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EFEITO DA RESISTENCIA À CAVITAÇÃO NA MORTALIDADE DE ARVORES DA AMAZÔNIA CENTRAL

EDHER CHECA CORDOBA

Manaus, Amazonas

Abril, 2018

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EFEITO DA RESISTENCIA À CAVITAÇÃO NA MORTALIDADE DE ARVORES DA AMAZÔNIA CENTRAL

Orientadora: Dra. Flávia Regina Capellotto Costa

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do o título de Mestre em Ciências Biológicas (Botânica).

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Manaus, Amazonas

Abril, 2018

Sinopse:

Relacionamos menor resistência a cavitação (menor P50) e outros rasgos hidráulicos do caule e folha na mortalidade de arvores jovens, que se distribuem em duas topografias contrastantes de disponibilidade hídrica localizado na Reserva Forestal Adolpho Ducke, município de Manaus- AM. Avaliamos a capacidade de predição de estas características hidráulicas na mortalidade de arvores. E determinamos os rasgos hidráulicos que se correlacionam significativamente com menor resistência a cavitação.

Palavras-chave: Cavitação, Rasgos hidráulicos, Mortalidade, Gradiente hidro-edáfico, Seca natural.

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Manaus (AM), 25 de abril de 2018.

OBS:_____

John Gilbert Hopkins
Coordenador do Programa de
Pós-Graduação em Botânica
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Nada mais havendo, foi lavrado a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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RESUMO

Os eventos extremos causados estão sendo cada vez mais frequente e intensos a nível mundial. Especialmente para Amazônia, os episódios de seca são cada vez mais frequentes variando em intensidade, com efeito no incremento da mortalidade de arvores na última década. Portanto, o interesse nos últimos anos é compreender os mecanismos de mortalidade das arvores através das caraterísticas funcionais, que permitiram predizer o nível de vulnerabilidade das espécies a estes eventos climáticos extremos. Esta pesquisa tem como objetivo, determinar o efeito da menor resistência a cavitação (menor P50) na mortalidade de arvores da Amazônia Central. A hipótese central é que as características da arquitetura hidráulica das árvores afetam suas taxas de mortalidade, e que estes efeitos dependem do ambiente hídrico ao qual a espécie está associada. Espera-se que as condições de solo sejam fatores determinantes desta performance, através dos gradientes de disponibilidade hídrica. O estudo foi desenvolvido na Reserva Forestal Adolpho Ducke, caraterizada como floresta de terra firme, apresentando ambientes de condições hidro edáficas contrastantes de platô e baixio. Foram amostradas 28 espécies, e realizamos medições das caraterísticas anatômicas de caule (diâmetro e densidade de vaso, comprimento da parede inter-vasos, percentual de agrupamento dos vasos) e folhas (comprimento e densidade dos estomas, e densidade de venação). Para 18 espécies com dados de resistência a cavitação, foram estimadas as taxas de mortalidade de arvores jovens (<10 cm DAP) entre os períodos 2001-2016. Encontramos que o menor P50 se relaciona com maior mortalidade de arvores jovens em ambientes de platô. A caraterística anatômica que predizem melhor a mortalidade de arvores foi o maior percentual de agrupamento de vasos. Menor P50 se correlaciono positivamente com rasgos de maior agrupamento dos vasos e comprimento da parede inter-vasos, que estão ligados à maior eficiência na condutividade hídrica, deteriorando à seguridade no transporte hídrico. Nosso resultado é considerado o primeiro registro do efeito do menor P50 na mortalidade de arvores jovens sob secas naturais em ambientes de platô, o qual sugere o importante efeito este ambiente como filtro na supervivência das arvores. As caraterísticas anatômicas da caule foram melhores preditores da alta mortalidade de arvores, comparada as de folha. As quais se correlacionam significativamente com menor resistência a cavitação, favorecendo a hipóteses de semeadura do ar, que estabelece que a maior conectividade entre os vasos, facilita a propagação da cavitação entre as pontuações de membrana. Consideramos estes resultados são importantes para entender as interações entre as condições hidro edáficas e os arvores, e como está dinâmica reflete na mudança da estrutura e composição das florestas, sob condições de eventos climáticos extremos futuros.

ABSTRACT

Extreme weather events are becoming more frequent and intense worldwide. Especially for Amazonia, drought episodes are increasingly frequent, varying in intensity, with an effect of increasing tree mortality in the last decade. Therefore, the interest in recent years is to understand the mechanisms of tree mortality through functional characteristics, which allowed predicting the level of vulnerability of species to these extreme weather events. This research aims to determine the effect of lower cavitation resistance (lower P50) on tree mortality in Central Amazonia. The central hypothesis is that the characteristics of trees' hydraulic architecture affect their mortality rates and that these effects depend on the water environment with which the species is associated. Soil conditions are expected to be determinant factors of this performance through the water availability gradients. The study was developed in the Adolpho Ducke Forestal Reserve, characterized as terra firme forest, with contrasting hydro-edaphic plateau and shoal environments. Twenty-eight species were sampled, and we performed measurements of stem anatomical characteristics (vessel diameter and density, inter vessel wall length, vessel cluster percentage) and leaves (stoma length and density, and venation density). For 18 species with cavitation resistance data, the mortality rates of trees juveniles (<10 cm DBH) were estimated between the periods 2001-2016. We found that the lowest P50 is related to higher mortality of trees juveniles in plateau environments. The anatomical characteristic that best-predicted tree mortality was the highest percentage of vessel grouping. Smaller P50 correlates positively with features of greater vessel grouping and inter-vessel wall length, which are linked to greater efficiency in water conductivity, deteriorating water transport safety. Our result is considered the first record of the effect of lower P50 on the mortality of trees juveniles under natural drought in plateau environments, which suggests the important effect of this environment as a filter on tree survival. The anatomical characteristics of the stem were better predictors of the high tree mortality compared to the leaf. These correlate significantly with lower cavitation resistance, favoring the air seeding hypothesis, which establishes that the greater connectivity between vessels facilitates the propagation of cavitation between membrane scores. We consider these results to be important for understanding the interactions between water and soil conditions, and how these dynamics reflect changes in the structure and composition of forests under conditions of future extreme weather events.

SUMARIO

INTRODUÇAO

Na atualidade os eventos climáticos extremos são cada vez mais frequentes e intensos na região da Amazônia central, com aumento de temperaturas e mudanças nas precipitações (Levine *et al.* 2016), afetando a disponibilidade da água no solo e a demanda de evaporação atmosférica (Martinez *et al.* 2014). Estes eventos de seca mais prolongados no tempo têm impulsado mudanças rápidas em diferentes escalas na estrutura e composição das florestas (Allen *et al.* 2010, Pivovaroff *et al.* 2015).

As caraterísticas hidráulicas e as respostas fisiológicas das plantas vão ser mediadoras de sua vulnerabilidade aos eventos de seca, dado o potencial de falhas no transporte da água no *continuo solo-planta-atmosfera* (*SPAC*) (Zach *et al.* 2010, Meinzer *et al.* 2001, Brodribb *et al.* 2010). Portanto, é fundamental entender as razões que levam às diferenças na sensibilidade à cavitar, essa cavitação que se define como ao presencia de de ar que se podem expandir devido as pressões negativas nos vasos do xilema, o que leva a inutilização destes vasos (embolismo) entre as espécies, do ponto de vista anatômico e hidráulico, o que afeta sua performance ecológica no ambiente (Markesteijn *et al.* 2011).

A arquitetura hidráulica das plantas se define como a estrutura e funcionamento dos tecidos do xilema desde raízes até folhas, que trabalham em conjunto para absorção da água, suas formas de movimentação respondendo a gradientes de pressão negativa, processos de condutividade estomática e transpiração (Hacke & Sperry, 2001, Loepfe *et al.* 2007, Ayup *et al.* 2012). Vários elementos compõe a arquitetura hidráulica das plantas, e afetam seu grau de sensibilidade à cavitação no transporte da água. Tem-se documentado que plantas com menor sensibilidade a cavitar ou mais tolerantes à seca tem caraterísticas gerais como maior densidade da madeira, maior comprimento dos vasos, menor diâmetro dos vasos, placas de perfuração reticulada, maior conteúdo de matéria seca foliar, folhas pequenas e maior controle da condutância estomática (Sherwin *et al.* 1998, Markesteijn *et al.* 2009, Iogna *et al.* 2011, Vinya *et al.* 2013, Jansen & Schenk 2015, Schenk *et al.* 2015)

Em geral estas caraterísticas são adaptações das plantas em direção à uma arquitetura hidráulica eficiente, mas ao mesmo tempo segura, já que as plantas terrestres perdem grandes quantidades de água através de seus estômatos, os quais ficam abertos para permitir a entrada de carbono. Esta perda de água na forma de vapor (transpiração) pode gerar eventos de estresse hídrico, se a perda não estiver em equilíbrio com a água absorvida pelas raízes, o que pode afetar sua

sobrevivência (Brodribb 2009, Manzoni *et al.* 2013). Sendo assim, as plantas terrestres têm que conseguir uma máxima eficiência hidráulica e ao mesmo tempo prevenir processos de cavitação, o que não se consegue de forma independente, e implica em um *trade-off* das características dos tecidos entre eficiência e segurança (Loepfe *et al.* 2007, Lopez *et al.* 2013). Gleason *et al.* (2015), corroborou este *trade-off* usando metadados de angiospermas e gimnospermas, ao não encontrar espécies com alta segurança e eficiência ao mesmo tempo. Poorter *et al.* (2009) e Markesteijn *et al.* (2011) também encontraram um forte *trade-off* entre vulnerabilidade a cavitar e eficiência hidráulica, refletido no tamanho e número de vasos em espécies de bosques secos e úmidos tropicais.

Estudos da distribuição das plantas tropicais tem mostrado fortes associações com a disponibilidade da água. Por exemplo, os estudos de Engelbrecht & Kursar (2003) e Engelbrecht *et al.* (2007), mostram que as espécies arbustivas e árvores que demostraram alta sensibilidade à seca em experimentos de campo, se distribuem com mais frequência em condições maiores taxas de pluviosidade ao longo de um gradiente climático. Por outro lado, temos as espécies associadas a condições secas, que desenvolveram diferentes estratégias de resistência e tolerância, como a absorção da água que se encontra em camadas profundas do solo, com um incremento da alocação de biomassa para a construção de raízes mais profundas, ao mesmo tempo troncos mais densos, com maiores comprimentos e menor diâmetro dos vasos, sendo mais seguros no transporte da água. Além disso, as folhas das espécies resistentes à secas tendem a ser menores e densas (algumas com comportamento caducifólio), e apresentam maior controle estomático e altas taxas fotossintéticas (Markesteijn & Poorter 2009, Vinya *et al.* 2013, Chmura *et al.* 2016).

Neste estudo, nosso objetivo é determinar o efeito da resistencia a cavitação na mortalidade de árvores em estado juvenil da Amazônia central. A hipótese central é que as características da arquitetura hidráulica das árvores afetam as taxas mortalidade, e que estes efeitos dependem do ambiente hídrico ao qual a espécie está associada. Espera-se que as condições de solo sejam fatores determinantes desta performance, através dos gradientes de disponibilidade hídrica. (Ernst 1990, Blom & Voesenek 1996, Razi & Mohd 1996, Schietti *et al.* 2013).

OBJETIVOS

Geral

Determinar o efeito da menor resistência a cavitação (menor negativo P50) na mortalidade de árvores na Amazônia central

Específicos

- Determinar o efeito da menor resistência a cavitação (menor negativo P50) na mortalidade de árvores jovens e como muda ao longo das condições hidro edáficas numa floresta de terra firme.

- Avaliar as relações das caraterísticas anatômicas e hidráulica na mortalidade de arvores jovens na Amazônia Central

- Determinar a relação das características anatômicas do caule e da folha com menor resistência à cavitação (menor negativo P50) em árvores de uma floresta da Amazônia central.

Capítulo 1

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Edher C. Cordoba, Rafael S. Oliveira, Lourens Poorter & Flávia R. C. Costa. (2018). Cavitation vulnerability and local hydrological environment together control drought-related tree mortality in Amazonia. *Plant, Cell & Env.*

Title page:

(i)Title: Cavitation vulnerability and local hydrological environment together control drought-related tree mortality in Amazonia

(ii) Authors: Edher Checa Cordoba[1], Rafael Oliveira[2], Lourens Poorter[3] ,Flavia R.C. Costa[4],

(iii)[1] Programa de Pós-graduação em Botânica, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. Ephigênio Sales 2239, 69060-20 Manaus, AM, Brazil. [2] Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas 13083-862, Brazil. [3]Forest Ecology and Forest Management Group, Wageningen University and Research, P.O. Box 47, 6700 AA Wageningen, the Netherlands. [4] Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. Ephigênio Sales 2239, 69060-20 Manaus, AM, Brazil.

(iv) Edher Checa Cordoba, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. Ephigênio Sales 2239, 69060-20 Manaus, echeca@uniamazonia.edu.co.

Abstract

Tree mortality is increasing under climate change, but is not fully understood. Increasing drought in Amazonia suggests that hydraulic traits should mediate tree response to climate change.

Here we tested whether hydraulic traits can predict tree mortality in central Amazonia, across contrasting hydrological environments previously shown to be associated with tree hydraulic vulnerability. We measured eight hydraulic traits of small individuals (<10cm DAP) of 28 tree species associated with either Shallow Water Table forests (SWTF) on valleys or deepWTF on plateaus of a terra-firme forest, and their mortality rates from 2001 to 2016.

P50 was the best predictor of mortality, with less negative P50 associated to high mortality within the more water-limited plateaus. Percentage of vessel grouping (VG) was the best anatomical predictor of mortality. VG and inter-vessel wall length were both related to lower resistance to cavitation, favoring the "pit-rare" hypothesis.

Hydraulic traits alone were not sufficient to predict mortality drought-responses to the same climate perturbations across environments, because local hydrological environment mediates the effect of droughts. Trees with more vulnerable traits were not vulnerable to droughts in SWTF where more available water buffered drought response. We conclude that accounting for hydrological environments is critical for assessing the future of forests under climate change.

Key-words: drought, mortality, cavitation vulnerability, hydro-topographic environments, hydraulics traits, Amazonian forest,

Introduction

Tree mortality induced by droughts has been increasing in recent decades (Anderegg *et al.* 2016, McDowell *et al.* 2018) , affecting the structure and composition of forests at different scales (Allen *et al.* 2010, Williams *et al.* 2013 , Pivovaroff *et al.* 2016). In the Amazon, droughts became increasingly frequent, with different levels of severity, leading sometimes to intense tree mortality (Phillips *et al.* 2010, Lewis, Brando, Phillips, Van Der Heijden & Nepstad 2011). The degree to which this reported sensitivity of the Amazon to drought-induced mortality is general is not yet resolved, due to the use of indirect climatic proxies, soft traits, individual analyzes of hard traits (Wright *et al.* 2010, Rowland *et al.* 2015, Esquivel-Muelbert *et al.* 2017) and lack of coverage of the wide variation in hydrological environments of the Amazon. Sensitivity to drought may not depend only on climate, but on the mean hydraulic traits of species of each site, on the local

hydrological properties of soils or an interaction of both, and this perspective is currently lacking.

At the local scale, topography defines hydrological environments ranging from waterlogged to seasonally dry (Hodnett, Vendrame, De O. Marques Filho, Oyama & Tomasella 1997). These filter the composition of species (Schietti *et al.* 2014) and their hydraulic traits (Cosme, Schietti, Costa & Oliveira 2017, Oliveira *et al.* 2018) and can modulate the effect of atmospheric droughts on vegetation. It can be expected that trees in the shallow water-table forests on valleys are more sensitive to droughts given their lower resistance to cavitation (Cosme *et al.* 2017 Oliveira *et al.* 2018), but at the same time, the permanently high levels of the water table in the valleys (Hodnett *et al.* 1997), could dampen the negative effect of atmospheric droughts on trees. Here we investigate how the mortality rates of trees vary across local hydrological environments (deepWTF on plateaus x ShallowWTF on valleys) within the same climatic regime, according to the hydraulic features of the species. We suggest that it is the interaction of hydraulic traits and local hydrological environments that controls the outcome of droughts.

Recent studies postulate that drought mortality is driven by hydraulic failure (Rowland *et al.* 2015 , Anderegg *et al.* 2016) caused by cavitation, which occurs by the seeding of air bubbles in the xylem vessels under conditions of high water stress (Tyree & Sperry 1988, Tyree & Sperry 2002, Schenk, Steppe & Jansen 2015), irreversibly interrupting the transport of water and its supply to the leaves (Tyree & Sperry, 1988, McDowell *et al.* 2008). The resistance to cavitation, estimated as P50, indicates the water potential at which 50% of the water's conductivity is lost (Anderegg *et al.* 2015). P50 has been used as an indicator of resistance to cavitation at the local, regional and global levels (Maherali, Pockman & Jackson 2004, Rowland *et al.* 2015, Oliveira *et al.* 2018), and it is potentially relevant for the modeling of forest mortality in recent decades (Hoffmann, Marchin, Abit & Lau 2011, Nardini, Battistuzzo & Savi 2013).

Besides P50, other characteristics of the hydraulic architecture can affect the resistance of species to drought (Mencuccini, Minunno, Salmon, Martínez-Vilalta & Höltta 2015, Venturas, Sperry & Hacke 2017). The association of wide vessels, larger pit membrane pores, higher density of pit membranes between vessels and lower wood density improve the efficiency of water conduction, but are linked to thin cell walls and greater seeding of air bubbles, which increase the risk of losing functionality when the negative pressure in the vessel increases (Baas *et al.* 2004, Wheeler, Sperry, Hacke & Hoang 2005, Choat, Cobb & Jansen 2008, Poorter *et al.* 2010). Different morphological, anatomical and hydraulic traits have been used as predictors of drought induced tree mortality in different biomes (Chave *et al.* 2009, Russo *et al.* 2010, Wright *et al.* 2010), but the comprehension of the relationships between hydraulic traits, physiology and the mechanisms of tropical tree mortality is still weak, which makes the prediction of the effects of a

rapidly changing climate uncertain (Markesteijn, Poorter, Paz, Sack & Bongers 2011, Anderegg *et al.* 2016, O'Brien *et al.* 2017). Moreover, measurements of P50 are laborious and time consuming, it would be possible to more widely rank species according to their drought vulnerability if easier to measure traits were available. Anatomical traits related to hydraulics have the potential to achieve that. We thus here evaluate how different anatomical traits of leaf and stem and P50 correlate among themselves and determine their relative ability to predict juvenile tree mortality rates.

We propose as a central hypothesis that the characteristics of the hydraulic architecture of trees affect their mortality rates and that these effects depend on the local hydrological environment to which the species is associated. Because the shallow WTF on valleys have a constantly high soil moisture, we expect that resistance to cavitation is less relevant to explain mortality in this environment. We also expect that values of anatomical traits theoretically associated with greater hydraulic efficiency (greater diameter of the vessel, greater grouping of vessels, greater stomatal length and lower density of venation) are correlated with lower resistance to cavitation and a higher mortality rate.

Materials and methods

Study area

The study was conducted in the Ducke Forest Reserve, a 10,000 ha terra-firme forest managed by the Amazon Research Institute (INPA), located in the outskirts of the city of Manaus, Amazonas, Brazil (2 ° 55 'S, 59 ° 59' W). The forest has a closed canopy of 30-37 m (Ribeiro *et al.* 1999). Average temperature is 26 °C with a minimum of 19 and maximum of 39 o C. Mean annual precipitation is ~2200 mm (range 1900 - 3300 mm) with a wet season from November to June and months of the dry season from July to September, with generally less than 100 mm of rain per month (Satyamurty, De Castro, Tota, Da Silva Gularte & Manzi 2010). The topography of the reserve is undulated with a dense drainage network, giving raise to plateaus dissected by small streams and their valleys, with an average height difference of about 30 m (Ribeiro *et al.* 1999). In the valleys, the water table is around 0 to 2 m deep year-round (Hodnett et al. xxx), while in plateaus and hillslopes it is under 20 m (Schietti et al. 2014). Clay content is higher in the plateaus and sand content increases in the valleys (Luizao *et al.* 2004). These soils are acidic and poor in phosphorus, calcium, magnesium, sodium and potassium, and in general the aluminum content is high (Ribeiro *et al.* 1999).

Selection of species

The 28 study species (Figure 1) were selected from previous studies across the network of permanent plots of the Biodiversity Research Program (PPBio). The selected species are dicotyledonedonous trees, paired across the hydrological environments within genera or families to decrease the potential bias of phylogenetic effects. We sought to cover the gradient of hydrological conditions, pairing within phylogeny one species associated to the shallowWTF on valleys and another to the deepWTF on plateaus.

Mortality rate

Mortality was calculated for each species from censuses conducted over 72 1-ha permanent plots systematically distributed over the Reserve, from 2001/02 to 2016. Fours census periods were available: 2001-2004, 2004-2008, 2008-2014, 2014-2016. Only species with a sufficient number of individuals in each census were selected (N≥ 20). The mortality rate (M) was calculated as in Sheil, Burslem & Alder (1995): $M = \ln No - \ln Nt / t$, t = time elapsed between the censuses, No= initial counts of individual trees, Nt = final counts of individual trees. We calculated mortality rates for each species/census period combination.

Resistance to cavitation

The water potential in which the plant loses 50% of its water conduction capacity (P50) was obtained for each species from the curves of the percentage of loss of conductivity, following the pneumatic method developed by Pereira *et al.* (2016). Between 3 and 6 individuals were selected per species (N=18), which ranged between 2 and 10 m in height; from each one a branch sample of 1 m in length was taken for measurements. The samples were induced to dehydrate repeatedly at a different water potential and their water discharge was measured simultaneously with a pressure chamber (PMS 1000, PMS Instruments Co., Albany, OR, USA). The branch was left inside a closed dark bag for 1 hour for leaf and xylem water potential equilibrate, then new measurement was taken and so on until the branch embolized completely. The percentage of conductance loss was estimated from the percentage of air discharge curves and P50 was calculated from an adjusted sigmoidal curve that relates the percentage of conductance loss with the water potential of the xylem.

Xylem anatomy

For the anatomical measurements of the xylem, we used fragments of branches (of three to five individuals of each species) of two centimeters in length, each sample was cut transversely in a sliding microtome (Leica SM2010 R). Cuts were treated with sodium hypochlorite (2%), stained

with 0.5% toluidine blue, and photographed under optical microscopy (Olympus DP71 digital camera coupled to Olympus BX51 microscope, Laboratory of Plant Anatomy, University of Campinas) in 10x and 20x magnifications, making two to four replicates of images per sample. Each image was analyzed with the Image J program, obtaining the area of each vessel (A) to be transformed into vessel diameter (µm) D = (4A / pi) 1/2. The density of vessels VD (mm^2) was calculated as the number of vessels per area. Also, a measure inter-vessel wall length (Lvw µm), and the percentage of vessels grouping (% VG) was estimated, as the ratio of the number of vessels grouped (with walls in contact) by the total number of vessels (Scholz, Klepsch, Karimi & Jansen 2013a).

Density of venation and stomata

Vein length per area (VLA mm mm^{-2}), stomatal density (SD mm^2) and length (SL µm) were measured on 1 cm^2 squares cut from the median region of the leaves of three to five individuals per species. For VLA, the leaf pieces went through diaphanization, following an adaptation of the protocol of Gardner (1975). Two to four image replicates were taken per sample with a magnifying glass (Leica DMC 2900 digital camera coupled to the Leica S8PA0 magnifying glass) obtained in a 40x magnification, and analyzed with the LEAF GUI program (www.leafgui.biology.gatech.edu, Price, Symonova, Mileyko, Hilley & Weitz 2011).

For SD and SL, the epidermis of the leaf pieces was dissociated using Franklin's solution (30% hydrogen peroxide and acetic acid, 1: 1) for 2 to 5 days at 60 °C, followed by manual peeling with brush. The side of the epidermis containing stomata was stained with 0.5% toluidine blue, photographed under a light microscope (Zeiss-Axio Lab1) coupled to a digital camera (Axiocam Erc5s) in 20x and 40x magnification, and SD and SL were measured with ImageJ.

Statistical analysis

All trait values were averaged for the species (Table S1), and these represent the units of analysis. To assess the association between the anatomical traits of the stem and the leaf (N = 28 species) and their relationships with the resistance to cavitation (this performed for 18 species with P50 data), a Pearson correlation analyses were performed. Significant relationships were visualized through trait correlation networks, using the qgraph package (Epskamp, Cramer, Waldorp, Schmittmann & Borsboom 2012). Traits were represented as nodes and their correlation as the edges that link them. A centrality test was performed for each trait, using the strength index, defined as the sum of all significant correlation coefficients of a node (Table S2).

Drought intensity was calculated as the maximum cumulative water deficit (MCWD) of each census period. For each month we calculated CWD following (Aragão *et al.* 2007) from precipitation records, as:

$$CWD_n = CWD_{n-1} + P_n - ET_n$$

where P_n is the monthly precipitation (observed at the Ducke meteorological station) and ET_n is the monthly evapotranspiration, assumed to be 100 mm per month, hence the deficits are negative numbers. Whenever calculated CWD_n exceeds zero in a given month, the excess water is assumed to runoff, and the CWD_n for that month is reset to zero, thus $CWD_n \leq 0$ for all months. MCWD across the census periods varied from -73.6 and -76.1 (above 1 SD from the 53-y historical mean) in the periods with moderate drought from 2001 to 2008, to -157.0 and -168.1 (above 2 SD from the historical mean) in the periods including the strong droughts of 2009-10 and 2015-16.

To test the effects of hydraulic traits on mortality rates, we used linear mixed-effect models, including species as random factors to control for the repeated measurements of mortality rates across censuses. Mixed models were implemented with lme from the R nlme package. All the possible combinations of traits alone, with topography (plateau vs valley), MCWD and interactions were tested, and the best models to predict mortality rates were ranked according to Akaike's information criterion corrected for small samples (AICc).

To determine if phylogenetic relationships might have affected the relationships between traits and mortality rates, we tested the phylogenetic signal associated to each trait. We reconstructed the phylogenetic relationships using PhyloMatic v.3 (Webb & Donoghue 2005), based on the phylogeny of angiosperms (Zanne *et al.* 2014). Phylogenetic trees were constructed in PHYLOCOM 4.2 and then used to calculate the Blomberg k (Blomberg, Garland & Ives 2003) and Pagel lambda (Pagel 1999), with significance tested by 999 permutations. All analyzes were carried out using R version 3.6.1 (R core Team, 2018).

Results

Best predictors of the mortality of juvenile trees

Resistance to cavitation (P50) and vessel grouping (VG) were the traits that best predict the mortality rates of trees juveniles. These traits were the only predictors included in the five best models ranked according to AICc (Table 2). Tree mortality rates were higher for species with lower resistance to cavitation (less negative P50) and a higher %VG (Figure 2a and 2b). However, these

relationships were dependent on the hydro-topographic environment: only the species associated to deepWTF on plateaus had higher mortality rates as P50 became less negative and vessel grouping increased (Figure 2a and 2c), while the mortality rates of the shallowWTF species were not affected by changes of these traits (Figure 2b and 2d). The intensity of the drought was also an important predictor of mortality (third and forth best models), but models including only drought intensity or drought intensity and P50 had a similar predictive power. Even if P50 had a small contribution to the model that already included drought intensity, it is clear that species with less negative P50 suffered more mortality in the strongest droughts (Figure 3). Our limited sample size may have not been enough to detect the interactions between drought intensity, P50 and topographical environments in best models (this model was tenth in the rank).

Association between resistance to cavitation, stem and leaf traits

Cavitation resistance (P50) was directly correlated with the anatomical features of the stem and only indirectly with leaf traits (Figure 4a). Lower resistance to cavitation was significantly associated with a higher percentage of vessel grouping (VG) and a greater inter-vessel wall length (Lvw), and indirectly with greater length of stomata, through its high relationship with VG. Inter-vessel wall length was the trait with the highest centrality value.

Examining correlations only between hydraulic anatomical features, we find that vessel diameter is the trait with the highest centrality value. There is a coordination between the features of the leaf and stem in the direction of high water efficiency, the greater diameter of vessels is associated with the greater stomata length and, in turn, is related to a high percentage of vessel grouping (Figure 4b). Among the features of the stem, we also find that greater inter-vessel wall length is associated to wider vessels. The leaf venation density was not associated with any of the other variables evaluated and may represent an independent axis of hydraulic regulation.

Phylogenetic signal

There was no phylogenetic signal for any of the evaluated traits, with *K* values in the 0.12-0.45 range (Table 3). All values of *K* are below 1 and not significantly different from expected under random evolution, so we conclude that these traits are not conserved throughout the phylogeny for the group of species evaluated (N=18 species for P50 and N=28 others anatomical traits).

Discussion

We studied the capacity of hydraulic traits in predicting mortality rates of juvenile Amazonian tree species across contrasting hydro-topographic conditions. We found that the combination of hydraulic traits and local hydrological environments best predicts mortality, and thus local hydrology is an important modulator of tree responses to drought, which not only depends on species hydraulic architecture. The hydraulic traits with best predictive capacity were P50 and the percentage of vessel grouping, which are positively related.

Hydraulic traits and local hydrology control mortality

This is the first record of lower resistance to cavitation (less negative P50) and higher percentage of vessel grouping (%VG) leading to higher mortality rates of tropical trees under natural droughts in Amazonia. Until now, only reports under artificially induced drought were known (Rowland *et al.* 2015, Powell *et al.* 2017). Moreover, we found this effect to be confined to plateau species, not affecting valley species. Differences in mortality rates of species associated with contrasting topographic habitats have been demonstrated previously (Nakagawa *et al.* 2000, Potts 2003, Itoh *et al.* 2012). However, this is the first time that these contrasting responses to natural drought across topographic environments are linked to a causal explanation, through hydraulic traits.

The composition of hydraulic traits of juvenile tree species is strongly influenced by hydro-topographical conditions, with more vulnerable trait values (less negative P50, wide diameter vessels, lower wood density) associated to valley species and more resistant trait values associated to plateaus (Cosme *et al.* 2017, Oliveira *et al.* 2018). Although the average trait values follow this pattern, the distribution of values has some overlap, which means that some vulnerable species also occur in the seasonally dry plateaus, and these species were the most affected by droughts. Plateaus and hillslopes in our study site lie 20 to 50 m over the water-table, which means that roots, especially of small trees, are probably not accessing this water source, given the root depths documented so far (Nepstad *et al.* 1994). Conversely, water table depth in valleys is constantly shallow (0 to 2 m) year-round (Hodnett *et al.* 1997). These differences in soil water availability imply that trees probably experience droughts in the plateaus, but not in valleys. Thus, hydraulically vulnerable plants in plateaus are therefore the most affected, due to the combination of limited rooting systems and low cavitation resistance. Therefore, the variation of hydro-topographic conditions at a local scale acts as an environmental filter, driving differential performance through hydraulic strategies and modulating the effects of droughts.

The lack of an association between P50 and mortality on trees associated to shallow water tables runs contrary to the potential expectation based on the less negative P50 values documented for this environment, in comparison to the deep water-table plateaus (Oliveira et al. 2019). Based solely on the distribution of P50 values across the hydro-topographical gradient, higher drought vulnerability would be naturally assigned to the shallowWTF on valleys. Our results highlight that the trait distribution across hydrological environments cannot be used alone to predict vulnerability, but must be coupled to layers of spatial variation and temporal fluctuation of the water-table, to inform models of vegetation dynamics in response to droughts.

Vessel grouping and communication are the best predictors of cavitation resistance
P50 was strongly correlated with the percentage of vessel grouping (%VG) and inter-vessel wall length (Lvw), while the expected correlation with vessel diameter was small and not significant. Current hypotheses suggest opposite effects of vessel grouping on cavitation resistance. The first postulates that a larger grouping of vessels contributes to prevent cavitation, by providing alternative routes for water transport (Carlquist 1984, 2009). The second hypothesis ("pit-rare" hypothesis, Loepfe, Martinez-Vilalta, Piñol & Mencuccini 2007, Martínez-Vilalta *et al.* 2012, Lens *et al.* 2013), postulates that the high connectivity between grouped vessels generates less resistance to cavitation, given the greater probability of embolism spread by air-seeding between pit membranes shared by grouped vessels. Our results support the "pit-rare" hypothesis, as species with higher VG and Lvw were the less resistant to cavitation. Similar results were found by Wheeler *et al.* (2005) for Rosaceae and Scholz *et al.* (2013b) for *Prunus* species. In addition, we find that favoring the propagation of cavitation due to greater grouping vessels and more connected by its walls, is an important mechanism of hydraulic failure linked to tree mortality in deepWTF.

We expected that a greater stomata length would be associated with lower resistance to cavitation, due to its influence on maximum stomatal conductance (Hetherington & Woodward 2003), which would imply risks to the hydraulic integrity. This relationship was not significant in our study, suggesting that hydraulic failure may depend more on the physiological behavior of the stoma (Sparks & Black 1999, Arango-Velez, Zwiazek, Thomas & Tyree 2011). We also did not find an association of venation density (VLA) and vulnerability to cavitation, as would be expected given the higher proportion of veins with large diameters and wide vessels associated to lower VLA (Sack *et al.* 2012), contributing to high leaf hydraulic conductivity (Sack & Holbrook 2006, Sack & Scoffoni 2013) but higher risk of cavitation (Brodribb *et al.* 2016, Martin-StPaul, Delzon & Cochard

2017). This suggests that the risk of cavitation at the leaf level may depend more on the architecture of the leaf venation network, such as its topology, the proportion of major and minor veins, and the proximity of smaller terminal veins to the stomata (Sack & Holbrook 2006). These characteristics deserve further investigation, to integrate the contributions of the anatomical properties of stems and leaves to the risk of cavitation.

The correlations between the anatomical traits show positive coordination between traits that increase the hydraulic conductivity at the leaf-stem interface. Higher Lvw, wide vessels and greater length of the stoma are positively correlated, linked to greater efficiency but reducing hydraulic safety (Scholz *et al.* 2013b), therefore were also associated to lower resistance to cavitation. In our study, VLA did not correlate with any of the anatomical traits. This can represent an independent hydraulic axis, which must be better understood, or the metric in itself may not be adequate to understand cavitation vulnerability, as discussed above. The complete understanding of the correlations between traits will allow better modeling of water transport and distribution, understanding how plants respond to drought events and climate change.

Conclusion

We conclude that local environments with lower water availability (DWTF in plateaus) act as survival filters for juvenile trees during droughts, given the limited access of their shallower roots to water, while at the same time, shallow WTF in valleys act as hydrological refugia under drought conditions, irrespective of plant hydraulic traits. These differential mortality rates of juvenile trees select species that will reach the canopy and, consequently, will affect the structure and composition of tree communities in the face of extreme climatic events. We also determined that some anatomical features of the stem (grouping and communication among vessel) are significantly correlated with resistance to cavitation, and can be used to rank species according to their potential sensibility to vascular damages in water deficit conditions.

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Table 1. Linear mixed-effect models to explain mortality rates of juvenile trees (<10 cm DBH), ranked by AIC.

Fixed effect(s)	AICc	ΔAICc	R^2
~ P50	147.3	0	0.23
~ P50 + topography	149.5	2.1	0.23
~ P50 + WCD	151.7	4.4	0.30
~ WCD	152.1	4.8	0.29
~ VG	153.0	5.7	0.28

Table 2. Phylogenetic contrast analysis (PIC) of the hydraulic traits for 18 species (P50) and 28 species for all other traits.

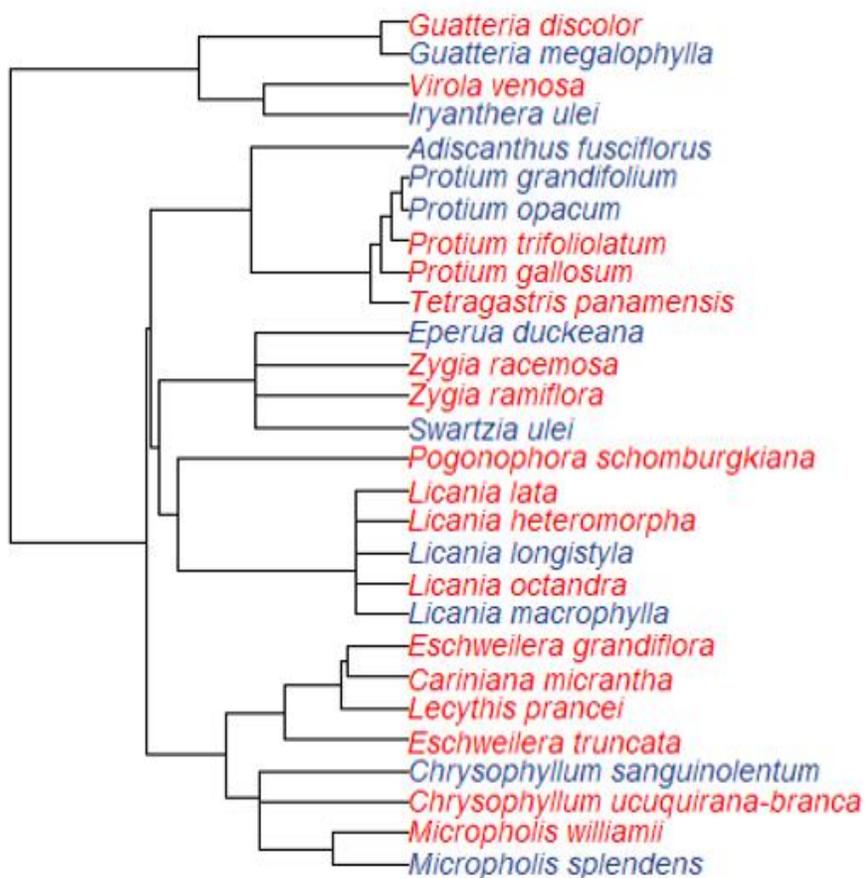| Traits	K	λ
P50	0.34	0.39
D	0.31	<0.001
VG	0.28	0.11
VD	0.21	<0.001
Lvw	0.45	<0.001
VLA	0.29	<0.001
SD	0.12	<0.001
SL	0.30	0.12

Figure 1

Figure 1. Evolutionary relationships among the 28 species of tropical trees selected for this study. The cladogram is based on the angiosperms phylogeny by Zanne *et al.* (2014). Colors indicate the hydro-topographic environment to each the species is associated (red: plateau; blue: valley).
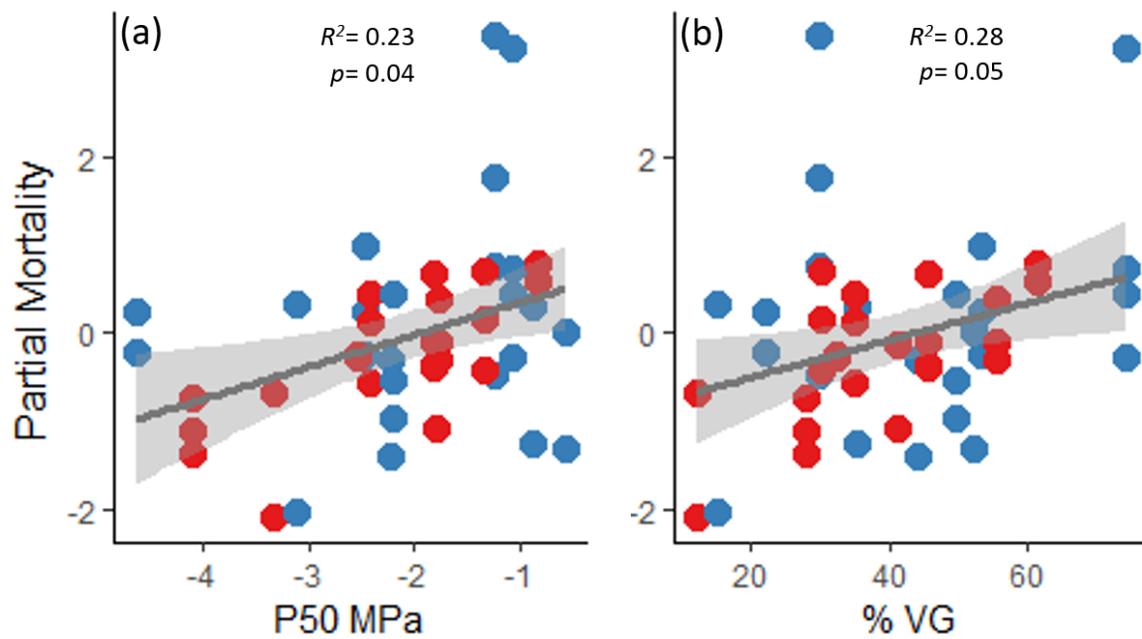
Figure 2

Figure 2. Relationships between the partial mortality of juvenile trees (<10 cm DBH) and (a) pressure causing 50% xylem cavitation, P50; (b) percentage of vessels grouping, %VG. Tree species belong to two contrasting hydrographic environments in the Central Amazon: plateau (red) and valley (blue). The gray line indicating the significant relationship.
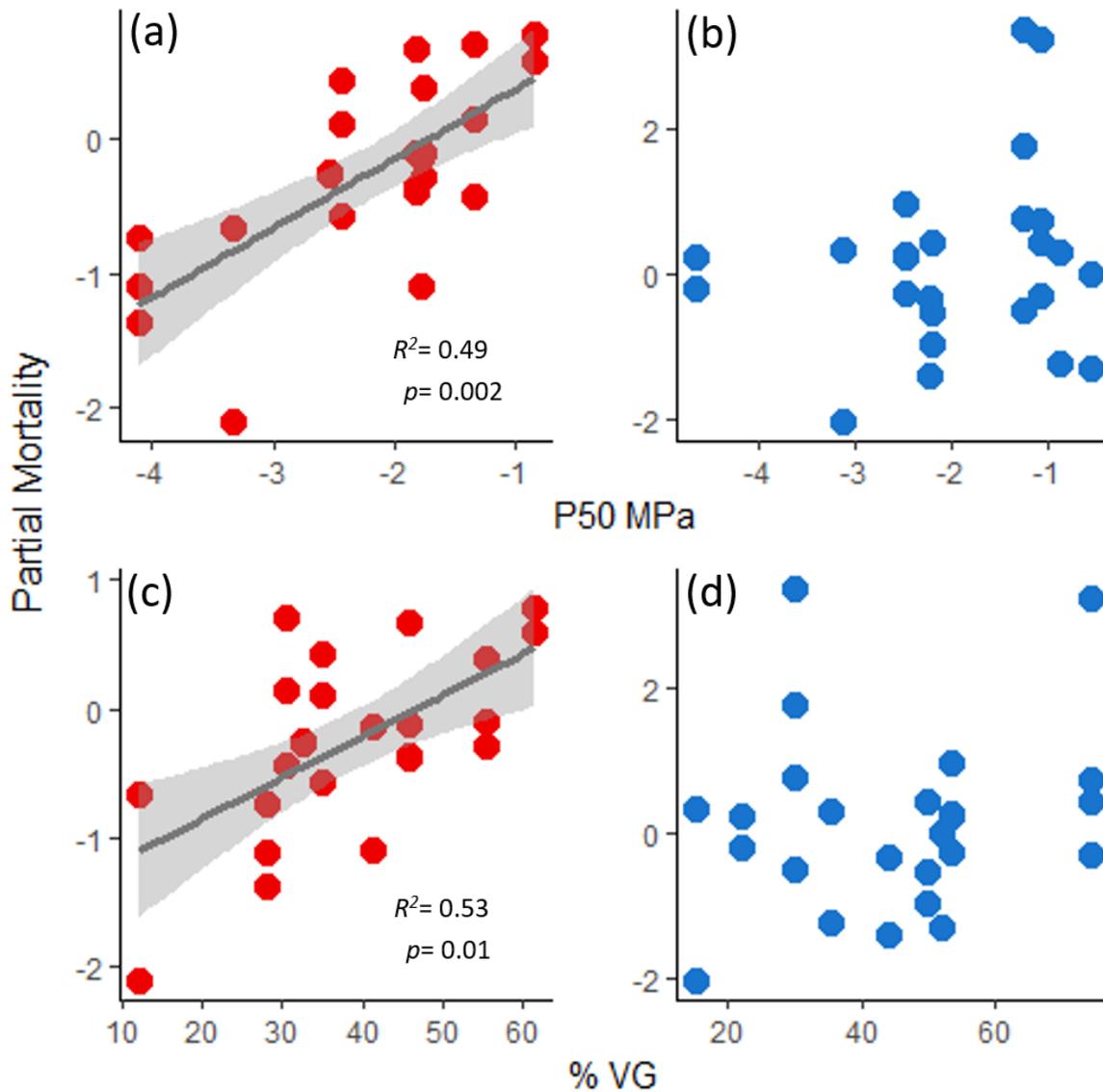
Figure 3

Figure 3. Relationships between the partial mortality of juvenile trees (<10 cm DBH): (a) and (b) pressure causing 50% xylem cavitation, P50; (c) and (d) percentage of vessel grouping, %VG, dependent on the hydro-topographic environment. The gray shadow shows the xx confidence interval around significant relationships. Colors indicate environment of the species: plateau (red) and valley (blue).
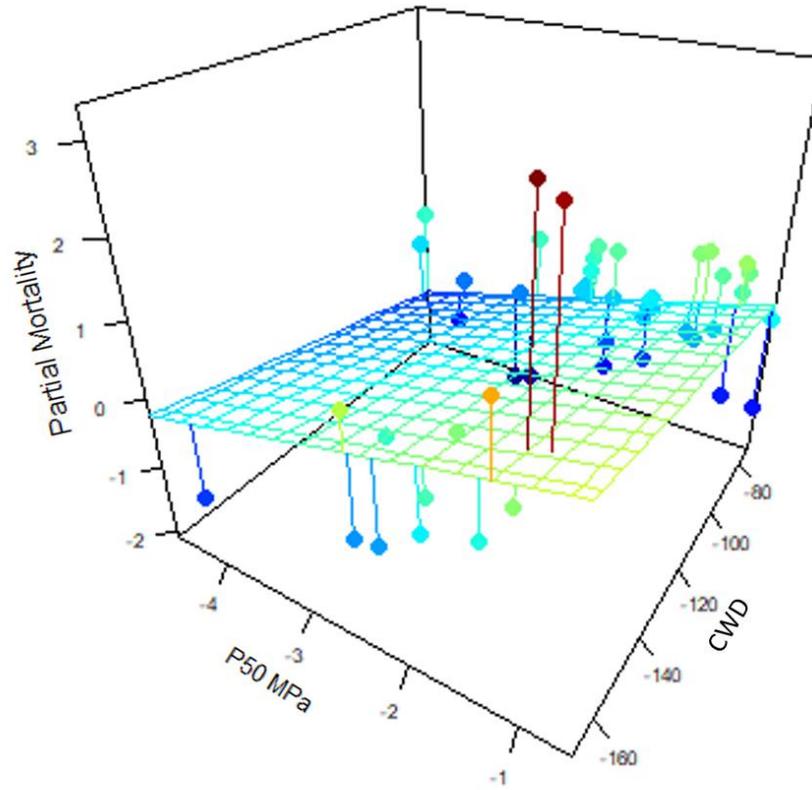
Figure 4

Figure 4. The effect of the interaction between the pressure causing 50% xylem cavitation (P50) and cumulative water deficit (CWD) on tree mortality (partials of the regression model).
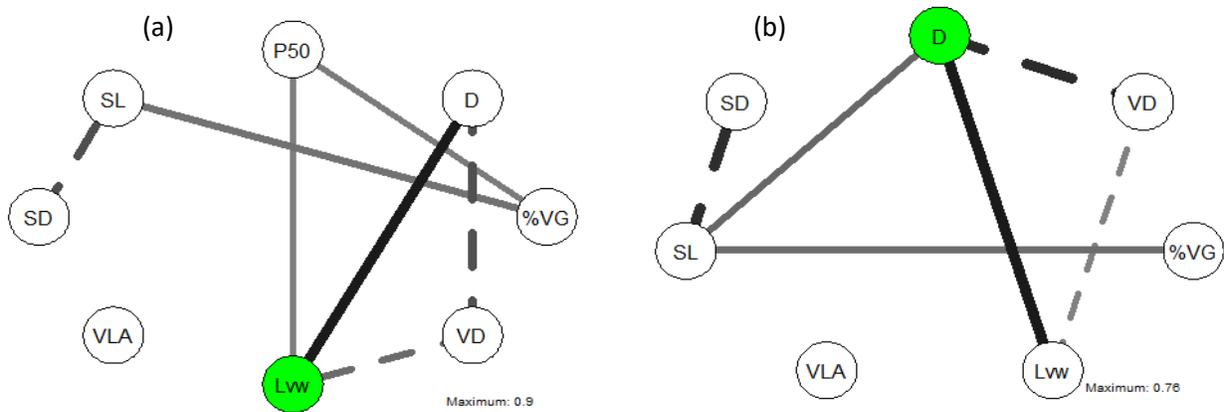
Figure 5

Figure 5. Trait correlation networks across traits (a) including P50 (N=18); or (b) without P50 (N=28). Solid black and grey dashed edges show positive and negative correlations, respectively. Correlation strength is represented by edge thickness. Only significant correlations are shown ($p < 0.05$). Traits identified by green circles show the highest centrality value in terms of strength (the sum of all the significant coefficients of correlation of a node). P50, pressure causing %50 xylem cavitation; D, vessel diameter; %VG, percentage of vessel grouping; VD, vessel density; Lvw, inter-vessel wall length; VLA, vein length per area; SD, stomatal density; SL, stomatal length.

Supporting Information

Table S1. Values average of traits evaluated for 28 species of tropical trees selected for this study. Values P50 only for 18 species.

| Species	P50	D	VD	%VG	Lvw	VLA	SL	SD
Adiscanthus fusciflorus	-1.08	17.5	559.5	74.3	7.9	15.5	34.6	66.0
Cariniana micrantha	–	41.2	73.5	50.0	95.3	29.6	30.9	145.0
Chrysophyllum sanguinolentum	-2.47	18.9	216.8	53.3	10.0	22.2	15.5	207.1
Chrysophyllum ucuquirana-branca	–	23.1	133.5	74.9	14.2	13.5	16.9	209.1
Eperua duckeana	-0.89	20.4	284.1	35.5	9.6	15.4	23.2	262.7
Eschweilera grandiflora	–	21.2	231.7	37.6	12.0	25.5	19.7	287.6
Eschweilera truncata	-2.43	17.0	289.7	35.0	7.4	23.4	22.3	254.9
Guatteria discolor	–	36.2	89.7	66.3	21.5	24.0	29.8	131.3
Guatteria megalophylla	-2.21	19.2	201.1	44.3	11.8	14.9	18.2	241.0
Iryanthera ulei	-0.56	29.6	147.0	52.1	16.8	15.5	28.6	133.0
Lecythis prancei	–	21.2	170.3	49.9	10.8	16.5	20.2	327.8
Licania heteromorpha	-3.33	16.5	298.9	12.2	9.3	34.6	21.6	301.8
Licania lata	–	13.8	226.0	17.9	7.4	37.2	13.4	353.2
Licania longistyla	-3.11	17.2	244.6	15.4	8.0	16.9	15.3	234.1
Licania macrophylla	-4.64	18.3	251.0	22.4	5.6	20.8	15.8	314.0
Licania octandra	–	16.2	341.2	21.4	6.7	20.6	13.4	259.7
Micropholis splendens	–	16.3	215.1	42.0	8.1	17.1	30.6	63.7
Micropholis williamii	-1.78	10.2	501.2	41.2	4.3	17.1	15.2	191.1
Pogonophora schomburgkiana	–	17.6	319.5	54.3	8.2	27.6	22.2	285.7
Protium gallosum	-2.54	16.4	414.1	32.7	7.5	11.9	10.7	675.2
Protium grandifolium	–	27.3	165.4	30.0	15.6	14.2	19.9	183.3
Protium opacum	-1.25	23.9	168.7	18.3	13.5	19.5	20.2	245.2
Protium trifoliolatum	-1.33	21.7	177.5	30.4	10.8	19.8	13.4	552.6
Swartzia ulei	-2.2	22.5	142.2	49.7	10.7	22.5	18.5	268.7
Tetragastris panamensis	-1.83	22.6	266.0	45.8	12.9	36.7	16.7	477.9
Virola venosa	-0.84	24.9	129.2	61.4	12.6	22.6	22.4	270.1
Zygia racemosa	-4.1	22.7	173.0	28.0	8.8	22.0	22.0	130.2
Zygia ramiflora	1.76	20.9	206.9	55.5	9.9	17.6	21.6	125.6
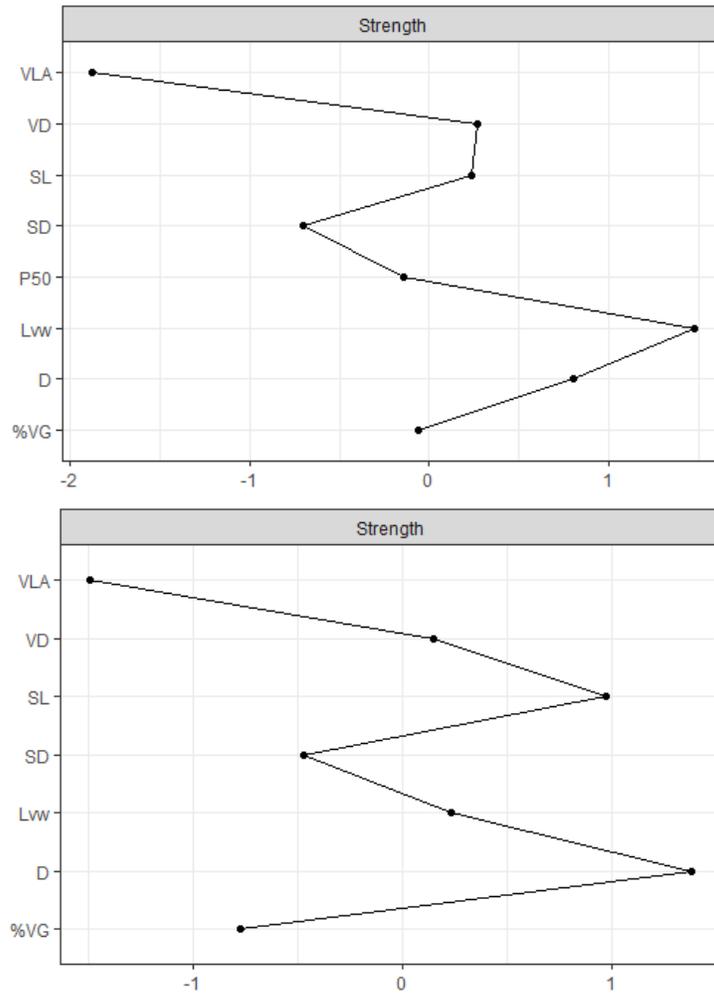
Figure S1. Values centrality for each trait, using the strength index, defined as the sum of all significant correlation coefficients of a node.

CONCLUSÕES

Se determino por primeira vez o efeito de menor resistência a cavitação nas altas taxas de mortalidade de arvores jovens, com maior efeito no platô. Nós sugerimos ao platô como filtro ambiental forte, que em eventos de secas naturais joga um papel importante na sobrevivência das arvores que iram a atingir no futuro o dossel. Consideramos estes resultados são importantes para entender as interações entre as condições hidro edáficas e os arvores, e como está dinâmica reflete na mudança da estrutura e composição das florestas, sob condições de futuros eventos climáticos extremos.

Para nosso estúdio, as características anatômicas do caule sao os melhores preditores da mortalidade das arvores, comparadas as de folha. Maior percentual de agrupamentos do vasos se relaciona a alta mortalidade das arvores densidade de venação é a caraterística que melhor prediz à alta mortalidade de pequenos arvores. Por tanto, achamos que o melhoramento da compreensão dos mecanismos mecanismos de mortalidade, na direção do funcionamento das respostas hídricas e de aquisição de carbono, são chaves para entender e modelar de forma cada vez mais integral os efeitos das mudanças climáticas sob a vegetação.

As caraterísticas que se correlacionam significativamente com menor resistência a cavitação estão ligas a maior eficiência na condutividade, mas ao mesmo tempo deterioram à seguridade do transporte hídrico na planta. Menor resistência a cavitação se relacionam positivamente com alto porcentagem de agrupamento do vaso e maior comprimento da parede inter-vasos. O resultado de nosso estudo apoia a teoria que maior área de contato e número de pontuações de membrana entre os vasos agrupados, facilita a propagação das bolhas do ar de vaso à vaso.