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RELAÇÕES ENTRE A OCORRÊNCIA DE RAÍZES ACIMA DO SOLO E FATORES INDIVIDUAIS E AMBIENTAIS NA RESERVA FLORESTAL ADOLPHO DUCKE

GABRIELA MACIEL ALENCAR

Manaus, Amazonas

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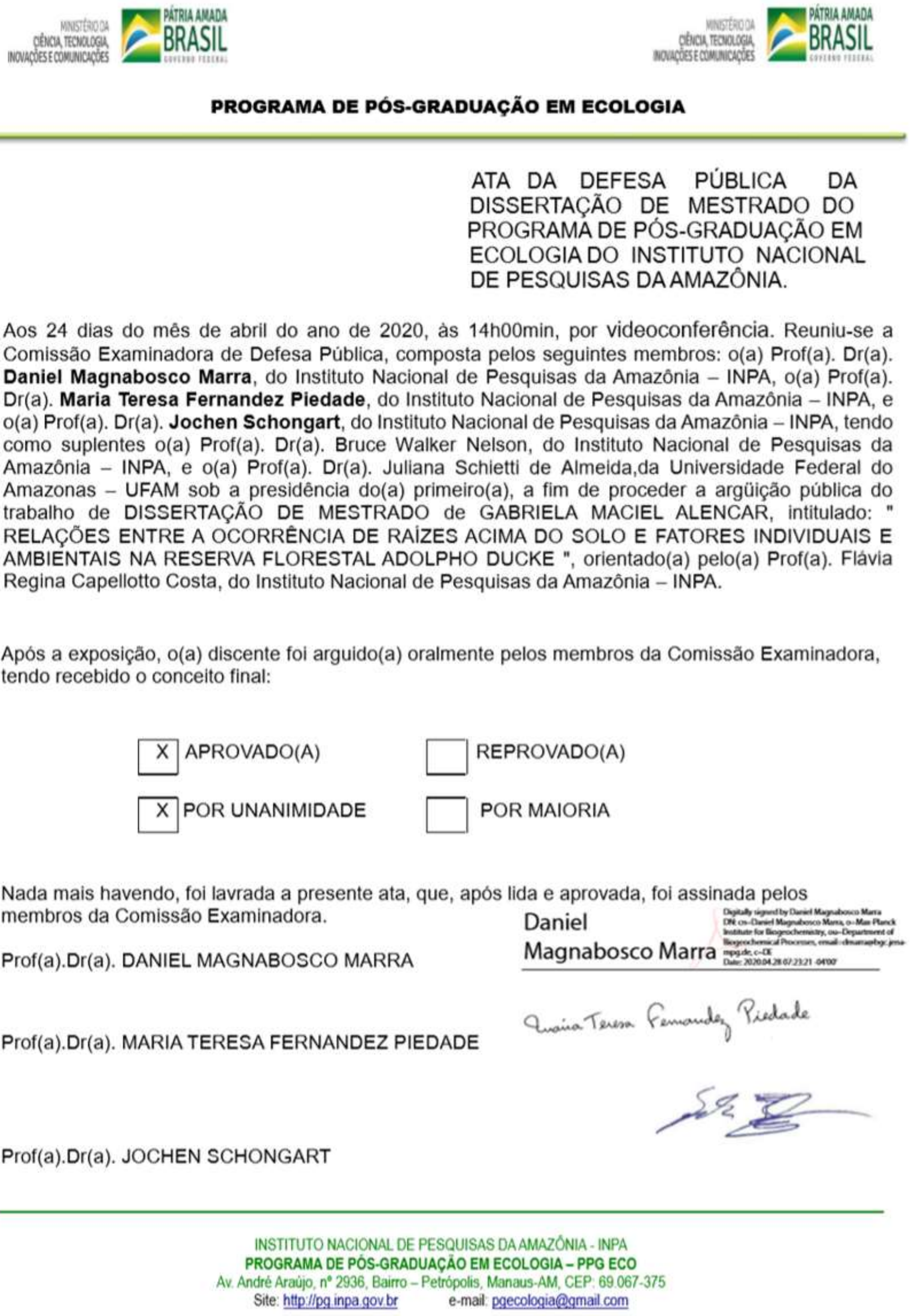

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Aos 24 dias do mês de abril do ano de 2020, às 14h00min, por videoconferência. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Daniel Magnabosco Marra**, do Instituto Nacional de Pesquisas da Amazônia – INPA, o(a) Prof(a). Dr(a). **Maria Teresa Fernandez Piedade**, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). **Jochen Schongart**, do Instituto Nacional de Pesquisas da Amazônia – INPA, tendo como suplentes o(a) Prof(a). Dr(a). Bruce Walker Nelson, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). Juliana Schietti de Almeida,da Universidade Federal do Amazonas – UFAM sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de DISSERTAÇÃO DE MESTRADO de GABRIELA MACIEL ALENCAR, intitulado: " RELAÇÕES ENTRE A OCORRÊNCIA DE RAÍZES ACIMA DO SOLO E FATORES INDIVIDUAIS E AMBIENTAIS NA RESERVA FLORESTAL ADOLPHO DUCKE ", orientado(a) pelo(a) Prof(a). Flávia Regina Capellotto Costa, do Instituto Nacional de Pesquisas da Amazônia – INPA.

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

☒ APROVADO(A) ☐ REPROVADO(A)

☒ POR UNANIMIDADE ☐ POR MAIORIA

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

Prof(a).Dr(a). DANIEL MAGNABOSCO MARRA — Daniel Magnabosco Marra — Digitally signed by Daniel Magnabosco Marra DN: cn=Daniel Magnabosco Marra, o=Max Planck Institute for Biogeochemistry, ou=Department of Biogeochemical Processes, email=dmarra@bgc-jena.mpg.de, c=DE Date: 2020.04.28 07:23:21 -04'00'

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Sinopse:

Avaliou-se as relações entre a ocorrência de raízes tabulares e raízes suporte com o ambiente e com as características da própria árvore na Reserva Florestal Adolpho Ducke.

Palavras-chave: floresta tropical, alometria, topografia.

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Resumo

Os determinantes da ocorrência de raízes tabulares e suporte ainda são pouco compreendidos. A estabilidade mecânica necessária para atingir grandes alturas requer aumento de diâmetro e, portanto, grandes custos para esse aumento poderiam ser atenuados com a realocação de investimentos em estruturas de apoio. Condições ambientais estressantes, como exposição ao vento, carga gravitacional e instabilidade de ancoragem em solos rasos, podem gerar demandas extras à estabilidade das árvores. Aqui, investigamos como as propriedades individuais e ambientais da árvore interagem para determinar a ocorrência de estruturas de suporte. A presença de raízes tabulares ou suporte e o diâmetro das árvores foram registrados em 8.415 árvores de 35 parcelas de 1 ha na Amazônia central. Em 67 árvores de duas espécies-alvo distribuídas pela topografia, também medimos a alometria e o tamanho da copa. A proporção de estruturas de suporte no nível da parcela e a probabilidade de ocorrência no nível individual foram modeladas com várias regressões lineares ou logísticas e árvores de regressão. A proporção de árvores com raízes tabulares foi maior nos baixios e platôs e raízes suporte foram mais frequentes nos baixios, quando mais inclinados. No nível individual, a probabilidade de ocorrência de qualquer estrutura de suporte aumentou com o diâmetro das árvores e nos baixios. Dentro das espécies, o diâmetro foi o preditor mais importante das raízes tabulares, mas 30% das espécies tiveram interações variadas e complexas com a inclinação e altitude do terreno. A ocorrência de estruturas de suporte foi mais provável em árvores robustas (menor proporção H: D), que possuíam áreas de copas menores. Em resumo, os ambientes mais instáveis, aqui representados pelos baixios com solos alagados, selecionaram uma maior frequência de árvores com estruturas de suporte no nível da comunidade. No entanto, relações alométricas coordenadas entre o tamanho do tronco e o tamanho da copa também influenciam a necessidade de estruturas de suporte. Assim, raízes tabulares e suporte não são características fixas da espécie, sua presença depende das relações alométricas de cada planta e das condições de instabilidade impostas pelo ambiente.

Palavras-chave: floresta tropical, raízes tabulares, raízes suporte, topografia, relações alométricas

Abstract

Determinants of the occurrence of buttress and stilt roots are still poorly understood. The mechanical stability required to reach large heights requires increasing diameter, and thus large construction costs that could be alleviated with reallocation of investments to support structures. Stressful environmental conditions such as exposure to wind, gravitational load and anchorage instability in shallow soils can place extra demands on the stability of trees. We here investigate how tree individual and environmental properties interact to determine the occurrence of support structures. Presence of buttress or stilt roots and tree diameter were recorded on 8.415 trees from 35 1-ha plots in central Amazon. On 67 trees of two target species distributed across topography, we also measured allometry and crown size. Proportion of support structures at the plot level and probability of occurrence at the individual level were modelled with multiple linear or logistic regressions, and boosted regression trees. The proportion of buttressed trees was higher in valleys and plateaus and stilt roots were more frequent in valleys, when more inclined. At the individual level, the probability of occurrence of any support structure increased with tree diameter and in valleys. Within species, diameter was the most important predictor of buttresses, but 30% of the species had varied and complex interactions with terrain slope and elevation. Occurrence of support structures was more likely on stout trees (lower H:D ratio), which had smaller crown areas. In summary, the most unstable environments, here represented by valleys with waterlogged soils, selected for a higher frequency of trees with support structures at the community level. However, coordinated allometric relationships among stem size and crown size also influence the need of support structures. Thus, support structures are not fixed species traits, their presence depending on individual plant´s allometric relationships and the instability conditions imposed by environment.

Keywords: rainforest, buttresses, stilt roots, topography, allometric relations

Sumário

Introdução

As raízes das plantas têm como funções a absorção de nutrientes e água, a sustentação nos substratos e também podem atuar no transporte de substâncias, bem como armazenar substâncias. Para facilitar o entendimento, as raízes são classificadas de acordo com suas funções e características, assim, de acordo com a adaptação ao ambiente, as raízes podem ser classificadas como terrestres, aquáticas ou aéreas. As raízes aéreas são consideradas raízes adventícias por surgirem dos caules das plantas e podem ser classificadas em: sugadoras ou haustórios, grampiformes, respiratórias ou pneumatóforos, assimiladoras, coletoras, estranguladoras, escoras ou suporte e sapopemas ou tabulares (Henriques et al., 2010; Jenik 1976).

Raízes tabulares são projeções em forma de tábuas, achatadas, que se formam nos caules das árvores aumentando a superfície respiratória e a sustentação do tronco e raízes suporte são adaptações de raízes adventícias jovens, que auxiliam na sustentação de plantas que crescem em ambientes instáveis (Jenik, 1970; Almeida e Almeida, 2014). Essas estruturas são encontradas nas florestas tropicais e temperadas e foram notadas por naturalistas há muito tempo (Navez, 1930).

Apesar da abundância das raízes tabulares e suporte nos trópicos ter chamado a atenção desde os primeiros pesquisadores, suas funções e relações com o ambiente são ainda pouco investigadas e entendidas (He, 2012; Young e Perkocha, 1994). Muitos autores sugerem uma função de suporte mecânico para as árvores mais altas das florestas tropicais (Chapman et al., 1998; Mehedi et al., 2012; Crook et al., 1997) e há também controvérsia em torno das condições ambientais que promoveriam a seleção de indivíduos com estas características (Ruslandi et al., 2015).

As raízes tabulares e suporte são consideradas estruturas de sustentação que protegem a árvore de estresses do ambiente que tenderiam a promover sua queda (Ribeiro et al., 1999). Dentre os estresses ambientais em que as raízes podem servir de apoio estão a força do vento, o peso das suas copas, o próprio peso da árvore contra a gravidade (He et al., 2012) e a instabilidade de ancoragem em solos rasos ou instáveis (Navez, 1930).

Nos estudos de Chapman et al. (1998) e Mehedi et al. (2012), árvores emergentes e de dossel apresentaram maior proporção de raízes tabular/suporte em comparação com árvores de sub-bosque, o que está de acordo com a hipótese de suporte mecânico. Richter (1984) mostrou que a presença de raízes tabulares/suporte reduziu em até 15% a vulnerabilidade de queda das árvores devido às forças dos ventos, porém, Chapman et al. (1998) mostraram que existe pouca evidência de que as raízes tabulares tenham sido usadas como suporte em algumas espécies devido às suas estratégias de vida, que podem usar outros meios de suporte. Crook et al. (1997) testaram a resistência das árvores que possuíam ou não raízes diferenciadas e seus resultados mostraram que as árvores sem raízes de suporte foram mais susceptíveis a desenraizamento e quebra quando submetidas experimentalmente a forças mecânicas. O modo de falha (desenraizamento ou quebra do tronco) diferiu conforme a arquitetura de raízes e à presença ou ausência de raízes tabulares em Eschweilera submetidas às forças mecânicas experimentais (Ribeiro, 2015). Diante disso, embora não exista consenso sobre a função de suporte mecânico das raízes tabulares e suporte, há alguma evidência de que estas raízes podem auxiliar as árvores contra os estresses ambientais a que são submetidas.

O suporte das árvores pode também estar associado a outras características da planta e, portanto, poderíamos esperar que a presença de raízes tabulares/suporte não seja a única forma de proteção contra os estresses e que múltiplas características poderiam estar associadas para promover maior sustentação. A estrutura da copa das árvores pode estar associada à forma como ocorre a sustentação da planta, então copas mais largas que profundas podem ocorrer em árvores com maior diâmetro sem precisar de sustentação com raízes de suporte, sendo o diâmetro da árvore suficiente para sustentar o peso da copa, como um centro de massa (McMahon, 1973). Já nas copas assimétricas é possível que exista a projeção de raízes tabulares para equilibrar o peso da árvore (Lewis, 1988; Young e Perkocha, 1994).

Se o ambiente filtra as espécies em função de suas características de suporte, e o desenvolvimento destas estruturas pode ser induzido em função do ambiente, deve-se esperar uma maior abundância de árvores com raízes tabulares e suporte nos ambientes onde as condições de fixação das árvores no solo são ruins, e os fatores estressantes como vento e gravidade são maiores. A inclinação do terreno que sustenta a árvore pode influenciar na formação de raízes tabulares, que podem estar direcionadas acima ou abaixo da inclinação permitindo que a árvore se mantenha na posição vertical (Richter, 1984).

Na Amazônia Central, a altitude, a inclinação do relevo e as características do solo estão relacionadas (de Castilho et al., 2006), de modo que nas áreas mais altas (platôs) o solo é argiloso, profundo e bem drenado, nas vertentes o solo possui uma transição de argila nas partes mais altas e areia nas partes mais baixas e o relevo é inclinado, enquanto que nas áreas mais baixas (baixios) o solo é arenoso e frequentemente encharcado (Ribeiro et al., 1999). As variações nas condições de fixação das plantas (solo e inclinação) entre os ambientes de platô, vertente e baixio e sua interação com os eventos de estresse mecânico, podem constituir filtros determinantes na proporção de árvores com raízes tabulares e suporte, ainda que seja possível observar a ocorrência de raízes tabulares e suporte em todos os ambientes.

Perguntas e hipóteses

A proporção de indivíduos com raízes tabulares e suporte varia entre ambientes topográficos diferentes?

A hipótese para essa pergunta é que exista diferença na proporção de indivíduos com raízes tabulares e suporte em ambientes diferentes. É esperado que ocorra maior proporção de indivíduos com raízes tabulares e suporte em ambientes com altitudes menores, com solos encharcados periodicamente e instáveis e em ambientes inclinados, auxiliando na sustentação das árvores.

A ocorrência de raízes tabulares e suporte varia entre indivíduos da mesma espécie? E entre ambientes?

Dentro da mesma espécie, é esperado que indivíduos maiores em tamanho apresentem estruturas de sustentação como as raízes tabulares e suporte diferentemente dos indivíduos menores, que ainda não passaram por momentos de estresse no ambiente e que, por isso não apresentam tais raízes em sua base. Porém, em ambientes estressantes como solos de difícil drenagem e instáveis fisicamente, indivíduos menores possuiriam base tabular ou raízes suporte para contornar o estresse mecânico. Além disso, características do tamanho de copa também poderia influenciar na ocorrência de raízes tabulares e suporte para estabilizar a árvore.

Capítulo único

Gabriela M Alencar, Carolina V de Castilho, Flávia R C Costa. When are buttresses and stilt roots necessary for a tree in terra-firme Amazonian forests? Submetido e em revisão na revista *Journal of Plant Ecology* – ISNN: 1752-9921.

Abstract

Determinants of the occurrence of buttress and stilt roots are still poorly understood. The mechanical stability required to reach large heights requires increasing diameter, and thus large construction costs that could be alleviated with reallocation of investments to support structures. Stressful environmental conditions such as exposure to wind, gravitational load and anchorage instability in shallow soils can place extra demands on the stability of trees. We here investigate how tree individual and environmental properties interact to determine the occurrence of support structures. Presence of buttress or stilt roots and tree diameter were recorded on 8.415 trees from 35 1-ha plots in central Amazon. On 67 trees of two target species distributed across topography, we also measured allometry and crown size. Proportion of support structures at the plot level and probability of occurrence at the individual level were modelled with multiple linear or logistic regressions, and boosted regression trees. The proportion of buttressed trees was higher in valleys and plateaus and stilt roots were more frequent in valleys, when more inclined. At the individual level, the probability of occurrence of any support structure increased with tree diameter and in valleys. Within species, diameter was the most important predictor of buttresses, but 30% of the species had varied and complex interactions with terrain slope and elevation. Occurrence of support structures was more likely on stout trees (lower H:D ratio), which had smaller crown areas. In summary, the most unstable environments, here represented by valleys with waterlogged soils, selected for a higher frequency of trees with support structures at the community level. However, coordinated allometric relationships among stem size and crown size also influence the need of support structures. Thus, support structures are not fixed species traits, their presence depending on individual plant´s allometric relationships and the instability conditions imposed by environment.

Keywords: rainforest, buttresses, stilt roots, topography, allometric relations

Introduction

Buttresses and stilt roots are morphological modifications of tree trunks, forming plank-shaped or root projections above the ground (Chapman et al. 1998). Although their abundance in the tropics has attracted attention since the first researchers (Richards 1952), the plant and environmental conditions that require these structures are still little understood (Young and Perkocha 1994; He et al. 2012). Many authors suggest a mechanical support function for the tallest trees in tropical forests (Crook et al. 1997; Chapman et al. 1998; Mehedi et al. 2012) others attribute their presence to phylogenetic conservatism (He et al. 2012) and there is also controversy surrounding the environmental conditions that would promote the selection of individuals with these structures (Navez 1930; Lewis 1988; Warren et al. 1988).

The mechanical stability required by trees to attain large heights demands investments in increasing diameter to avoid buckling by the gravity imposed static loading, which increases with the weight of individual parts, or by wind (McMahon 1973). Trees never attain the buckling limit set by the elastic criteria of stem length proportional to the 2/3 power of diameter (McMahon 1973), but this may require large costs of construction of stems for tall trees that could be alleviated if investments were reallocated to support structures in the trunk base, such as buttresses and stilt roots. The mechanical formulation of (McMahon 1973) assumes that crowns have uniform size and shape across trees, which in other words, means that it does not consider crowns. However, many aspects of crown architecture (crown area, depth, density, and location on the bole) may affect susceptibility to wind damage (Hutte 1968; Grace 1977; Jackson et al. 2019). Crown properties can then be expected to modify the demands of supporting structures in the base of stems, since the whole architecture of a tree must be adjusted to the biomechanical demands imposed by gravity and wind. Wider than deeper, or asymmetric crowns, may require support structures to help equilibrate tree weight (Lewis 1988; Young and Perkocha 1994). This suggests that, in order to understand the prevalence of buttress and stilt roots, we need to understand the combinations of tree height and diameter (the H:D relationship), crown size and shape.

Besides tree size and shape, environmental properties can impose extra demands on tree stability. Among the environmental stressors requiring increased tree support are wind strength, gravity load in sloping terrains (He et al. 2012) and anchorage instability in shallow or unconsolidated soils (Navez 1930). In central Amazonia, the prevalence of such stressors varies across topographic gradients, from shallow loose soils on valleys, to gravity load on slopes and potentially higher wind exposure in the upper parts of slopes and plateaus.

Small increases in rooting depth result in considerable increases in resistance to uprooting (Fraser 1962), and soil shear strength (i. e., the soil's ability to resist torsional forces) decreases with increasing soil-moisture content (Hough 1957). Shallow and waterlogged soils are then expected have a larger probability of uprooting, being where we should expect a higher frequency of supporting structures to aid trees stand still. Moreover, rooting depth is superficial on waterlogged soils, given the anoxic conditions as depth increases (Fan et al. 2017). Superficial roots may provide low anchorage, so any tree growing more in height than diameter in these conditions should benefit from stilt roots or buttresses, which provide a large support base without the need of large investments in wood (Jenik 1970).

Treefall rates can be taken as an indication of the susceptibility to death faced by trees in each environment. Across topography, these rates tend to be higher in bottomlands then in hilltops (Ferry et al. 2010) and large gaps are frequent on floodplains and wind-exposed areas (Goulamoussène et al. 2017). At the same time, wind exposure is related to higher elevations that inflate the occurrence of larger gaps (Negrón-Juárez et al. 2018). These patterns suggest that bottomland valleys are susceptible to large disturbance rates, probably due to the soil properties as revised above, while in other topographic positions, such as slopes and high plateaus, trees may be better anchored in deep soils but more exposed to winds. Sloping terrain by itself may also challenge tree´s stability, especially if crowns are asymmetric, increasing the gravity imposed static load.

Environmental conditions may also affect the need of supporting structures indirectly, via selection of tree sizes and allometry. Average tree diameter (D), height (H), and the H:D allometry change with soil structure and depth (Ferry et al. 2010; Feldpausch et al. 2011; Goulamoussène et al. 2017) as well as disturbance rates (Niklas et al. 2003). Environmental selection of trees that are either shorter, have low H:D, or have small canopies can potentially solve the biomechanical demands for stability without the need of buttresses or stilt roots.

Taking advantage of a large database (8.415 individuals from 35 1-ha plots) on the occurrence of support structures over a 10 x 10 km landscape of a hyper-diverse forest in central Amazonia, and adding architectural and allometric data for two model species, we examined how individual tree properties and topographic conditions affect the occurrence of support structures. We hypothesize that (1) if the development of support structures can be induced according to the environment, and the environment filters species according to these structures, a greater proportion of trees with buttresses and stilt roots should be expected in environments where the conditions for tree anchorage to the ground are poor (such as in the valleys), and where stressors such as wind and gravity play a larger role (such as in slopes). Moreover, this leads to the general expectation that support structures are not fixed characteristics of the species, but that environment and individual properties, such as size and architecture, may interact to determine its occurrence. Alternatively, allometric adjustments of trees to their topographic environments may solve the stability needs and support structures may not be required.

Material and methods

Study site

The study was conducted at the Ducke Forest Reserve (RFD), a 10,000 ha mature forest in the Central Amazon, 26 km north of the city of Manaus (02 ° 55'S, 59 ° 59'W). Climate is tropical humid, with average temperature is 26 ° C, and an average of 2,300 mm of rain per year. The rainy season occurs between November and June, with greater precipitation in March and April and the dry season (precipitation monthly <100 mm) occurs between July and September (Marques Filho et al. 1981). Vegetation is of lowland dense terra-firme forest and the average canopy height is estimated between 26 - 30 m (M. Smith unpl. data), with emergent trees that reach maximum heights above 35 m, with the tallest tree having 55 m (Guillaumet 1987). In the plateaus, the altitude varies from 80 to 140 m and the average canopy height is 30.8 m, in the slopes, the average altitude is 71 m and the average canopy height is 26.9 m and the valleys have an average altitude of 51 m and the average canopy height is 26.8 m (Ribeiro et al. 1999). Soils vary across topography, from flat well-drained plateaus with clayey soils of the alic-yellow latosol type, to slopes with sandy-clay soils, and the clay fraction decreases towards the valleys, where soils are almost pure sand. Valleys are over shallow-water table and get waterlogged during the rainy season (Hodnett et al. 1997). The topography of the RFD has altitudes ranging from 39 m to 109 m. The highest and flatest areas constitute the central plateau that divides the two watersheds (Ribeiro et al. 1999).

Sampling design

RFD is a research site of the Brazilian Biodiversity Research Program (PPBio) and a LTER since 1999, encompassing a large grid of 18 trails and 72 1-ha plots covering 64 km^2, for standardized biodiversity and forest dynamics studies (Magnusson et al. 2005). Plots are 250 m long and follow the terrain contour to minimize variation of drainage and soils, and are distributed in the grid keeping a minimum distance of 1 km. Plot width is adjusted according to the size of trees: individuals with DBH ≥ 30 cm were sampled in 1 ha (40 x 250 m), individuals with DBH between 10-30 cm in 0.5 ha (20 x 250 m) and individuals with DBH between 1-10 cm in 0.1 ha (4 x 250 m).

Data collection

The type of the tree stem base was recorded during floristic inventories of plots between 2001 and 2004 by Carolina Castilho and her field team, as either straight (no projections), stilt roots, buttress or a combination of buttress and stilt roots. We revisited a set of the trees classified as having both structures to check if there were misclassifications, and ascertained that the occurrence of both structures in the same tree is real. Tree diameters of all trees in plots used here were measured between 2009 and 2016 following the protocol described in Castilho et al. (2010). Plot ground-elevation was measured with a theodolite by a professional topographer. Terrain slope was measured with a clinometer every 50 m along a central line running along the main axis of each plot, totaling 5 points in each plot, summarized by the average (de Castilho et al. 2006).

Since the plot data has only information on tree diameters, to better understand the effects of other dimensions of tree size and shape on the occurrence of buttresses, we choose two species for detailed measurements. These were the two most abundant species that can present buttress and are widely distributed across topography. Information from the database of the 72 plots shows that, although individuals of *Eperua glabrifolia* occur more frequently in the valleys (166 individuals) than in plateaus (91) and slopes (120), and *Eschweilera coriacea* occurs more frequently in slopes (376 individuals) than in plateaus (180) or valleys (245), there is good coverage of all the topographic gradient. We selected 10 to 12 individuals of each species (*Eschweilera coriacea* N=35 and *Eperua glabrifolia* N=32) with and without buttress, in each topographic environment (plateau, slope and valley), thus covering the gradient of elevation and slope of our study site. We measured for each individual the diameter at 1.30 m height or 50 cm above buttress, total height, stem height, crown depth and crown area.

The total tree height was measured with the help of a climber who used his pole-pruner to take a measuring tape measure to the top of the crown and this tape was stretched to the ground. While climbing, the tape was also taken to the height of the first branch, to record the stem height. Crown depth was then calculated as the difference between total tree height and stem height. We measured the projection of the crown on the ground with four measuring tapes, stretched first in the North-South direction (when the trees were on flat ground) or the direction aligned with the slope (in the hillside trees) and then crossing at 90° and 45° to delimit 8 radii. The crown was observed with binoculars by an observer walking along the tape to determine its length. From these measurements we generated the crown polygon from which crown area was calculated on ImageJ software. Terrain slope was also measured for each individual with a clinometer, along a 6 m line centered on the tree, and passing by the direction of the slope.

Data analysis

To understand the effects of topography on the proportion of individuals with either buttress or stilt roots, the sample units were the 35 plots for which at least 60% of the individuals above 10 cm DBH had information on the type of stem base. White sand plots were also excluded, as they were very few (two plots among those previously selected), and have a very distinct floristic composition. Dependent variables were checked for normality, independent variables tested for collinearity, and all conformed to the requirements of classical multiple linear models. The dependent variables were the proportions of individuals with either buttress or stilt roots in relation to the total number of individuals per plot. The independent variables were elevation, slope, average diameter of trees per plot, and their interactions. Since tree size is expected to affect tree stability and thus the need of supporting structures, we tested models for the effect of topography controlling for the effect of plot mean tree diameter, for trees above 20 cm. Twenty centimeters DBH was the most likely minimum size limit for the occurrence of support structures at individual level (see analyses below), and was then used to remove potential false negatives.

The variation in the probability of occurrence of buttresses or stilt roots among individuals of the same species was evaluated for the 29 most abundant species with this trait in the database, to ensure a large enough sample (N_{min} = 27 individuals, N_{max} = 260, N_{mean} = 77). The binary dependent variable (presence or absence of supporting structure) was modelled with a logit function in multiple logistic models, with tree diameter, tree slope, elevation and interactions as predictors. The same analysis was conducted at the individual level for the pooled sample of species with either buttress, stilt roots or combining species with any of these support structures.

The variation in the probability of occurrence of buttresses or stilt roots among individuals of the two model species (N = 67 individuals) was modelled as a function of individual size and shape (tree height and diameter, canopy area and depth, and height to diameter ratio - H:D) and topographic features (ground-elevation and slope). Slope was measured for each individual, and altitude came from the plot measurements. We used a boosted regression tree (gbm.step function, gbm package, (Pistón et al. 2019) to find the relative influences of each predictor, and from that select variables for the multiple logistic models. The multiple logistic models (glm in R base package, family binomial, link logit) included the best predictor selected from the individual metrics in the step described above and the topographic features, allowing both simple effects of predictors and their interactions.

For all the models described above, we established a best-fitting subset model based on AIC ranking, using unsupervised model selection (dredge function, MuMIn package, Bartón 2016). All analyzes were performed using the R Studio software version 3.6.1 (The R Foundation for Statistical Computing).

Results

There were 8.415 individuals with recorded information on the type of stem base, of which 71.3% (5.883) have 10 to 30 cm DBH and 28.7% (2.366) have DBH ≥ 30 cm. Twenty-eight percent of the trees 10-30 cm DBH had buttress, 4.5 % had stilt roots and 61.8 % did not have support structures. Sixty percent of trees above 30 cm DBH had buttress, 2 % had stilt roots and 30.8 % no support structures.

Plot-level analyses

Controlling the effect of the average diameter of trees in the plot (for trees ≥ 20 cm DBH), the best model to explain the proportion of trees with buttress included only the effect of slope ($b_{std} = -0.35$, $p = 0.035$), and contrary to the expectation, the proportion of buttressed trees decreased with terrain inclination (Fig. 1a). Thus, buttressed trees were more common on both the non-sloping topographic conditions, the valleys and plateaus. The best model to explain the proportion of trees with stilt roots included elevation ($b_{std} = -0.68$, $p < 0.001$) and the interaction between slope and elevation ($b_{std} = -0.45$, $p = 0.045$). This means that controlling for the average diameters, the proportion of trees with stilt roots was higher in lower elevations (valleys) and especially in more inclined terrains when they are in lower elevations, i.e. lower slopes close to valleys (Fig. 1b).

Individual level analyses

The probability that individuals had any type of support structure, either buttress or stilt root, increased with tree diameter ($b_{std} = 0.80$, $p < 0.001$, Fig. 2a) and decreased with elevation ($b_{std} = -0.16$, $p < 0.001$, Fig. 2b). The probability of having buttress was determined by diameter ($b_{std} = 0.94$, $p < 0.001$), elevation ($b_{std} = -0.10$, $p = 0.002$) and an interaction of tree size, elevation and slope ($b_{std} = 0.12$, $p = 0.008$), increasing for large trees in low elevation and low to moderate sloping terrains (Fig. 2c). The probability of having stilt roots was determined by elevation ($b_{std} = -0.51$, $p < 0.001$) and an interaction of tree size and elevation ($b_{std} = -0.14$, $p = 0.023$), increasing slightly with tree size in low elevations, but decreasing with tree size in higher elevations (Fig. 2d).

Among the 29 species with buttress and large enough populations for analyses, 69% (20 species) had the probability of having buttress increasing with tree diameter. The size where trees start to present buttress was around 20 to 30 cm DBH across all species. Among these 20 species, tree diameter was the only predictor of buttress in 55% of them, but environment affected this probability together with tree size in the remaining 45% (9 spp.), sometimes in complex interactions (Table 1, Fig. 1S, the supplementary material is available on-line). Slope was included in all but one of these nine models, having a simple effect on buttress probability (5 spp.), or an interaction with DBH (3 spp.) or elevation (2 spp.). The effect of slope was mostly positive, increasing the probability of buttresses, but was sometimes negative, especially when interacting with elevation or diameter. The probability of having buttress was not related to any predictors in eight species (27.6 %), and one species (*Eperua duckeana*) was affected only by slope.

Among the 93 that may have stilt roots, the majority (85 sp) had too few individuals to allow modeling ($N \leq 10$). Three species (*Licania hereromorfa* N=25 trees, *Porouma tomentosa* N=20 and *Micrandra spruceana* N=14) always presented this trait regardless of size or environment. Five species had enough individuals to fit a multiple logistic regression model (*Eperua duckeana*, *Eperua glabriflora*, *Zigia racemosa*, *Eschweilera coriacea* and *Rinorea racemosa*), but no significant model other than null was found to explain the probability of occurrence of stilt roots.

Analyses of model species

Before modelling the occurrence and size of buttresses, we investigated tree allometric relationships. Tree height and diameter were correlated ($r^2 = 0.56$, $p <0.001$). Crown area increased with height ($r^2 = 0.22$, $p < 0.001$, for the log linearized relationship, Fig. 3a) and diameter ($r^2 = 0.42$, $p < 0.001$, for the log linearized relationship, Fig. 3b), but slender trees (higher H:D) always had a smaller crown area, while stout trees may have small or large crowns, tending towards larger crowns ($r^2 = 0.36$, $p < 0.001$, for the log linearized relationship, Fig. 3c). The slope of the relationship between slenderness (H:D) and canopy area (log linearized) differed between environments, being larger for slopes ($b_{std} = -0.67$) and valleys ($b_{std} = -0.68$) than plateaus ($b_{std} = -0.53$). This means that slopes and valleys have trees with proportionally larger crowns for the same H:D (Fig. 4).

The probability of having any support structure was influenced by tree H:D, diameter and crown size, according to the regression tree, but the best predictor was the H:D ratio (Fig 5 a, b). Including H:D and the topographical variables in a multiple regression, H:D was still the single predictor of a support structure presence. The relationship was negative, with slender trees (higher H:D ratio) being less likely to have a support structure ($b_{std} = -1.57$, $p < 0.001$, Fig 5c).

Discussion

We have shown here that the proportion of trees with buttress or stilt roots does vary across topography, even when we control the effect of varying tree size associated to topography. Both support structures decrease with terrain slope (contrary to expectation) and stilt roots also increase in lower elevations. Tree size was the foremost important determinant of buttress occurrence at the individual level, but terrain properties also affected that in 30% of the species. Slope was the more frequently selected topographic predictor of the buttress probability at the within-species level. Conversely, elevation was the most important predictor of stilt root occurrence at this level, and higher occurrence was associated to low elevations, i.e. to valleys. In close detail, the analysis of the model species indicated that tree allometry (here, the height to diameter ratio) was actually more important to predict buttress occurrence than any other plant or topographic feature.

We tested the hypothesis that potentially unstable environments, such as the valleys with seasonally waterlogged sandy soils, or sloping terrains, would have an increased frequency of trees with stilt roots and buttresses. Although stilt roots are common in mangroves and low varzea forests, which are daily or seasonally flooded (Wittmann and Parolin 2005; Méndez-Alonzo et al. 2015), this is the first study to demonstrate that valleys of small streams, that are not subjected to predictable floods, also have a higher frequency of stilt roots than other topographical environments within the same forest. Buttresses were more common in less inclined terrains, which mean both the valleys and plateaus. Valleys are characterized by seasonal to permanent waterlogging, with roots limited to the surface due to the mostly hypoxic conditions of the soils (Fan et al. 2017). Moreover, valley trees have on average lower wood density (Toledo et al. 2016; Cosme et al. 2017) than trees in the higher elevations, which may increase susceptibility to buckling. Our analysis of the model species allometry also suggest that valley trees tend to have larger investments on crown size to the same H:D than trees in plateaus. This all suggests that valleys select for acquisitive strategies (low wood density, large crown to stem H:D) while limiting the capacity of anchorage by roots, which combined may render trees more susceptible to uprooting. Allocation of investments to buttress and stilt roots can potentially increase anchorage at a low carbon investment, which would be compatible to the acquisitive strategy. Beyond anchorage, stilt roots may contribute to the provision of oxygen to the active roots (Jeník 1973; Almeida and Almeida 2014) and thus have an obvious selective value in hypoxic soils.

We also detected a larger proportion of stilt roots in sloping than in flat terrains at low elevations and this is in accordance with the expectation that sloping terrains increase the likelihood of tree fall due to the asymmetry of gravitational load and increase the canopy exposure to winds, thus requiring extra support structures (Ennos 1993; Ataíde et al. 2015). However, buttresses, which are also expected to increase support and stability, were not more frequent in slopes, but actually the opposite. These seemingly contradictory results suggest that 1) the main function of stilt roots may not be anchorage, but aeration in waterlogged or flooded conditions, and species associated to these environments may retain this trait even when occurring in the slopes neighboring the valleys, or 2) buttresses or stilt roots may not be needed in sloping areas if trees adjust their allometry and architecture, decreasing their susceptibility to gravity or wind loads. Canopy height, estimated from LIDAR, is lower on slopes (26.9 m) than in plateaus (30.8 m) (M. Smith unpl. data), which may be a factor decreasing the vulnerability of trees on slopes. At the same time, trees of our model species had larger crown areas on slopes than trees of comparable H:D on plateaus, and if this pattern holds on the rest of the tree community, it would constitute a risk factor for uprooting or stem buckling. So far it is not clear why there is lower proportion of trees with buttresses in sloping terrain, and which strategies trees may be adopting to increase stability. Unfortunately, at the moment there is no wide mapping of canopy sizes and tree allometries across topography, which would probably help clarify that.

Buttresses were more common in less inclined terrains, which mean both the valleys and plateaus. Although plateau soils are deep and provide good anchorage (Quesada et al. 2010; De Toledo et al. 2011) and we did not expect plateaus to be more exposed to winds than slopes, larger tree heights may be the selective pressure for buttresses in this habitat. Taller trees are more exposed to wind and require support structures even if the other risk factor - crown size - was relatively smaller in plateaus as compared to the other habitats, in our model species. Actually, the challenge of increasing instability as trees grow taller can potentially be solved with either decreased crown area and/or investments in buttress.

At the individual level within species, the probability of having buttress increased mostly with tree size (here represented by diameter). Buttresses appear on tree trunks during periods of stress, as when trees reach the canopy (Chapman et al. 1998; He et al. 2012) and become more exposed to wind. In our studied forests trees tends to reach the canopy when they are around 20 to 30 cm DBH, regardless of species (Camargo 2018), and this was also the size where buttresses became more likely. Despite this large effect of tree size, the occurrence of buttress was also modulated by the topography in nine of the 29 abundant species, and these responses tended to be species-specific, despite of a more congruent effect of slope. It is interesting that at the individual level within species, the effect of slope was positive in four cases, while we saw a negative effect at the plot level. Thus, although the hillslope habitat may not select buttress specifically as the only strategy to provide stability, some species may use it. This points to the potentially diverse strategies adopted by species to cope with the same challenge of standing still in the face of external stress, and the need of a stronger emphasis in understanding this diversity.

In our model species, the probability of having a support structure, in spite of being influenced by tree diameter and the size of the crown, was mainly associated to a decreased height:diameter ratio. This indicates that regardless of the environment in which the tree grows, the slender trees tend to not have support structures. This seems contradictory with the mechanical laws indicating that slender trees are more susceptible to buckling (McMahon 1973; Chapman et al. 1998). However, on these species, trees with a higher H:D had a smaller canopy area, which can be a form of decreasing the risks associated to wind exposure and crown weight (Lewis 1988; Young and Perkocha 1994). On the other side, large crowns, even on stout trees, seem to be an important instability factor requiring support structures. Slender trees tend to develop where tree density and thus light competition is high, imposing the development of smaller crowns. Therefore, constraints along tree establishment may determine the allocation route that will lead to either the development of buttresses on large trees with large crowns, probably developing in more open and exposed conditions requiring investments on structures for stability, or slender trees with smaller crowns developing in crowded conditions, which may require less investments on stability. These model species illustrate the plasticity of above-ground allocation that trees may have, generating multiple ways to solve the problem of mechanical stability.

We have shown here that the most unstable environments, here represented by valleys with sandy and seasonally waterlogged soils, select a higher frequency of trees with support structures at the community level. However, individual traits, linked to stem size, crown size and their allometric relationships also influence the need of support structures. We conclude that support structures are not fixed species traits, their presence depending on individual plant´s allometric relationships and the instability factors imposed by environment.

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Table 1. Statistical summary of the best multiple logistic regression, selected by the AIC criteria, to explain the probability of occurrence of buttresses on 21 species as a function of diameter (D), environment (elevation and slope) and interactions. Standardized regression coefficients followed by the associated probability. Significance codes * p<0.05, ** p<0.01, ***p<0.001.

Species	**Diameter (D)**	**Elevation (E)**	**Slope (S)**	**D*E**	**D*S**	**E*S**
Eschweilera wachenheimii	1.17***	-	-	-	-	-
Eschweilera atropetiolata	0.84**	-	-	-	-	-
Brosimum rubescens	1.86***	-	-	-	-	-
Zygia racemosa	1.19***	-	-	-	-	-
Eschweilera pseudodecolorans	0.97*	-	-	-	-	-
Pouteria freitasii	1.74***	-	-	-	-	-
Swartzia recurva	1.78**	-	-	-	-	-
Brosimum parinarioides	2.81**	-	-	-	-	-
Eschweilera bracteosa	2.50**	-	-	-	-	-
Vantanea macrocarpa	1.28*	-	-	-	-	-
Iryanthera juruensis	1.08*	-	-	-	-	-
Osteophloeum platyspermum	2.80*	ns	ns	-	-	ns
Eperua duckeana	-	-	-0.84*	-	-	-
Eschweilera coriacea	2.25***	ns	-0.41*	-	-	-
Eschweilera truncata	0.98***	ns	0.86***	-	-	0.66*
Protium hebetatum	1.35***	0.55*	0.60*	-	-	-
Andira micranta	1.95*	1.83*	1.92*	-	-	2.48*
Micropholis guyanensis	ns	ns	-	-2.05*	-	-
Eperua glabriflora	2.22***	ns	ns	-1.65*	-1.76*	ns
Ecclinusa guianensis	ns	-	ns	-	-1.12*	-
Protium apiculatum	ns	-	ns	-	-1.91*	-

Figure legends

Figure 1: Partial plots of the best multiple linear regression models, selected by the AIC criteria, to explain the proportion of trees with buttresses (a) or stilt roots (b) by plot. The proportion of trees with stilt roots increases with slope on low elevations, but decreases with slope in higher elevations, as illustrated in the interaction on (b).

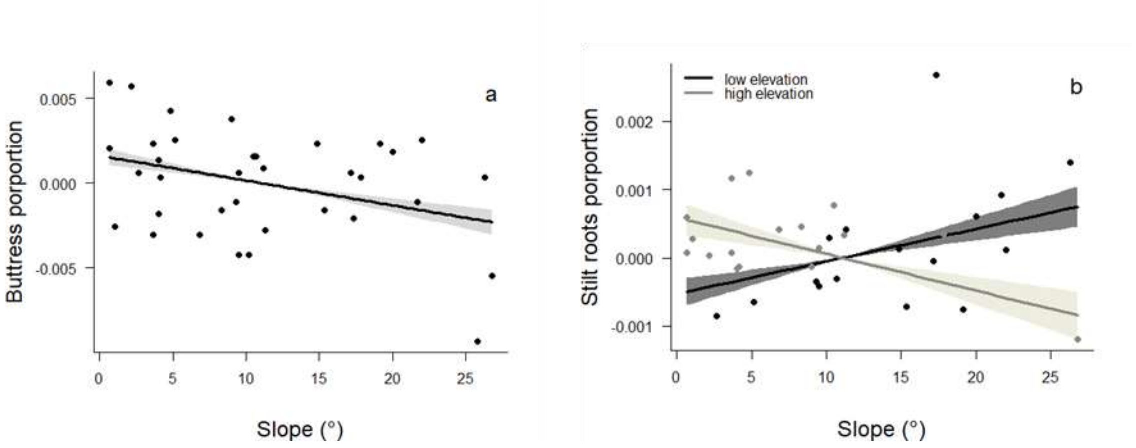
Figure 2: Partial plots of the best multiple logistic regression models, selected by the AIC criteria, to explain the probability of having a support structure (either buttress or stilt root) (a, b), the probability of having only buttress (c) or having only stilt roots (d), at the individual level.

Figure 3: Allometric relationships for two model species (Eschweilera coriacea and Eperua glabriflora) that may present buttress. H:D is the height to diameter ratio.

Figure 4: Variation of the allometric relationship between crown area and the ratio height:diameter (H:D) among topographic conditions. (a) the contrast among plateaus and slopes, and b) the contrast among valleys and slopes.

Figure 5: Boosted regression tree for the probability of buttress on two model species (a), the relative importance of predictors (b) and the partial plot of the best multiple logistic regression model, selected by the AIC criteria to explain the probability of buttress (c).

Figure 1. Partial plots of the best multiple linear regression models, selected by the AIC criteria, to explain the proportion of trees with buttresses (a) or stilt roots (b) by plot. The proportion of trees with stilt roots increases with slope on low elevations, but decreases with slope in higher elevations, as illustrated in the interaction on (b).



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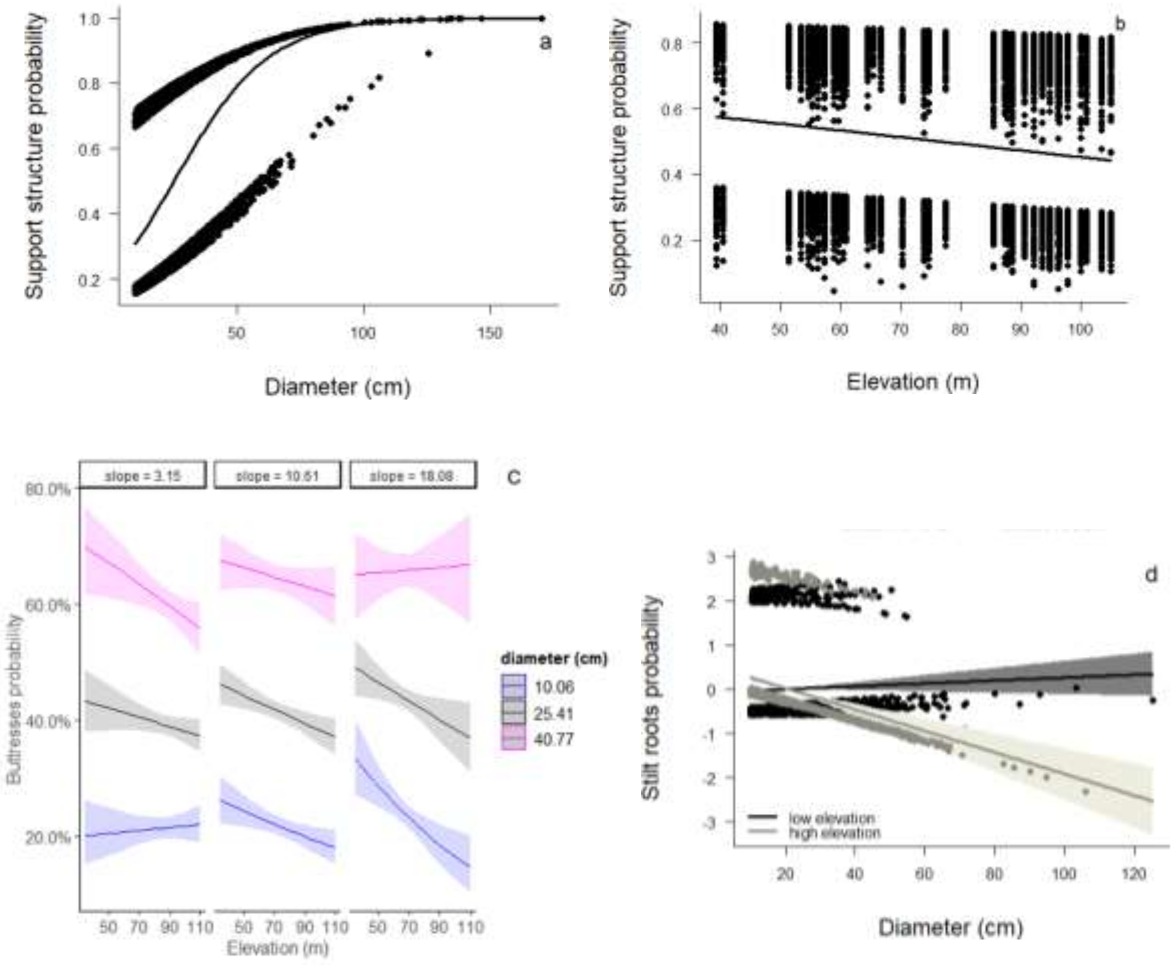


Figure 3. Allometric relationships for two model species (Eschweilera coriacea and Eperua glabriflora) that may present buttress. H:D is the height to diameter ratio.

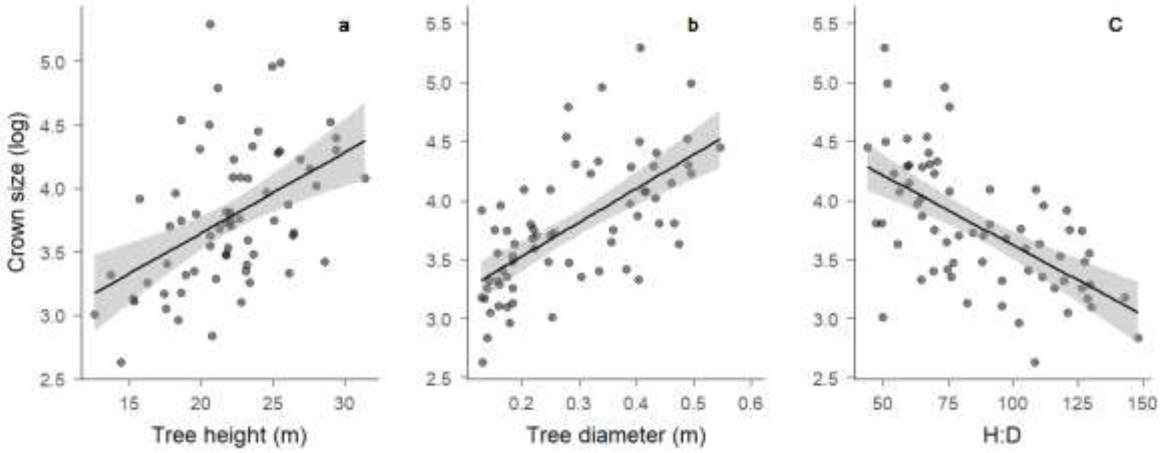


Figure 4: Variation of the allometric relationship between crown area and the ratio height to diameter (H:D) among topographic conditions. (a) the contrast among plateaus and slopes, and b) the contrast among valleys and slopes.

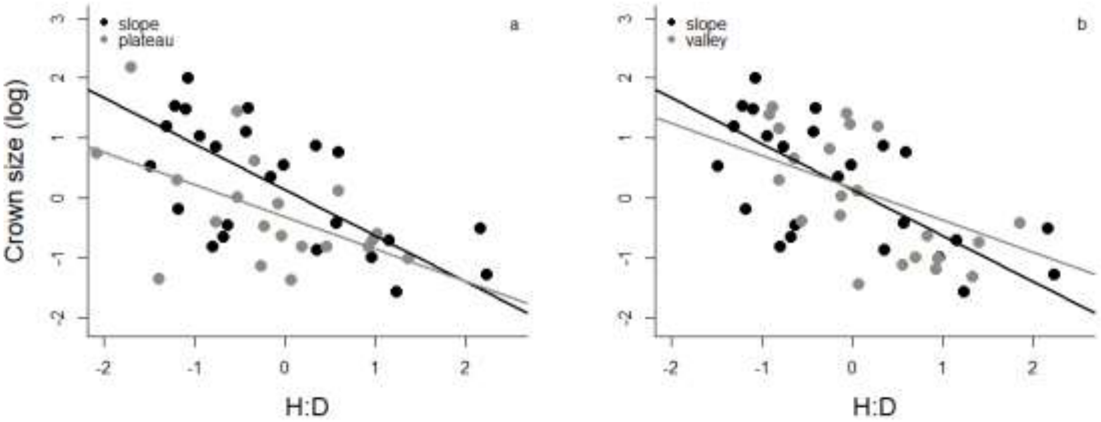
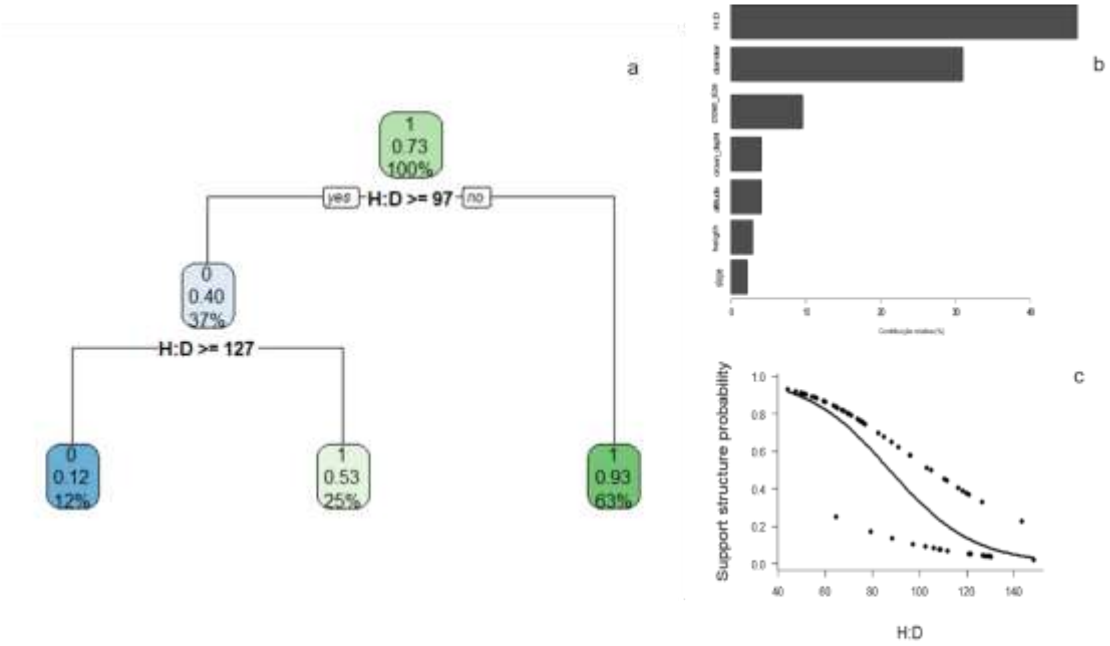


Figure 5. Boosted regression tree for the probability of buttress on two model species (a), the relative importance of predictors (b) and the partial plot of the best multiple logistic regression model, selected by the AIC criteria to explain the probability of buttress analysis, the H: D ratio of the model species.



Conclusão

As estruturas de suporte das árvores não são características fixas das espécies, mas dependem das relações alométricas de cada planta e das condições que o ambiente impõe. Os ambientes mais instáveis selecionam uma maior frequência de estruturas de suporte no nível da comunidade, mas as características individuais ligadas ao tamanho das árvores, tamanho de copa e às relações alométricas influenciam na necessidade de estruturas de apoio, de modo que a ocorrência destas estruturas depende das interações entre as características das plantas e dos fatores de instabilidade.

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