

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?**

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Manaus, Amazonas

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 30 dias do mês de Setembro do ano de 2021, às 14h00min, por videoconferência. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: a Dra. **Gabriela de Paula Souza Zuquim**, da University of Turku, o Dr. **Ethan Householder**, da Institut für Geographie und Geoökologie – KIT, e o Dr. **Ben Hur Marimon Junior**, da Universidade do Estado de Mato Grosso - UNEMAT, tendo como suplentes o Dr. Fabricio Beggiato Baccaro, da Universidade Federal do Amazonas - UFAM e a Dra. Flavia Delgado Santana, do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência da orientadora, a fim de proceder a arguição pública do trabalho de DISSERTAÇÃO DE MESTRADO do **MANUEL JESÚS MARCA ZEVALLOS**, intitulado: "**COMO AS CONDIÇÕES HIDRO-TOPOGRÁFICAS LOCAIS INFLUENCIAM NOS PADRÕES DE DIVERSIDADE E COMPOSIÇÃO ARBÓREA NAS FLORESTAS DA BACIA AMAZÔNICA?**", orientado pela Dra. Flávia Regina Capellotto Costa, do Instituto Nacional de Pesquisas da Amazônia – INPA e Co-orientado pelo Dr. Gabriel Massaine Moulatlet.

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

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

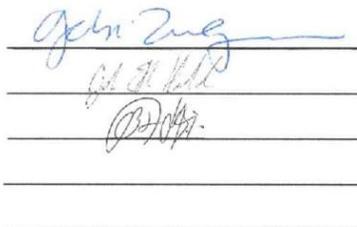
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**Sinopse:**

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.

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## 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 firme, 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

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## 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; Schiatti *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 secas 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; Schiatti *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

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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 Baidier, Jos Barlow, Joice Ferreira, Erika Berenguer, Juliana Stropp, Roel Brienens, 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*.

## 1 **Abstract**

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

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

## 24 **Introduction**

25           Large-scale patterns of floristic diversity and composition across tropical forests have  
26 been well explained by annual precipitation and seasonality (Clinebell *et al.*, 1995; ter Steege  
27 *et al.*, 2003; Stropp *et al.*, 2009; Esquivel-Muelbert *et al.*, 2017). Nevertheless, the water  
28 availability actually experience by plants within any given climatic regime is modulated by

29 local topographical and edaphic conditions (Daws *et al.*, 2002; Gibbons & Newbery, 2003;  
30 Moeslund *et al.*, 2013), which affect the local hydrology and thus the distribution of plants  
31 along these gradients (e. g., ter Steege *et al.*, 1993; Svenning, 2001; Jirka *et al.*, 2007; Schiatti  
32 *et al.*, 2013; Moulatlet *et al.*, 2017; Zuleta *et al.*, 2020). Within Amazonia, world's largest  
33 tropical forests, we now understand how local hydrological conditions can modulated the  
34 effects of Amazon droughts (Sousa *et al.*, 2020; Esteban *et al.*, 2021), with locally wetter  
35 areas constituting potential refuges for diversity (McLaughlin *et al.*, 2017). Therefore, and  
36 especially since global heating is leading to a reduction in water availability in many tropical  
37 environment (Pascolini-Campbell *et al.*, 2021) and an increase in the frequency of drought  
38 (Marengo *et al.*, 2018) which cause higher tree mortality and biomass loss (Phillips *et al.*,  
39 2009; Brienen *et al.*, 2015; Berenguer *et al.*, 2021), it is important to properly consider the  
40 influence of local hydrological conditions on forest diversity, structure and composition.

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

59           The hydro-topographic conditions in non-flooded forests are mainly determined by  
60 elevation (relief), terrain aspect and slope (Moeslund *et al.*, 2013). These characteristics  
61 control the land's drainage capacity, the local redistribution of precipitation runoff, and the  
62 vertical distance to groundwater (Rennó *et al.*, 2008; Nobre *et al.*, 2011; Moeslund *et al.*,  
63 2013). Along a topographic profile, lower areas are moist, often water-saturated and have  
64 soils with low drainage capacity due to the proximity to the water table (Rennó *et al.*, 2008;  
65 Nobre *et al.*, 2011; Moeslund *et al.*, 2013). These conditions restrict the establishment and  
66 rooting of trees (Fan *et al.*, 2017). On the other hand, the upper areas, such as hilltops, are  
67 typically drier and have well-drained soils due to the distance to the water table (Rennó *et*  
68 *al.*, 2008; Nobre *et al.*, 2011; Moeslund *et al.*, 2013; Fan *et al.*, 2017). Trees with shallow  
69 roots are at a disadvantage in these environmental conditions, especially during drought  
70 periods (Giardina *et al.*, 2018) when the soil water depletion may cause tree mortality  
71 (Nepstad *et al.*, 2007). Furthermore, along hydro-topographic gradient, soil conditions such  
72 soil texture can regulate the infiltration and the capillary rise of water from groundwater  
73 towards upper soil profiles, and this can affect moisture retention and water availability for  
74 plants (Hacke *et al.*, 2000; Fan *et al.*, 2017). Therefore, an effect of the interaction between  
75 local hydro-topographic conditions with the precipitation and edaphic gradients on Amazon  
76 forests is expected. These effects can allow a better understanding of the maintenance and  
77 organization of tree diversity and composition at Amazon basin scale.

78           A functional ecology approach allows to understand the species filtering and  
79 communities structuring along environmental gradients through the morpho-physio-  
80 phenological traits use which affect the individual's growth, reproduction and survival  
81 (Violle *et al.*, 2007). For example, wood density is associated with plant hydraulics (Hacke  
82 *et al.*, 2001) and can allow to understand the functional traits filtering along the water  
83 availability gradient. Local studies of non-flooded Amazonian forests indicate that hydro-  
84 topographic conditions in addition to influencing tree diversity and composition (Valencia *et*  
85 *al.*, 2004; Schietti *et al.*, 2013; Féret and Asner, 2014; Moulatlet *et al.*, 2014; Zuleta *et al.*,  
86 2020), influence the functional composition, such as wood density (Ferry *et al.*, 2010; Cosme  
87 *et al.*, 2017), leaf functional traits (Kraft, Valencia and Ackerly, 2008; Cosme *et al.*, 2017;  
88 Schmitt *et al.*, 2020), hydraulic resistance (Oliveira *et al.*, 2019; Fontes *et al.*, 2020), seed  
89 mass (Kraft, Valencia and Ackerly, 2008) and canopy chemical traits (Asner *et al.*, 2015).

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

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

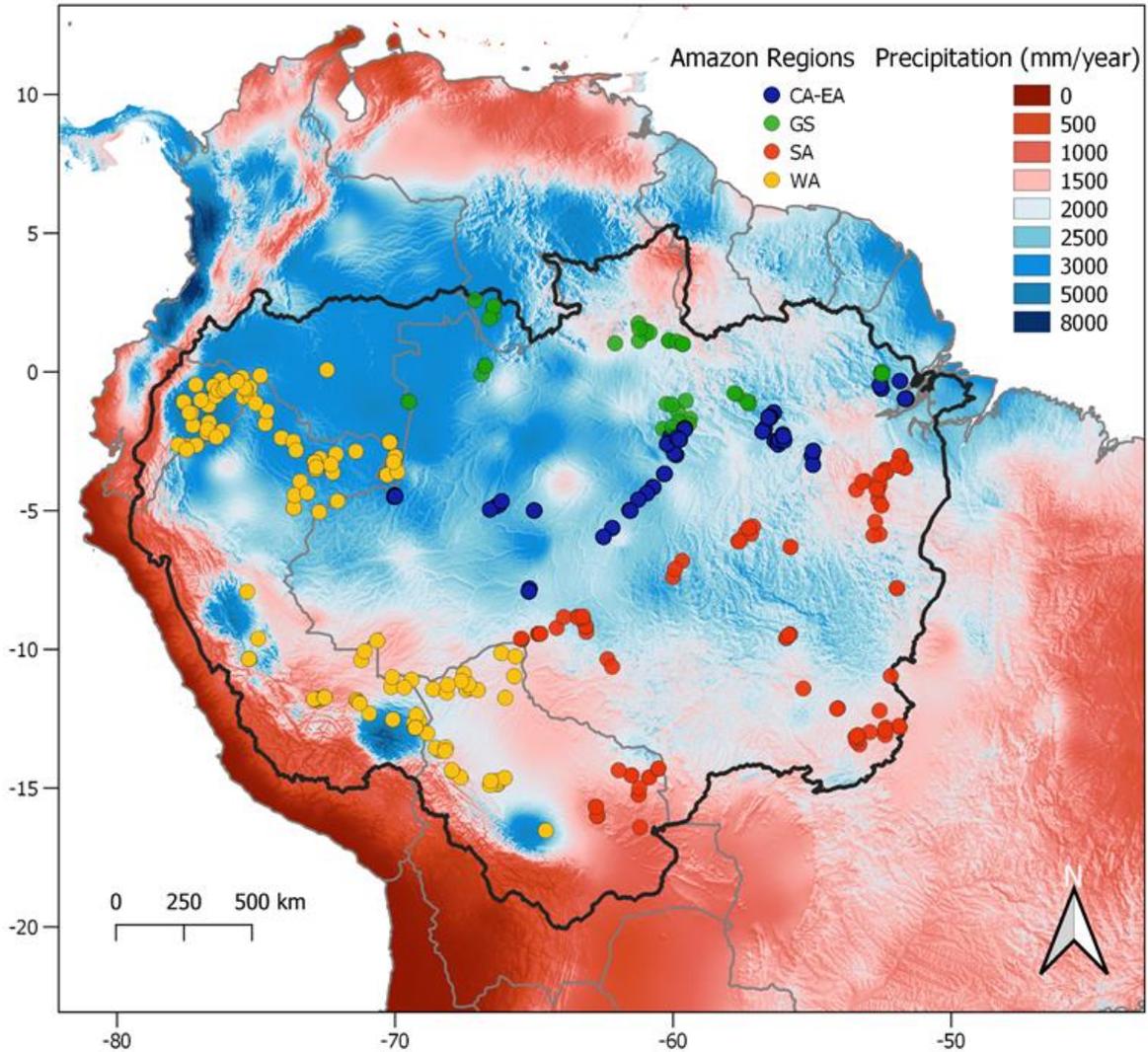
- 107         (a) The effects of hydro-topographic conditions will result in greater diversity in the  
108             upland parts of the humid forests with well-draining (not waterlogged) soils; while in  
109             drier forests, diversity will be greater in lowland areas with greater water availability.
- 110         (b) Hydro-topographic conditions will promote opposing patterns of species composition  
111             change between wet and dry forests, where the tree composition change will  
112             divergence towards upland parts because the water availability effect provided by  
113             climate will be greater in these areas. Furthermore, greater changes in species  
114             composition along hydro-topographic gradient is expected in terrains with an ancient  
115             edaphic structure and well-dissected relief, such as in the Guiana Shield and Southern  
116             Amazon, compared to other regions of Amazonia with young edaphic structure and  
117             flatter topographies.
- 118         (c) Forests on soil with greater drainage capacity and less water availability will have a  
119             higher wood density.

120

## 121 **Methods**

### 122 **Vegetation data**

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



138

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

146

### 147 **Environmental variables**

148 To represent the hydro-topographic condition of each plot, we used the height above  
 149 the nearest drainage (HAND). HAND is calculated by normalizing the topography as a

150 function of the relative height over the nearest drainage, using information from digital  
151 elevation models (DEM). This variable is directly related to the gravitational potential of soil  
152 water and, therefore, its values are correlated with the water table depth, providing a  
153 representation of the local water conditions (Rennó *et al.*, 2008; Nobre *et al.*, 2011). High  
154 HAND values mean high drainage potential and low HAND values indicates proximity to  
155 the water table, where drained water accumulates and may create waterlogged conditions  
156 (Nobre *et al.*, 2011). We extracted HAND data from layers elaborated by Banon & Novo  
157 (2018) (available at: <http://www.dsr.inpe.br/amazondrainage/home.php?content=hand>) with  
158 ~30m x 30m spatial resolution. We reprojected the layers to ~100m x 100m resolution to  
159 correspond to the 1-ha plots using bilinear extraction. The HAND layer that we used in the  
160 analyses was based on Strahler's sixth order drainages, as it provides more stable information  
161 about the drainage capacity and the water condition of the environment across varying  
162 geomorphologies. Finally, HAND data was log-transformed (base 2) to meet normality  
163 assumptions.

164 The climatic information for each plot was represented by the historical average of  
165 its maximum accumulated water deficit (MCWD). MCWD is the measure of the annual water  
166 deficit that considers both the duration and the intensity of the dry season (Aragão *et al.*,  
167 2007). MCWD represents the most negative value of water deficit (WD), given by the  
168 difference between precipitation (P) and evapotranspiration (E) within each year, where for  
169 each month (n), WD is quantified as: *if*  $WD_{n-1} - E_n + P_n < 0$  ; then  $WD_n = WD_{n-1} -$   
170  $E_n + P_n$  ; *else*  $WD_n = 0$ . For this calculation, we considered the hydrological year, so the  
171 starting point is not necessarily the first month of the calendar year, but the wettest month (n-  
172 1) of the first year of the time series, according to calculations made by Esquivel-Muelbert  
173 *et al.*, (2019). The precipitation data was obtained from the TerraClimate platform  
174 (Abatzoglou *et al.*, 2018) with ~4 x 4 km spatial resolution from 1959 to 2018. We assumed  
175 the evapotranspiration to be fixed at 100 mm per month, being an approximation (mean) from  
176 soil evapotranspiration obtained in different locations in Amazonia (Aragão *et al.*, 2007).

177 We defined the soil fertility as the sum of the concentration of exchangeable cations  
178 (SCC, Na<sup>+</sup>, Mg<sup>+2</sup>, Ca<sup>+2</sup> and K<sup>+1</sup>), which is an indicator of soil fertility correlated with  
179 phosphorus availability (Figueiredo *et al.*, 2017; Moulatlet *et al.*, 2017; Quesada *et al.*, 2009).

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

183 The soil texture, which determines the water retention capacity of the soil (Hacke *et*  
184 *al.*, 2000), was represented by the percentages of sand and clay. We extracted soil texture  
185 data for a depth of 15 cm for each plot from the SoilGrids platform (Hengl *et al.*, 2017) with  
186 ~250 x 250 m spatial resolution.

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

## 201 **Vegetation metrics**

### 202 **Species diversity**

203 We quantified diversity for each plot using Fisher's Alpha, which is based on the  
204 number of individuals and species in each plot and is relatively insensitive to the difference

205 in the number of individuals among plots (Fisher, Corbet and Williams, 1943). We calculated  
206 Fisher's Alpha at the species, genus and family levels.

### 207 **Species composition**

208 To summarize the species composition, we used Non-Metric Multidimensional  
209 Scaling (NMDS) ordinations. We excluded species with less than two occurrences, to reduce  
210 the potential noise generated by the inclusion of rare species in the analysis (Cao and Larsen,  
211 2001; McCune and Grace, 2002). The final number of species and individuals included was  
212 2,417 and 206,459, respectively. We used three dimensions for the ordination to maintain  
213 stress  $< 2$  (McCune and Grace, 2002), and was based on the quantitative data using the Bray-  
214 Curtis distances, calculated on the data matrix standardized by plot. Standardization involves  
215 dividing the abundance of each species by the total abundance in each plot, in order to obtain  
216 the relative abundance of species in each plot (McCune and Grace, 2002). The ordination  
217 based on quantitative data allows capturing the patterns generated mainly by the most  
218 abundant species, which tend to have larger contributions to the difference or similarity  
219 between plots (Costa, Magnusson and Luizao, 2005; Costa *et al.*, 2009). The variation of the  
220 original data captured by the NMDS axes was obtained by regression of the matrix of original  
221 floristic distances among samples calculated with the same dissimilarity index used in the  
222 ordination method, and the matrix of distances among samples obtained from the final  
223 NMDS solution (McCune and Grace, 2002).

224 We quantified the differences in floristic composition among regions using  
225 PERMANOVA (Anderson, 2001), using 999 permutations on the original distance matrix  
226 given by the Bray-Curtis dissimilarity distance. This method tests whether plots from the  
227 same region are floristically more similar to each other than it would be expected by chance.  
228 We applied the PERMANOVA method using the *adonis* function from the *vegan* R package  
229 (Oksanen *et al.*, 2020). In addition, we quantified the floristic variability within each region  
230 using the multivariate dispersion method (Anderson, 2006). This method tests how  
231 floristically similar plots are to one another within each region. The multivariate dispersion  
232 method was applied using the *betadisper* function from the R package *vegan* (Oksanen *et al.*,  
233 2020) on the original distance matrix using the Bray-Curtis dissimilarity distances.

## 234 **Wood Density**

235           We obtained wood density data from the global wood density database (Chave *et al.*,  
236 2009, Zanne *et al.*, 2009) for the species considered in the species composition analyses.  
237 When the wood density of a species was not available, we used the mean wood density at the  
238 genus, family or plot level (Baker *et al.*, 2004; Rozendaal *et al.*, 2020). We used genus level  
239 wood density data for 1,381 species out of the 2,417 species, and family and plot level data  
240 for 170 and 10 species, respectively. Then, we calculated the community weighted mean  
241 (CWM) of each plot, which is the estimated mean wood density of the individuals in the plot  
242 (Garnier *et al.*, 2004).

243

## 244 **Data analyses**

### 245 **Species diversity**

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

## 264 **Species and functional composition**

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

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

285 The analyses were carried out in R (R version 4.0.2), using the *nlme* (Pinheiro *et al.*,  
286 2021) packages.

## 287 **Results**

### 288 **Tree diversity**

289         The species and genus diversity were significantly associated with the interaction  
290 between HAND and MCWD ( $P = 0.012$  and  $P = 0.004$ , respectively) and by the individual  
291 effect of MCWD ( $P = <.0001$ , species;  $P = <.0001$ , genus). Family diversity was influenced  
292 by the individual effect of MCWD ( $P = <.0001$ ) and soil fertility ( $P = 0.002$ ) (Table 1). The  
293 interaction between MCWD and HAND indicated that in wetter forests (MCWD between -  
294 136.7 mm and -1.60 mm, corresponding approximately to 1-2 dry months in the year, 222  
295 plots) the diversity of species and genera were higher in well-drained areas with deep water  
296 tables, such as the plateaus and hilltops (Fig. 2A, B, blue). However, in drier forests (MCWD  
297 between -429.6 mm and -138.0 mm, >2 dry months, 221 plots), there was a subtle tendency  
298 towards greater diversity in the zones with higher water availability and water table close to  
299 the surface, corresponding to bottomlands and riparian forests (Fig.2A, B, red). Although the  
300 interaction effect between MCWD and HAND was not significant at the family level ( $P =$   
301 0.173), the diversity patterns in relation to this interaction were similar to those observed for  
302 species and genus levels (Fig. 2C).

303         The diversity at all taxonomic levels evaluated was affected by MCWD, which  
304 always had the largest relative contribution in the models (Fig. 4 A - C). Diversity increased  
305 towards wetter forests, this relationship being more pronounced at the species and genus  
306 levels (Supporting information, Fig. S1). Soil fertility had a positive effect on species ( $P =$   
307 0.335) and genus diversity ( $P = 0.093$ ), but was more evident on family diversity (Fig. 4A –  
308 C, Table 1, Supporting information, Fig. S1). Soil texture did not contribute significantly at  
309 any taxonomic level (Table 1).

## 310 **Floristic composition**

311           The three-dimensional NMDS solution produced high congruence between species  
312 composition distances observed in the original space and those obtained in the reduced space  
313 (non-metric fit  $r^2 = 0.96$ , linear fit  $r^2 = 0.73$ ). The stress value was 0.19, and the variance  
314 captured by the three dimensions altogether was 56%. Floristic composition differed  
315 significantly among geological regions (PERMANOVA:  $P = 0.001$ ,  $R^2 = 0.10$ ). Furthermore,  
316 the multivariate dispersion method showed a greater variability in the floristic composition  
317 within Southern Amazonia, the Guiana Shield and Western Amazonia, which had a greater  
318 mean distances to the medians of the sets of plots (0.64, 0.62, 0.61, respectively). This  
319 variability was lower in Central and Eastern Amazonia (0.57) (Supporting information, Fig.  
320 S2).

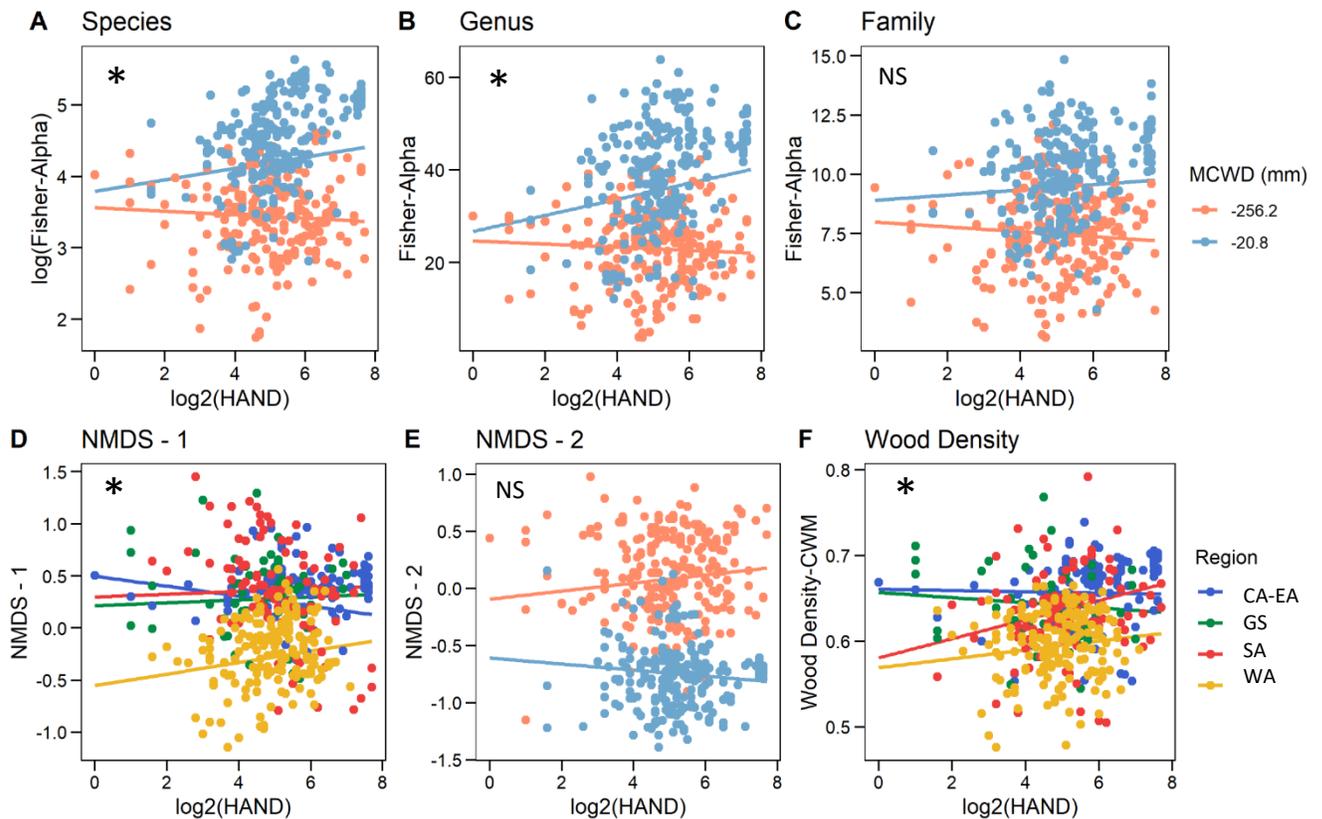
321           The first NMDS axis was influenced by HAND (Table 1), interacting with geological  
322 regions ( $P = 0.001$ ). This interaction indicated that species composition converged among  
323 regions in the upper topographic zones, with greater drainage capacity (higher HAND  
324 values), and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

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

#### 344 **Wood Density**

345 Wood density was influenced by interactions between HAND and geological regions  
346 ( $P = 0.03$ , Table 1). This interaction effect was more evident in Southern and Western  
347 Amazonian forests, indicating a higher wood density towards uplands and well-drained areas  
348 (Fig. 2F). Furthermore, the individual effect of HAND indicated an increase in wood density  
349 towards forests with greater soil drainage capacity (Fig. 4F, Supporting information, Fig. S5),  
350 but this effect was not statistically significant ( $P = 0.14$ ). Wood density was mainly  
351 influenced by the simple effects of soil fertility and geological regions (Fig. 4F), decreasing  
352 with soil fertility (Supporting information, Fig. S5). In addition, wood density was higher in  
353 Central, Eastern Amazonia and Guiana Shield forests, and lower in Southern and Western  
354 Amazonian forests, respectively (Supporting information, Fig S5). The effects of MCWD ( $P$   
355 = 0.81), soil texture (% sand,  $P = 0.63$ ; % clay,  $P = 0.2$ ) and the interactions of HAND with  
356 MCWD ( $P = 0.71$ ), were not significant.

357



358

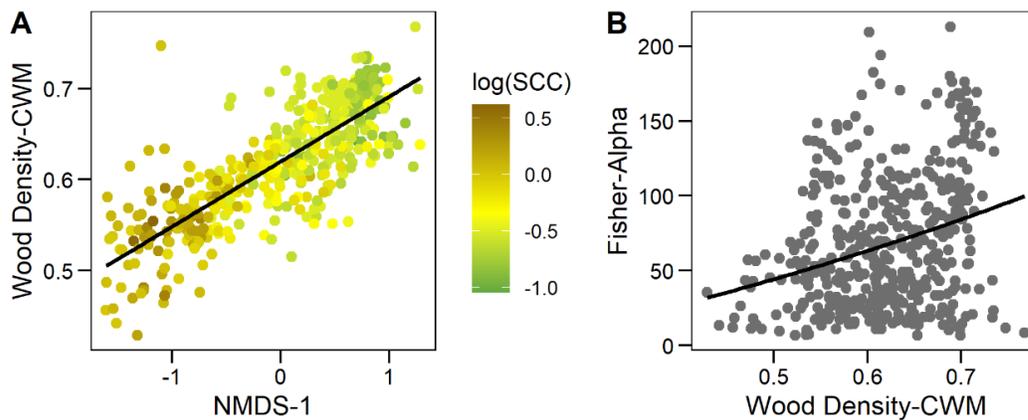
359 **Figure 2.** Partial effect of the interaction between HAND and MCWD on the species (A), genus (B),  
 360 and family diversity(C). Panels A-C show the HAND effect on wetter forests (blue) and drier forests  
 361 (red). MCWD = -256.2 (red), is the median MCWD value of the plots with the higher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

371

372 **Correlations between diversity, floristic composition and wood density**

373 The first NMDS ordination axis was strongly associated with wood density ( $\rho =$   
374  $0.80, P > 0.001$ ). This relationship indicates that along this axis, the species composition  
375 varies from forests with lower wood density in more fertile soils (more negative scores) to  
376 forests with higher wood density in poor soils (more positive scores) (Fig. 3A). The wood  
377 density also had a positive relationship with tree diversity ( $\rho = 0.26, P > 0.001$ ), where  
378 forests with higher wood density tend to have greater tree diversity (Fig. 3B). Furthermore,  
379 the tree diversity was related with the second NMDS ordination axis ( $\rho = -0.68, P > 0.001$ )  
380 (Supporting information, Table S3).

381



382

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

386

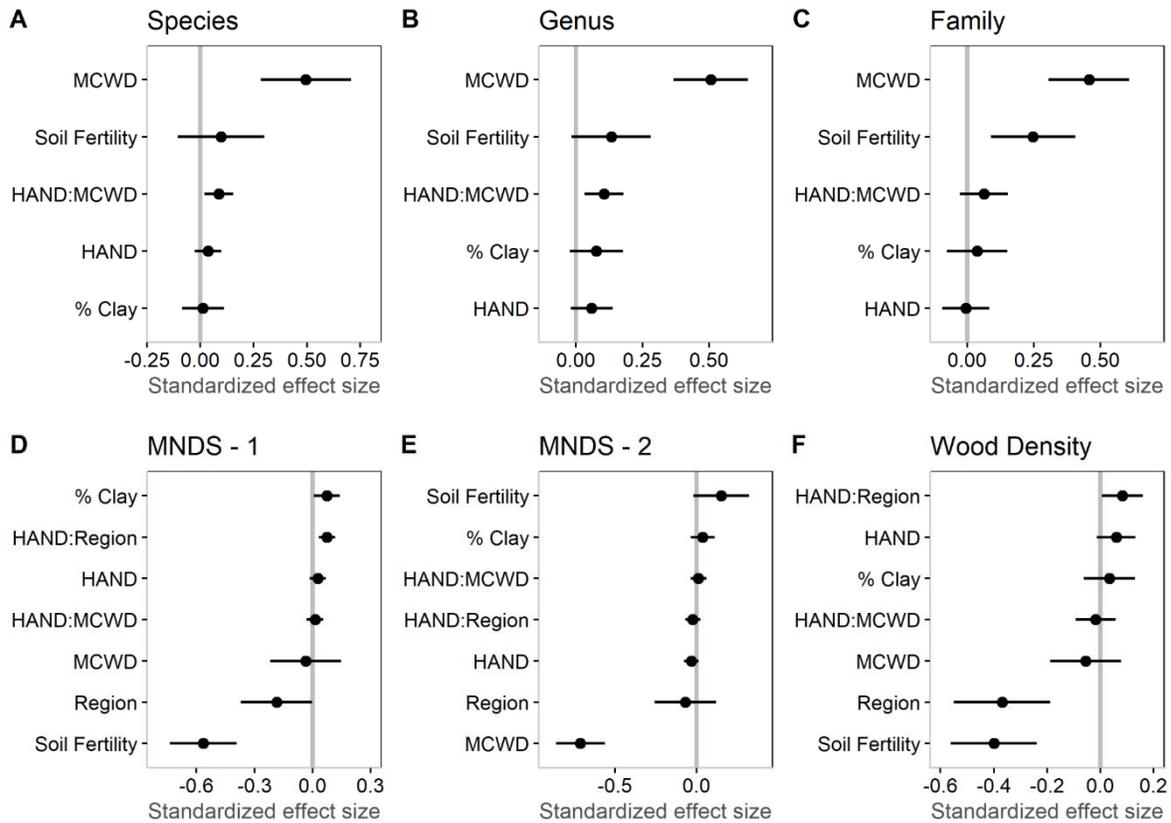
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393 **Figure 4.** Standardized effect of variables for the GLS models for diversity, floristic composition and  
394 wood density in the Amazon basin. Species (A), genus (B) and family (C) diversity were mainly  
395 influenced by MCWD. The higher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

406

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

	MCWD	HAND	Soil Fertility	% Clay	HAND:MCWD	Region	HAND:Region	R <sup>2</sup>
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

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

413

## 414 Discussion

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

427 Our results show the interaction between hydro-topographic conditions (HAND) and  
 428 climatic water deficit (MCWD) on species and genus diversity, which modifies the diversity  
 429 patterns previously described based only on climate. We showed that within wetter climatic  
 430 conditions, tree diversity can be either higher or lower depending on the hydro-topographic  
 431 conditions, and thus that fine-scale diversity patterns are also determined by soil water

432 availability, which has important implications to biodiversity conservation under climate  
433 change. In humid forests, the excess water generated by high precipitation and water  
434 convergence to the bottomlands, which have a lower drainage capacity given the shallow  
435 water table, generate poorly structured and water-saturated soils (Ferry *et al.*, 2010; Fan *et*  
436 *al.*, 2017; Roebroek *et al.*, 2020). These conditions can cause stress due to excess water,  
437 which leads to a reduction in oxygen (hypoxia or anoxia) (Araya, Gowing and Dise, 2013;  
438 Silvertown, Araya and Gowing, 2015; Roebroek *et al.*, 2020) and nitrogen in the soil (Ferry  
439 *et al.*, 2010; Araya, Gowing and Dise, 2013). These effects can decrease survival and inhibit  
440 the growth and development, especially of species that do not have specific adaptations in  
441 the root system, such as adventitious root structure or aerenchyma tissue (Parolin, 2001;  
442 Parolin *et al.*, 2004). Superficial and waterlogged soils also limit root depth (Fan *et al.*, 2017)  
443 and can limit the establishment and survival of trees without efficient attachment structures  
444 such as buttress or tabular roots that compensate for the absence of deep roots. Species that  
445 attain larger sizes would be especially unstable under these conditions (Wittmann and  
446 Parolin, 2005). Thus, the physical and physiological limitations for the establishment and  
447 performance of many species in waterlogged sites may filter out a small set of species,  
448 reducing tree diversity. On the other hand, waterlogged areas with superficial water table  
449 represent only ~36% of whole Amazonian basin (Fan and Miguez-Macho, 2010), so the  
450 lower diversity in these areas could also be a result of the reduced extent of these  
451 environments over a larger timescale (ter Steege *et al.*, 2000).

452         The effects of hydro-topographic conditions on tree diversity agree with an earlier  
453 study at small scale in Southwestern Amazonia, although the reported effect of the hydro-  
454 topographic conditions was not very pronounced (Féret and Asner, 2014). In Central  
455 Amazonia, Laurance *et al.*, (2010) found lower tree diversity in forests with sandy soils,  
456 which correspond to environments with a shallow water table in this region (Chauvel, Lucas  
457 and Boulet, 1987). Valencia *et al.*, (2004) reported a larger number of species in the lower  
458 lying areas, although the difference in diversity to the upper and well-drained areas was not  
459 significant. On the other hand, flooded forests show a pattern similar to that reported here,  
460 along the flooding gradient, with alpha diversity increasing towards lower levels of flooding  
461 (Wittmann *et al.*, 2006; Wittmann, Schöngart and Junk, 2010; Assis *et al.*, 2015). Due to the  
462 connection with terra-firme forests, environments with low levels of flooding in floodplains

463 and igapós can be colonized by terra-firme species adapted to some waterlogging, increasing  
464 their alpha diversity (Wittmann *et al.*, 2006, 2010). We conclude that the patterns of lower  
465 tree diversity associated with water excess, either due to flooding or shallow water table  
466 under wet climates, can now be generalized to the whole Amazon basin.

467 In forests with higher water deficit, lower topographic areas harbour a more equal  
468 complement of biological diversity to higher topographic areas than they do in wet forests.  
469 The higher soil water availability in topographic bottomlands (Oliveira-Filho *et al.*, 1998;  
470 Segura *et al.*, 2003; Balvanera *et al.*, 2011; Fan *et al.*, 2017), allows better establishment and  
471 greater plant diversity in forests in more seasonal climates, than on hilltops with deep water  
472 tables (Segura *et al.*, 2003). However, the higher dynamics in the higher and well-drained  
473 areas in drier climates (Segura *et al.*, 2003; Brando *et al.*, 2014; Marimon *et al.*, 2014;  
474 Johnson *et al.*, 2016) may also favour an increase in diversity (Connell, 1978; Bongers *et al.*,  
475 2009). Although our data does not allow us to determine whether these are in fact the  
476 mechanisms in action, the hypothesis that disturbances could be regulating the effect of  
477 hydro-topographic conditions on diversity in Amazonian forests with greater climatic water  
478 deficit could be tested in future studies.

479 Our results also showed a weak trend for an interaction effect between hydro-  
480 topographic conditions and climate on species composition change, generating opposite  
481 patterns between drier and wetter forests towards upland areas with well-drained soils (Fig.  
482 2E). Therefore, our results suggest that local hydro-topographic conditions can generate  
483 different responses of forests according to the climate context in the face of global warming  
484 and climate change in the largest tropical forests on the Earth.

485 Wood density tends to increase towards higher topographic positions, with better  
486 drained soils and deep water table, indicating that the effect of local hydro-topographic  
487 conditions is widespread over large extensions of the Amazon basin, especially in the  
488 Southern and Western Amazonian forests. The effect of hydro-topographic conditions on  
489 wood density at the Amazon basin scale is supported by earlier local scale studies done on  
490 different parts of Amazonia (Kraft, Valencia and Ackerly, 2008; Ferry *et al.*, 2010; Araujo-  
491 Murakami *et al.*, 2014; Cosme *et al.*, 2017) and on other biomes (Cornwell and Ackerly,  
492 2009; Liu, Yunhong and Slik, 2014; Jucker *et al.*, 2018; Blanchard *et al.*, 2019). At the same

493 time, in contrast to the studies of Chave *et al.*, (2006) and Ibanez *et al.*, (2017), we found that  
494 climate did not have a significant effect on wood density when other environmental factors  
495 are taken into account, which agrees with other studies of tropical and Amazonian forests  
496 (ter Steege and Hammond, 2001; Muller-Landau, 2004; Umaña *et al.*, 2021). Blanchard *et*  
497 *al.*, (2019) showed a larger effect of hydro-topographic conditions on wood density in drier  
498 than in wetter forests, but in the present study this dependence on the climatic context was  
499 not observed. High wood density tends to be associated with hydraulic safety and resistance  
500 to drought-induced embolism (Hacke *et al.*, 2001), but Southern Amazonian forests have  
501 relatively low wood density (Supporting information, Table S4) and suffer larger water  
502 deficits (Supporting information, Fig. S6), so it is likely that tree species of these drier forests,  
503 rather than investing in a higher wood density, have developed alternative strategies to deal  
504 with low water availability. These strategies may be related to root systems that can reach  
505 and absorb water from deeper soil layers (Fan *et al.*, 2017), smaller leaves (Wright *et al.*,  
506 2017), leaf deciduousness (Araujo-Murakami *et al.*, 2014; Blanchard *et al.*, 2019) or higher  
507 concentration of soluble sugars in the leaves (Signori-Müller *et al.*, 2021) that may favour  
508 osmoregulation.

509         The filtering of higher wood density in well-drained soils with a deep water table, and  
510 the opposite in wet conditions, is part of a broader selection of functional strategies along  
511 hydro-topographic gradients. Several local studies indicate the selection of functional  
512 characteristics by hydro-topographic conditions (Kraft, Valencia and Ackerly, 2008; Ferry *et*  
513 *al.*, 2010; Cosme *et al.*, 2017; Oliveira *et al.*, 2019; Fontes *et al.*, 2020; Schmitt *et al.*, 2020).  
514 In better drained areas, with lower water availability and deep water table, species converge  
515 towards more conservative traits related to resource use and conservation, with a reduced  
516 specific leaf area (SLA) and higher dry matter content (Kraft, Valencia and Ackerly, 2008;  
517 Liu, Yunhong and Slik, 2014; Cosme *et al.*, 2017; Schmitt *et al.*, 2020) and higher seed mass  
518 (Kraft *et al.*, 2008; Liu *et al.*, 2014), in addition to higher wood density. Furthermore, species  
519 from these zones have hydraulic systems with greater resistance to water stress and thus to  
520 drought events (Oliveira *et al.*, 2019; Fontes *et al.*, 2020). Root depth also increases with  
521 water table depth (Fan *et al.*, 2017). These trait strategies make communities less dynamics  
522 in the well-drained and deep water table environments (Ferry *et al.*, 2010; Toledo *et al.*,  
523 2012), which may lead to a lower variability in floristic composition than in low lying

524 environments, with lower drainage capacity and greater soil water availability (Schietti *et al.*,  
525 2013; Féret and Asner, 2014; Zuleta *et al.*, 2020).

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

549         On the other hand, the absence of an effect of the hydro-topographic conditions on  
550 floristic composition in the Southern Amazonia and in the Guiana Shield forests may be due  
551 to the fact that these regions present a greater variability in tree composition compared to  
552 other regions. This variability may be a result of short-distance variation in edaphic  
553 conditions (Sombroek, 2000; Quesada *et al.*, 2011) and, although soils in these regions are

554 formed from older substrates, they often have a low pedogenic development compared to the  
555 other regions (Quesada *et al.*, 2010). In Southern Amazonia, soil physical characteristics are  
556 similar along the hydro-topographic gradient, but some soils in the upper areas are shallow  
557 compared to soils in the lower areas (Araujo-Murakami *et al.*, 2014), which may limit root  
558 development (Fan *et al.*, 2017). Furthermore, although there is a marked difference in soil  
559 water availability between the lower and upper areas (Araujo-Murakami *et al.*, 2014), the  
560 high rate of dynamism experienced by forests in this region (Johnson *et al.*, 2016; Esquivel-  
561 Muelbert *et al.*, 2020) can lead to greater species composition variability, limiting the effect  
562 of local hydro-topographic conditions. The effect of hydro-topography on wood density in  
563 the Southern Amazonian forests may indicate that the change in functional composition along  
564 hydro-topographic gradients is not necessarily accompanied by a change in species  
565 composition in this region. In the case of the Guiana Shield, there are studies outside the  
566 limits of the Amazon basin that have demonstrated the effect of soil drainage conditions on  
567 local species distribution (ter Steege *et al.*, 1993; Sabatier *et al.*, 1997) and of hydro-  
568 topographic conditions on the dynamics of communities (Ferry *et al.*, 2010) and their  
569 functional traits (Schmitt *et al.*, 2020). However, in our case, the absence of a pattern in  
570 species composition change as a function of the hydro-topography observed may also have  
571 been influenced by the low representation of this region (52 plots) compared to the others  
572 (CA-EA = 122, SA = 102, WA = 167 plots).

573         Soil fertility had a strong influence in species composition and wood density, which  
574 agrees with previous studies carried out in tropical and Amazonian forests (Muller-Landau,  
575 2004; ter Steege *et al.*, 2006; Quesada *et al.*, 2012; Umaña *et al.*, 2021). Furthermore, soil  
576 fertility had a positive influence on tree diversity, but it was only significant at the family  
577 level. Local scale studies indicate that soil fertility can have both a positive (Tuomisto *et al.*,  
578 2002; Laurance *et al.*, 2010; Tuomisto, Zuquim and Cárdenas, 2014) and negative effect on  
579 plant diversity (Clinebell *et al.*, 1995). However, the effect of soil fertility may not  
580 necessarily be associated with resource availability (Clinebell *et al.*, 1995), but rather with  
581 the dynamics and intensity of disturbance in Amazonian forests, where greater soil fertility  
582 leads to selection of plants with short life cycle (e.g., species with lower wood density),  
583 generating a higher mortality and recruitment rates (Quesada *et al.*, 2012). However, other  
584 local scale studies indicate that disturbances negatively affect tree diversity (Marra *et al.*,

585 2014), or simply have no measurable effect (Carreño-Rocabado *et al.*, 2012). Our results are  
586 in agreement with previous large-scale studies of tropical (Phillips *et al.*, 1994) and Amazon  
587 forests (Baker *et al.*, 2016), where disturbances are associated with a higher tree diversity,  
588 although in our results that was more evident at the family level.

### 589 **Limitations of this study**

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

### 603 **Conclusions**

604         At the Amazon basin scale, we have shown that the effect of hydro-topographic  
605 conditions on tree diversity depends on the climate context. Furthermore, the influence of  
606 hydro-topographic conditions on the functional and floristic composition is generalized and  
607 is given according to the edaphic and geomorphological conditions of the Amazon regions.  
608 These findings reinforce the importance of hydro-topographic factors as determinants of  
609 plant communities at large scales. Considering that most Neotropical forests species are  
610 restricted to wetter conditions (Esquivel-Muelbert *et al.*, 2017), climatic events such as  
611 extreme droughts that have been more frequent in recent decades (Marengo *et al.*, 2018), can  
612 be a serious threat to the diversity and functioning of the most diverse forests on the planet.  
613 In future scenarios of increase of global temperature and reduction of water availability  
614 (IPCC 2021), topographic and hydrological conditions can play an important role in the

615 ecology and distribution of plants. Low topographic environments with a shallow water table  
616 can reduce the impact of extreme climatic events (Esteban et al., 2020; Schwartz et al., 2020;  
617 Sousa et al., 2020), being potential refuges for diversity (McLaughlin et al., 2017). Therefore,  
618 it is important to consider the hydro-topographic conditions in modelling studies of species  
619 distribution and forecasting the fate of forests under climate change, to allow the promotion  
620 of socio-political strategies of conservation and sustainable use of forests.

621

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630

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985

986 **Supporting Information**

987 **Supplementary tables**

988 **Supplementary table 1.** 1-ha Plots that were excluded for having less than 30 species.  
989 *Tabebuia aurea* (Bignoniaceae), which is a typical species of transitional forests, has a high  
990 abundance in BENI\_04 (318 individuals) and BENI\_06 (115). Furthermore, *Machaerium hirtum*  
991 (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

992

**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  $\Delta$  AIC.

<b>DIVERSITY</b>			
Variance Models	Variance Structure	AIC	$\Delta$ 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	<b>varExp(MCWD)</b>	<b>4244.00</b>	<b>0.00</b>
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	$\Delta$ AIC
Fisher sp ~ MCWD + HAND + Fertility	<b>Exp</b>	<b>460.59</b>	<b>0.00</b>
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
<b>SPECIES COMPOSITION</b>			
Autocorrelation Models	AutoCorStruct	AIC	$\Delta$ AIC
NMDS ~ MCWD + Fertility + Region	<b>Exp</b>	<b>400.68</b>	<b>0</b>
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
<b>WOOD DENSITY</b>			
Autocorrelation Models	AutoCorStruct	AIC	$\Delta$ AIC
WD-cwm~MCWD + Fertility + Region	<b>Exp</b>	<b>-1639.85</b>	<b>0</b>
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

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**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
<b>Fisher Alpha</b>	1.00	–	<b>0.26</b>	0.00	0.20	0.00	<b>0.68</b>	0.00	<b>0.30</b>	0.00
<b>Wood Density</b>	0.26	0.00	1.00	–	<b>0.80</b>	0.00	0.04	0.38	0.13	0.00
<b>NMDS-1</b>	0.20	0.00	0.80	0.00	1.00	–	0.02	0.68	0.04	0.42
<b>NMDS-2</b>	0.68	0.00	0.04	0.38	0.02	0.68	1.00	–	0.05	0.34
<b>NMDS-3</b>	0.30	0.00	0.13	0.00	0.04	0.42	0.05	0.34	1.00	–

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

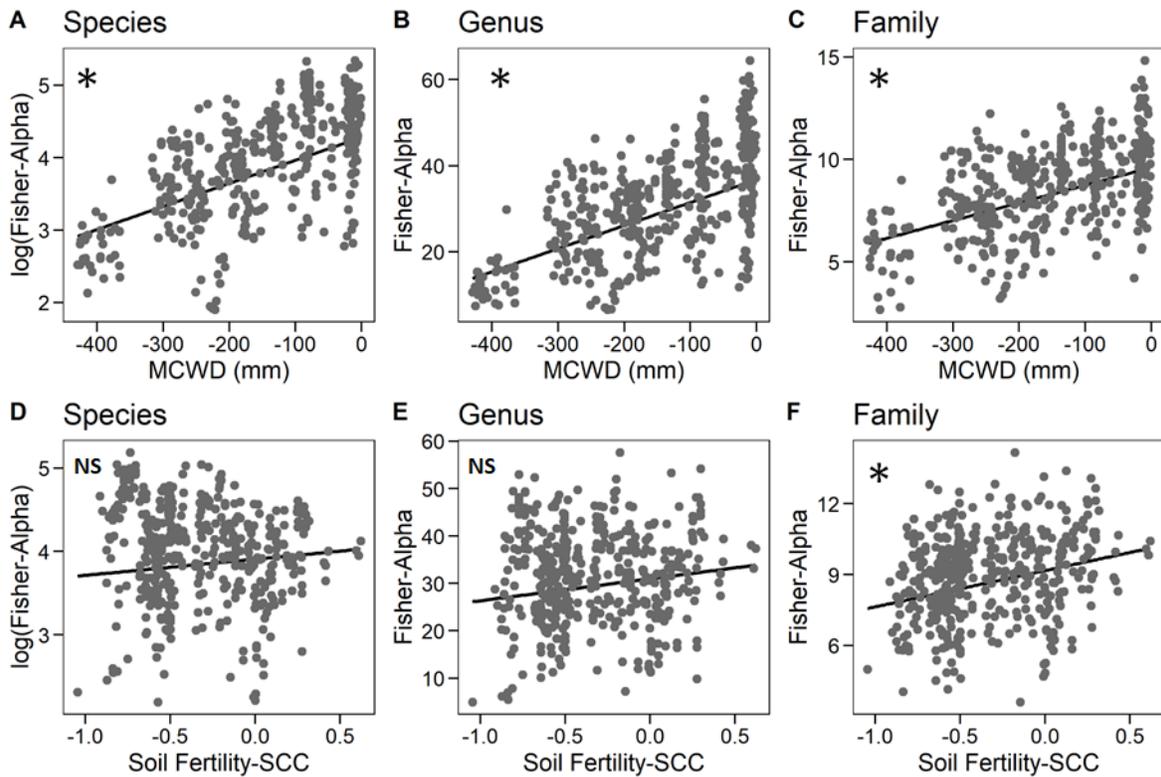
Geological Regions	N	Species Composition	Wood Density	
		Mean multivariate dispersal	Mean	SE
East-Central Amazon	122	0.57	0.675	± 0.003
Guiana Shield	52	0.62	0.655	± 0.006
South Amazon	102	0.64	0.618	± 0.005
Western Amazon	167	0.61	0.569	± 0.004

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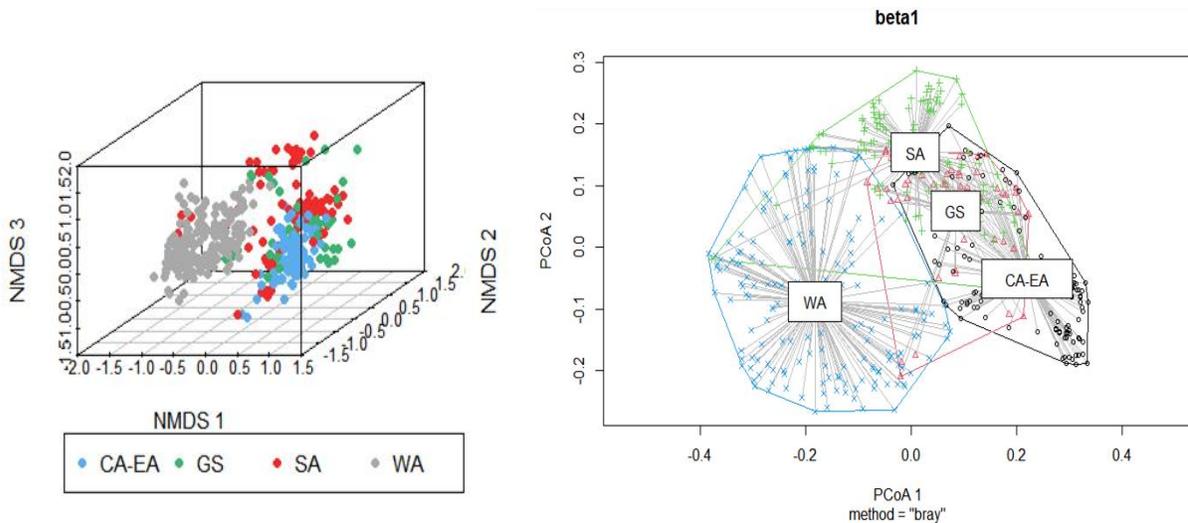
1002 **Supplementary figures**

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**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.



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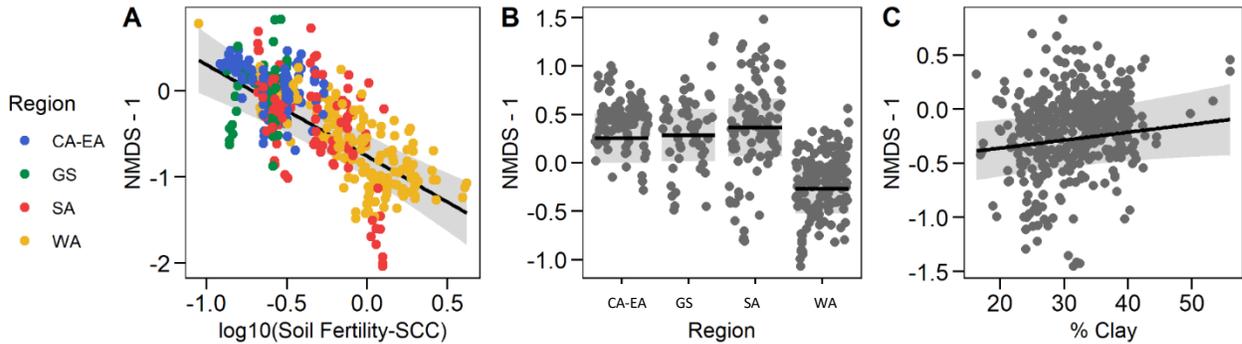
**Figure S2.** 3D plot of the three ordination axes (left) used in the GLS models. (right) Dispersion plot based on the first two PCoA axes used in the dispersion analyses. The first axis of the PCoA represents 16% of the data variation, and the second axis represents 9%. The PCoA method was used only for

1014 the multivariate dispersion analysis which was incorporated into the *betadisper* function of the *Vegan*  
1015 package. The Bray-Curtis dissimilarity distance was used.

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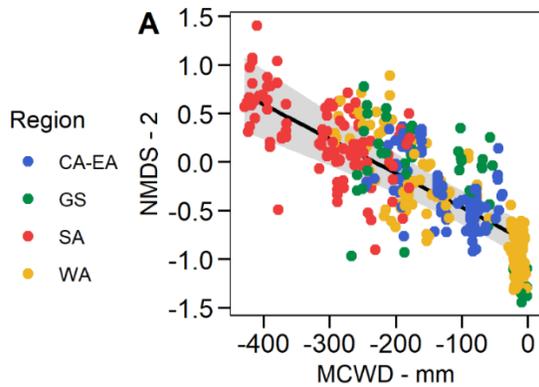
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1021 **Figure S3.** Significant partial effect of soil fertility (A), geological regions (B) and clay content (C)  
1022 on the first ordination axis of the species composition for the GLS model, considering an Exponential  
1023 spatial autocorrelation structure. Central-Eastern Amazonia (CA-EA), Guiana Shield (GS), Southern  
1024 Amazonia (SA) and Western Amazonia (WA).

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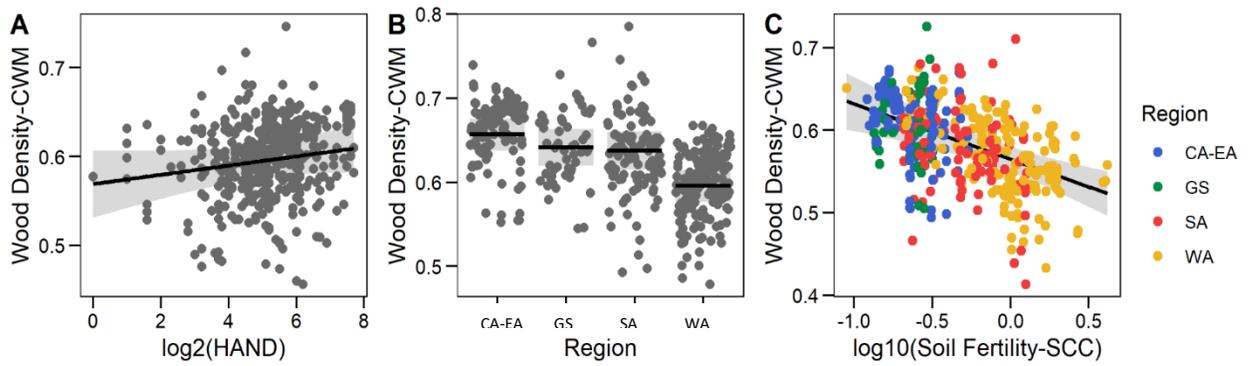
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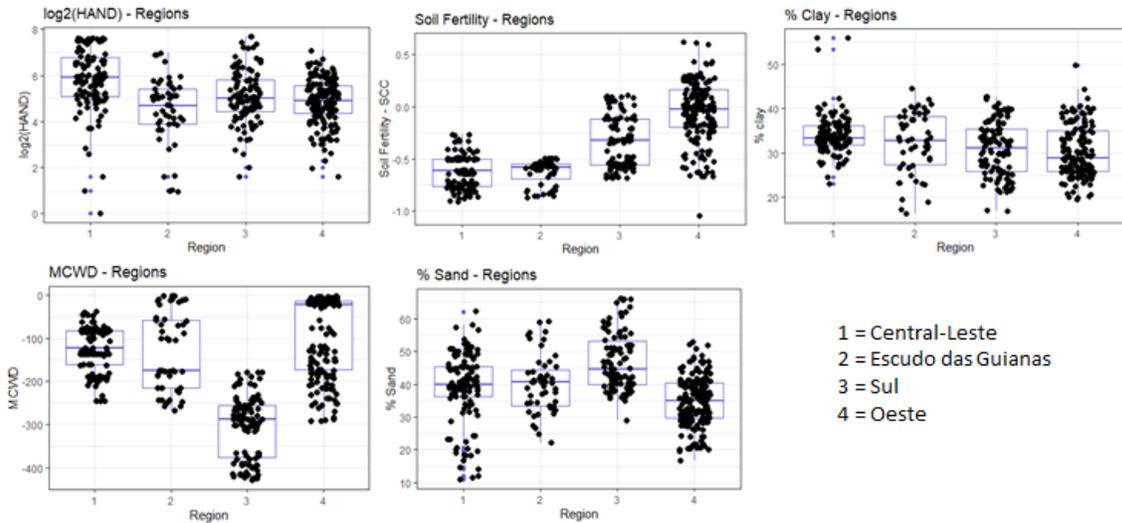
1029 **Figure S4.** Significant partial effect of MCWD on the second ordination axis for the GLS model,  
1030 considering an exponential spatial autocorrelation structure. Central-Eastern Amazonia (CA-EA),  
1031 Guiana Shield (GS), Southern Amazonia (SA) and Western Amazonia (WA).

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**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).



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**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

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1048           Na escala da bacia Amazônica, nós mostramos que o efeito das condições hidro-  
1049 topográficas na diversidade arbórea depende do contexto climático. Ademais, a influência  
1050 das condições hidro-topográficas na composição florística e funcional é generalizada e está  
1051 dada de acordo às condições edáficas e geomorfológicas das regiões amazônicas. Estes  
1052 achados reforçam a importância dos fatores hidro-topográficos nas comunidades de plantas  
1053 em grande escala. Considerando que a maioria das espécies das florestas Neotropicais estão  
1054 restritas a condições muito úmidas (Esquivel-Muelbert *et al.*, 2017), eventos climáticos como  
1055 as secas extremas estão sendo mais frequentes nas últimas décadas (Marengo *et al.*, 2018),  
1056 podem ser uma séria ameaça para a diversidade e o funcionamento das florestas mais diversas  
1057 do planeta. Em cenários de aumento da temperatura global e redução da disponibilidade de  
1058 água (IPCC 2021), condições topográficas e hidrológicas podem cumprir um papel  
1059 importante na ecologia e na distribuição das plantas. Ambientes topográficos baixos, com  
1060 lençol freático superficial podem reduzir o impacto de eventos climáticos extremos  
1061 relacionados com as secas (Esteban *et al.*, 2020; Schwartz *et al.*, 2020; Sousa *et al.*, 2020),  
1062 sendo potenciais refúgios para a diversidade (McLaughlin *et al.*, 2017). Portanto, é  
1063 importante considerar as condições hidro-topográficas nos estudos de modelagem de  
1064 distribuição de espécies e na previsão do destino das florestas sob cenários de mudanças  
1065 climáticas para permitir a promoção de estratégias sociopolíticas de conservação e uso  
1066 sustentável das florestas.

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