	-3.31	-54.94	100	0.25	3
Brazil	TAP-52	-3.31	-54.94	100	0.25	3
Brazil	TAP-53	-3.31	-54.94	100	0.25	3
Brazil	TAP-54	-3.31	-54.95	100	0.25	3
Brazil	TAP-55	-3.31	-54.95	100	0.25	3
Brazil	TAP-56	-3.31	-54.95	100	0.25	3
Brazil	TAP-57	-3.31	-54.95	100	0.25	3
Brazil	TAP-58	-3.31	-54.94	100	0.25	3
Brazil	TAP-59	-3.31	-54.94	100	0.25	3
Brazil	TAP-60	-3.31	-54.94	100	0.25	3
Brazil	TAP-61	-3.31	-54.94	100	0.25	3
Brazil	TEC-01	-1.71	-51.46	15	1	11
Brazil	TEC-02	-1.74	-51.49	15	1	11
Brazil	TEC-03	-1.73	-51.51	15	1	11
Brazil	TEC-04	-1.75	-51.52	15	1	11
Brazil	TEC-05	-1.78	-51.59	15	1	11
Brazil	TEC-06	-1.73	-51.43	15	1	11
Brazil	TEM-01	-2.97	-59.9	120	1	10
Brazil	TEM-02	-2.93	-59.95	120	1	10
Brazil	TEM-03	-2.41	-59.9	100	1	9
Brazil	TEM-04	-2.43	-59.79	100	1	9
Brazil	TEM-05	-2.62	-60.21	100	1	9
Brazil	TEM-06	-2.6	-60.11	100	1	10
Brazil	TIC-01	-3.54	-59.22	13	0.25	4
Brazil	TIC-03	-3.53	-59.22	12	0.25	4

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Brazil	VCR-02	-14.83	-52.17	297	0.6	6
Brazil	VIR-11	1.49	-61.01	94	1	3
Brazil	VIR-12	1.49	-61.02	53	1	3
Brazil	VIR-13	1.49	-61.03	50	1	3
Brazil	VIR-14	1.49	-61.03	52	1	3
Brazil	VIR-15	1.49	-61.04	48	1	3
Brazil	VIR-22	1.48	-61.02	130	1	3
Brazil	VIR-23	1.48	-61.03	58	1	3
Brazil	VIR-24	1.48	-61.03	49	1	3
Brazil	VIR-25	1.48	-61.04	49	1	3
Brazil	VIR-31	1.47	-61.01	55	0.5	3
Brazil	VIR-32	1.47	-61.02	56	1	3
Brazil	VIR-33	1.47	-61.03	58	1	3
Brazil	VIR-34	1.47	-61.03	56	1	3
Brazil	VIR-35	1.47	-61.04	49	0.5	3
Brazil	VIR-41	1.46	-61.01	52	0.9	3
Brazil	VIR-42	1.46	-61.02	55	1	3
Brazil	VIR-43	1.46	-61.03	57	1	3
Brazil	VIR-45	1.46	-61.04	50	0.5	3
Brazil	VIR-51	1.45	-61.01	50	1	3
Brazil	VIR-52	1.45	-61.02	50	1	3
Brazil	VIR-53	1.45	-61.03	49	1	3
Brazil	VIR-54	1.45	-61.03	48	1	3
Brazil	VIR-55	1.45	-61.04	48	1	3
Brazil	VIR-61	1.44	-61.01	52	1	3
Brazil	VIR-62	1.44	-61.02	49	1	3
Brazil	VIR-63	1.44	-61.03	49	1	3
Brazil	VIR-65	1.44	-61.04	50	1	3
Colombia	AGP-01	-3.72	-70.31	120	1	5
Colombia	AGP-02	-3.72	-70.3	120	1	5
Colombia	LOR-01	-3.06	-69.99	94	1	3
Colombia	LOR-02	-3.06	-69.99	93	0.52	4
Colombia	LOR-03	-3.06	-69.99	93	0.48	3
Colombia	ZAR-03	-3.99	-69.9	130	1	4
Colombia	ZAR-04	-3.99	-69.91	146	1	3
Ecuador	BOG-01	-0.7	-76.48	257	1	6
Ecuador	BOG-02	-0.7	-76.47	284	1	6
Ecuador	JAS-02	-1.07	-77.62	452	1	9

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Ecuador	JAS-03	-1.08	-77.61	384	1	9
Ecuador	JAS-04	-1.07	-77.61	430	0.96	6
Ecuador	TIP-02	-0.63	-76.14	243	0.8	6
French Guiana	NOU-01	4.09	-52.67	110	1	5
French Guiana	NOU-02	4.09	-52.67	110	1	5
French Guiana	NOU-03	4.09	-52.68	110	1	5
French Guiana	NOU-04	4.09	-52.68	110	1	5
French Guiana	NOU-05	4.09	-52.68	110	1	4
French Guiana	NOU-06	4.09	-52.68	110	1	4
French Guiana	NOU-07	4.08	-52.68	110	1	4
French Guiana	NOU-08	4.08	-52.68	110	1	4
French Guiana	NOU-09	4.08	-52.68	110	1	4
French Guiana	NOU-10	4.09	-52.68	110	1	4
French Guiana	NOU-11	4.08	-52.68	110	1	5
French Guiana	NOU-12	4.08	-52.68	110	1	4
French Guiana	NOU-13	4.08	-52.68	127	1	4
French Guiana	NOU-14	4.08	-52.68	110	1	4
French Guiana	NOU-15	4.08	-52.68	118	1	4
French Guiana	NOU-16	4.08	-52.68	110	1	4
French Guiana	NOU-17	4.08	-52.68	110	1	4
French Guiana	NOU-18	4.08	-52.68	123	1	4
French Guiana	NOU-19	4.08	-52.68	110	1	4
French Guiana	NOU-21	4.08	-52.68	110	1	4
French Guiana	NOU-22	4.08	-52.67	110	1	4
French Guiana	PAB-01	5.27	-52.92	40	6.25	28
French Guiana	PAR-20	5.28	-52.92	20	0.49	7
French Guiana	PAR-21	5.28	-52.92	20	0.49	7
French Guiana	PAR-22	5.28	-52.92	20	0.49	7
French Guiana	PAR-23	5.28	-52.92	20	0.49	7
French Guiana	PAR-24	5.28	-52.92	20	0.49	7
French Guiana	PAR-25	5.28	-52.92	20	0.49	7
French Guiana	PAR-26	5.28	-52.92	20	0.49	7
French Guiana	PAR-27	5.28	-52.92	20	0.49	7
French Guiana	PAR-28	5.28	-52.92	20	0.49	7
French Guiana	PAR-29	5.28	-52.92	35	0.49	7
Guyana	FMH-01	5.17	-58.69	98	1	8
Guyana	FMH-02	5.17	-58.69	122	1	4
Guyana	FMH-03	5.18	-58.7	115	1	4

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Guyana	IWO-03	4.53	-58.78	100	1	3
Guyana	IWO-09	4.61	-58.73	116	1	3
Guyana	IWO-12	4.73	-58.72	61	1	3
Guyana	IWO-21	4.63	-58.74	97	1	5
Guyana	IWO-22	4.62	-58.72	139	1	5
Guyana	PIB-05	5.02	-58.62	93	1	4
Guyana	PIB-06	5.01	-58.62	81	1	4
Guyana	PIB-12	5.03	-58.6	94	1	4
Peru	ALM-01	-11.8	-71.47	400	2	5
Peru	BAR-01	-11.9	-71.42	345	0.813	5
Peru	CUZ-01	-12.54	-69.06	190	1	9
Peru	CUZ-02	-12.54	-69.06	190	1	9
Peru	CUZ-03	-12.53	-69.05	190	1	9
Peru	CUZ-04	-12.54	-69.05	190	1	9
Peru	IND-01	-3.52	-72.85	111	1	2
Peru	JEN-11	-4.88	-73.63	151	1	8
Peru	LAS-02	-12.57	-70.09	235	1	4
Peru	MNU-03	-11.9	-71.4	312	2	5
Peru	MNU-04	-11.9	-71.4	358	1	6
Peru	MNU-08	-12	-71.24	295	2	6
Peru	MNU-09	-12.04	-71.21	332	2	5
Peru	PAK-01	-11.94	-71.28	345	1	4
Peru	PNY-04	-10.34	-75.25	414	1	5
Peru	PNY-05	-10.35	-75.25	448	1.002	5
Peru	PNY-07	-10.35	-75.26	414	1	5
Peru	PNY-22	-10.38	-75.26	463	1.026	4
Peru	RCS-05	-9.62	-74.93	251	1	3
Peru	SUC-01	-3.25	-72.91	107	1	10
Peru	SUC-02	-3.25	-72.9	98	1	10
Peru	SUC-04	-3.25	-72.89	107	1	8
Peru	SUC-05	-3.26	-72.89	118	1	8
Peru	TAM-01	-12.84	-69.29	205	1	10
Peru	TAM-02	-12.83	-69.29	210	1	13
Peru	TAM-04	-12.84	-69.28	210	0.42	9
Peru	TAM-05	-12.83	-69.27	220	1	12
Peru	TAM-06	-12.84	-69.3	200	0.96	12
Peru	TAM-07	-12.83	-69.26	225	1	10
Peru	TAM-08	-12.83	-69.27	220	1	6

Country	Plot Code	Lat.	Long.	Alt. (m asl)	Area (ha)	N censuses
Peru	TAM-09	-12.83	-69.28	199	1	5
Peru	YAN-02	-3.43	-72.84	109	1	7
Venezuela	ELD-01	6.11	-61.41	220	0.25	26
Venezuela	ELD-02	6.11	-61.41	244	0.25	26
Venezuela	ELD-04	6.09	-61.35	366	0.25	26
Venezuela	RIO-01	8.11	-61.69	312	0.25	25

Table S2. Statistical summary of the multiple linear models tested to investigate the effects of environmental variables on vegetation structure and dynamics of Amazon forests. Standardized beta coefficients for the simple effects of variables (but not for interactions) are shown. Significant effects are shown in bold.

Forest metric	Regression coefficients for predictors	P	R^2
AGWP	0.45 MCWD	**<0.001**	0.36
	0.18 water table depth	**0.008**	
	0.39 clay content	**<0.001**	
	-0.09 maximum temperature	0.33	
	0.51 soil fertility	**<0.001**	
	-0.0004 water table depth*MCWD	**<0.001**	
	0.00007 water table depth*MCWD*clay	**0.01**	
	-0.00009 MCWD*clay	0.55	
AGB stock	20.25 MCWD	**<0.001**	0.33
	14.19 water table depth	**0.003**	
	23.87 clay content	**<0.001**	
	-18.06 maximum temperature	**0.007**	
	-4.20 soil fertility	0.45	
	-0.01 water table depth*MCWD	0.16	
	0.003 water table depth*MCWD*clay	0.15	
	-0.03 MCWD*clay	**0.02**	
Annual mortality rate	-0.27 MCWD	**<0.001**	0.29
	-0.08 water table depth	0.11	
	-0.17 clay content	**0.03**	
	0.13 maximum temperature	0.09	
	0.16 soil fertility	**0.01**	
	0.00005 water table depth*MCWD	0.57	
	0.000008 water table depth*MCWD*clay	0.67	
	0.0005 MCWD*clay	**<0.001**	

Forest metric	Regression coefficients for predictors	P	R^2
Annual recruitment rate	-0.14 MCWD	**0.03**	0.10
	-0.05 water table depth	0.38	
	-0.13 clay content	0.08	
	0.04 maximum temperature	0.61	
	0.13 soil fertility	**0.04**	
	-0.0001 water table depth*MCWD	0.13	
	-0.000003 water table depth*MCWD*clay	0.90	
	0.00002 MCWD*clay	0.85	
Annual turnover rate	-0.20 MCWD	**<0.001**	0.24
	-0.07 water table depth	0.14	
	-0.14 clay content	**0.03**	
	0.09 maximum temperature	0.14	
	0.16 soil fertility	**0.004**	
	-0.00003 water table depth*MCWD	0.66	
	0.000005 water table depth*MCWD*clay	0.79	
	0.0003 MCWD*clay	**0.01**	
AGB mortality rate	-0.0008 MCWD	0.14	0.10
	-0.0005 water table depth	0.23	
	-0.0007 clay content	0.25	
	0.00007 maximum temperature	0.92	
	0.002 soil fertility	**0.005**	
	-0.0000008 water table depth*MCWD	0.28	
	0.000003 water table depth*MCWD*clay	0.08	
	0.000003 MCWD*clay	**0.004**	

Table S3. Multicollinearity test to check the associations between predictor variables in the linear models. Variance Inflation Factor (VIF) less than 5 indicates low multiple correlation of that predictor with others.

Predictors	VIF	SE factor
MCWD	1.54	1.24
Water table depth	1.14	1.07
Soil fertility	1.64	1.28
Clay content	2.19	1.48
Maximum temperature	2.25	1.50

Table S4. Comparison of models with and without a random factor to assess spatial autocorrelation between plots. AIC0 is the model without random factor, AIC1 is the model with random factor and DIF is AIC0-AIC1.

Forest metric	AIC0	AIC1	DIF
AGWP	1268.53	1238.16	30.37
AGB	4037.11	3976.27	60.84
Mortality rate	1869.88	1607.16	262.72
Recruitment rate	863.77	800.41	63.66
Turnover rate	1387.79	1177.87	209.92
AGB mortality rate	4342.20	4393.22	-51.02

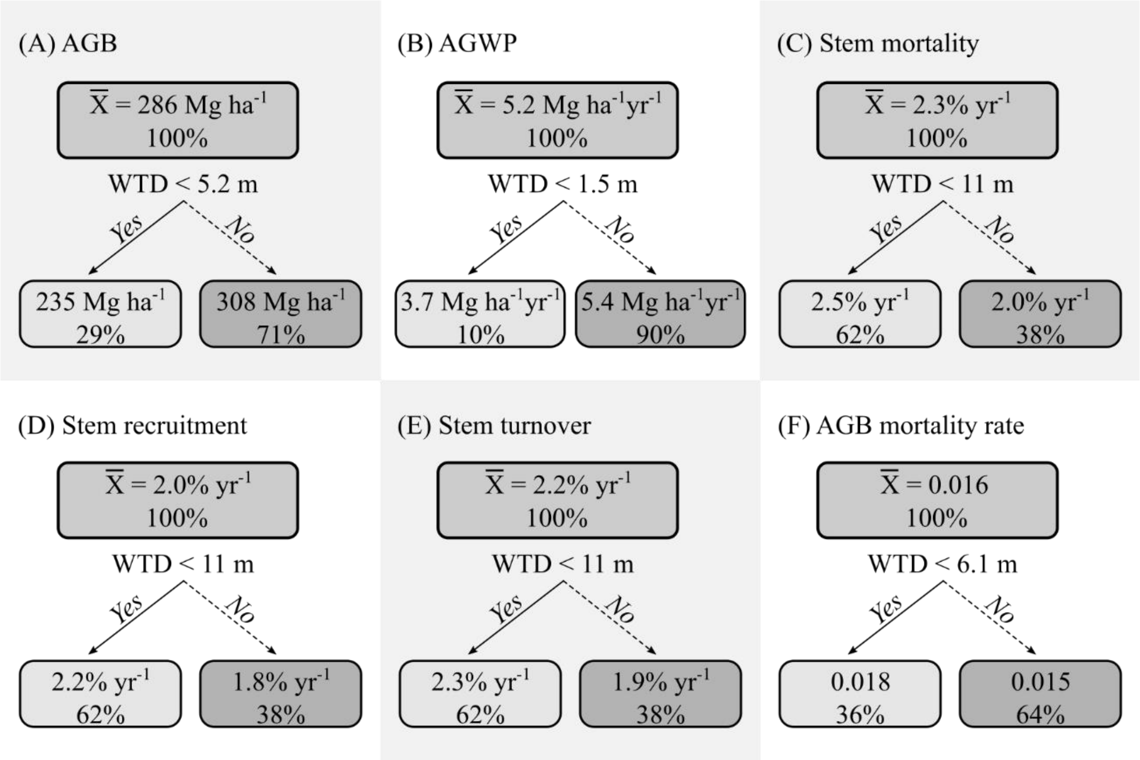

Figure S1. Regression trees showing the relationships and cutoff between water-table depth and the response variables: (A) AGB stock, (B) AGWP, (C) Annual stem mortality, (D) Annual stem recruitment, (E) Annual stem turnover, and (F) AGB mortality rate.

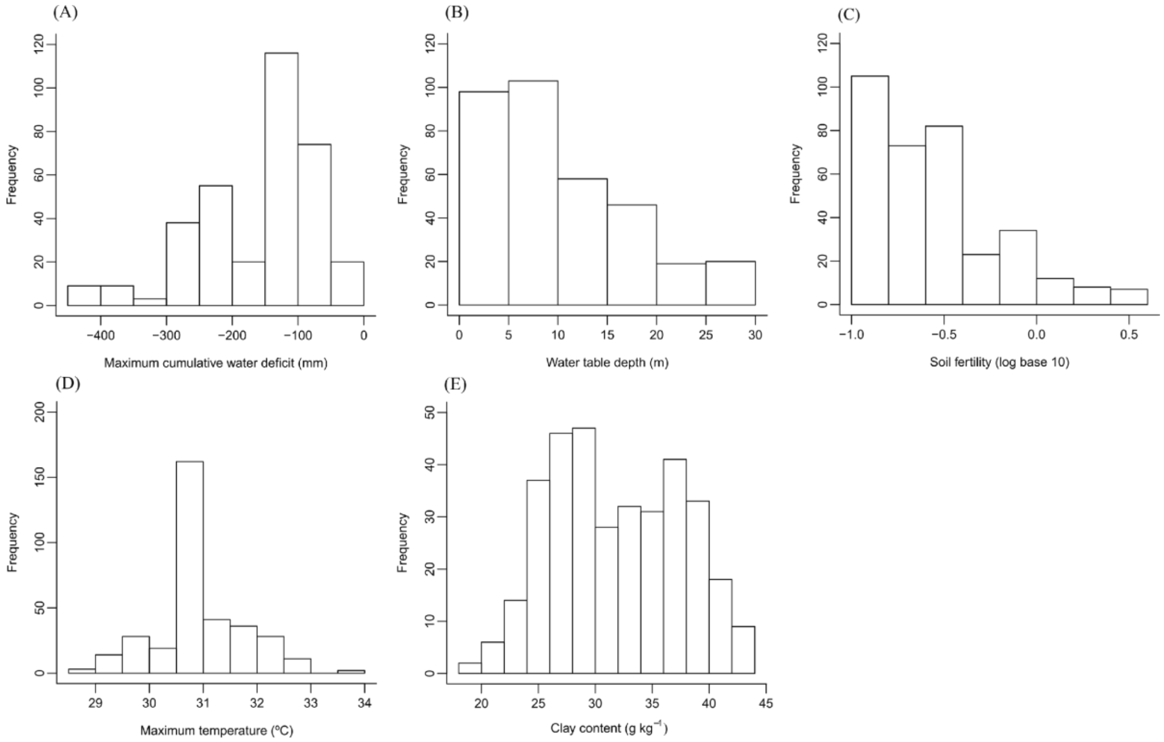

Figure S2. Histograms of the distribution of environmental variables in the plots used in this study are as follows: (A) Maximum cumulative water deficit; (B) Water-table depth; (C) Soil fertility; (D) Maximum temperature; and (F) Clay content.

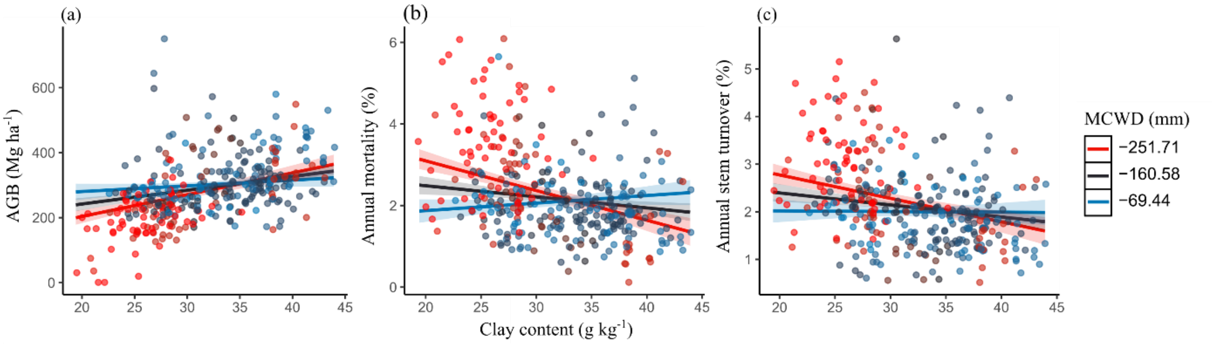

Figure S3. Partial-dependence plot of the interaction between MCWD and water table depth on biomass productivity without plots with very low productivity (AGWP < 2 Mg ha^{-1} yr^{-1}). These were eight plots in white sand forests that are dominated by very thin trees (<10 cm DBH). In order to visualize interactions, climate was divided in three classes based on the standard deviation around the mean. Red colour is for plots with MCWD values less than one standard deviation below the mean; black is for plots with MCWD values within one standard deviation of the mean; and blue is for plots with MCWD values greater than one standard deviation above the mean. Shaded regions represent confidence intervals.

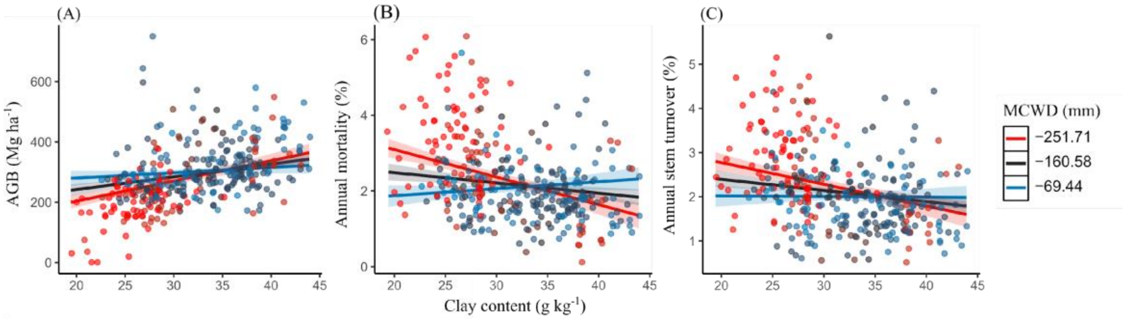

Figure S4. Multiple regression models investigating the effect of interactions among clay content and MCWD in Amazon forests. (A) biomass stock; (B) mortality rate; and (C) stem turnover. We used partial-dependence plots to visualize the shape of the relationships between response and predictor variables. In order to visualize interactions, clay content and climate deficit were divided in three classes based on the standard deviation around the mean of each of these variables. *Red* color is for plots with MCWD values less than one standard deviation below the mean; *black* is for plots with MCWD values within one standard deviation of the mean; and *blue* is for plots with MCWD values greater than one standard deviation above the mean. Shaded regions represent confidence intervals.

CAPÍTULO 2

Sousa, T.R. et al., 2020. Palms and trees resist extreme drought in Amazon forests with shallow water tables. *Journal of Ecology, doi:10.1111/1365-2745.13377*

Title: Palms and trees resist extreme drought in Amazon forests with shallow water tables

Abstract

1. The intensity and frequency of severe droughts in the Amazon region has increased in recent decades. These extreme events are associated with changes in forest dynamics, biomass and floristic composition. However, most studies of drought response have focused on upland forests with deep water tables, which may be especially sensitive to drought. Palms, which tend to dominate the less well-drained soils, have also been neglected. The relative neglect of shallow water tables and palms is a significant concern for our understanding of tropical drought impacts, especially as one third of Amazon forests grow on shallow water tables (<5m deep).

2. We evaluated the drought response of palms and trees in forests distributed over a 600 km transect in central-southern Amazonia, where the landscape is dominated by shallow water table forests. We compared vegetation dynamics before and following the 2015-16 El Nino drought, the hottest and driest on record for the region (-214 mm of cumulative water deficit).

3. We observed no change in stand mortality rates and no biomass loss in response to drought in these forests. Instead, we observed an increase in recruitment rates, which doubled to 6.78% y-1 ± 4.40 (mean ± SD) during 2015-16 for palms and increased by half for trees (to 2.92% y-1 ± 1.21), compared to rates in the pre-El-Nino interval. Within these shallow water table forests, mortality and recruitment rates varied as a function of climatic drought intensity and water table depth for both palms and trees, with mortality being greatest in climatically and hydrologically wetter environments and recruitment greatest in drier environments. Across our transect there was a significant increase over time in tree biomass.

4. Synthesis: Our results indicate that forests growing over shallow water tables – relatively under-studied vegetation that nonetheless occupies one-third of Amazon forests - are remarkably resistant to drought. These findings are consistent with the hypothesis that local hydrology and its interactions with climate strongly constrain forest drought effects, and has implications for climate change feedbacks. This work enhances our understanding of integrated drought effects on tropical forest dynamics and highlights the importance of incorporating neglected forest types into both the modeling of forest climate responses and into public decisions about priorities for conservation.

Keywords: water table, groundwater, Arecaceae, drought, extreme events, forest dynamics, tropical forest, climate change.

Introduction

There has been an increase in the frequency and intensity of severe droughts in the Amazon. The most recent three extreme drought events occurred at a very short interval (2005, 2010 and 2015-16) and the last two were possibly the most severe in a century (Anderson et al., 2018; Jiménez-Muñoz et al., 2016; Marengo et al., 2011). Due to its extensive area (≈6 million km^2), large carbon stores, and exceptional species richness (including as many as 15,000 tree species), the responses of the Amazon forests to extreme events is likely to affect not only the basin itself, but also global climates and biodiversity (Nobre et al., 2016; Saatchi et al., 2011; Ter Steege et al., 2013). It is already clear that the water deficits associated with recent droughts has slowed growth rates (e.g., Feldpausch et al., 2016) and increased tree mortality rates (e.g., Phillips et al., 2009; Zuleta et al., 2017), resulting in biomass loss (Brienen et al., 2015; Feldpausch et al., 2016; Leitold et al., 2018; Phillips et al., 2009). These evidences of vulnerability reinforce concerns that Amazon ecosystems may be vulnerable if drought frequency continues to increase (Esquivel-Muelbert et al. 2017*b*). However, most assessments of drought effects have ignored the soil hydrological conditions and assumed that precipitation is the only source of water deficit to plants. The balance between precipitation and estimated evapotranspiration is the basis of the most used metrics to quantify drought, e.g. the maximum accumulated water deficit, and belowground water sources, such as provided by the water table, are not explicitly included. The water table may be the main source over considerable large expanses of the Amazon. Thousands of square kilometers of the Amazon basin are covered by poorly drained areas (Junk 1993) and at least 36% of whole Amazonian basin is covered by forests over shallow water table (<5m deep) (Fan & Miguez-Macho, 2010). The belowground water source can be expected to minimize the effects of droughts on plants and change the predictions of forest vulnerability to drought.

Water table depth is an important driver of rooting depth and plant water uptake. Under deep water table conditions, the vegetation relies on local precipitation and rooting depth is determined by the depth of rainfall infiltration into the soil (Fan et al. 2017). On the other hand, shallow water table prevents drainage and creates frequently waterlogged soil conditions. Thus, roots remain shallow, to minimize the stress due to anaerobiosis (Fan and Miguez-Macho 2011, Fan et al. 2017). In deep water table forests (DWTF), the drier and warmer climate conditions during extreme droughts decrease soil moisture leading to reduced photosynthesis and net primary production (Santos et al., 2018; Zhao & Running, 2010).

However, this should not apply to shallow water table forests (SWTF), as the soil waterlogging tend to decrease during droughts in leading to an increase the growth window, and thus promote growth in a similar way to what has been observed in floodplain forests (Schöngart et al., 2004; Schöngart et al., 2005).

Our current understanding on the effect of drought on Amazonian forests have neglected how palms, a fundamental functional group within these forests, have responded to the changes in climate. Responses to drought have been mostly evaluated for dicotyledonous trees and lianas and have typically either excluded palms or included them within a broad category of 'trees' (e.g., Brienen et al., 2015; Fauset et al., 2012; Laurance et al., 1999; Lewis et al., 2011; Phillips et al., 2004). However, palm's xylem anatomy, architecture and growth strategies are fundamentally different from dicotyledonous trees (Castilho et al., 2006; Emilio et al., 2013; Tomlinson, 2006). Thus, the changing patterns in dynamics and biomass stocks described for trees across the Amazon may simply not apply to palms. The responses of palms to climate are likely to have important basin-wide implications, as palm-dominated forests cover 20% of the Brazilian Amazon and contribute up to 23% of the basal area in the western Amazon (Emilio et al., 2013; IBGE, 1997). Moreover, this group comprises no less than six of the top ten most abundant tree species of the Amazon basin (ter Steege et al. 2013), being highly useful for people (Levis et al. 2018). To date the only analysis we are aware of in which the effect of Amazon climate drying on long-term population changes of Amazon trees has been probed, found that palms are especially drought-vulnerable, having declined in abundance in many long-term Amazon forest plots (Esquivel-Muelbert et al. 2019). Thus, forests on shallow water table (SWTF) and palms both represent important and currently neglected components that need to be understood to properly evaluate the future of Amazon forests under climate change.

Trees and arborescent palms differ in growth strategies, rooting and vascular systems (Gale & Barfod, 1999; Renninger et al, 2013). Furthermore, palms and trees are associated to different soil physical conditions, palms being more abundant on less structured soils, e.g. environments that limit root development. Moreover, palms are more physically stable due to characteristics of their stem anatomy that allows firm anchorage to the ground (Tomlinson 1990, Emilio et al. 2013). Palms lack vascular cambium and thus, as opposed to trees, cannot add additional vessels to increase stem diameter and cannot replace embolized xylem vessels (Tomlinson, 2006). The palm root system is shorter than in trees, and therefore, is naturally restricted to superficial soil layers (Tomlinson, 1990). These morphological differences between palms and trees should affect their responses to droughts. Notably, the absence of secondary xylem vessels production and shallow roots could make palms more sensitive to drought-induced embolism (Rich 1987, Tomlinson 2006, Renninger et al. 2013).

Considering the limited understanding of forest dynamics in areas of shallow water table and the great importance of palms to the structure of the tropical forests, here we seek to address these gaps. Our study takes advantage of a unique permanent plot initiative, which has established and monitored sites accessible from the Central-southern Amazon BR-319 road. This made possible for the first time to track forest dynamics and biodiversity over a huge and otherwise largely inaccessible landscape. Using this plot network, we monitored the dynamics of palms and trees in forests along a 600 km transect, through landscapes dominated by shallow water table forests, and during a period that captures the intense 2010 and 2015-16 droughts. We specifically addressed the following questions: 1) Are palms more vulnerable to extreme drought than trees?; 2) What is the impact of different climatological drought intensities on palm and tree dynamics?; 3) How do local water table depth and soil properties interact with climatological droughts to influence palm and tree dynamics?

We considered two alternative hypotheses: 1) palms here will be more sensitive to droughts than trees, so that intense droughts (such as in 2015-16) cause strong reduction in water availability of these normally water saturated soils, leading to higher mortality and lower recruitment rates, and a consequent loss of biomass stocks; or 2) droughts will instead promote a decrease in the water table level and a consequent reduction in the stressful soil anoxic condition, and so ameliorate the growing conditions for both palms and trees. In this scenario, plants will benefit from droughts, with no changes in their mortality and an increase in recruitment rates would be expected. In addition, independent of the drought events, higher soil physical constraints, i.e., shallow, compact and anoxic soils, will promote greater recruitment and lower palm mortality, given the palms preference for these conditions (Emilio et al., 2013).

Materials and methods

Study area and sampling design

The study was conducted along a 600 km transect along the interfluvial region between the Purus and Madeira rivers, south of the Amazon River in Central-southern Amazonia. The water table is shallow (2.81 m ± 2.38 deep (mean ± SD)), and topography in the region is generally flat with elevation above sea level varying from 30–80 m over large distances (estimated by Shuttle Radar Topography Mission - SRTM data) (Rodríguez et al.

2006). Mean annual precipitation in this area varies from 2100–2700 mm (Hijmans et al., 2005), with on average two to three consecutive months with less than 100 mm rainfall (dry months) per year (Sombroek 2001). Soils are predominantly Plinthosols and Gleysols, the predominant texture is silt to fine sand, with poor drainage, and varying degrees of soil water saturation and anoxic conditions (Sombroek 2000, Martins et al. 2014). Soils physical structure is generally dense and restrictive to root growth, with varying degrees of hardness and effective soil depth (Quesada et al. 2010).

We sampled 25-1 ha plots systematically distributed in 8 research sites along 600 km of the BR-319 highway. In each site, two to five plots were sampled in regular grids of 5 x 1 km, keeping a 1 km minimum distance among plots (Figure 1). Plots were established at least 1 km distance from the road to avoid sampling forests which had been recently disturbed by human activity. Permanent plots were 250 m long and followed the terrain altitudinal contour, in order to reduce edaphic and hydrological variation within plots (Magnusson et al. 2005).

Vegetation data

Diameter at breast height (dbh) of approximately 1,700 palm stems and 15,000 trees were measured in the 25 plots. We used a nested design to measure palms and trees along the 250 m plot main axis (Magnusson et al. 2005). All stems with dbh ≥ 30 cm were sampled in the full 1 ha (250 x 40 m), stems with 10 cm ≤ dbh < 30 cm were measured in a subplot of 0.5 ha (250 x 20 m) and stems with 1 cm ≤ dbh < 10 cm were measured in a subplot of 0.025 ha (250 x 1 m). Each stem from clonal species (mostly palms) was considered as an individual stem in the analyses. The three censuses for vegetation monitoring were conducted during dry season in the years 2010 (Schietti et al. 2016), 2015 and 2016. All palms and trees with above-ground stems measured were considered in the analyses. Palm and tree data were uploaded and curated in the ForestPlots.net data management system (Lopez-Gonzalez et al, 2011).

Above-ground biomass of individual palms was calculated based on dry mass fraction (dmf), stem diameter (dbh) and stem height (H_{stem}), according to the family-level allometric equation for Amazonian palms developed by Goodman et al. (2013):

$$Palm\,biomass = 0.55512^{4} \times (dmf \times dbh^{2} \times H_{stem})$$

The Goodman et al. (2013) equation is largely supported by local studies such as Silva et al. (2015) and Avalos et al. (2019) who both studied a subset of the species in our dataset.

Palm heights were measured using a Vertex hypsometer (Vertex Laser VL400 Ultrasonic-Laser Hypsometer III, Haglöf of Sweden). Stem heights could only be estimated during the second census in 2015, when 70% of the total number of palms registered in the plots had their height measured. For those stems that did not have their height measured, we used species-level means, either the site-level mean height for the most abundant species (*Lepidocaryum tenue* and *Oenocarpus bataua*) or the overall mean height for remaining species. We disregarded changes in palm height over time and used the height measurements from 2015 for all censuses (2010, 2015 and 2016).

Our evaluation of changes in the palm biomass stock is based on only on the population changes, i.e. recruitment and mortality. We assumed zero stem diameter growth, as palm diametric variations are mostly governed by fluctuations in water content (Stahl et al. 2010). We note that palm growth occurs via increasing height, with the addition of new metamers (Tomlinson 1990), so quantifying biomass increases in individual palms requires repeated height measurements which were not possible here.

Above-ground biomass of individual trees was calculated based on diameter (D), wood density (ρ) and tree height (H), according to the pantropical allometric model developed by Chave et al. (2014):

$$Tree\ biomass\ =\ 0.0673\ x\ (\rho D^2 H)^{0.976}$$

Tree height was estimated using D-H allometric equations adjusted for each of the 8 research sites along the transect (Schietti et al. 2016). Species wood density was obtained from the global wood-density data base (Chave et al., 2009; Zanne et al., 2009).

Annual mortality rates (λ) were calculated as: $\lambda = \frac{[lnln\ (N_0) - lnln\ (N_s)\ ]}{t}$, where N_0 and N_s are the number of stems counted of the initial population, and the number of stems surviving to time t, respectively (Sheil et al. 1995). Annual recruitment rates (μ) were calculated following Phillips et al (1994) equation: $\mu =\ (N_f /\ N_s)]/t$, where N_f is the final number of stems, N_s is the original number of stems surviving to final inventory and t is the number of years between inventories. Mortality and recruitment rates were calculated for the intervals 2010-2015 and for 2015-2016. In this paper stand mortality and stand recruitment were treated as mortality and recruitment rates, respectively.

Long and irregular census intervals may lead to some underestimation of mortality and recruitment rates, since they have a greater probability of including unobserved mortality and recruitment especially of fast turnover sub-populations (Lewis et al., 2004). The proposed correction factor $\lambda_{corr} = \lambda \times t^{0.08}$, where λ is the rate and t is time between censuses in years, was applied for all the demographic rates calculated in this study.

Environmental data

To assess meteorological drought, i.e., atmospheric drought based on the balance between precipitation and evapotranspiration, we estimated maximum cumulative water deficit (MCWD) between census intervals, considering the month of the initial and final census of each plot. MCWD corresponded to the maximum value of the monthly accumulated climatic water deficit reached for each location. This metric represents the sum of water deficit values (i.e. the difference between precipitation and estimated evapotranspiration for the forest) over consecutive months when evapotranspiration is greater than precipitation (Aragão et al., 2007). Precipitation data were extracted from the Tropical Rainfall Measuring Mission satellite (TRMM, 3B43 7A) (Huffman et al. 2007) produced from 2010 to 2016, at 0.25º spatial resolution. Monthly evapotranspiration was assumed fixed at 100 mm month^{-1}, considering that moist tropical canopies have approximately constant evapotranspiration rate (Shuttleworth 1988, Rocha et al. 2004).

As a proxy to the plant access to belowground water, which can affect the hydrological drought experienced by roots, we characterized the local hydrological condition as the average water table depth (WTD) monitored using piezometers between the years of 2010 and 2013 in all plots (Figure S1). Each plot had one piezometer 7 m deep in the ground, monitored every one or four months in this period. Although the hydrological drought would be more correctly described by WTD values measured along the full census period, this concomitant temporal data was not available. However, the seasonal fluctuation of WTD in each plot is similar across years, i.e. plots with shallow minimum and maximum values along the year (thus shallow WTD average) in general do not attain deeper WTD values in dry years than plots with deeper min, max and average WTD (Figure S6). This means that we can use these average values to rank plots along a gradient of WTD that is indicative of the potential hydrological drought experienced by plants.

Since forest dynamics is known to be linked not only to climate but also to soil properties (Quesada et al. 2012), we included an index of soil physical restriction developed by Quesada et al. (2010) in our analyses, to represent the magnitude of soil physical limitation. This semi-quantitative index is based on soil effective depth, soil structure, anoxic conditions and topography. Higher scores denote more limited soil conditions for plant roots. Soil physical classification was determined in 2 m deep pits dug in each research site and in soil-profile samples from all plots (Martins et al., 2014). As a proxy of soil fertility we used the available phosphorus content (extracted with Mehlich-1) (EMBRAPA 2011) determined from a compound sample derived from 6 subsamples from the first 30 cm soil depth (Schietti et al. 2016).

Data analyses

All analyses were conducted in R version 3.4.2 software (The R Core Team 2018). To evaluate the changes in recruitment and mortality over time on a plot basis we used paired *t-tests* between the moderate (2010-2015) and severe (2015-2016) droughts, this was also applied to assess changes in rates considering different diameter size classes. Biomass stocks were analyzed by repeated-measures ANOVA between the years of 2010, 2015 and 2016. To investigate the relationships of palm and tree dynamics with environmental conditions, we used generalized linear mixed models, with package GAMLSS (Stasinopoulos and Rigby 2007), assuming a Beta distribution for demographic rates. Site was included in the models as a random effect, to control for potential spatial autocorrelation between plots nested in the same site. We tested models relating palms and trees demographic rates to a set of combinations of environmental variables describing hydrology and soil constraints (Supporting information Tables S3 and S4). Hydrological conditions were represented by meteorological drought (maximum cumulative water deficit: MCWD) and water in soil (average water table depth); soil constraints were represented by an index of soil physical restriction and available phosphorus. We hypothesized that water table depth would modulate the effects of the drought intensity on demographic rates, so we included the interactions among these factors. The models were built and evaluated based on the continuous values of MCWD, however for visualization of interactions our outputs were categorized into “more negative” and “less negative”. The classification of MCWD in these two classes was data-driven based on the frequency distribution of values observed in the plots - thus in the moderate drought the MCWD threshold was -90 mm, while in strong drought MCWD threshold was -130 mm (Figure S2). Best models were selected according to the Akaike’s information criterion (AIC). Models with lower AIC, fewer parameters and significant relationships between the response and the predictor variables were selected as the best models.

Results

In our dataset we recorded 19 palm species distributed in 13 genera, with *Lepydocaryum tenue* and *Oenocarpus bataua* being the most abundant species (Supporting information Table S1). According to precipitation data recorded from 1998 to 2016, the study region experienced MCWD annual anomalies up to -1σ in 2010 (MCWD = 107 mm;

accumulated annual precipitation = 2438 mm) and MCWD annual anomalies up to -3σ in 2015 (MCWD = 308 mm; accumulated annual precipitation = 2053mm) (Figure 1). Due to the MCWD anomalies recorded in the years 2010 and 2015 in relation to the historical series, the first interval can be considered as a moderate drought (2010-2015) and the second interval as a severe drought (2015-2016) for this study region.

Palm and tree annual recruitment dynamics changed between moderate and strong droughts. There was a strong increase in palm annual recruitment rates from the first to the second period ($t = -4.02$; $df = 24$; $p < 0.001$). Palm recruitment averaged 3.30% ± 1.94 (mean ± SD) per year in the period 2010 to 2015 and doubled to 6.78% ± 4.40 (mean ± SD) per year during 2015-2016 (Figure 2a). Annual recruitment rates also increased among trees from the first to the second interval ($t = -4.70$; $df = 24$; $p < 0.001$), averaging 1.85% ± 0.52 (mean ± SD) per year from 2010 to 2015, and was 1.5 times greater between 2015 and 2016 (2.92% ± 1.21, mean ± SD) (Figure 2c). However, there was no change in annual mortality rates over the same intervals for palms (3.67% ± 1.93, 2010-2015 and 4.28% ± 3.69, 2015-2016) or trees (1.56% ± 0.62, 2010-2015 and 1.69% ± 0.91, 2015-2016) (Figures. 2b-2d). Considering the variation among diameter classes, we find that annual recruitment rates increased from the first to the second interval only for small diameter classes ($1 \text{ cm} \leq dbh < 10 \text{ cm}$), for both trees and palms. On the other hand, annual mortality rates do not differ among size classes between intervals, i.e. large trees ($dbh \geq 30$ cm) did not have higher mortality in years of severe drought (Figure S5).

The association between demographic rates of both palms and trees (described by the models below) and environmental predictors varied across time periods (Supporting information Tables S3 and S4). Variation in mortality rates was significantly associated to the environmental conditions only in the period with moderate drought (2010-2015), while variation in recruitment was significantly associated to environment only in the period with the strongest drought (2015-2016).

The best model to explain palm mortality rates included the interaction between cumulative water deficit and average water table depth, and soil physical restriction index (Table 1). In the interval from 2010 to 2015, sites that experienced less negative water deficit (MCWD > -90 mm) and with shallowest water table (Figure 3a, grey points on the right of the dashed line) had higher palm annual mortality rate ($\underline{x}$ = 4.12%). In contrast, forests sites that experienced more negative water deficit (MCWD < -90 mm) and shallowest water table

(Figure 3a, black points on the right dashed line) had lower palm mortality rates ($\underline{x}$ = 2.36%). Palm mortality was also higher in soils with lower physical constraints (Figure 3b).

The best model for palm recruitment included only hydrological variables, i.e. an interaction between the maximum cumulative water deficit and average water table depth in the interval from 2015 to 2016 (Table 1). On average, during this interval, palm annual recruitment rates did not differ between plots that experienced less negative water deficit (MCWD > -130 mm) ($\underline{x}$ = 7.06%) and those that experienced more negative water deficit (MCWD < -130 mm) ($\underline{x}$ = 6.52%). However, recruitment was lower (1.68%) in plots with shallower water table (< 2.5 m deep) and under strong drought (Figure 3e, black points on the right of dashed line). Plots on the same shallow water table level, but experiencing less negative water deficit, had higher recruitment rates (5.98%, Figure 3e, grey points on the right of dashed line).

For trees, in the interval from 2010 to 2015, models with higher support to explain mortality rates included the average water table depth and the available soil phosphorus (Table 1). Tree mortality was higher in soils with the shallowest water table and greater fertility (Figures. 3c-3d). During the 2015- 2016 interval, the best recruitment rates model included an interaction between maximum cumulative water deficit and average water table depth (Table 1). In this period, recruitment rates were lower in plots that experienced less negative water deficit (MCWD > -130 mm) ($\underline{x}$ = 2.28%) than in those that experienced more negative water deficit (MCWD < -130 mm) ($\underline{x}$ = 3.50%). Among plots with higher water deficit, recruitment increased with water table depth, and decreased for plots with lower water deficit (Figure 3f).

Spatially, palm biomass stocks (AGB) varied widely from 1.12 to 12.33 Mg ha^{-1} (Figure 4a) and contributed with 1% to 5% per hectare to the total amount of alive above-ground biomass (Table S2). Biomass stocks were respectively 5.84 ± 3.17 (mean ± SD) in 2010, 5.84 ± 3.18 in 2015 and 5.86 ± 3.17 in 2016 for palms, and 227.94 ± 55.39, 233.95 ± 55.73 and 234.48 ± 56.57 (mean ± SD) for trees. There was no significant change in palm biomass stock between the three censuses (F= 0.014; p= 0.91) considering the balance between recruitment and mortality of individuals. For trees, biomass varied spatially from 97.15 to 328.75 Mg ha^{-1} (Figure 4b). However, unlike palms, trees had an increase in the biomass stock from 2010 to 2015 (F= 17.69; p < 0.001). Analyzing plot-by-plot 80% of them had biomass gain in this interval (Figure S4b).

Discussion

We analyzed for the first time the effect of droughts of different intensities over shallow water table Amazonian forests (SWTF). Our results show that palms were no more vulnerable to extreme droughts than trees in these forests. The strong drought of 2015 did not increase palm or tree mortality rates, but instead, promoted increased recruitment rates. The drought responses in terms of recruitment and mortality were mediated by the local hydrological conditions, soil fertility and soil physical restriction. There was an increase in tree above-ground biomass stock from 2010 to 2015, but no significant change over time of palm AGB. Overall, extreme droughts did not have a negative impact on either trees or palms growing over shallow water table. Our study reveals the complex interplay between climatological droughts and belowground water access on forest dynamics. Our results indicate the crucial need to incorporate the interaction between precipitation and belowground properties for a more realistic estimation of local hydrological conditions on environmental impact evaluations and models to forecast drought effects in the Amazon.

We hypothesized that more intense droughts could sufficiently reduce water availability of these normally water-saturated soils, leading to higher mortality and lower recruitment rates, resulting in biomass loss, particularly of palms. However, our results did not support this hypothesis. Palms and trees have structural differences in their vascular anatomy, which are reflected on different sensitivities to drought. Palms tend to have large vessels, high hydraulic conductivity and high demand for water (Aparecido et al. 2015; Kunert et al. 2013), which could be expected to generate a larger vulnerability to drought, however this was not what observed in SWTF. Our results are partially in accordance with our alternative hypothesis: droughts are likely to lead to moderate soil drying, which is enough to reduce the anoxic conditions of waterlogged soils and hence promote palm and tree growth, with increased recruitment and no increase in mortality rates. This suggests that both palms and trees on shallow water table forests are resistant to extreme droughts because the belowground hydrological environment buffers climatological water deficit. Thus, shallow water table may offer a relief from the atmospheric water stress projected by climate models for decades to come, functioning as hydrologic refugia (Pokhrel et al. 2014, McLaughlin et al. 2017).

Higher tree mortality in soils with higher phosphorus concentration may be related to the functional properties selected by fertile soils and the resulting vegetation dynamics. Low wood density is selected on fertile soils, which generally have high phosphorus availability and physical restrictions, leading to high turnover rates (Baker et al., 2004; Phillips et al., 2004) and low biomass stock (Quesada et al. 2012, Schietti et al. 2016).

Higher recruitment rates observed during the 2015-16 interval are likely to be directly associated with climatological changes, though they could potentially be an indirect result of previous disturbances that increase light. The importance of light availability to forest growth and dynamics is well known (Augspurger, 1984; Bentos et al. 2017; Jakovac et al. 2012), however responses still depend on specific requirements of each species (Ley-López et al. 2016). Our study did not include direct metrics of light availability, however, we evaluated whether previous disturbances (i.e., the mortality rates in the previous period, a proxy for canopy openness) could be leading to increased recruitment. We found no effect of previous disturbances on recruitment rates on the following period (Figure S3), thus it is likely that the higher recruitment in 2015-16 is associated with the environmental conditions during the 2015-16 El Niño event. In seasonally flooded forests, drought prolongs the non-flooded period, which is when plants grow due to the reduction of anoxic stressful conditions (Schöngart et al., 2002). Under the drier conditions observed in El Niño years, floodplain forests show increased wood growth (Schöngart et al. 2004). Our findings of increased recruitment in the 2015-16 El Niño in SWTF are consistent with those observations on floodplain forests. However, this increase in recruitment during the strongest drought cannot be solely attributed to the temporal decrease in stress due to anoxia. Forest plots that experienced higher climatological water deficits and deeper water table had higher recruitment rates than plots that experienced similar drought conditions, but located in shallow water table. It must be acknowledged that all sites studied here have shallower water table (average depth < 7m; Figure S1) than most other studied plots in the Amazon (i.e. from 10 to more than 40 m deep, S. Chen personal communication). We can speculate that during the strong drought, anoxia was sufficiently reduced in soils with water table deeper than 3 m, but not enough where the water table was shallow. However, detailed monitoring of belowground water level fluctuation during drought periods is still required, through field monitoring and / or eco-hydrological modeling (Chitra-Tarak et al. 2018). This information may provide additional support to our hypothesis or elucidate other mechanisms that may be involved on forest responses.

Over our 600 km of monitored forests, there was no increase in mortality from the moderate to the strong drought periods, and neither larger mortality rates associated to sites that experienced the strongest climatic water deficits. We expected stronger negative drought effects on palms, as their anatomy and growth form are likely to make this group more drought-vulnerable (Tomlinson, 2006). Indeed highly increased mortality (7%) of the most abundant palm species of a *terra firme* forest over deep water table was observed after the strong 1997 drought (Williamson et al. 2000), and a long-term decline trend of wet-affiliated palms was detected across the Amazon basin as climate becomes drier (Esquivel-Muelbert et al. 2019). Surprisingly, we found no evidence that palms are more vulnerable to drought than trees in the wet conditions experienced by SWTF. This is consistent with the findings of no increases in palm mortality after droughts in wet forests of western Amazonia (Olivares et al. 2017) and Central America (Condit et al. 2004). Our results suggest that even if Amazon palms are intrinsically susceptible to drought, their response to drought events can be highly variable and contingent to local belowground hydrological conditions. The fact that even the more drought-sensitive palms did not suffer increased mortality in the strong 2015 drought supports the assertion that forests with the shallowest water tables are more resistant to drought than forests with deep water table.

Our result of an increase in the tree biomass stock is the contrary of what has been observed (biomass loss) on most tropical forests after droughts. Studies in Amazon forests have evidenced its vulnerability to drought through the reduction in above-ground biomass along the last decades (Brienen et al., 2015; Phillips et al., 2009). In the 2010 drought, the estimated biomass loss of Amazon forests was on average 1.45 Mg ha^{-1}, leading to a projected reduction of carbon uptake of 1.1 Pg (Feldpausch et al. 2016). Biomass stock of the Amazon has a wide spatial variation, from 200 to 350 Mg ha^{-1}, according to the geographic region (Baker et al., 2004; Lewis et al., 2013). In the present study, forest biomass stock was comparable to that of the Southwestern region, which has lower biomass compared to Central and Eastern Amazonia (Baker et al., 2004). Although palms do not contribute heavily to biomass in most dense *terra firme* forests (~ 1%) (Castilho et al. 2006), their contribution is often considerably greater in other environments as open forests and swampy conditions (Kahn et al., 1990; Lähteenoja et al., 2009), as represented in our plots. More stable biomass stocks in the shallow water table forests, which cover around a third of the Amazon basin (Junk et al. 2011), may thus provide a counterbalance to losses on the deep water table forests during droughts.

We have shown here that, contrary to the previous results from studies conducted at forest over deep water table across the Amazon basin (Brienen et al., 2015; Feldpausch et al., 2016; Phillips et al., 2009), palms and trees on SWTF are more resistant to drought. Therefore, it is important to consider the local belowground hydrological environment for a better assessment of drought effects on tropical forests. In addition, as previously reported for lianas (Lewis et al., 2004; Nepstad et al., 2007; Phillips et al., 2002; Van Der Heijden et al., 2013), different life forms may respond differently to global climate changes according to their biology and the effect on these should be investigated separately. Considering the progression of climate change, SWTF can be considered as potential refuges for biodiversity, conservation of the Amazon forest and may provide an important counterbalance to the biomass loss in forests affected by both atmospheric and soil moisture deficits. Given the extent of these forests, and their differential responses to drought, more research in shallow water table tropical forests is urgently needed. Not only will it be important to better account for soil water supply in modeling the dynamics and carbon fluxes of tropical forests, but a wider recognition of the importance of these systems can contribute to the development of public policies including prioritizing conservation areas on SWTF, which may be best-suited to help Amazonia resist climate change.

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Author contributions

TRS, FRCC and JS conceived the ideas; TRS, FCS, AEM, JS and TE collected the data; TRD, IOR and PACLP analysed the data; TRS led the writing of the manuscript; FRCC and OP made important intellectual contributions. All authors revising and contributed critically to the drafts and gave final approval for publication.

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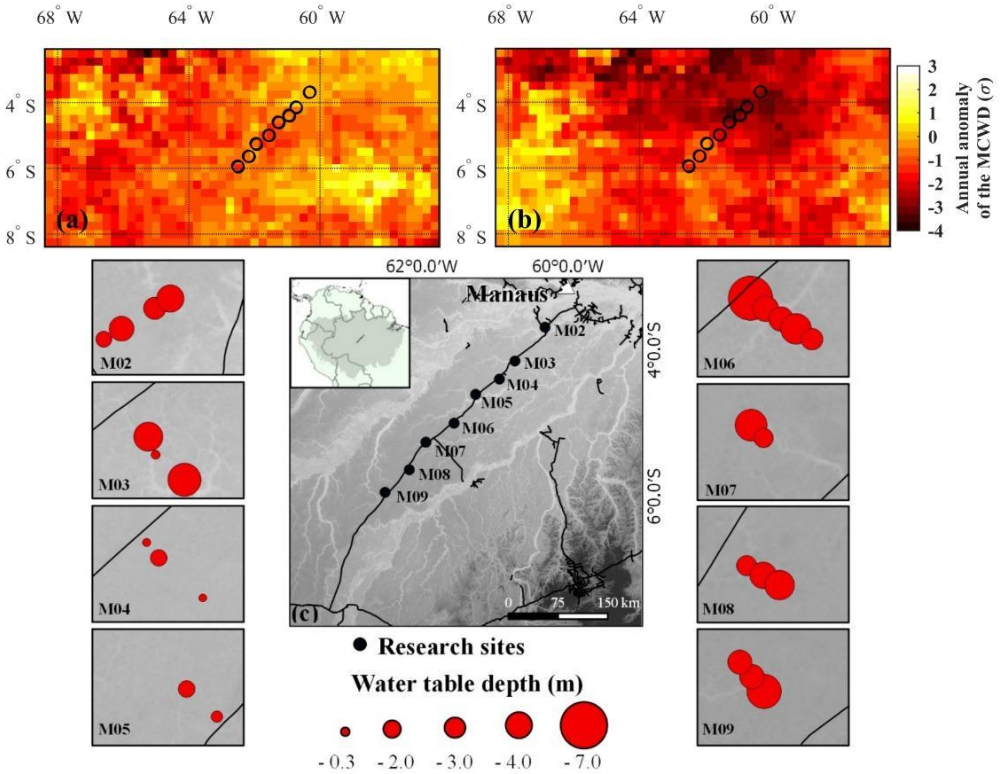

Figure 1. Characterization of the drought intensity (MCWD, in mm) across the study region in 2010 (a), and 2015 (b), and the average water table depth of the plots in each of the 8 research sites along the Purus–Madeira interfluve, in central-southern Amazonia (c).

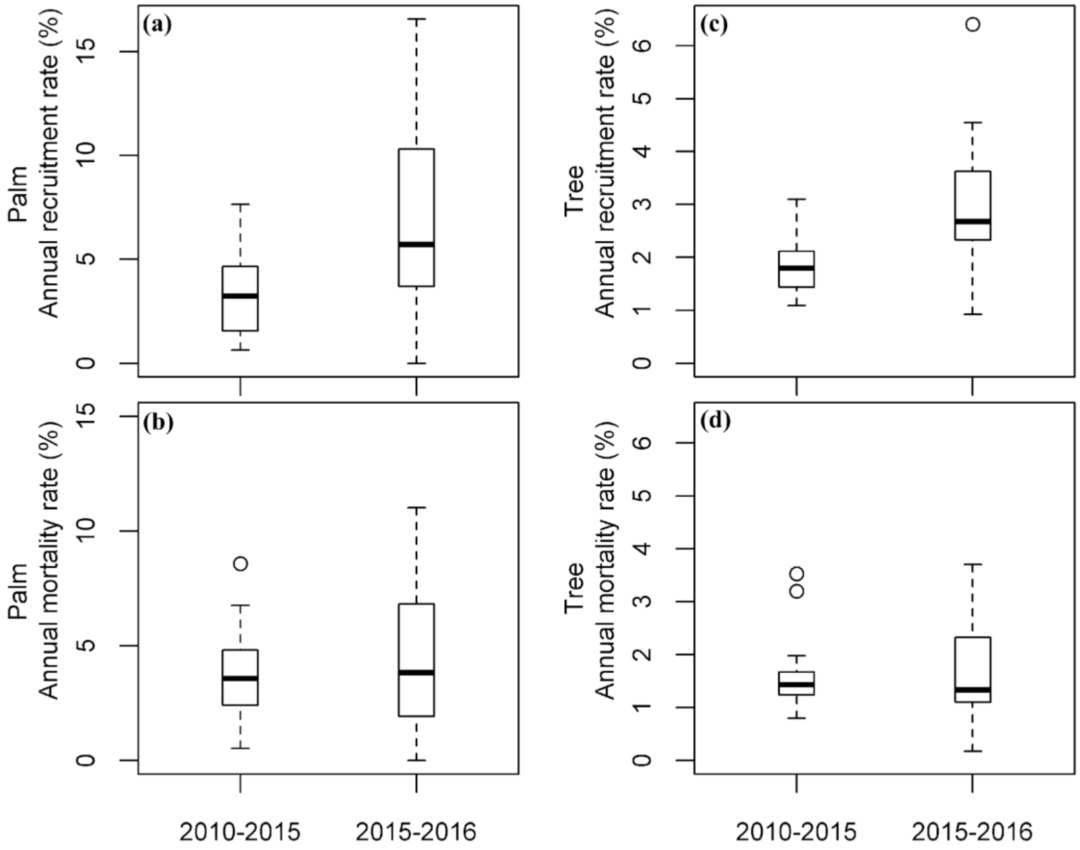

Figure 2. Palm annual recruitment (a) and mortality rates (b); Tree annual recruitment (c) and mortality rates (d), between the two censuses in forests along the Purus–Madeira interfluve, in central-southern Amazonia.

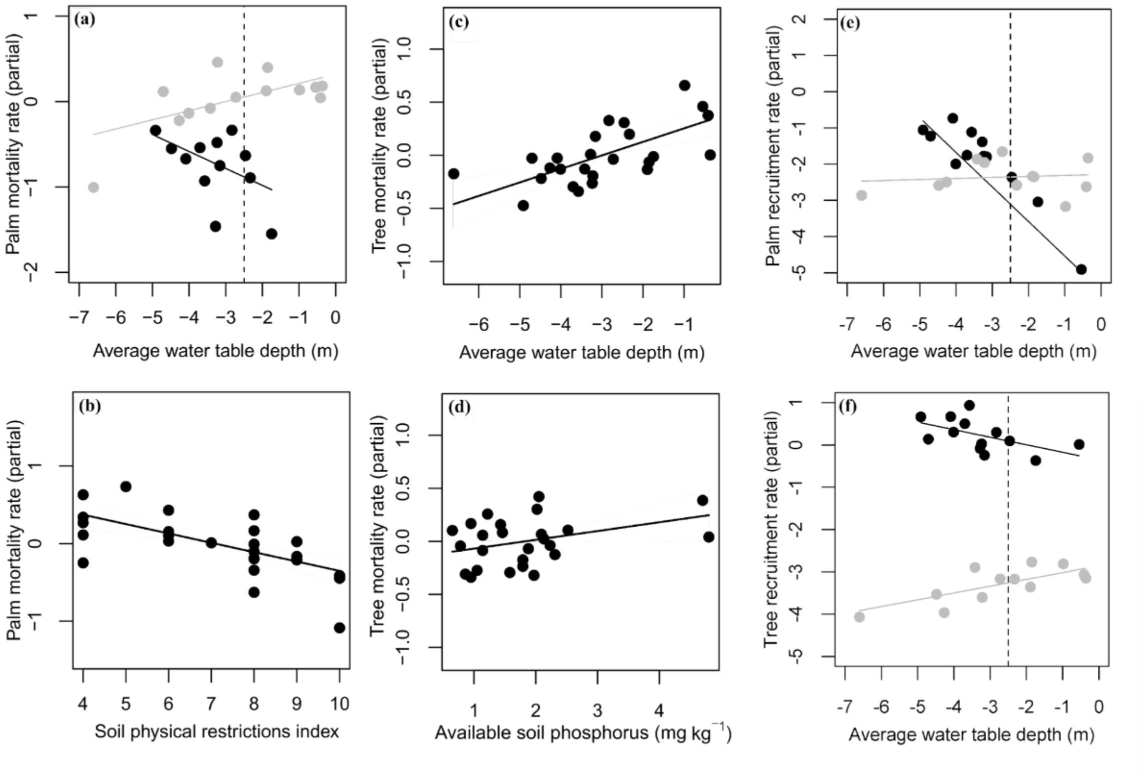

Figure 3. Partial regressions derived from the multiple regression models investigating the effects of maximum cumulative water deficit (MCWD), average water table depth (m), soil physical restriction index and available soil phosphorus on mortality and recruitment in Central-Southern Amazonia. (a) Partial effect of the interaction between MCWD and average water table depth and (b) partial effect of the soil physical restriction index on palm mortality, during the 2010 to 2015 interval; (c) Partial effect of the average water table depth (m) and (d) partial effect of available soil phosphorus on tree mortality, during 2010 to 2015 interval; (e) Partial effect of the interaction between MCWD and average water table depth on palm recruitment, and (f)) partial effect of the interaction between MCWD and average water table depth on tree recruitment, during the 2015 to 2016 interval. For mortality, grey points are plots that experienced less negative MCWD (> -90 mm) in the analyzed period, black points are plots that experienced more negative MCWD (< -90 mm). For recruitment, grey points are plots that experienced less negative MCWD (> -130 mm) in the analyzed period, black points are plots that experienced more negative MCWD (< -130 mm). Dashed lines indicate 2.5 m water table depth.

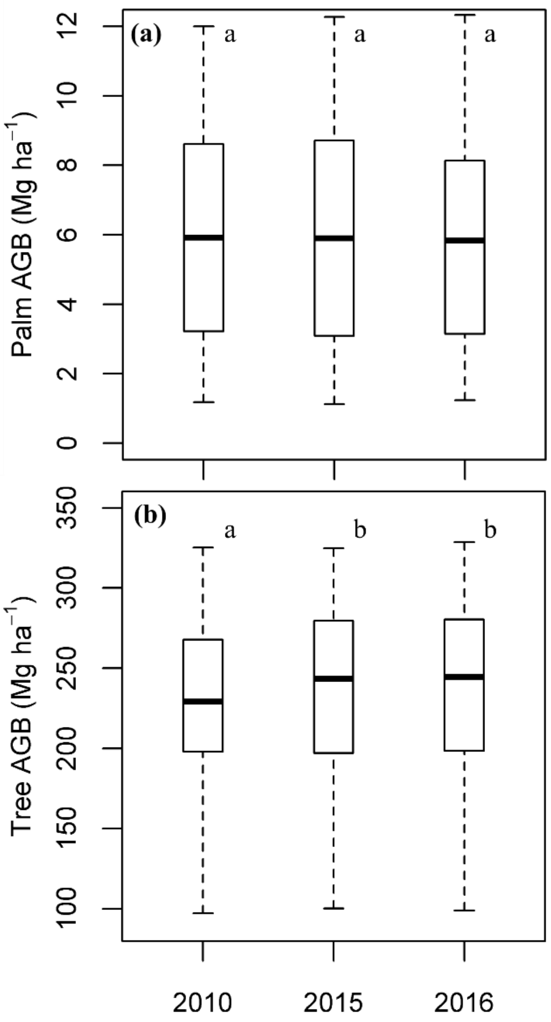

Figure 4. Variation in palm (a) and tree (b) biomass stocks (AGB) in 25 plots measured along the Purus–Madeira interfluve, in Central-southern Amazonia. Different letters indicate significant differences in biomass stock between years ($p < 0.001$; Tukey method).

Table 1. Statistical summary of the best generalized mixed models to explain the relationship between palm and tree dynamics and environmental variables. Intercept and slopes of each predictor included in the regressions are presented; ΔAIC is the difference between the model with the lowest AIC and the model chosen.

Models	Predictors	p	ΔAIC	R2
Palm mortality (2010-2015)	0.02 MCWD	0.002	0	0.84
	0.47 average water table depth	0.001		
	-0.13 soil physical restriction index	<0.001		
	0.005 MCWD*average water table depth	0.004		
Palm recruitment (2015-2016)	0.05 MCWD	< 0.001	-0.64	0.70
	1.37 average water table depth	0.001		
	0.01 MCWD*average water table depth	0.0004		
Tree mortality (2010-2015)	0.12 average water table depth	<0.001	0	0.61
	0.08 available soil phosphorus	0.05		
Tree recruitment (2015-2016)	0.004 MCWD	0.34	0	0.52
	0.43 average water table depth	0.02		
	0.003 MCWD*average water table depth	0.04		

Abbreviations: AIC, Akaike's information criterion; MCWD, maximum cumulative water deficit; WTD, water table depth.

Supporting Information

Table S1. Floristic composition, abundance and relative abundance of palms registered in 2016 in the 25 plots along the Purus–Madeira interfluve, in central-southern Amazonia.

Species	Abundance (stems)	Relative abundance (%)
Lepidocaryum tenue	733	45.44
Oenocarpus bataua	461	28.58
Non-identified	146	9.05
Astrocaryum gynacanthum	54	3.35
Oenocarpus bacaba	41	2.54
Euterpe precatoria	40	2.48
Socratea exorrhiza	28	1.74
Attalea speciosa	25	1.55
Attalea maripa	20	1.24
Mauritia flexuosa	17	1.05
Iriartella setigera	12	0.74
Astrocaryum spp	8	0.50
Astrocaryum murumuru	7	0.43
Leopoldinia pulchra	7	0.43
Mauritiella armata	6	0.37
Oenocarpus minor	3	0.19
Bactris spp	2	0.12
Attalea spp	1	0.06
Geonoma spp	1	0.06
Maximiliana maripa	1	0.06

Table S2. Forest biomass stocks (palm+tree) and vegetation structure of 25 plots measured in three censuses, along the Purus–Madeira interfluve, in central-southern Amazonia.

Site	Plot id	Stand biomass (Mg ha^{-1}) Year 2010	Stand biomass (Mg ha^{-1}) Year 2015	Stand biomass (Mg ha^{-1}) Year 2016	Average biomass stock (Mg ha^{-1})	Palm biomass contribution (%)	Tree biomass contribution (%)	Palm stems (unit)	Tree stems (unit)
2	M02_TN_0500	226.77	233.53	222.43	227.58	5	95	66	466
2	M02_TN_1500	249.92	265.9	259.49	258.44	4	96	51	521
2	M02_TN_3500	203.77	213.93	215.07	210.92	3	97	34	552
2	M02_TN_4500	312.7	309.91	312.27	311.63	3	97	65	468
3	M03_TN_4500	142.65	145.15	148.34	145.38	1	99	59	635
3	M03_TS_1500	177.13	183.76	184.64	181.84	1	99	68	708
3	M03_TS_2500	99.88	102.47	101.15	101.17	2	98	21	413
4	M04_TN_(-)0500	178.68	186.47	186.33	183.83	5	95	54	641
4	M04_TN_0500	255.9	265.28	266.7	262.63	2	98	37	752
4	M04_TN_3500	244.68	253.6	249.5	249.26	3	97	85	699
5	M05_TN_(-)0500	220.21	212.98	215.47	216.22	1	99	52	597
5	M05_TN_1500	276.6	283.86	283.71	281.39	1	99	78	637
6	M06_TN_(-)0500	282.98	290.57	293.18	288.91	3	97	68	565
6	M06_TN_0500	311.86	306.8	309.83	309.50	2	98	54	558
6	M06_TN_1500	262.06	270.38	264.16	265.53	1	99	50	483
6	M06_TN_2500	293.73	301.13	305.24	300.03	1	99	41	598
6	M06_TN_3500	189.22	191.73	186.83	189.26	2	98	103	571
7	M07_TS_3500	210.49	209.95	212.94	211.13	5	95	113	581
7	M07_TS_4500	210.67	206.19	207.57	208.14	5	95	109	596
8	M08_TS_0500	327.26	326.98	330.91	328.38	1	99	68	479
8	M08_TS_1500	222.17	245.17	254.2	240.51	4	96	71	601
8	M08_TS_2500	275.19	286.85	291.18	284.41	3	97	50	576
9	M09_TS_2500	236.24	250.82	253.87	246.98	3	97	116	612

Site	Plot id	Stand biomass (Mg ha^{-1}) Year 2010	Stand biomass (Mg ha^{-1}) Year 2015	Stand biomass (Mg ha^{-1}) Year 2016	Average biomass stock (Mg ha^{-1})	Palm biomass contribution (%)	Tree biomass contribution (%)	Palm stems (unit)	Tree stems (unit)
9	M09_TS_3500	264.48	278.7	280.67	274.62	2	98	116	604
9	M09_TS_4500	169.3	172.62	172.87	171.60	3	97	83	645

Table S3. Statistical summary of the generalized mixed models tested to investigate the relationship between palm dynamics and environmental variables.

Models	Predictors	P	AIC
Palm mortality (2010-2015)	MCWD	0.06	-138.09
	average water table depth	0.12	
	MCWD*average water table depth	0.15	
	available soil phosphorus	0.77	-143.33
	soil physical restriction index	0.02	
	MCWD	0.002	-144.06
	average water table depth	0.001	
	soil physical restriction index	<0.001	
	MCWD*average water table depth	0.004	
Palm mortality (2015-2016)	MCWD	0.12	-127.47
	average water table depth	0.08	
	MCWD*average water table depth	0.04	
	Available soil phosphorus	0.55	-127.35
	soil physical restriction index	0.01	
	MCWD	0.11	-129.25
	average water table depth	0.03	
	soil physical restriction index	0.05	
	MCWD*average water table depth	0.02	
Palm recruitment (2010-2015)	MCWD	0.25	-125.03
	average water table depth	0.39	
	MCWD*average water table depth	0.29	
	available soil phosphorus	0.86	-124.91
	soil physical restriction index	0.71	
	MCWD	0.25	-123.33
	average water table depth	0.37	
	soil physical restriction index	0.62	
	MCWD*average water table depth	0.28	

Models	Predictors	P	AIC
Palm recruitment (2015-2016)	MCWD	< 0.001	-110.11
	average water table depth	0.001	
	MCWD*average water table depth	0.0004	
	available soil phosphorus	0.31	-95.38
	soil physical restriction index	0.03	
	MCWD	< 0.0001	-110.74
	average water table depth	0.0008	
	soil physical restriction index	0.11	
	MCWD*average water table depth	0.0003	

Table S4. Statistical summary of the generalized mixed models tested to investigate the relationship between tree dynamics and environmental variables.

Models	Predictors	p	AIC
Tree mortality (2010-2015)	MCWD	0.68	-197.87
	average water table depth	0.48	
	MCWD*average water table depth	0.49	
	MCWD	0.48	-199.71
	average water table depth	0.0001	
	available phosphorus	0.02	-190.47
	soil physical restriction index	0.68	
	average water table depth	<0.001	-200.57
	available soil phosphorus	0.05	
Tree mortality (2015-2016)	MCWD	0.42	-161.8
	average water table depth	0.95	
	MCWD*average water table depth	0.89	
	MCWD	0.06	-163.79
	average water table depth	0.40	
	available soil phosphorus	0.40	-160.84
	soil physical restriction index	0.86	
	MCWD	0.08	-161.79
	average water table depth	0.44	
	available soil phosphorus	0.97	
Tree recruitment (2010-2015)	MCWD	0.80	-193.96
	average water table depth	0.10	
	MCWD*average water table depth	0.30	
	MCWD	0.04	-194.85
	average water table depth	0.03	
	available soil phosphorus	0.35	-188.23
	soil physical restriction index	0.62	
	MCWD	0.03	-193.08
	average water table depth	0.03	
	available soil phosphorus	0.60	

Models	Predictors	p	AIC
Tree recruitment (2015-2016)	MCWD	0.34	-155.24
	average water table depth	0.02	
	MCWD*average water table depth	0.04	
	MCWD	0.009	-153.48
	average water table depth	0.13	
	available soil phosphorus	0.09	-153.38
	soil physical restriction index	0.58	
	MCWD	0.35	-153.88
	average water table depth	0.02	
	available soil phosphorus	0.58	
	MCWD*average water table depth	0.04	

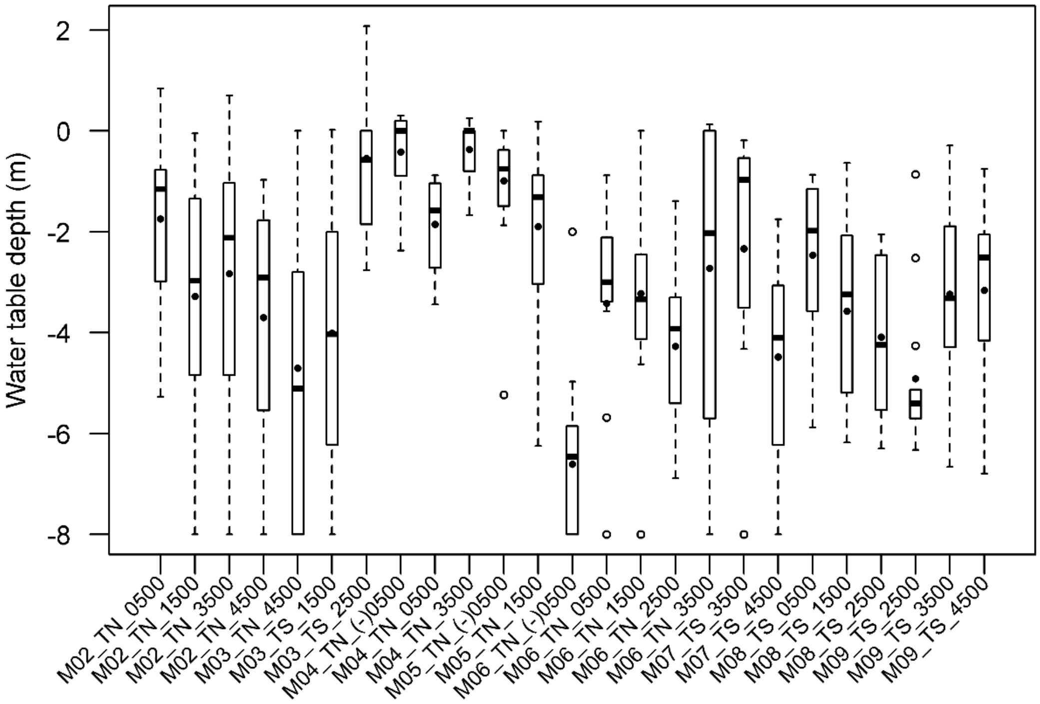

Figure S1. Water table depth variation of each studied plot along the Purus–Madeira interfluve, central-southern Amazonia, from 2009 to 2013. Black dots in the bars show the average water table depth for the plot across the measurement period. This figure depicts all the intra and inter annual variation recorded over the measurement period (check Figure S6 for the intra-annual vs. interanual comparison).

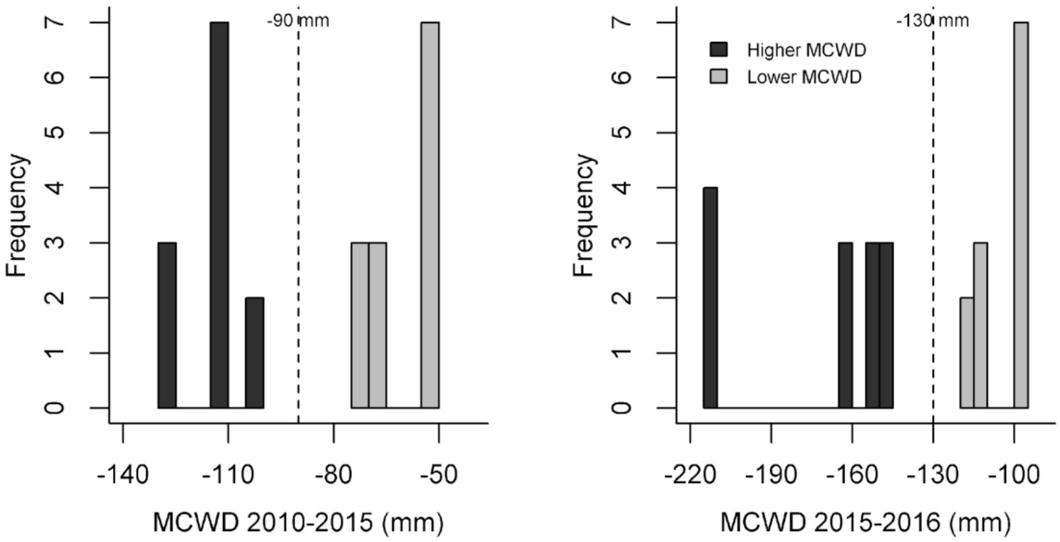

Figure S2. Frequency of MCWD values observed in the plots during the two monitoring periods. In the moderate drought (2010-2015) the MCWD threshold was -90 mm (left dashed line), in the strong drought (2015-2016) the MCWD threshold was -130 mm (right dashed line).

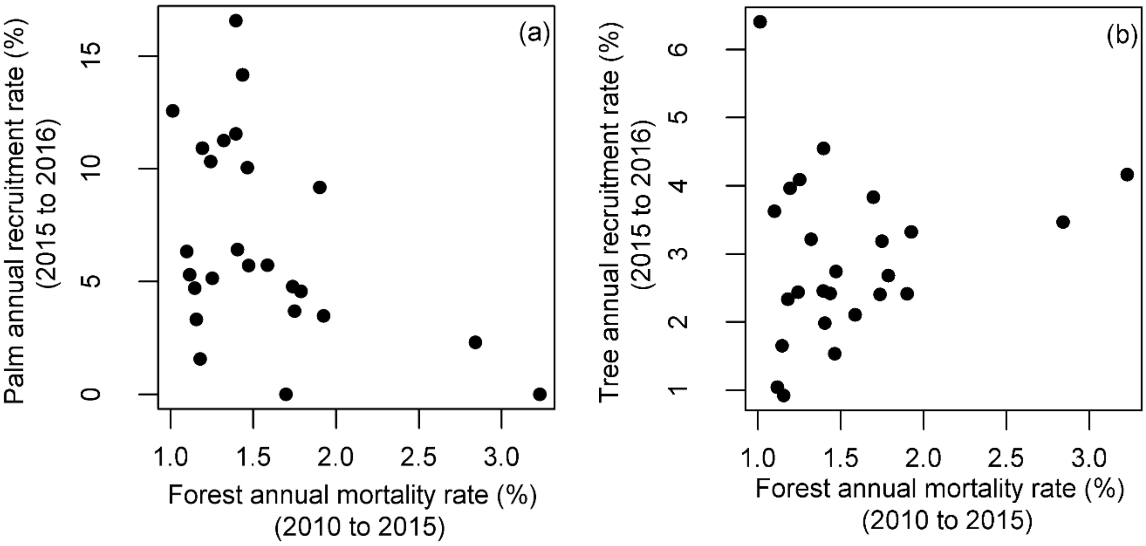

Figure S3. Relationships between recruitment rates in the 2015-2016 interval and forest mortality (trees + palm) rates in the previous 2010-2015 interval for palm (a) and trees (b).

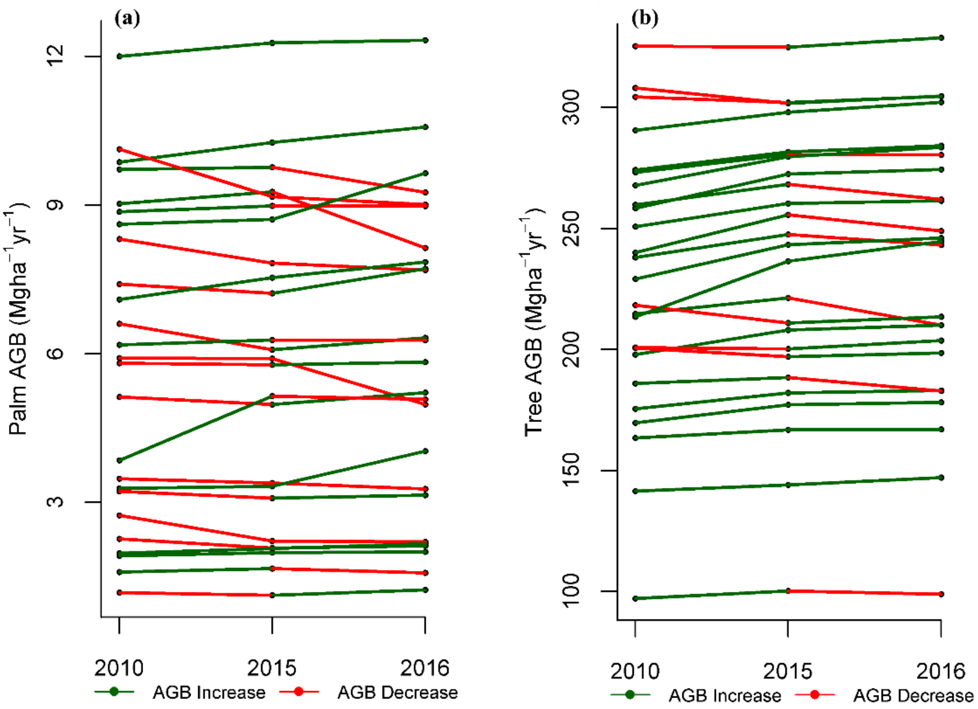

Figure S4. Temporal variation of biomass stocks (AGB) of individual plots for palms (a) and trees (b) along the Purus–Madeira interfluve, in central-southern Amazonia.

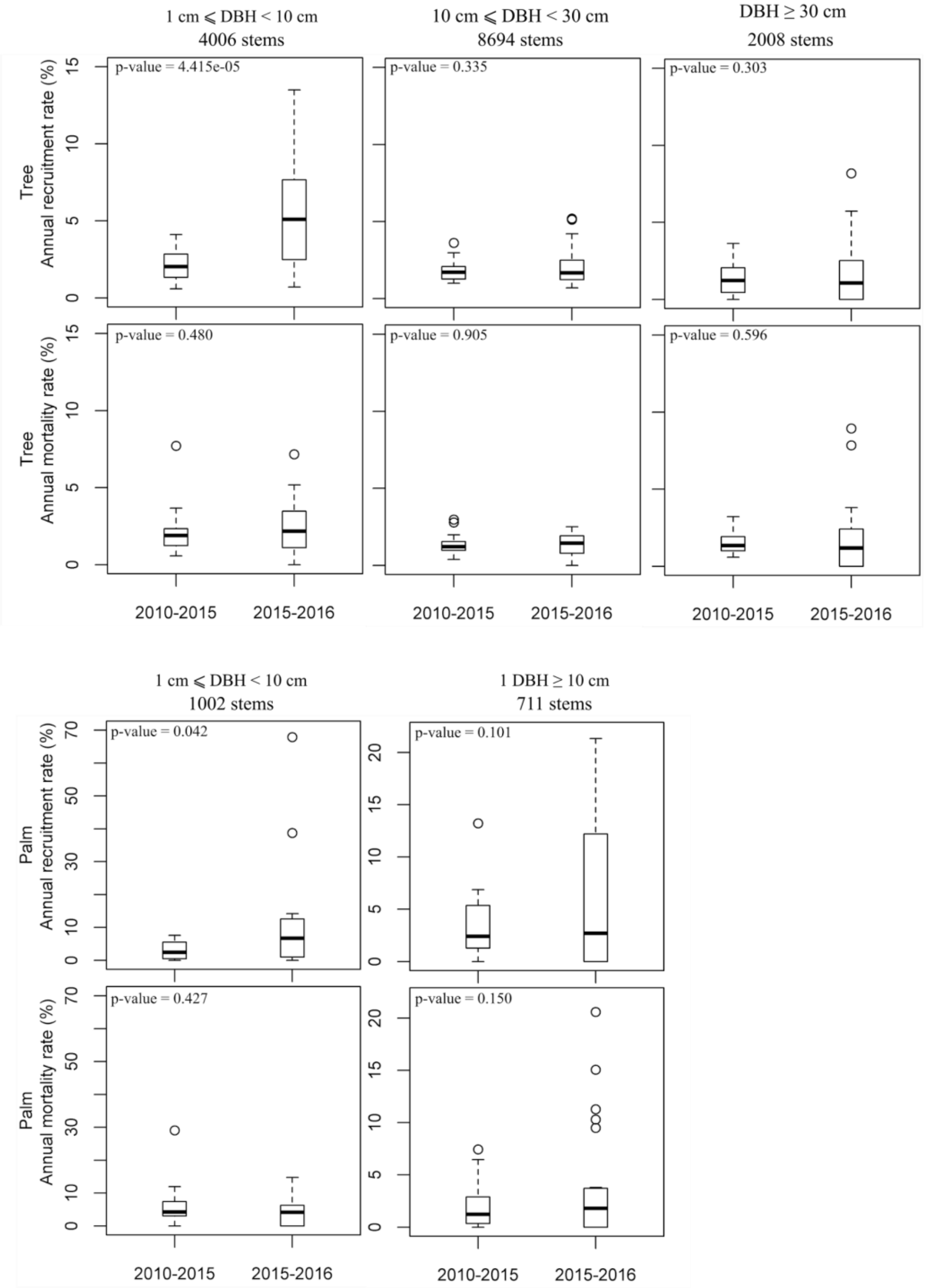

Figure S5. Tree and palm annual recruitment and mortality rates according to diameter size class, between the two censuses in forests along the Purus–Madeira interfluve, in central-southern Amazonia.

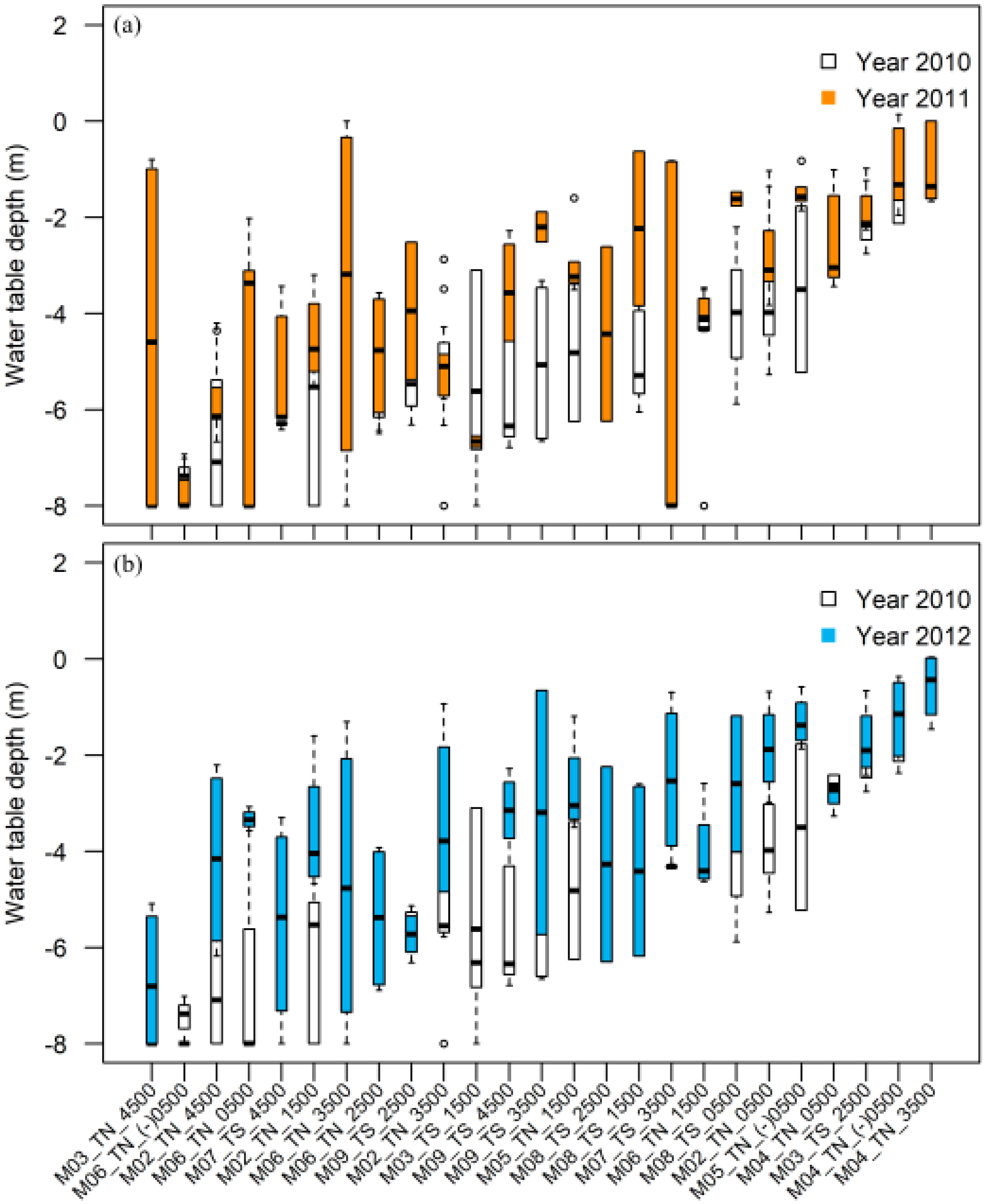

Figure S6. Water table depth variation of each studied plot along the Purus–Madeira interfluve, central-southern Amazonia, comparing years 2010-2011 (a) and 2010-2012 (b).

Síntese

A presente tese de doutorado teve por objetivo central avaliar a influência da profundidade do lençol freático na estrutura e dinâmica da floresta amazônica de terra firme, bem como no amortecimento dos efeitos de secas intensas. Para isso utilizei um robusto banco de dados de monitoramento da vegetação, sendo que a primeira abordagem abrangeu toda a bacia amazônica, e a segunda abrangeu uma importante região de floresta sobre lençol freático superficial, o interflúvio Purus-Madeira. Os resultados mostraram que a profundidade do lençol freático foi determinante nos padrões estruturais encontrados na bacia amazônica, onde florestas com lençol freático superficial apresentaram menor estoque e produtividade de biomassa lenhosa acima do solo, bem como maiores taxas de mortalidade e recrutamento de caules, portanto são florestas mais dinâmicas. Considerando eventos de secas intensas, florestas sobre lençol freático superficial são mais resistentes à seca pois durante o El Niño de 2015-16 não foi observado aumento na mortalidade de caules de árvores e palmeiras, por outro lado houve um aumento nas taxas de recrutamento, o que pode indicar aumento do crescimento neste período. Além disso, houve um aumento da biomassa arbórea do período de 2010 para 2015. Sendo assim, esta tese permitiu um avanço no conhecimento sobre o papel da hidrologia local no funcionamento da floresta no longo prazo e em anos de secas intensas.

A umidade do solo é um fator determinante para o desenvolvimento da vegetação, neste sentido a profundidade do lençol freático é um indicador indireto bastante eficaz da acessibilidade hídrica das plantas (Fan et al. 2017). O nível de acessibilidade das plantas à água, dado pelo contato das raízes com o lençol freático, é determinante para o ritmo de crescimento e dinâmica da vegetação. Apesar de suas adaptações morfofisiológicas, a condição de anoxia do solo em florestas com lençol freático superficial (< 5 m de profundidade) proporciona uma importante limitação para o desenvolvimento do sistema radicular e crescimento das plantas (Lopez and Kursar 2003, Fan and Miguez-Macho 2010, Cintra et al. 2013, Fan et al. 2017). Estudos locais mostraram que florestas que vivem em solos saturados de água tendem a apresentar menor produtividade de biomassa acima do solo e maiores taxas de mortalidade (Castilho et al. 2006, 2010, Ferry et al. 2010), porém na escala da bacia amazônica ainda não havia sido realizado um estudo tão amplo com dados de monitoramento de campo para confirmação deste padrão, conforme avaliado no capítulo 1 desta tese. Além disso, em períodos de seca moderada, seguindo a definição proposta por Costa *et al.* (2022) em que mesmo com essa alteração climática as raízes das plantas ainda conseguem alcançar a água disponível no lençol freático, há a hipótese das florestas sobre lençol freático superficial atuarem como refúgios hidrológicos, mitigando o efeito das secas já relatados para florestas sobre lençol freático profundo (Phillips et al. 2009, Zhao and Running 2010, Lewis et al. 2011), e isto foi avaliado para uma importante região no coração da Amazônia no capítulo 2 desta tese. Entender o papel da profundidade do lençol freático no funcionamento da floresta e sua resposta à seca é especialmente importante porque uma porção considerável (~ 50%) da floresta amazônica está sobre lençol freático superficial (Fan and Miguez-Macho 2010, Costa et al. 2022).

Os resultados do capítulo 1 mostraram que tanto o excesso quanto o déficit hídrico têm um efeito prejudicial no funcionamento da floresta. Além disso, existem combinações críticas de abastecimento de água dadas pelo clima e solo que, juntas, podem mitigar o estresse hídrico e maximizar o crescimento da floresta e o armazenamento de carbono. Florestas com lençol freático superficial têm, em média, menor produtividade e estoque de biomassa, maior mortalidade e turnover de caules, bem como observado em florestas localizadas em climas mais secos. O excesso de água no solo promove efeitos deletérios no metabolismo e fisiologia das plantas, portanto a maior parte do crescimento das plantas é restrita a uma curta janela de tempo, quando os níveis do lençol freático diminuem e a condição de anoxia é aliviada. Tais janelas de crescimento têm sido descritas em áreas inundadas, onde o maior crescimento em diâmetro ocorre no período não inundado (Schöngart et al. 2002, 2004). A maior mortalidade de caules pode estar associada à fraca ancoragem da árvores causada pela camada de água subterrânea que impede o crescimento das raízes em profundidade, isso também está geralmente associado à textura de solo mais desagregada (Gale and Barfod 1999, Toledo et al. 2011*a*), proporcionando assim menor aderência no solo e maior suscetibilidade ao desenraizamento (Madelaine et al. 2007). Em climas mais secos, a combinação de lençol freático superficial e solo argiloso tem potencial de amenizar o déficit hídrico na estação seca, levando a uma maior produtividade do que em florestas sobre lençol freático profundo nas mesmas condições climáticas e de solo. No entanto, as mesmas condições de lençol freático superficial e clima seco, mas combinadas com solos arenosos, levam à redução da produtividade da biomassa. A maior agregação de partículas de argila resulta em melhores características de retenção de água (Richter and Babbar 1991), melhorando a disponibilidade de água para as plantas principalmente durante a estação seca (Damasco et al. 2013). Em geral, os efeitos ecológicos do regime hídrico do solo dependerão do grau de saturação do solo nos meses úmidos, do grau e frequência dos períodos de déficit hídrico, da capacidade de retenção de água e da distribuição das raízes no solo (Franco and Dezzeo 1994). Portanto, este estudo separou a contribuição relativa do lençol freático e do clima, melhorando a compreensão do funcionamento do ecossistema tropical.

Dada a demonstração clara da influência da água subterrânea nos padrões de funcionamento da floresta em anos “normais”, no capítulo 2 busquei entender o funcionamento da floresta nos anos com secas intensas, como as associadas a anomalias positivas da temperatura da superfície do mar no Pacífico Equatorial (El Niño) e Atlântico Tropical Norte. Os resultados indicaram que na escala avaliada, região do interflúvio Purus-Madeira, as florestas que crescem sobre lençol freático superficial – vegetação relativamente pouco estudada que, no entanto, ocupa 50% das florestas amazônicas – são notavelmente resistentes à seca, efeito oposto do observado em florestas sobre lençol freático profundo (Phillips et al. 2009, Brienen et al. 2015, Feldpausch et al. 2016). A forte seca de 2015 não aumentou as taxas de mortalidade de árvores e palmeiras, mas sim promoveu o aumento das taxas de recrutamento. Provavelmente o El Niño 2015-16 promoveu uma seca moderada do solo que foi suficiente para reduzir as condições anóxicas de encharcamento e, portanto, promoveu melhores condições para o crescimento de palmeiras e árvores, aumentando as taxas de recrutamento e não alterando a mortalidade de caules. Houve um aumento no estoque de biomassa acima do solo de árvores do ano 2010 para 2015. Além disso, nossos resultados mostraram que as palmeiras não foram mais vulneráveis a secas extremas do que as árvores nessas florestas. Essas descobertas estão de acordo com a hipótese de que a hidrologia local e suas interações com o clima afetam a resposta das florestas às mudanças climáticas (Costa et al. 2022), amortecendo o déficit hídrico climatológico. Assim, o lençol freático superficial pode oferecer um alívio do estresse hídrico atmosférico projetado pelos modelos climáticos para as próximas décadas, funcionando como refúgios hidrológicos (Pokhrel et al. 2014, McLaughlin et al. 2017). Portanto, é importante considerar o ambiente hidrológico local abaixo do solo para uma melhor avaliação dos efeitos da seca nas florestas tropicais. Este capítulo contribuiu para compreensão dos efeitos integrados da seca na dinâmica das florestas tropicais e destacou a importância de incorporar estes tipos de ambientes nas modelagens das respostas climáticas da floresta e nas políticas públicas sobre áreas prioritárias para conservação.

Os resultados dos dois capítulos desta tese evidenciaram a importância do lençol freático na estrutura e dinâmica da floresta, bem como no amortecimento dos efeitos deletérios das secas intensas. Florestas sobre lençol freático superficial em geral têm menor produtividade e estoque de biomassa e são mais dinâmicas do que florestas sobre lençol freático profundo. Todas as limitações impostas pelo excesso de água no solo fazem com que estas florestas tenham um funcionamento diferenciado do observado para florestas de terra firme sobre lençol freático profundo. Nesse sentido, o efeito das secas intensas também é diferente em florestas sobre lençol freático superficial, pois o alívio na condição de anoxia do solo em anos de seca intensa beneficia as plantas desses ambientes, e isso foi observado através do aumento das taxas de recrutamento após o El Niño 2015-16 e da não alteração nas taxas de mortalidade neste período para a área de estudo. Como conclusão destaco a grande importância das florestas sobre lençol freático superficial, que apesar de ocuparem uma extensa área na região amazônica, ainda precisam ser estudadas mais profundamente. Compreender seu funcionamento e papel na mitigação das secas intensas na escala da bacia amazônica é essencial para elaboração de uma legislação ambiental específica para sua conservação.

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Apêndice A

Artigos publicados como co-autora:

DRAPER, F. C.; COSTA, F. R.; ARELLANO, G.; PHILLIPS, O. L.; DUQUE, A.; MACÍA, M. J.; ... **SOUSA, T. R.**; ... et al. Amazon tree dominance across forest strata. *Nature Ecology & Evolution*, v. 1, p. 1, 2021. https://doi.org/10.1038/s41559-021-01418-y

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