INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA PROGRAMA DE
PÓS-GRADUACIÓN EM ECOLOGIA

COMO AS CONDIÇÕES HIDRO-TOPOGRÁFICAS LOCAIS INFLUENCIAM NOS PADRÕES DE DIVERSIDADE E COMPOSIÇÃO ARBÓREA NAS FLORESTAS DA BACIA AMAZÔNICA?

MANUEL JESÚS MARCA ZEVALLOS

Manaus, Amazonas

Setembro, 2021

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Dissertação apresentada à Coordenação do Programa de Pós-Graduação em Ecologia, como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

Manaus, Amazonas

Setembro, 2021

PG·ECO·INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
UNIDADE DE PESQUISA DO MCTIC

MINISTÉRIO DA CIÊNCIA, TECNOLOGIA E INOVAÇÕES

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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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M313c ZEVALLOS, MANUEL
COMO AS CONDIÇÕES HIDRO-TOPOGRÁFICAS LOCAIS INFLUENCIAM NOS PADRÕES DE DIVERSIDADE E COMPOSIÇÃO ARBÓREA NAS FLORESTAS DA BACIA AMAZÔNICA? / MANUEL ZEVALLOS; orientadora Flávia Reggina Capellotto Costa; coorientador Gabriel Massaine Moulatlet. -- Manaus:[s.l], 2021.
48 f.

Dissertação (Mestrado - Programa de Pós Graduação em Ecologia) -- Coordenação do Programa de Pós-Graduação, INPA, 2021.

1. Hidrologia local. 2. Ecologia de comunidades. 3. Bacia Amazônica. 4. floresta tropical. I. Capellotto Costa, Flávia Reggina, orient. II. Massaine Moulatlet, Gabriel, coorient. III. Título.

CDD: 598

Sinopse:

Avaliou-se a influência das condições hidro-topográficas locais nos padrões de diversidade e composição de espécies de árvores nas florestas da bacia Amazônica.

Palavras-chave: hidrologia local, ecologia de comunidades, florestas tropicais.

Agradecimentos

Agradeço ao Instituto Nacional de Pesquisas da Amazônia (INPA) e ao Programa de Pós-Graduação em Ecologia pela oportunidade de me capacitar e fazer ciência. À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) por ter me concedido a bolsa de mestrado.

Agradeço à Dra. Flávia Costa por ter me acolhido dentro da Família Vegetal, pela compreensão e a paciência em me guiar durante esse processo de muito aprendizado, obrigado pela confiança e por ter me permitido trabalhar com a Amazônia toda! Ao Dr. Gabriel Moulatlet pelas ideias que permitiram enriquecer o trabalho e a preocupação no andamento do projeto. Ao Dr. Hans ter Steege e a todos os membros da rede ATDN (Amazon Tree Diversity Network) por terem disponibilizado e permitido o uso da base de dados para o presente estudo. Ao Dr. Oliver Phillips ao Dr. William Ernest Magnusson e à Dra. Natalia Umaña pelos comentários e as sugestões pertinentes ao manuscrito. Ao Dr. Bruce Nelson, ao Davieliton Mesquita e ao Flavio Costa pela paciência e a ajuda na obtenção e processamento de dados climáticos, obrigado por ter compartilhado seus conhecimentos comigo. Ao Dr. Fabricio Baccaro pela ajuda na organização dos dados que me permitiram agilizar a análise dos dados. Ao grupo de Modelos Lineares, em especial ao Dr. Pedro Pequeno e ao Thiago Cavalcante pela ajuda pertinente nas questões estatísticas. À Dra. Juliana Schietti, à Thaiane Sousa e a todos os integrantes da Família Vegetal pelos comentários e as contribuições ao trabalho.

Agradeço aos meus pais, Sabino e María, pelo amor e o apoio nas minhas decisões, sempre me lembrando "*Diosq'a nin: mañakuwaychis, nuq'a q'usaykichis*", "*atiyq'a munallaymi*". Aos meus irmãos, Dina, Abraham, Gloria, Isaac e María, pelo carinho e o suporte. Estou orgulhoso de tê-los. À Lourdes, ao Eduardo e à Mariane por formar parte da minha família manauara, obrigado pela companhia e pelos momentos compartilhados. Ao João (el gran campeón) e à Laura pelas reuniões dos quase mestres que sem dúvida, ajudaram a relaxar e recarregar as energias. Aos meus amigos da turma de 2019 pelo companheirismo e as experiências compartilhadas e aos professores do programa por toda a disponibilidade e por ter compartilhado seus conhecimentos conosco. Por último (não menos importante), agradeço à Mara, companheira e guia a traves do rio Amazonas e outras belas paisagens, obrigado por ter me acompanhado nos primeiros meses em Manaus, por confiar em mim, por me encorajar a sair da minha zona de conforto e seguir para frente. Gracias pe!

Resumo

Foi demonstrado que a diversidade e a composição arbórea na Amazônia estão fortemente determinadas pela disponibilidade de água fornecida pela precipitação. Porém, dentro do mesmo regime climático, a disponibilidade de água está modulada pela topografia e as características edáficas (referidas como condições hidro-topográficas), variando desde áreas saturadas de água e mal drenadas para áreas secas e bem drenadas que se espera influenciem na distribuição das espécies. No entanto, o efeito das condições hidro-topográficas nos padrões de diversidade e composição arbórea é pouco conhecida, sobre tudo na escala da bacia Amazônica. Usando uma base de dados de 443 parcelas de 1ha de terra firma, distribuídas ao longo da bacia, investigamos como as condições hidro-topográficas influenciam nos padrões de i) diversidade alpha de árvores, ii) densidade da madeira e iii) composição de espécies arbóreas. Nós encontramos que o efeito das condições hidro-topográficas sobre a diversidade arbórea depende do contexto climático, sendo mais evidente nas florestas mais úmidas, onde a diversidade aumenta em direção às áreas com solos bem drenados e livres de encharcamento. A densidade da madeira foi influenciada pelas condições hidro-topográficas, também aumentando em direção dos ambientes com solos bem drenados. A composição de espécies converge para comunidades com espécies similares com características conservativas no uso de recursos nas condições hidro-topográficas bem drenadas, mas diverge em condições pobremente drenadas entre as regiões geomorfológicas. Nossos resultados sugerem que a hidro-topografia local modula a filtragem de espécies influenciando a diversidade e composição das florestas amazônicas. Em geral, o presente estudo mostra que o efeito das condições hidro-topográficas é generalizada e se estende por amplas regiões da Amazônia e, reforça a importância em considerar a topografia e a hidrologia local para entender a resposta e a resiliência das florestas em cenários de aumento de eventos climáticos extremos e da temperatura global.

Palavras-chave: condições hidro-topográficas, diversidade arbórea, densidade da madeira, composição de espécies, bacia Amazônica.

Abstract

Tree diversity and composition in Amazonia is known to be strongly determined by the water supplied by precipitation. Nevertheless, within the same climatic regime, water availability is modulated by local topography and soil characteristics (hereafter referred to as hydro-topographic conditions), varying from saturated and poorly drained to dry and well-drained areas. While these may be expected to influence species distribution. However, the impacts of hydro-topographic conditions on tree diversity and composition remain poorly understood, especially at the whole Amazon basin scale. Using a data set of 443 1-ha non-flooded forests plots distributed across the basin, we investigate how hydro-topographic conditions influence i) tree alpha diversity, ii) wood density, and iii) tree species composition. We find that the effect of hydro-topographic conditions on tree diversity depends on climate, being more evident in wetter forests, where diversity increases towards locations with well-drained soils. Wood density is influenced by hydro-topographic conditions, also increasing toward better drained soils. Tree species compositional response are more complicated, with consistent community convergence associated with conservative resource use traits in well-drained locations, but diverging among different geomorphological regions for poorly drained conditions. Our results suggest that local hydro-topographic gradients filter species, influencing the diversity and composition of Amazonian forests. Overall, this study shows that the effect of hydro-topographic conditions is pervasive, extending over wide Amazon regions, and reinforces the importance of accounting local topography and hydrology to better understand the likely response and resilience of forests to increased frequency of extreme climate events and rising temperatures.

Keywords: hydro-topographic conditions, tree diversity, wood density, species composition, Amazon basin

Sumário

Introdução

Os padrões de diversidade e composição florística em grande escala têm sido bem explicados pela sazonalidade climática e a precipitação anual (Clinebell *et al.*, 1995; ter Steege *et al.*, 2003; Stropp *et al.*, 2009; Esquivel-Muelbert *et al.*, 2017). Porém, a disponibilidade de água experimentada pelas plantas dentro de qualquer regime climático está modulada pelas condições topográficas e edáficas locais (Daws *et al*., 2002; Gibbons & Newbery, 2003; Moeslund *et al*., 2013), os quais afetam a hidrologia local e assim a distribuição das plantas ao longo desses gradientes (e. g., ter Steege *et al.*, 1993; Svenning, 2001; Jirka *et al.*, 2007; Schietti *et al.*, 2013; Moulatlet *et al.*, 2017; Zuleta *et al.*, 2020). Na Amazônia, a maior floresta tropical do mundo, as condições hidrológicas locais podem modular o efeito das secas (Sousa *et al.*, 2020; Esteban *et al.*, 2021), com as áreas localmente mais úmidas constituindo potenciais refúgios para a diversidade (McLaughlin *et al.*, 2017). Portanto, considerando que o aquecimento global está levando a uma redução na disponibilidade de água nos ambientes tropicais (Pascolini-Campbell *et al.*, 2021) e a um aumento na frequência de secas (Marengo *et al.*, 2018) que causa uma alta mortalidade de árvores e perda de biomassa (Phillips *et al.*, 2009; Brienen *et al.*, 2015; Berenguer *et al.*, 2021), é importante considerar apropriadamente a influência das condições hidrológicas locais na diversidade, estrutura e composição das florestas.

Além da disponibilidade de água, processos neutros podem afetar a diversidade e composição arbórea na Amazônia (e. g., Condit *et al.*, 2002; Coronado *et al.*, 2009; Stropp *et al.*, 2009; Emilio *et al.*, 2010), mas têm evidência considerável que fatores determinísticos como as interações bióticas (e.g. Fine et al., 2004) e condições edáficas (Phillips *et al.*, 2003; ter Steege *et al.*, 2006; Cámara-Leret *et al.*, 2017; Figueiredo *et al.*, 2018) têm um papel importante. Outros importantes determinantes da composição florística na Amazônia são a fertilidade e o desenvolvimento e estrutura do solo, que variam desde solos ricos em nutrientes e menos desenvolvidos no Oeste até solos pobres em nutrientes e mais estruturados e desenvolvidos no Leste da bacia (ter Steege *et al.*, 2006; Quesada *et al.*, 2009). Condições edáficas como a disponibilidade de nutrientes e textura do solo podem estar associadas às condições topográficas locais (Chauvel, Lucas and Boulet, 1987; Vormisto *et al.*, 2000; Ferry *et al.*, 2010). Estas associações dependem da geomorfologia e a história evolutiva da paisagem, diferindo entre as regiões amazônicas (Sombroek, 2000). Formações geológicas, devido a suas diferenças nas características edáficas e do relevo, também afetam a composição florística (Rossetti *et al.*, 2010, 2019; Higgins *et al.*, 2011, 2015; Figueiredo *et al.*, 2014) e a dinâmica das florestas amazônicas (Johnson *et al.*, 2016; Esquivel-Muelbert *et al.*, 2020). Estas condições precisam então, ser tomadas em consideração para entender os efeitos da topografia e hidrologia local nas florestas.

As condições hidro-topográficas nas florestas não inundáveis (terra firme) estão determinadas principalmente pela elevação (relevo), o aspecto e a declividade do terreno (Moeslund *et al.*, 2013). Estas características controlam a capacidade de drenagem do terreno, a redistribuição local do escoamento da precipitação e a profundidade do lençol freático (Rennó *et al.*, 2008; Nobre *et al.*, 2011; Moeslund *et al.*, 2013). Ao longo do perfil topográfico, áreas mais baixas são úmidas, frequentemente saturadas de água e apresentam solos com baixa capacidade de drenagem devido à proximidade do lençol freático (Rennó *et al.*, 2008; Nobre *et al.*, 2011; Moeslund *et al.*, 2013). Estas condições podem restringir o estabelecimento e enraizamento das árvores (Fan *et al.*, 2017). Por outro lado, as áreas mais altas, como as encostas e colinas, são mais secos e apresentam solos bem drenados devido à distância do lençol freático (Rennó *et al.*, 2008; Nobre *et al.*, 2011; Moeslund *et al.*, 2013; Fan *et al.*, 2017). Árvores com raízes superficiais podem ser mais desfavorecidas nesses ambientes, especialmente em períodos de seca (Giardina *et al.*, 2018) quando o esgotamento da água do solo pode causar mortalidade de árvores (Nepstad *et al.*, 2007). Além disso, ao longo do gradiente hidro-topográfico, as condições do solo como a textura podem regular a infiltração e a ascensão capilar da água do lençol freático para os estratos superiores do solo, e assim pode afetar na retenção da umidade e a disponibilidade de água para as plantas (Hacke *et al.*, 2000; Fan *et al.*, 2017).

Uma abordagem da ecologia funcional permite entender a filtragem das espécies e a estruturação das comunidades ao longo dos gradientes ambientais a través do uso de traços morfológicos, fisiológicos e fenológicos, os quais afetam no crescimento, reprodução e a sobrevivência dos indivíduos (Violle *et al.*, 2007). Por exemplo, a densidade da madeira está associada com a hidráulica das plantas (Hacke *et al.*, 2001) e pode ajudar a entender a filtragem dos traços funcionais ao longo do gradiente de disponibilidade de água. Estudos locais em florestas de terra firme indicam que as condições hidro-topográficas locais além de influenciar na diversidade e composição florística (Valencia *et al.*, 2004; Schietti *et al.*, 2013; Féret and Asner, 2014; Moulatlet *et al.*, 2014; Zuleta *et al.*, 2020), influenciam na composição funcional, como na densidade da madeira (Ferry *et al.*, 2010; Cosme *et al.*, 2017), características da folha (Kraft, Valencia and Ackerly, 2008; Cosme *et al.*, 2017; Schmitt *et al.*, 2020), resistência hidráulica (Oliveira *et al.*, 2019; Fontes *et al.*, 2020), massa da semente (Kraft, Valencia and Ackerly, 2008) e características químicas do dossel (Asner *et al.*, 2015). No entanto, nenhum estudo até agora determinou se esses padrões se repetem em toda a bacia Amazônica e como eles dependem de outros fatores ambientais. Estudos em outras florestas tropicais indicam que o efeito das condições hidro-topográficas na estrutura e composição funcional das florestas dependem do clima (Blanchard *et al.*, 2019; Muscarella *et al.*, 2019). Na bacia Amazônica, onde o clima varia desde não sazonal até sete meses secos por ano e as condições edáficas, geológicas e do relevo variam entre as regiões da Amazônia, espera-se diferentes combinações da hidro-topografia com o clima e as condições das regiões que podem afetar os padrões de diversidade e composição de espécies e suas características funcionais nas florestas.

Perguntas e hipóteses

Como as condições hidro-topográficas influenciam nos padrões de diversidade arbórea nas florestas da bacia Amazônica?

O efeito das condições hidro-topográficas na diversidade vai depender do contexto climático.

Nós prevemos que nas florestas mais úmidas a diversidade será maior nas partes mais altas com solos bem drenados; enquanto que nas florestas mais secas, a diversidade será maior nas partes topográficas baixas com maior disponibilidade de água.

Como as condições hidro-topográficas afetam a mudança da composição de espécies arbóreas ao longo dos gradientes ambientais?

A magnitude do efeito das condições hidro-topográficas na mudança da composição florística vai depender do contexto climático e das condições edáficas e do relevo das regiões geológicas da Amazônia.

Nós prevemos que as condições hidro-topográficas vão gerar padrões opostos de mudança da composição de espécies entre florestas secas e úmidas, onde a mudança da composição arbórea vai divergir em direção às partes mais altas e solos bem drenados devido ao efeito da disponibilidade de água fornecida pela precipitação será maior nessas áreas. Ademais, o efeito das condições hidro-topográficas na composição de espécies será maior em regiões com estrutura edáfica antiga e relevo bem dissecado, e menor nas regiões com estrutura edáfica recente e pouca variabilidade topográfica.

Como as condições hidro-topográficas influenciam na densidade da madeira?

As condições hidro-topográficas vão afetar na densidade da madeira independentemente das outras variáveis.

Nós prevemos que as florestas em solos com maior capacidade de drenagem e menor disponibilidade terão uma maior densidade da madeira.

Capítulo único

Manuel J. Marca-Zevallos, Gabriel Moulatlet, Thaiane R. Sousa, Juliana Schietti, Maria Natalia Umaña, Luiz de Souza Coelho, Juan Ernesto Guevara, Rafael P. Salomão, José Ferreira Ramos, Nigel C.A. Pitman, Diogenes de Andrade Lima Filho, Marcelo de Jesus Veiga Carim, José Renan da Silva Guimarães, Percy Núñez Vargas, Iêda Leão Amaral, William F. Laurance, Ana Andrade, Abel Monteagudo Mendoza, José Luís Camargo, Susan G.W. Laurance, Rodolfo Vasquez, Francisca Dionízia de Almeida Matos, Hugo F. Mogollón, Ben Hur Marimon-Junior, Beatriz S. Marimon, Timothy J. Killeen, Emanuelle de Sousa Farias, Lorena M. Rincón, David Neill, Marcelo Brilhante de Medeiros, Marcelo Fragomeni Simon, Juan David Cardenas Revilla, John Terborgh, Juan Carlos Montero, Bonifacio Mostacedo, Roosevelt García-Villacorta, Alejandro Araujo-Murakami, Nállarett Dávila, James A. Comiskey, Marcelo Petratti Pansonato, Carolina V. Castilho, Fernanda Coelho de Souza, Fernanda Antunes Carvalho, Jon Lloyd, Marcos Ríos Paredes, Alfonso Alonso, Francisco Dallmeier, Nicolás Castaño Arboleda, Rogerio Gribel, Juan Carlos Licona, Gerardo A. Aymard C., Dairon Cárdenas López, Anthony Di Fiore, Isau Huamantupa-Chuquimaco, Agustín Rudas, Adriana Prieto, Flávia Rodrigues Barbosa, Janaína Costa Noronha, Euridice N. Honorio Coronado, Domingos de Jesus Rodrigues, Carlos A. Peres, William Milliken, Alfredo Fuentes, Luzmila Arroyo, Rainiellen de Sá Carpanedo, Leandro Valle Ferreira, Carlos Cerón, J. Sebastián Tello, Bente Klitgaard, Milton Tirado, Edelcilio Marques Barbosa, Kenneth R. Young, Gonzalo Rivas-Torres, Dário Dantas do Amaral, Pablo R. Stevenson, Rodrigo Sierra, Alexandre A. Oliveira, Ires Paula de Andrade Miranda, Ophelia Wang, Cláudia Baider, Jos Barlow, Joice Ferreira, Erika Berenguer, Juliana Stropp, Roel Brienen, Manuel Augusto Ahuite Reategui, Italo Mesones, Therany Gonzales, Susamar Pansini, Vincent Antoine Vos, Walter Palacios Cuenca, Angela Cano, Angelo Gilberto Manzatto, Neidiane Farias Costa Reis, William Farfan-Rios, William Farfan-Rios, Miles R. Silman, Adeilza Felipe Sampaio, Patricio von Hildebrand, Marcelino Carneiro Guedes, Luis Valenzuela Gamarra, Karina Garcia-Cabrera, Juan Fernando Phillips, César I.A. Vela, José Julio de Toledo, Corine Vriesendorp, Daniel Villarroel, Daniela Pauletto, Janaina Barbosa Pedrosa Costa, Henrik Balslev, Fernando Cornejo Valverde, Elvis H. Valderrama Sandoval, Luiz Carlos de Matos Bonates, Oliver L. Phillips, William E. Magnusson, Hans ter Steege, Flávia R. C. Costa. Local hydro-topographic influences tree diversity and composition across the Amazon basin. Manuscrito submetido para *Ecography*.

Abstract

Tree diversity and composition in Amazonia has been demonstrated to be strongly determined by the water availability provided by precipitation. Nevertheless, within the same climatic regime, water availability is modulated by local topography and soil characteristics (hereafter referred to as hydro-topographic conditions), running from water-saturated and poorly drained areas to dry and well-drained areas which is expected to influence on species distribution patterns. However, the effect of hydro-topographic conditions on tree diversity and composition patterns is still poorly understood, especially at the whole Amazon basin scale. Using a data set of 443 1-ha terra-firme plots distributed across the basin, we investigate how hydro-topographic conditions influence the i) tree alpha diversity, ii) wood density, and iii) tree species composition patterns. We found that the effect of hydro-topographic conditions on tree diversity depends on climate, being more evident in wetter forests, where diversity increases towards areas with well-drained soils free of waterlogging. Wood density is higher towards well-drained soils regardless of climate and soil fertility. Finally, we find that tree species composition converges to similar species communities associated with conservative traits in resource use in well-drained topographic conditions, but diverges in poorly drained conditions among geomorphological regions. Our results suggest that local hydro-topographic modulates the filtering of species giving rise to the structure and composition of Amazonian forests. Overall, this study shows that the effect of hydro-topographic conditions is pervasive, extending over wide Amazon regions, and reinforces the importance in considering the local topography and hydrology to understand the response and resilience of forests in scenarios of increased frequency of extreme climate events and global temperature.

Keywords: hydro-topographic conditions, tree diversity, wood density, species composition, Amazon basin

Introduction

Large-scale patterns of floristic diversity and composition across tropical forests have been well explained by annual precipitation and seasonality (Clinebell *et al.*, 1995; ter Steege *et al.*, 2003; Stropp *et al.*, 2009; Esquivel-Muelbert *et al.*, 2017). Nevertheless, the water availability actually experience by plants within any given climatic regime is modulated by local topographical and edaphic conditions (Daws *et al*., 2002; Gibbons & Newbery, 2003; Moeslund *et al*., 2013), which affect the local hydrology and thus the distribution of plants along these gradients (e. g., ter Steege *et al*., 1993; Svenning, 2001; Jirka *et al*., 2007; Schietti *et al.*, 2013; Moulatlet *et al.*, 2017; Zuleta *et al.*, 2020). Within Amazonia, world's largest tropical forests, we now understand how local hydrological conditions can modulated the effects of Amazon droughts (Sousa *et al.*, 2020; Esteban *et al.*, 2021), with locally wetter areas constituting potential refuges for diversity (McLaughlin *et al.*, 2017). Therefore, and especially since global heating is leading to a reduction in water availability in many tropical environment (Pascolini-Campbell *et al.*, 2021) and an increase in the frequency of drought (Marengo *et al.*, 2018) which cause higher tree mortality and biomass loss (Phillips *et al.*, 2009; Brienen *et al.*, 2015; Berenguer *et al.*, 2021), it is important to properly consider the influence of local hydrological conditions on forest diversity, structure and composition.

In addition to water availability, neutral processes can affect tree composition and diversity in Amazonia (e. g., Condit *et al.*, 2002; Coronado *et al.*, 2009; Stropp *et al.*, 2009; Emilio *et al.*, 2010), but there is considerable evidence that deterministic factors, such as biotic interactions (e.g. Fine et al., 2004) and edaphic conditions (Phillips *et al.*, 2003; ter Steege *et al.*, 2006; Cámara-Leret *et al.*, 2017; Figueiredo *et al.*, 2018) play important roles. Other important determinants of floristic composition changes in the Amazon are soil fertility and edaphic development and structure, which range from nutrient-rich and less developed soils in the west to nutrient-poor, more structured and developed soils in the east of the basin (ter Steege *et al.*, 2006; Quesada *et al.*, 2009). Nevertheless, edaphic conditions such nutrient availability and soil texture are associated to local topographic conditions (Chauvel, Lucas and Boulet, 1987; Vormisto *et al.*, 2000; Ferry *et al.*, 2010). These associations depend on the geomorphology and evolutionary history of landscape, differing between Amazonian regions (Sombroek, 2000). Geomorphological formations, due to their differences in edaphic and relief characteristics, also affect floristic composition (Rossetti *et al.*, 2010, 2019; Higgins *et al.*, 2011, 2015; Figueiredo *et al.*, 2014) and dynamics of Amazonian forests (Johnson *et al.*, 2016; Esquivel-Muelbert *et al.*, 2020). These conditions then need to be taken into account to understand the local hydrology and topographic (hydro-topography) effects on forests.

The hydro-topographic conditions in non-flooded forests are mainly determined by elevation (relief), terrain aspect and slope (Moeslund *et al.*, 2013). These characteristics control the land's drainage capacity, the local redistribution of precipitation runoff, and the vertical distance to groundwater (Rennó *et al.*, 2008; Nobre *et al.*, 2011; Moeslund *et al.*, 2013). Along a topographic profile, lower areas are moist, often water-saturated and have soils with low drainage capacity due to the proximity to the water table (Rennó *et al.*, 2008; Nobre *et al.*, 2011; Moeslund *et al.*, 2013). These conditions restrict the establishment and rooting of trees (Fan *et al.*, 2017). On the other hand, the upper areas, such as hilltops, are typically drier and have well-drained soils due to the distance to the water table (Rennó *et al.*, 2008; Nobre *et al.*, 2011; Moeslund *et al.*, 2013; Fan *et al.*, 2017). Trees with shallow roots are at a disadvantage in these environmental conditions, especially during drought periods (Giardina *et al.*, 2018) when the soil water depletion may cause tree mortality (Nepstad *et al.*, 2007). Furthermore, along hydro-topographic gradient, soil conditions such soil texture can regulate the infiltration an the capillary raise of water from groundwater towards upper soil profiles, and this can affect moisture retention and water availability for plants (Hacke *et al.*, 2000; Fan *et al.*, 2017). Therefore, an effect of the interaction between local hydro-topographic conditions with the precipitation and edaphic gradients on Amazon forests is expected. These effects can allow a better understanding of the maintenance and organization of tree diversity and composition at Amazon basin scale.

A functional ecology approach allows to understand the species filtering and communities structuring along environmental gradients through the morpho-physio-phenological traits use which affect the individual's growth, reproduction and survival (Violle *et al.*, 2007). For example, wood density is associated with plant hydraulics (Hacke *et al.*, 2001) and can allow to understand the functional traits filtering along the water availability gradient. Local studies of non-flooded Amazonian forests indicate that hydro-topographic conditions in addition to influencing tree diversity and composition (Valencia *et al.*, 2004; Schietti *et al.*, 2013; Féret and Asner, 2014; Moulatlet *et al.*, 2014; Zuleta *et al.*, 2020), influence the functional composition, such as wood density (Ferry *et al.*, 2010; Cosme *et al.*, 2017), leaf functional traits (Kraft, Valencia and Ackerly, 2008; Cosme *et al.*, 2017; Schmitt *et al.*, 2020), hydraulic resistance (Oliveira *et al.*, 2019; Fontes *et al.*, 2020), seed mass (Kraft, Valencia and Ackerly, 2008) and canopy chemical traits (Asner *et al.*, 2015).

However, no study has so far determined if these patterns hold true over the whole Amazon basin and how they depend on other environmental factors. Studies in other tropical forests indicate that the effect of hydro-topographic conditions on the structure and functional composition of trees depends on the climate (Blanchard *et al.*, 2019; Muscarella *et al.*, 2019). In the Amazon basin, where the climate varies from non-seasonal to seven dry months per year and edaphic, geological and relief conditions vary between Amazon regions, different combinations of hydro-topography with climate and conditions of the regions are expected, which can affect patterns of diversity, species composition and their functional characteristics of forests.

Considering the limited understanding of the influence and importance of topographically-driven local hydrological conditions on tropical forests, the aim of this study is to understand the effects of hydro-topographic conditions on patterns of tree diversity, species composition and wood density at the scale of the whole Amazon basin. We address the following specific questions: (a) How do hydro-topographic conditions influence tree diversity? (b) How do hydro-topographic conditions affect tree species composition change along environmental gradients? (c) How do hydro-topographic conditions influence wood density? We raise the following hypotheses:

(a) The effects of hydro-topographic conditions will result in greater diversity in the upland parts of the humid forests with well-draining (not waterlogged) soils; while in drier forests, diversity will be greater in lowland areas with greater water availability.

(b) Hydro-topographic conditions will promote opposing patterns of species composition change between wet and dry forests, where the tree composition change will divergence towards upland parts because the water availability effect provided by climate will be greater in these areas. Furthermore, greater changes in species composition along hydro-topographic gradient is expected in terrains with an ancient edaphic structure and well-dissected relief, such as in the Guiana Shield and Southern Amazon, compared to other regions of Amazonia with young edaphic structure and flatter topographies.

(c) Forests on soil with greater drainage capacity and less water availability will have a higher wood density.

Methods

Vegetation data

We used the ATDN data set (Amazon Tree Diversity Network), with plots distributed throughout the Amazon basin (Fig. 1). Our analyses were restricted to 1-ha lowland terra-firme forest plots below 500 a.s.l. (excluding plots on white sand and inundated forests) and to individuals with a diameter ≥ 10 cm, excluding all lianas. In addition, we considered only plots with at least 80% of individuals identified to species level. As species identification was done by different taxonomists, we excluded individuals that were not identified to the species level to avoid confusion with morphospecies synonymy. By including only those individuals identified at the species level, more robust patterns of diversity and composition are expected (Pos *et al.*, 2014). We also excluded plots with georeferencing problems, such as plots whose coordinates were displaced from terra-firme towards rivers or lakes. Finally, we excluded 6 plots with less than 30 species, as they have a high abundance of a few species that may decrease the confidence in diversity and composition patterns and 18 plots from areas without hydro-topographic data (Supporting information, Table S1). Thus, we carried out the analyses using 443 plots, which total 210,801 individuals of 3,527 species, distributed in 619 genera and 104 families.

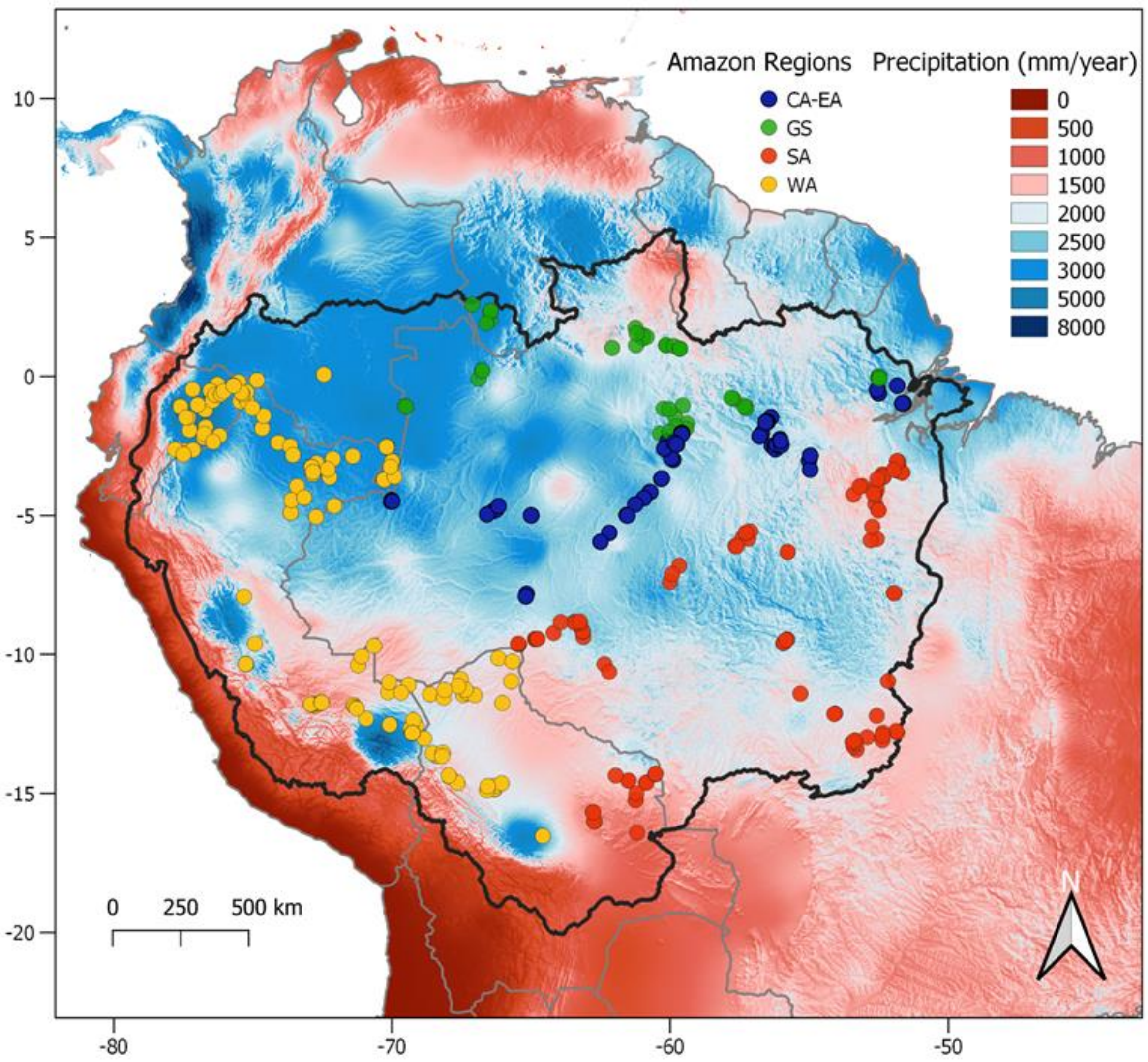

Figure 1. Location of 443 1-ha plots used in this study. The map shows the distribution of plots (coloured dots) across the Amazon basin. The limits of the Amazon basin (black outline) were defined according to Mayorga et al., (2012). Background information shows the annual precipitation layer obtained from CHELSA v1.2 (1979-2013, 30 arcsec of resolution) (http://chelsa-climate.org/). The different colours of the dots indicate which of the four geological regions they belong to: Central – East (blue, CA-EA = 122 plots), Guiana Shield (green, GS = 52 plots), South (red, SA = 102 plots) and West (yellow, WA = 167 plots).

Environmental variables

To represent the hydro-topographic condition of each plot, we used the height above the nearest drainage (HAND). HAND is calculated by normalizing the topography as a function of the relative height over the nearest drainage, using information from digital elevation models (DEM). This variable is directly related to the gravitational potential of soil water and, therefore, its values are correlated with the water table depth, providing a representation of the local water conditions (Rennó *et al.*, 2008; Nobre *et al.*, 2011). High HAND values mean high drainage potential and low HAND values indicates proximity to the water table, where drained water accumulates and may create waterlogged conditions (Nobre *et al.*, 2011). We extracted HAND data from layers elaborated by Banon & Novo (2018) (available at: http://www.dsr.inpe.br/amazondrainage/home.php?content=hand) with ~30m x 30m spatial resolution. We reprojected the layers to ~100m x 100m resolution to correspond to the 1-ha plots using bilinear extraction. The HAND layer that we used in the analyses was based on Strahler's sixth order drainages, as it provides more stable information about the drainage capacity and the water condition of the environment across varying geomorphologies. Finally, HAND data was log-transformed (base 2) to meet normality assumptions.

The climatic information for each plot was represented by the historical average of its maximum accumulated water deficit (MCWD). MCWD is the measure of the annual water deficit that considers both the duration and the intensity of the dry season (Aragão *et al.*, 2007). MCWD represents the most negative value of water deficit (WD), given by the difference between precipitation (P) and evapotranspiration (E) within each year, where for each month (n), WD is quantified as: $if\ WD_{n-1} - E_n + P_n < 0$; then $WD_n = WD_{n-1} - E_n + P_n$; $else\ WD_n = 0$. For this calculation, we considered the hydrological year, so the starting point is not necessarily the first month of the calendar year, but the wettest month (n-1) of the first year of the time series, according to calculations made by Esquivel-Muelbert et al., (2019). The precipitation data was obtained from the TerraClimate platform (Abatzoglou *et al.*, 2018) with ~4 x 4 km spatial resolution from 1959 to 2018. We assumed the evapotranspiration to be fixed at 100 mm per month, being an approximation (mean) from soil evapotranspiration obtained in different locations in Amazonia (Aragão *et al.*, 2007).

We defined the soil fertility as the sum of the concentration of exchangeable cations (SCC, Na^+, Mg^{+2}, Ca^{+2} and K^{+1}), which is an indicator of soil fertility correlated with phosphorus availability (Figueiredo et al., 2017; Moulatlet et al., 2017; Quesada et al., 2009).

We obtained SCC values from the layer produced by Zuquim et al., (2019), with ~11 x 11 km spatial resolution, which was reprojected to ~5 x 5 km resolution using the bilinear method.

The soil texture, which determines the water retention capacity of the soil (Hacke *et al.*, 2000), was represented by the percentages of sand and clay. We extracted soil texture data for a depth of 15 cm for each plot from the SoilGrids platform (Hengl *et al.*, 2017) with ~250 x 250 m spatial resolution.

Based on the characteristics and geological age of the soil substrate, the Amazon basin was classified into four regions: Central and Eastern Amazonia, Guiana Shield, Southern Amazonia and Western Amazonia (Feldpausch *et al.*, 2011; Johnson *et al.*, 2016). Central and Eastern Amazonia are characterized by having soils derived from reworked rocks and sediments belonging to the late Cretaceous that experienced more or less continuous weathering for more than 20 million years, and are thus nutrient-poor (Irion, 1978; Quesada *et al.*, 2010). These regions present an alternation of flat and undulating land, especially in the east (Sombroek, 2000). The Guiana Shield and Southern Amazonia have soils formed on ancient Cretaceous crystalline substrates (Irion, 1978; Quesada *et al.*, 2010), characterized by hilly dissected lands and rounded hills (Sombroek, 2000). Western Amazonia is formed on more recent pre-Andean sediments from the Cretaceous-Tertiary and Pliocene periods, characterized by undulating to rolling land (Sombroek, 2000). Furthermore, there are large areas dominated by shallow soils that can contribute to the fertility of the underlying soils through the weathering of the source material (Irion, 1978; Quesada *et al.*, 2010).

Vegetation metrics

Species diversity

We quantified diversity for each plot using Fisher's Alpha, which is based on the number of individuals and species in each plot and is relatively insensitive to the difference in the number of individuals among plots (Fisher, Corbet and Williams, 1943). We calculated Fisher's Alpha at the species, genus and family levels.

Species composition

To summarize the species composition, we used Non-Metric Multidimensional Scaling (NMDS) ordinations. We excluded species with less than two occurrences, to reduce the potential noise generated by the inclusion of rare species in the analysis (Cao and Larsen, 2001; McCune and Grace, 2002). The final number of species and individuals included was 2,417 and 206,459, respectively. We used three dimensions for the ordination to maintain stress < 2 (McCune and Grace, 2002), and was based on the quantitative data using the Bray-Curtis distances, calculated on the data matrix standardized by plot. Standardization involves dividing the abundance of each species by the total abundance in each plot, in order to obtain the relative abundance of species in each plot (McCune and Grace, 2002). The ordination based on quantitative data allows capturing the patterns generated mainly by the most abundant species, which tend to have larger contributions to the difference or similarity between plots (Costa, Magnusson and Luizao, 2005; Costa *et al.*, 2009). The variation of the original data captured by the NMDS axes was obtained by regression of the matrix of original floristic distances among samples calculated with the same dissimilarity index used in the ordination method, and the matrix of distances among samples obtained from the final NMDS solution (McCune and Grace, 2002).

We quantified the differences in floristic composition among regions using PERMANOVA (Anderson, 2001), using 999 permutations on the original distance matrix given by the Bray-Curtis dissimilarity distance. This method tests whether plots from the same region are floristically more similar to each other than it would be expected by chance. We applied the PERMANOVA method using the *adonis* function from the *vegan* R package (Oksanen *et al.*, 2020). In addition, we quantified the floristic variability within each region using the multivariate dispersion method (Anderson, 2006). This method tests how floristically similar plots are to one another within each region. The multivariate dispersion method was applied using the *betadisper* function from the R package *vegan* (Oksanen *et al.*, 2020) on the original distance matrix using the Bray-Curtis dissimilarity distances.

Wood Density

We obtained wood density data from the global wood density database (Chave *et al*., 2009, Zanne *et al*., 2009) for the species considered in the species composition analyses. When the wood density of a species was not available, we used the mean wood density at the genus, family or plot level (Baker *et al*., 2004; Rozendaal *et al*., 2020). We used genus level wood density data for 1,381 species out of the 2,417 species, and family and plot level data for 170 and 10 species, respectively. Then, we calculated the community weighted mean (CWM) of each plot, which is the estimated mean wood density of the individuals in the plot (Garnier *et al*., 2004).

Data analyses

Species diversity

To determine the influence of hydro-topographic conditions (HAND) on the tree species diversity, we used generalized least squares regressions (GLS). We applied a logarithmic transformation to species diversity values to ensure normal distribution of residuals. This transformation was not necessary for genus and family diversity. We built models where diversity was modelled as a function of climate variation (MCWD), soil fertility, soil texture (clay, sand) and HAND. To avoid multicollinearity between texture variables, we included sand and clay percentages in different models. We included a term to account for the spatial autocorrelation, specifying an exponential autocorrelation structure. Furthermore, after inspection of residuals, we included an exponential variance structure for MCWD to reduce the effect of heteroscedasticity on models. The selection of both the spatial correlation and the variance structure was based on the lowest values of the Akaike Information Criterion (AIC) (Zuur *et al*., 2009) (Supporting information, Table S2). We built one general model for each response variable (based on species, genus, or family). This model, included the additive effect of MCWD (water availability given by precipitation, which has been considered the main determinant of diversity patterns in Amazonian forests [ter Steege *et al*., 2003; Stropp *et al*., 2009; Esquivel-Muelbert *et al*., 2017]), soil texture, HAND and soil fertility. This model included the interaction effect between HAND and MCWD.

Species and functional composition

To investigate the influence of HAND, controlling the other relevant environment variables on the floristic composition and wood density, we used each NMDS ordination axis and the community weighted mean of wood density (WD-cwm) as response variables. Since there was no correlation among NMDS axes (Supporting information, Table S3), the axes containing most of the variation were used as separate response variables. We modelled species composition and WD-cwm as a function of HAND, soil texture, MCWD, soil fertility and geological regions, using GLS models. We included an exponential spatial autocorrelation structure (Supporting information, Table S2). For each ordination axis and the WD-cwm, we constructed one general model including the additive effect of soil fertility, MCWD, geological regions (variables that are already known to determine changes in floristic composition [ter Steege *et al.*, 2006; Figueiredo *et al.*, 2018; Tuomisto *et al.*, 2019], and in wood density [Chave *et al.*, 2006; ter Steege *et al.*, 2006; Quesada *et al.*, 2012] at the Amazon basin scale), soil texture, HAND and the interaction effect of HAND with MCWD and geological regions.

To visualize the individual or interaction effects of the explanatory variables on the response variables (diversity, floristic composition and WD-cwm), we used partial plots of the significant effects ($P > 0.05$) identified by the GLS models. To compare the effect size of the explanatory variables on the response variables, all variables were standardized to have mean of zero and standard deviation of one. We also examined the bivariate relationships between diversity, ordination axes and WD-cwm, using Spearman's correlation tests.

The analyses were carried out in R (R version 4.0.2), using the *nlme* (Pinheiro *et al.*, 2021) packages.

Results

Tree diversity

The species and genus diversity were significantly associated with the interaction between HAND and MCWD (*P* = 0.012 and *P* = 0.004, respectively) and by the individual effect of MCWD (*P* = <.0001, species; *P* = <.0001, genus). Family diversity was influenced by the individual effect of MCWD (*P* = <.0001) and soil fertility (*P* = 0.002) (Table 1). The interaction between MCWD and HAND indicated that in wetter forests (MCWD between -136.7 mm and -1.60 mm, corresponding approximately to 1-2 dry months in the year, 222 plots) the diversity of species and genera were higher in well-drained areas with deep water tables, such as the plateaus and hilltops (Fig. 2A, B, blue). However, in drier forests (MCWD between -429.6 mm and -138.0 mm, >2 dry months, 221 plots), there was a subtle tendency towards greater diversity in the zones with higher water availability and water table close to the surface, corresponding to bottomlands and riparian forests (Fig.2A, B, red). Although the interaction effect between MCWD and HAND was not significant at the family level (*P* = 0.173), the diversity patterns in relation to this interaction were similar to those observed for species and genus levels (Fig. 2C).

The diversity at all taxonomic levels evaluated was affected by MCWD, which always had the largest relative contribution in the models (Fig. 4 A - C). Diversity increased towards wetter forests, this relationship being more pronounced at the species and genus levels (Supporting information, Fig. S1). Soil fertility had a positive effect on species (*P* = 0.335) and genus diversity (*P* = 0.093), but was more evident on family diversity (Fig. 4A – C, Table 1, Supporting information, Fig. S1). Soil texture did not contribute significantly at any taxonomic level (Table 1).

Floristic composition

The three-dimensional NMDS solution produced high congruence between species composition distances observed in the original space and those obtained in the reduced space (non-metric fit $r^2 = 0.96$, linear fit $r^2 = 0.73$). The stress value was 0.19, and the variance captured by the three dimensions altogether was 56%. Floristic composition differed significantly among geological regions (PERMANOVA: $P = 001$, $R^2 = 0.10$). Furthermore, the multivariate dispersion method showed a greater variability in the floristic composition within Southern Amazonia, the Guiana Shield and Western Amazonia, which had a greater mean distances to the medians of the sets of plots (0.64, 0.62, 0.61, respectively). This variability was lower in Central and Eastern Amazonia (0.57) (Supporting information, Fig. S2).

The first NMDS axis was influenced by HAND (Table 1), interacting with geological regions ($P = 0.001$). This interaction indicated that species composition converged among regions in the upper topographic zones, with greater drainage capacity (higher HAND values), and diverged in areas with less drainage capacity and greater water availability (lower HAND values) (Fig. 2D). The effect of this interaction was more evident in Western, and in Central and Eastern Amazonian forests. This means that species composition tends to be more similar in well-drained areas of Central, Eastern and Western Amazonia, but tends to differ between low and poorly-drained areas of these regions. However, the mean effect of HAND (i.e. apart from interactions) was not significant ($P = 0.53$). The first NMDS axis was mainly associated with soil fertility ($P = <.0001$, Fig. 4D) indicating that the floristic composition changes from forests with poor soils mostly in the Eastern-Central Amazonia and Guiana Shield to forests with fertile soils mostly in the West Amazonia (Supporting information, Fig. S3). Furthermore, the individual effect of geological regions and clay content had a significant effect on the first NMDS axis ($P = 0.05$ and $P = 0.027$, respectively) (Fig. 4D, Table 1, Supporting information, Fig. S3). On the other hand, the change in species composition in the second NMDS axis was mainly associated with MCWD (Fig. 4E, Table

1), which ranges from forests with higher water deficit in South Amazonia to humid forests with lesser water deficit in Northwestern Amazonia (Supporting information, Fig. S4). Furthermore, although the effect of the interaction between HAND and MCWD was not significant on this axis (*P* = 0.67), there was a weak HAND effect causing a divergence on species composition between wetter and drier forests towards areas with well-drained soils (Fig. 2E). The effect of sand content was not significant for neither of the two ordination axes (*P* = 0.43 and *P* = 0.3, respectively).

Wood Density

Wood density was influenced by interactions between HAND and geological regions (*P* = 0.03, Table 1). This interaction effect was more evident in Southern and Western Amazonian forests, indicating a higher wood density towards uplands and well-drained areas (Fig. 2F). Furthermore, the individual effect of HAND indicated an increase in wood density towards forests with greater soil drainage capacity (Fig. 4F, Supporting information, Fig. S5), but this effect was not statistically significant (*P* = 0.14). Wood density was mainly influenced by the simple effects of soil fertility and geological regions (Fig. 4F), decreasing with soil fertility (Supporting information, Fig. S5). In addition, wood density was higher in Central, Eastern Amazonia and Guiana Shield forests, and lower in Southern and Western Amazonian forests, respectively (Supporting information, Fig S5). The effects of MCWD (*P* = 0.81), soil texture (% sand, *P* = 0.63; % clay, *P* = 0.2) and the interactions of HAND with MCWD (*P* = 0.71), were not significant.

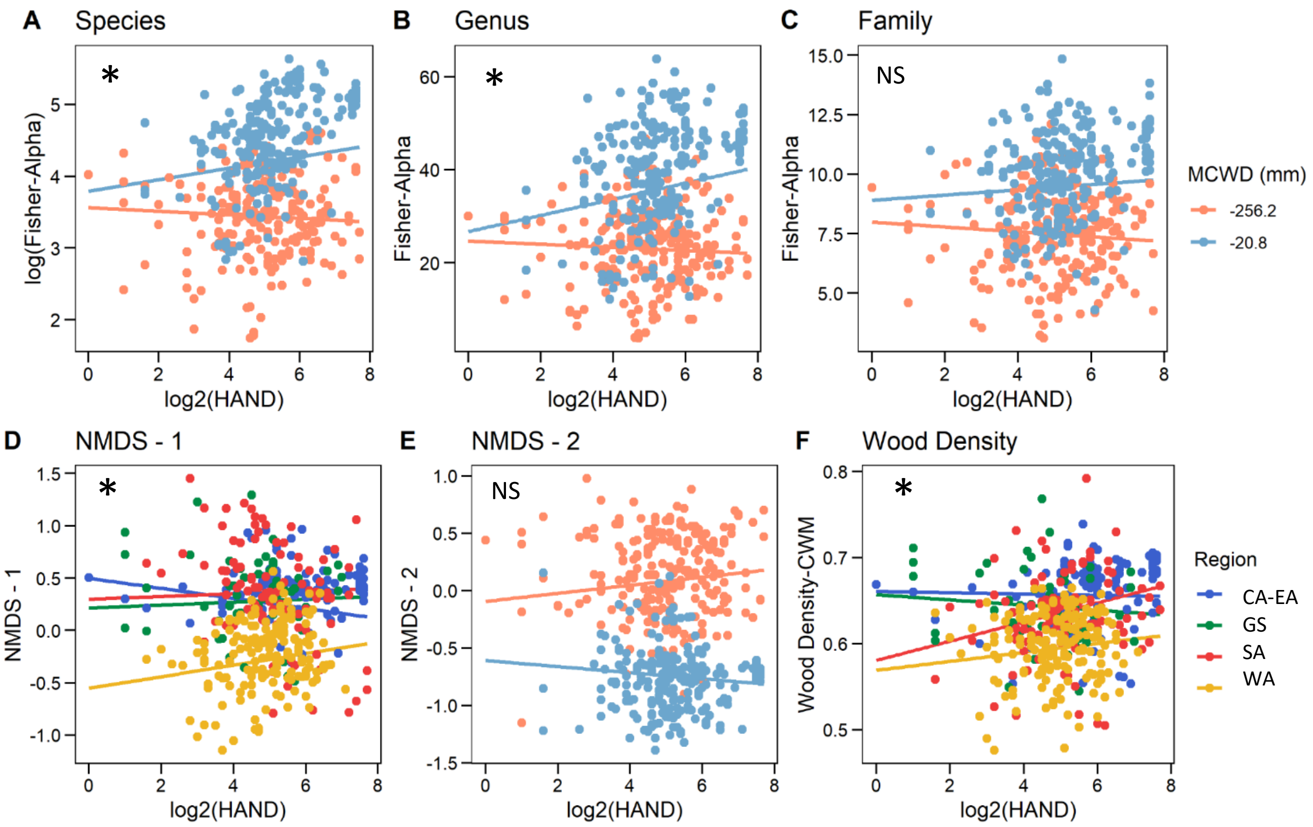

Figure 2. Partial effect of the interaction between HAND and MCWD on the species (**A**), genus (**B**), and family diversity(**C**). Panels A-C show the HAND effect on wetter forests (blue) and drier forests (red). MCWD = -256.2 (red), is the median MCWD value of the plots with the higher water deficit (between -429.6 and -138.0, 221 plots); MCWD = -20.8 (blue), is the median MCWD value of the plots with less water deficit (between -136.7 and -1.60, 222 plots). **(D)** shows the partial effect of the interaction between HAND and geological regions on the first NMDS ordination axis. **E**, shows the partial effect of the interaction between HAND and MCWD on the second NMDS ordination axis. **F**, shows the partial effect of the interaction between HAND and geological regions on wood density. In panel D and F, the different colours represent the four geological regions: Central and Eastern Amazonia (blue, CA-EA = 122 plots), Guiana Shield (green, GS = 52 plots), Southern Amazonia (red, AS = 102 plots) and West Amazonia (yellow, WA = 167 plots). “ * ” indicates a significant effect, and “NS” indicates a non-significant effect.

Correlations between diversity, floristic composition and wood density

The first NMDS ordination axis was strongly associated with wood density (rho = 0.80, *P* > 0.001). This relationship indicates that along this axis, the species composition varies from forests with lower wood density in more fertile soils (more negative scores) to forests with higher wood density in poor soils (more positive scores) (Fig. 3A). The wood density also had a positive relationship with tree diversity (rho = 0.26, *P* > 0.001), where forests with higher wood density tend to have greater tree diversity (Fig. 3B). Furthermore, the tree diversity was related with the second NMDS ordination axis (rho = -0.68, *P* > 0.001) (Supporting information, Table S3).

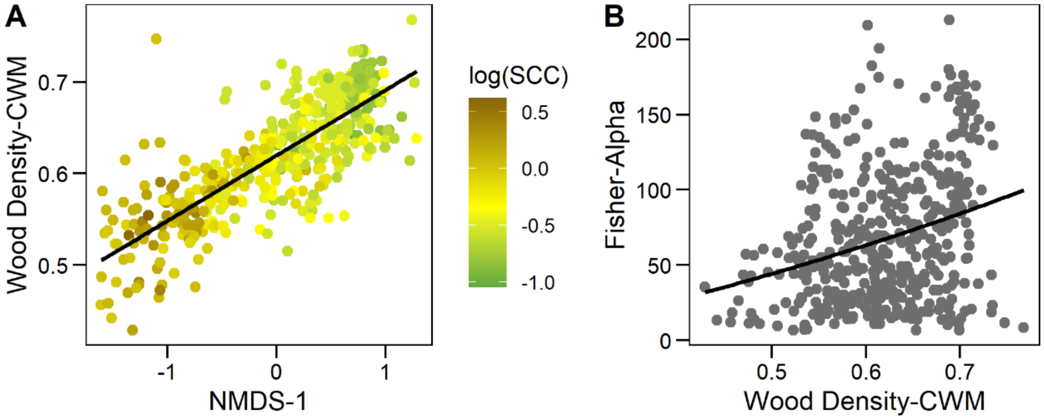

Figure 3. (**A**) Relationship between the first NMDS ordination axis and mean wood density, including the soil fertility gradient (log(SCC)), which varies from plots with low fertility soils (green) to plots with more fertile soils (brown). (**B**) Relationship between tree diversity and wood density.

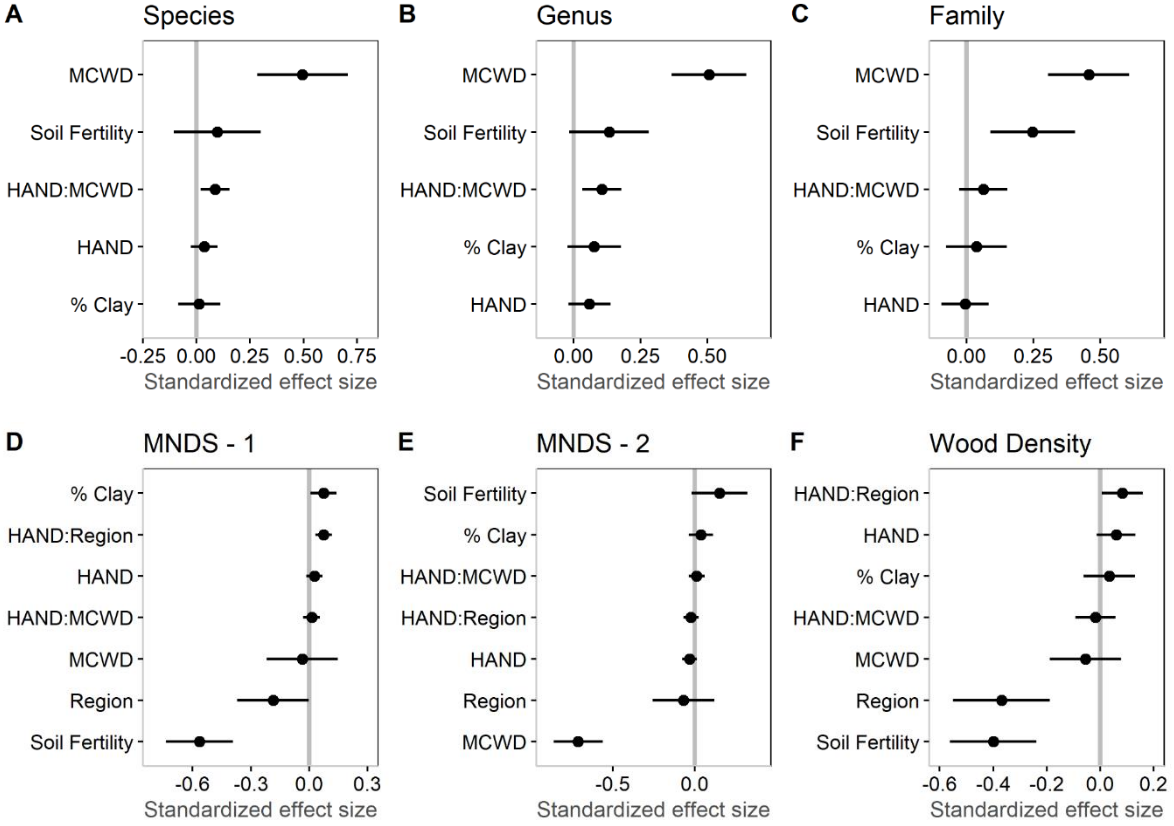

Figure 4. Standardized effect of variables for the GLS models for diversity, floristic composition and wood density in the Amazon basin. Species (**A**), genus (**B**) and family (**C**) diversity were mainly influenced by MCWD. The higher floristic diversity is found in the wetter forests, with less water deficit. The interaction effect between HAND and MCWD were weak, but significance on species and genus diversity (Table 1). In addition, soil fertility had a positive and more evident effect on family diversity. The first NMDS ordination axis (**D**) was mainly influenced by soil fertility and geological regions. The effects of the interaction between HAND and geological regions and the clay content were weak, but significance on the first ordination axis (Table 1). The floristic composition in the second NMDS ordination axis (**E**) was mainly influenced by the climate. Wood density is mainly influenced by soil fertility and geological regions (**F**). For each term in the model, the points represent the standardized effect and the lines represent standard deviation 1. See in the supporting information the bivariate relationships between the response variables and the explanatory variables (MCWD, region, fertility and soil texture). ":" = interaction.

Table 1. Standardized coefficients and their respective significance probabilities, as resulted from the GLS models for Alpha diversity (species, genus and family), floristic composition (NMDS 1 and NMDS 2) and wood density for 443 1-ha plots in the Amazon basin. In the construction of the models, the spatial autocorrelation was considered using an exponential correlation structure (Supporting information – Table S2). ":" = interaction.

	MCWD	HAND	Soil Fertility	% Clay	HAND:MCWD	Region	HAND:Region	R^2
Species	0.495***	0.035	0.097	0.012	0.086*	_	_	0.64
Genus	0.507***	0.06	0.133	0.078	0.107**	_	_	0.63
Family	0.457***	-0.006	0.247**	0.037	0.063	_	_	0.57
NMDS-1	-0.035	0.026	-0.565***	0.074*	0.013	-0.186*	0.074**	0.87
NMDS-2	-0.70***	-0.032	0.15	0.036	0.011	-0.068	-0.023	0.86
Wood Density	-0.055	0.06	-0.4***	0.034	0.14	-0.369**	4.58*	0.76

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Discussion

In this study, we investigated whether local hydro-topographic conditions influence tree diversity, floristic composition and wood density across the Amazon basin. Our results indicated that: 1) Amazonian tree diversity was affected by hydro-topographic conditions as a function of the climatic context, increasing towards well-drained topographic conditions in humid forests, 2) wood density was affected by hydro-topographic conditions depending on geological regions and increased towards well-drained topographic conditions, 3) the floristic composition converged among Amazonian geological regions, to more similar species assemblages on well-drained topographic conditions, but diverged on poorly-drained conditions. We conclude, therefore, that local hydro-topographic conditions interact with large-scale gradients in the Amazon, and this changes the perception of the important role that fine-scale environmental heterogeneity plays on biodiversity organization on the landscape.

Our results show the interaction between hydro-topographic conditions (HAND) and climatic water deficit (MCWD) on species and genus diversity, which modifies the diversity patterns previously described based only on climate. We showed that within wetter climatic conditions, tree diversity can be either higher or lower depending on the hydro-topographic conditions, and thus that fine-scale diversity patterns are also determined by soil water availability, which has important implications to biodiversity conservation under climate change. In humid forests, the excess water generated by high precipitation and water convergence to the bottomlands, which have a lower drainage capacity given the shallow water table, generate poorly structured and water-saturated soils (Ferry *et al.*, 2010; Fan *et al.*, 2017; Roebroek *et al.*, 2020). These conditions can cause stress due to excess water, which leads to a reduction in oxygen (hypoxia or anoxia) (Araya, Gowing and Dise, 2013; Silvertown, Araya and Gowing, 2015; Roebroek *et al.*, 2020) and nitrogen in the soil (Ferry *et al.*, 2010; Araya, Gowing and Dise, 2013). These effects can decrease survival and inhibit the growth and development, especially of species that do not have specific adaptations in the root system, such as adventitious root structure or aerenchyma tissue (Parolin, 2001; Parolin *et al.*, 2004). Superficial and waterlogged soils also limit root depth (Fan *et al.*, 2017) and can limit the establishment and survival of trees without efficient attachment structures such as buttress or tabular roots that compensate for the absence of deep roots. Species that attain larger sizes would be especially unstable under these conditions (Wittmann and Parolin, 2005). Thus, the physical and physiological limitations for the establishment and performance of many species in waterlogged sites may filter out a small set of species, reducing tree diversity. On the other hand, waterlogged areas with superficial water table represent only ~36% of whole Amazonian basin (Fan and Miguez-Macho, 2010), so the lower diversity in these areas could also be a result of the reduced extent of these environments over a larger timescale (ter Steege *et al.*, 2000).

The effects of hydro-topographic conditions on tree diversity agree with an earlier study at small scale in Southwestern Amazonia, although the reported effect of the hydro-topographic conditions was not very pronounced (Féret and Asner, 2014). In Central Amazonia, Laurance *et al.*, (2010) found lower tree diversity in forests with sandy soils, which correspond to environments with a shallow water table in this region (Chauvel, Lucas and Boulet, 1987). Valencia *et al.*, (2004) reported a larger number of species in the lower lying areas, although the difference in diversity to the upper and well-drained areas was not significant. On the other hand, flooded forests show a pattern similar to that reported here, along the flooding gradient, with alpha diversity increasing towards lower levels of flooding (Wittmann *et al.*, 2006; Wittmann, Schöngart and Junk, 2010; Assis *et al.*, 2015). Due to the connection with terra-firme forests, environments with low levels of flooding in floodplains and igapós can be colonized by terra-firme species adapted to some waterlogging, increasing their alpha diversity (Wittmann et al., 2006, 2010). We conclude that the patterns of lower tree diversity associated with water excess, either due to flooding or shallow water table under wet climates, can now be generalized to the whole Amazon basin.

In forests with higher water deficit, lower topographic areas harbour a more equal complement of biological diversity to higher topographic areas than they do in wet forests. The higher soil water availability in topographic bottomlands (Oliveira-Filho *et al.*, 1998; Segura *et al.*, 2003; Balvanera *et al.*, 2011; Fan *et al.*, 2017), allows better establishment and greater plant diversity in forests in more seasonal climates, than on hilltops with deep water tables (Segura *et al.*, 2003). However, the higher dynamics in the higher and well-drained areas in drier climates (Segura *et al.*, 2003; Brando *et al.*, 2014; Marimon *et al.*, 2014; Johnson *et al.*, 2016) may also favour an increase in diversity (Connell, 1978; Bongers *et al.*, 2009). Although our data does not allow us to determine whether these are in fact the mechanisms in action, the hypothesis that disturbances could be regulating the effect of hydro-topographic conditions on diversity in Amazonian forests with greater climatic water deficit could be tested in future studies.

Our results also showed a weak trend for an interaction effect between hydro-topographic conditions and climate on species composition change, generating opposite patterns between drier and wetter forests towards upland areas with well-drained soils (Fig. 2E). Therefore, our results suggest that local hydro-topographic conditions can generate different responses of forests according to the climate context in the face of global warming and climate change in the largest tropical forests on the Earth.

Wood density tends to increase towards higher topographic positions, with better drained soils and deep water table, indicating that the effect of local hydro-topographic conditions is widespread over large extensions of the Amazon basin, especially in the Southern and Western Amazonian forests. The effect of hydro-topographic conditions on wood density at the Amazon basin scale is supported by earlier local scale studies done on different parts of Amazonia (Kraft, Valencia and Ackerly, 2008; Ferry *et al.*, 2010; Araujo-Murakami *et al.*, 2014; Cosme *et al.*, 2017) and on other biomes (Cornwell and Ackerly, 2009; Liu, Yunhong and Slik, 2014; Jucker *et al.*, 2018; Blanchard *et al.*, 2019). At the same time, in contrast to the studies of Chave et al., (2006) and Ibanez et al., (2017), we found that climate did not have a significant effect on wood density when other environmental factors are taken into account, which agrees with other studies of tropical and Amazonian forests (ter Steege and Hammond, 2001; Muller-Landau, 2004; Umaña *et al.*, 2021). Blanchard et al., (2019) showed a larger effect of hydro-topographic conditions on wood density in drier than in wetter forests, but in the present study this dependence on the climatic context was not observed. High wood density tends to be associated with hydraulic safety and resistance to drought-induced embolism (Hacke et al., 2001), but Southern Amazonian forests have relatively low wood density (Supporting information, Table S4) and suffer larger water deficits (Supporting information, Fig. S6), so it is likely that tree species of these drier forests, rather than investing in a higher wood density, have developed alternative strategies to deal with low water availability. These strategies may be related to root systems that can reach and absorb water from deeper soil layers (Fan *et al.*, 2017), smaller leaves (Wright *et al.*, 2017), leaf deciduousness (Araujo-Murakami *et al.*, 2014; Blanchard *et al.*, 2019) or higher concentration of soluble sugars in the leaves (Signori-Müller *et al.*, 2021) that may favour osmoregulation.

The filtering of higher wood density in well-drained soils with a deep water table, and the opposite in wet conditions, is part of a broader selection of functional strategies along hydro-topographic gradients. Several local studies indicate the selection of functional characteristics by hydro-topographic conditions (Kraft, Valencia and Ackerly, 2008; Ferry *et al.*, 2010; Cosme *et al.*, 2017; Oliveira *et al.*, 2019; Fontes *et al.*, 2020; Schmitt *et al.*, 2020). In better drained areas, with lower water availability and deep water table, species converge towards more conservative traits related to resource use and conservation, with a reduced specific leaf area (SLA) and higher dry matter content (Kraft, Valencia and Ackerly, 2008; Liu, Yunhong and Slik, 2014; Cosme *et al.*, 2017; Schmitt *et al.*, 2020) and higher seed mass (Kraft et al., 2008; Liu et al., 2014), in addition to higher wood density. Furthermore, species from these zones have hydraulic systems with greater resistance to water stress and thus to drought events (Oliveira *et al.*, 2019; Fontes *et al.*, 2020). Root depth also increases with water table depth (Fan *et al.*, 2017). These trait strategies make communities less dynamics in the well-drained and deep water table environments (Ferry *et al.*, 2010; Toledo *et al.*, 2012), which may lead to a lower variability in floristic composition than in low lying environments, with lower drainage capacity and greater soil water availability (Schietti *et al.*, 2013; Féret and Asner, 2014; Zuleta *et al.*, 2020).

Given the filtering of functional traits along the hydro-topography gradient, we expected to see a concomitant shift in species composition, as traits selection can be attributed to species filtering. Species composition was associated with wood density. Thus, species compositional changes due to hydro-topographic conditions in the Western Amazon region clearly reflects a filtering of species with lower wood density in lower lying areas with greater water availability, and higher wood density in well-drained areas, where species composition converges to sets more similar to those found in the Central and Eastern regions, which on average have high wood density (Supporting information, Table S4). The pattern of compositional changes in Western Amazon is corroborated by the effect of hydro-topography on wood density in this region. We suggest that he absence of hydro-topography effect on wood density in Central and Eastern Amazon indicates that change in species composition along hydro-topography gradients in these regions may be associated with other characteristics different to wood density. Furthermore, species composition changes along the hydro-topographic gradient in the Central - Eastern and Western Amazonian forests, indicates that species composition tends to converge towards more similar species sets in the upper and well-drained areas of these regions, but diverge among their low and poorly drained areas between these regions. This can indicate that regional diversity in the Amazon forests may be maintained by high species variability in low topographical areas and low variability in high topographical areas. Therefore, we can conclude that the influence of hydro-topographic conditions on species composition extends over the Amazon, but in different ways in each geological region, suggesting that an effect of geological and geomorphological conditions over hydro-topographic patterns, which then affect regional species diversity and composition.

On the other hand, the absence of an effect of the hydro-topographic conditions on floristic composition in the Southern Amazonia and in the Guiana Shield forests may be due to the fact that these regions present a greater variability in tree composition compared to other regions. This variability may be a result of short-distance variation in edaphic conditions (Sombroek, 2000; Quesada *et al.*, 2011) and, although soils in these regions are formed from older substrates, they often have a low pedogenic development compared to the other regions (Quesada *et al.*, 2010). In Southern Amazonia, soil physical characteristics are similar along the hydro-topographic gradient, but some soils in the upper areas are shallow compared to soils in the lower areas (Araujo-Murakami *et al.*, 2014), which may limit root development (Fan *et al.*, 2017). Furthermore, although there is a marked difference in soil water availability between the lower and upper areas (Araujo-Murakami *et al.*, 2014), the high rate of dynamism experienced by forests in this region (Johnson *et al.*, 2016; Esquivel-Muelbert *et al.*, 2020) can lead to greater species composition variability, limiting the effect of local hydro-topographic conditions. The effect of hydro-topography on wood density in the Southern Amazonian forests may indicate that the change in functional composition along hydro-topographic gradients is not necessarily accompanied by a change in species composition in this region. In the case of the Guiana Shield, there are studies outside the limits of the Amazon basin that have demonstrated the effect of soil drainage conditions on local species distribution (ter Steege *et al.*, 1993; Sabatier *et al.*, 1997) and of hydro-topographic conditions on the dynamics of communities (Ferry *et al.*, 2010) and their functional traits (Schmitt *et al.*, 2020). However, in our case, the absence of a pattern in species composition change as a function of the hydro-topography observed may also have been influenced by the low representation of this region (52 plots) compared to the others (CA-EA = 122, SA = 102, WA = 167 plots).

Soil fertility had a strong influence in species composition and wood density, which agrees with previous studies carried out in tropical and Amazonian forests (Muller-Landau, 2004; ter Steege *et al.*, 2006; Quesada *et al.*, 2012; Umaña *et al.*, 2021). Furthermore, soil fertility had a positive influence on tree diversity, but it was only significant at the family level. Local scale studies indicate that soil fertility can have both a positive (Tuomisto *et al.*, 2002; Laurance *et al.*, 2010; Tuomisto, Zuquim and Cárdenas, 2014) and negative effect on plant diversity (Clinebell *et al.*, 1995). However, the effect of soil fertility may not necessarily be associated with resource availability (Clinebell *et al.*, 1995), but rather with the dynamics and intensity of disturbance in Amazonian forests, where greater soil fertility leads to selection of plants with short life cycle (e.g., species with lower wood density), generating a higher mortality and recruitment rates (Quesada *et al.*, 2012). However, other local scale studies indicate that disturbances negatively affect tree diversity (Marra *et al.*, 2014), or simply have no measurable effect (Carreño-Rocabado *et al.*, 2012). Our results are in agreement with previous large-scale studies of tropical (Phillips et al., 1994) and Amazon forests (Baker *et al.*, 2016), where disturbances are associated with a higher tree diversity, although in our results that was more evident at the family level.

Limitations of this study

Given the varied nature of the plots included in the ATDN, some issues regarding plot design and geographic coordinates may have affected the results presented here. Although all the plots used in this study are 1-ha, the plot design was not standardized. Some plots were installed following an elevation isoline, which reduces the topographic variation within the plot (Magnusson *et al.*, 2005) and thus improve the representation of hydrological conditions. However, most plots are quadrangular or rectangular, and may incorporate within-plot hydrological variation, which could make it difficult to adequately represent their hydro-topographic condition. Furthermore, only one geographic coordinate per plot was available, without additional information about the exact place where the coordinates were taken. Our hydro-topographic data (HAND) was obtained from a 30 m^2 resolution layer, but given the described issues, we had to reproject the HAND layer to a resolution of 100 m^2 to account for the variety of plot designs and possible inaccuracies in geographic location. Thus, the explanatory power of HAND may have been reduced.

Conclusions

At the Amazon basin scale, we have shown that the effect of hydro-topographic conditions on tree diversity depends on the climate context. Furthermore, the influence of hydro-topographic conditions on the functional and floristic composition is generalized and is given according to the edaphic and geomorphological conditions of the Amazon regions. These findings reinforce the importance of hydro-topographic factors as determinants of plant communities at large scales. Considering that most Neotropical forests species are restricted to wetter conditions (Esquivel-Muelbert *et al.*, 2017), climatic events such as extreme droughts that have been more frequent in recent decades (Marengo *et al.*, 2018), can be a serious threat to the diversity and functioning of the most diverse forests on the planet. In future scenarios of increase of global temperature and reduction of water availability (IPCC 2021), topographic and hydrological conditions can play an important role in the ecology and distribution of plants. Low topographic environments with a shallow water table can reduce the impact of extreme climatic events (Esteban et al., 2020; Schwartz et al., 2020; Sousa et al., 2020), being potential refuges for diversity (McLaughlin et al., 2017). Therefore, it is important to consider the hydro-topographic conditions in modelling studies of species distribution and forecasting the fate of forests under climate change, to allow the promotion of socio-political strategies of conservation and sustainable use of forests.

Acknowledgments

This work was made possible thanks to all ATDN (Amazonian Tree Diversity Network) members for having made available a very rich database. We thank Pedro Pequeno and Thiago Cavalcante for helping in data analysis, Fabricio Baccaro for helping with data organization, Bruce Nelson and Davieliton Mesquita for helping with the processing of climatic data, all members of Plant Ecology Laboratory of the Instituto Nacional de Pesquisas da Amazônia (INPA) for comments and suggestion. The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) granted a scholarship to M. J. M.

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Supporting Information

Supplementary tables

Supplementary table 1. 1-ha Plots that were excluded for having less than 30 species. *Tabebuia aurea* (Bignoniaceae), which is a typical species of transitional forests, has a high abundance in BENI_04 (318 individuals) and BENI_06 (115). Furthermore, *Machaerium hirtum* (Fabaceae), which is a pioneer species, has 458 individuals in BENI_11.

PlotCode	Country	Region	N	Species Richness
BENI_04	Bolivia	WA	438	11
BENI_06	Bolivia	WA	209	13
BENI_11	Bolivia	WA	592	15

Supplementary table 2. GLS models to select the structure of variance and spatial correlation for tree diversity, ordination axes and wood density. The variance structure with the highest performance for tree diversity was an Exponential structure. The structure of the spatial correlation with the highest performance for all response variables (tree diversity, ordination axes and wood density) was an Exponential. The selection of the structure of variance and spatial autocorrelation was given by the lowest values of AIC and Δ AIC.

DIVERSITY			
Variance Models	Variance Structure	AIC	Δ AIC
Fisher sp ~ MCWD + HAND + Fertility	_	4363.91	119.60
Fisher sp ~ MCWD + HAND + Fertility	varPower (MCWD)	4302.37	58.06
Fisher sp ~ MCWD + HAND + Fertility	**varExp(MCWD)**	**4244.00**	**0.00**
Fisher sp ~ MCWD + HAND + Fertility	varContPower(MCWD)	4304.37	60.06
Fisher sp ~ MCWD + HAND + Fertility	varFixed (MCWD)	4907.21	662.90
Autocorrelation Models	AutoCorStruct	AIC	Δ AIC
Fisher sp ~ MCWD + HAND + Fertility	**Exp**	**460.59**	**0.00**
Fisher sp ~ MCWD + HAND + Fertility	Gaus	476.84	16.24
Fisher sp ~ MCWD + HAND + Fertility	Spher	472.55	11.96
Fisher sp ~ MCWD + HAND + Fertility	Ratio	468.59	7.50
SPECIES COMPOSITION			
Autocorrelation Models	AutoCorStruct	AIC	Δ AIC
NMDS ~ MCWD + Fertility + Region	**Exp**	**400.68**	**0**
NMDS ~ MCWD + Fertility + Region	Gaus	453.93	43.64
NMDS ~ MCWD + Fertility + Region	Ratio	429.68	25.03
NMDS ~ MCWD + Fertility + Region	Spher	779.24	304.34
WOOD DENSITY			
Autocorrelation Models	AutoCorStruct	AIC	Δ AIC
WD-cwm~MCWD + Fertility + Region	**Exp**	**-1639.85**	**0**
WD-cwm~MCWD + Fertility + Region	Gaus	-1560.39	79.46
WD-cwm~MCWD + Fertility + Region	Ratio	-1638.99	0.86
WD-cwm~MCWD + Fertility + Region	Spher	-1560.41	79.45

Table S2. Bivariate relationship between alpha species diversity, ordination axes (NMDS1, NMDS2, NMDS3) and wood density (WD-cwm). The magnitude of the simple bivariate relationship was given by Spearman's correlation coefficient (rho). p - value < 0.05 means a significant relationship.

	Fisher Alpha		Wood Density		NMDS-1		NMDS-2		NMDS-3	
	rho	p - value	rho	p - value	rho	p - value	rho	p - value	rho	p - value
Fisher Alpha	1.00	_	**0.26**	0.00	0.20	0.00	**-0.68**	0.00	**-0.30**	0.00
Wood Density	0.26	0.00	1.00	_	**0.80**	0.00	0.04	0.38	-0.13	0.00
NMDS-1	0.20	0.00	0.80	0.00	1.00	_	0.02	0.68	-0.04	0.42
NMDS-2	-0.68	0.00	0.04	0.38	0.02	0.68	1.00	_	-0.05	0.34
NMDS-3	-0.30	0.00	-0.13	0.00	-0.04	0.42	-0.05	0.34	1.00	_

Table S3. Species composition and wood density in the regions of the Amazonia basin. N represents the number of plots in the regions. The multivariate mean of dispersion was obtained using the Bray-Curtis distance in a multivariate PCoA space, given by the betadisper function of the Vegan package. Finally, the mean and standard error (SE) of wood density in the regions.

Geological Regions	**N**	**Species Composition**	**Wood Density**	
		Mean multivariate dispersal	Mean	SE
East-Central Amazon	122	0.57	0.675	± 0.003
Guiana Shield	52	0.62	0.655	± 0.006
South Amazon	102	0.64	0.618	± 0.005
Western Amazon	167	0.61	0.569	± 0.004

Supplementary figures

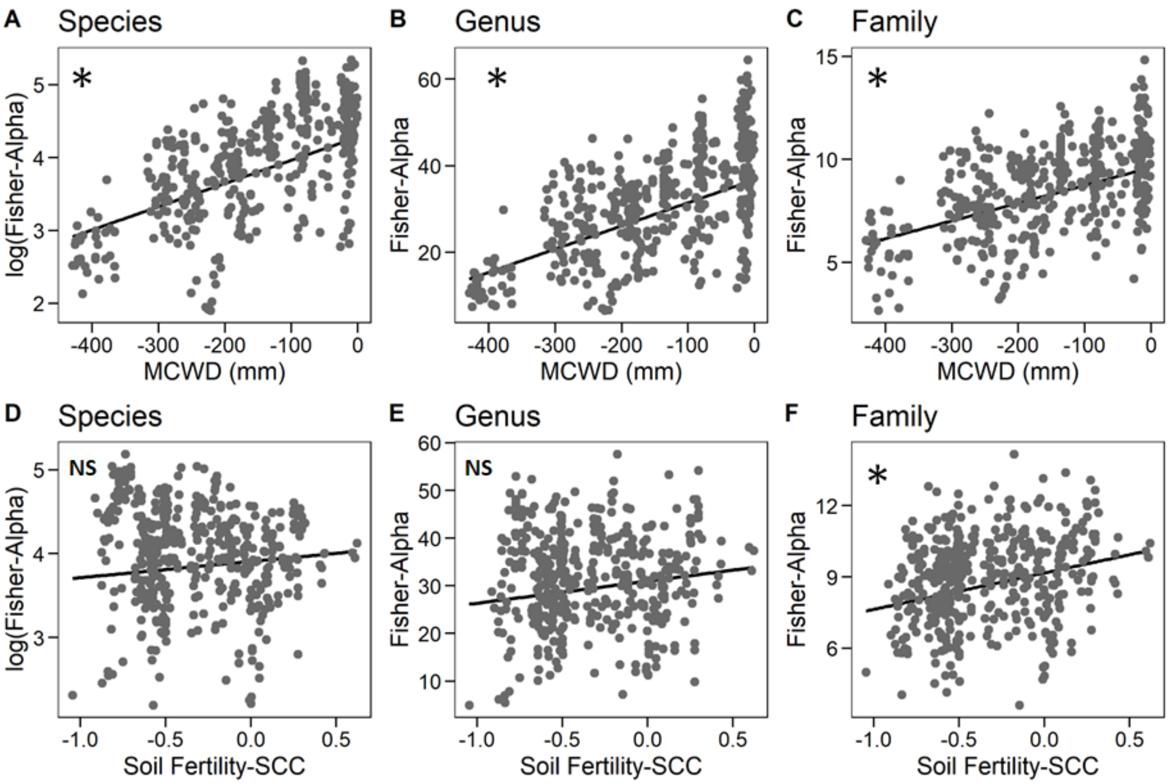

Figure S1. Partial effect of climatic water deficit (MCWD) on species (A), genus (B) and family (C) diversity. Partial effect of soil fertility on species (D), genus (E) and family (F) diversity for the GLS models, considering an exponential spatial autocorrelation structure. * = significant effect and NS = non-significant effect.

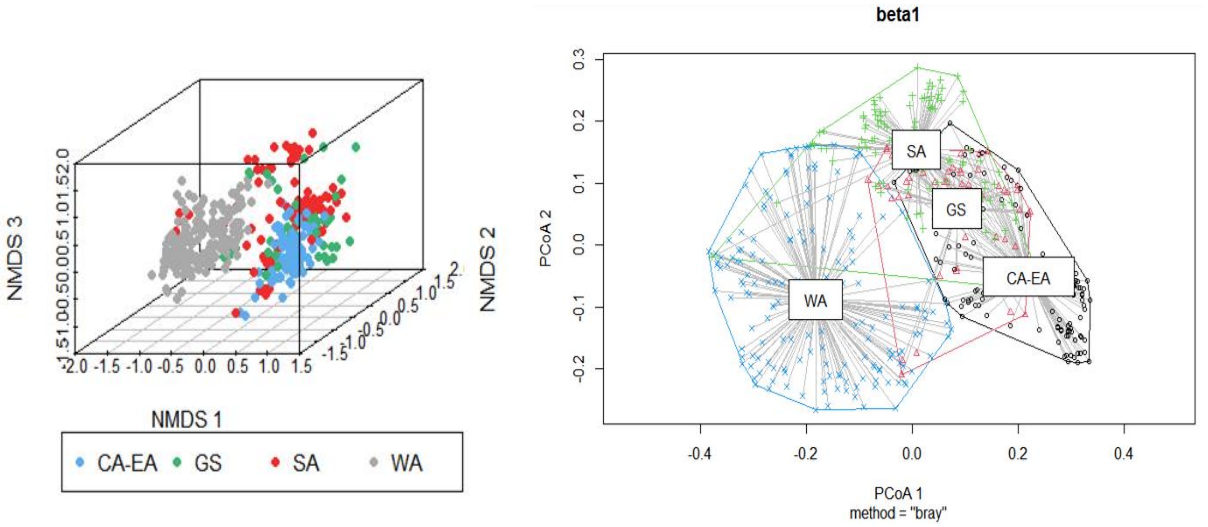

Figure S2. 3D plot of the three ordination axes (left) used in the GLS models. (right) Dispersion plot based on the first two PCoA axes used in the dispersion analyses. The first axis of the PCoA represents 16% of the data variation, and the second axis represents 9%. The PCoA method was used only for the multivariate dispersion analysis which was incorporated into the *betadisper* function of the *Vegan* package. The Bray-Curtis dissimilarity distance was used.

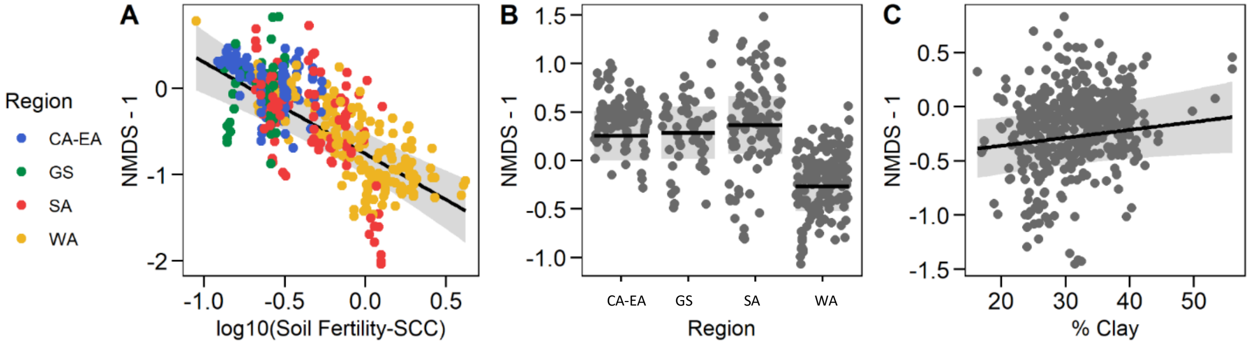

Figure S3. Significant partial effect of soil fertility (A), geological regions (B) and clay content (C) on the first ordination axis of the species composition for the GLS model, considering an Exponential spatial autocorrelation structure. Central-Eastern Amazonia (CA-EA), Guiana Shield (GS), Southern Amazonia (SA) and Western Amazonia (WA).

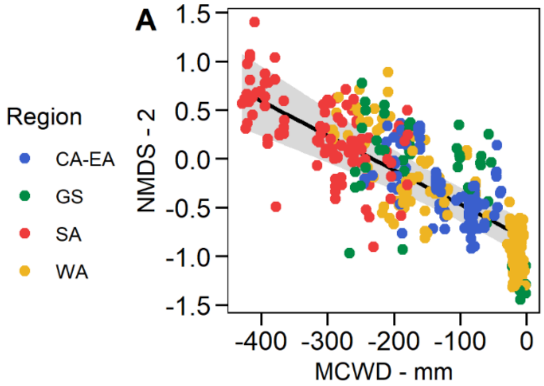

Figure S4. Significant partial effect of MCWD on the second ordination axis for the GLS model, considering an exponential spatial autocorrelation structure. Central-Eastern Amazonia (CA-EA), Guiana Shield (GS), Southern Amazonia (SA) and Western Amazonia (WA).

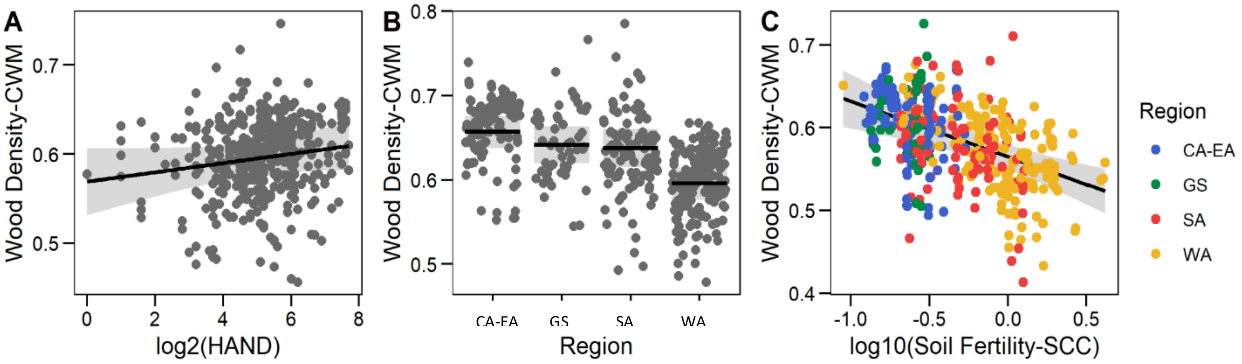

Figure S5. Positive partial, but not significant effect of HAND on wood density (A). Significant partial effect of geological regions (B) and soil fertility (C) on the wood density for the GLS model, considering an exponential spatial autocorrelation structure. Central-Eastern Amazonia (CA-EA), Guiana Shield (GS), Southern Amazonia (SA) and Western Amazonia (WA).

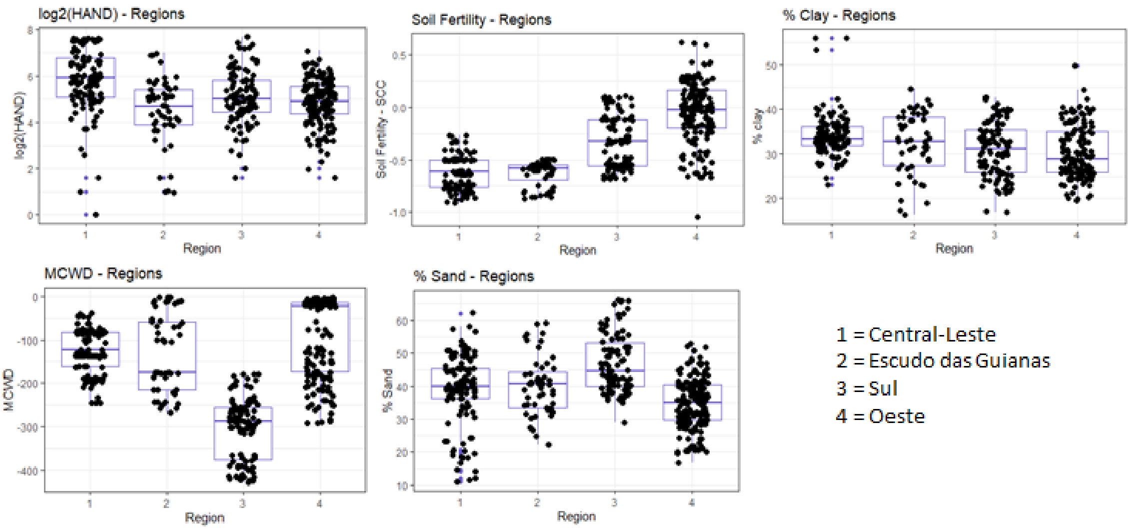

Figure S6. Environment variables in the Amazon regions. 1 = Central-Eastern Amazonia (CA-EA), 2 = Guiana Shield (GS), 3 = Southern Amazonia (SA) and 4 = Western Amazonia (WA).

Conclusão

Na escala da bacia Amazônica, nós mostramos que o efeito das condições hidro-topográficas na diversidade arbórea depende do contexto climático. Ademais, a influência das condições hidro-topográficas na composição florística e funcional é generalizada e está dada de acordo às condições edáficas e geomorfológicas das regiões amazônicas. Estes achados reforçam a importância dos fatores hidro-topográficos nas comunidades de plantas em grande escala. Considerando que a maioria das espécies das florestas Neotropicais estão restritas a condições muito úmidas (Esquivel-Muelbert *et al.*, 2017), eventos climáticos como as secas extremas estão sendo mais frequentes nas últimas décadas (Marengo *et al.*, 2018), podem ser uma séria ameaça para a diversidade e o funcionamento das florestas mais diversas do planeta. Em cenários de aumento da temperatura global e redução da disponibilidade de água (IPCC 2021), condições topográficas e hidrológicas podem cumprir um papel importante na ecologia e na distribuição das plantas. Ambientes topográficos baixos, com lençol freático superficial podem reduzir o impacto de eventos climáticos extremos relacionados com as secas (Esteban et al., 2020; Schwartz et al., 2020; Sousa et al., 2020), sendo potenciais refúgios para a diversidade (McLaughlin et al., 2017). Portanto, é importante considerar as condições hidro-topográficas nos estudos de modelagem de distribuição de espécies e na previsão do destino das florestas sob cenários de mudanças climáticas para permitir a promoção de estratégias sociopolíticas de conservação e uso sustentável das florestas.