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87	Dedico este trabalho à minha mãe, por todo apoio e
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89	para que eu pudesse estar aqui. Por nunca ter
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109	Sinopse
110	Avaliou-se o efeito das condições hidro-edáficas na distribuição de espécies de árvores em
111	uma floresta de terra firme da Amazônia Central. Buscou-se evidências de co-relação entre
112	atributos funcionais hidráulicos e condições hidro-edáficas no solo, desde o nível do ramo,
113	caule e planta inteira em 28 espécies congenericas de 12 generos, em uma escala local. Cada
114	par de espécie dentro do gênero apresenta abundância diferencial em um ambiente (baixio e
115	platô).
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117	Palavras-chave: Filtro ambiental, densidade da madeira, anatomia da madeira, Reserva
118	Adolpho Ducke.
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#### 149

#### 150 **Resumo**

151

Filtros ambientais atuam diretamente sobre a distribuição e composição de espécies. No 152 entanto, não se sabe como solo e as condições hídricas abaixo do solo estão relacionados às 153 154 características hidráulicas do xilema. Nós examinamos a densidade da madeira e anatomia da madeira, altura, área foliar, área foliar específica e a razão entre área foliar: área de xilema 155 156 ativo no nível do ramo em espécies de árvore que ocorrem no baixio e platôs em uma floresta 157 de terra-firme. Esses ambientes apresentam diferenças na profundidade do lençol freático e 158 textura do solo. Nós medimos 20 traços funcionais em 28 pares de espécies congenéricas de 12 gêneros. Cada par com uma espécie associada a baixio e uma espécie associada platô. 159 160 Espécies associadas aos platô ou baixios mostraram diferenças que indicam investimentos distintos na prevenção contra a falha hidráulica e eficiência de condução, respectivamente. 161 162 Em platôs, as espécies apresentaram maior densidade da madeira, as médias mais baixas de 163 diâmetro do vaso e diâmetro hidráulico do vaso, menor área de xilema ativo no caule e menor área foliar específica. A relação entre alguns atributos se alterou nas condições ambientais 164 165 contrastantes, e espécies de diferentes alturas nos diferentes ambientes parecem investir em eficiencia e segurança hidráulica de maneiras distintas. Concluímos que mesmo em uma 166 167 escala fina, com poucos metros separando ambientes com condições contrastantes de textura do solo e profundidade do lençol freático, filtros ambientais podem impor restrições 168 ecológicas em árvores que poderiam explicar espécies de distribuição complementar na 169 170 Amazônia Central. Estas restrições podem ser mais fortes em espécies filogeneticamente 171 relacionadas, que mostram mais semelhanças e competem pelos mesmos recursos. Sugerimos que os atributos hidráulicos e suas relações com o meio ambiente devem ser melhor 172 173 compreendidos, especialmente a nível local. 174

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#### 180 Abstract

181 The importance of hydraulic architecture to the distribution patterns of trees in a Central182 Amazonian forest

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184 Environmental filters act directly on the distribution and composition of species. However, it 185 is not known how soil and belowground hydric conditions are related to hydraulic 186 characteristics of the xylem, branches and of the whole plant on a local scale. We examined wood density and anatomy, height, leaf area, specific leaf area, and the leaf area:sapwood area 187 188 ratio at the branch level in valleys and plateaus of the *terra-firme* forest in Central Amazonia. These environments present contrasting table water depths and soil textures. We measure 20 189 traits related to branches, stem, and whole plant in 28 congeneric species pairs from 12 190 191 genera, each containing one valley and one plateau species. Species associated with the 192 plateaus or valleys showed trait differences that indicate distinct investments in prevention against hydraulic failure and driving efficiency, respectively. On plateaus, species had higher 193 194 wood density, lower averages of vessel size and hydraulic diameter of the vessel, smaller stem 195 sapwood area and smaller specific leaf area. Some correlations between traits change 196 according to the contrasting environmental conditions, demonstrating that species have 197 different investments in traits according to the water conditions in the soil. The maximum 198 adult stature in contrast environments was associated with different investing in conductivity 199 efficiency through the xylem anatomy. We conclude that even in a fine scale, with few meters 200 separating contrasting soil texture and water table depth conditions, environmental filters may 201 impose ecological restrictions on trees that could explain species complementary distribution 202 in Central Amazonia. These filter may be stronger in phylogenetically closely related species, 203 which show more similarities and compete for the same resources. Thus, contrasting soil 204 texture and water table depth conditions may be important determinants of species composition and diversity. Thus, we suggest that hydraulic attributes and their relationships 205 206 with the environment must be better understood, especially on a local level.

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#### 262 Introdução

Em florestas tropicais, a disponibilidade hídrica no solo é um dos principais fatores que determinam a
distribuição (Balvanera, Quijas, and Pérez-Jiménez 2011; Engelbrecht et al. 2007), e a composição de
espécies de plantas (Jirka et al. 2007; Schietti et al. 2013). A disponibilidade de água no solo pode
exercer uma forte pressão seletiva na anatomia e na estrutura do xilema, resultando em variações
dessas características entre espécies que ocorrem em ambientes úmidos e entre espécies que ocorrem

268 em ambientes secos (Carlquist 1977; Fonti et al. 2010; Gleason et al. 2012; Gotsch et al. 2010).

A arquitetura hidráulica, isto é, a estrutura do sistema de transporte de água das plantas (Melvin T.

270 Tyree and Ewers 1991), influencia o transporte ascendente de água e nutrientes da raiz até as folhas.

271 Diferenças na estrutura dos vasos afetam a eficiência no uso da água, as taxas de fotossíntese, o

272 crescimento, e a sobrevivência (Santiago et al. 2004). Dessa maneira, a interação entre disponibilidade

hídrica e arquitetura hidráulica pode influenciar a distribuição de espécies de plantas ao longo de um

gradiente hídrico (Pockman and Sperry 2000).

Ao longo do gradiente de distância vertical do lençol freático na Reserva Adolpho Ducke há um

276 gradiente de disponibilidade hídrica do solo, que está relacionado com mudanças na composição de

277 espécies (Schietti et al. 2013). Diversos pares de espécies congenéricas em diferentes famílias parecem

278 se substituir ao longo do gradiente de distância vertical do lençol freático e é comum a ocorrência de

279 espécies relativamente restritas às áreas de entorno dos corpos d'água (baixios), onde o lençol aflora, e

espécies que ocorrem em áreas mais altas, ao longo das encostas e nos divisores de águas (vertentes e

281 platôs). Ainda não se tem conhecimento se os traços funcionais exibidos pelas espécies se relacionam

- com as condições hidro-edáficas no solo, e se poderia auxiliar na compreensão dos padrões de
- 283 distribuição de espécies em uma escala local.
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292	Objetivo geral:	
293	Avaliar se os atributos do xilema e da arquitetura hidráulica da planta podem explicar a	
294	distribuição espécies de árvores ao longo de um gradiente hídrico em uma floresta de terra firme na	
295	Amazônia Central.	
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297	Objetivos específicos:	
298	(i) Investigar se pares de espécies de árvore dentro de um gênero variam o investimento	
299	nas características da arquitetura hidráulica e do xilema de acordo com a disponibilidade de água no	
300	solo;	
301	(ii) Compreender qual a combinação de atributos do xilema e da arquitetura hidráulica	
302	permite que as espécies se estabeleçam em diferentes condições hídricas;	
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321		Capítulo 1
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324	of hydraulic architecture to distribution	
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#### **The importance of hydraulic architecture to the distribution**

338 patterns of trees in a Central Amazonian forest

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#### 349 **Summary**

- Species distribution and community composition may be the result of trait selection
   through environmental filters. If and how soil hydric conditions filter species in a local
   scale through their hydraulic traits could be the basis of hydric microhabitat
   partitioning.
- We analyzed hydraulic characteristics at the tissue (wood density and anatomy),
   branch (leaf area, specific leaf area, and the leaf area:sapwood area ratio) and whole
   plant level (height) for 28 pairs of congeneric species from 12 genera restricted to
   either valleys or plateaus of a *terra-firme* forest in Central Amazonia. These
   environments have contrasting table water depths and soil properties.
- Species associated with plateaus or valleys had characteristics that indicate distinct
   investments in prevention against hydraulic failure or hydraulic efficiency. On
   plateaus, species had higher wood density, lower average vessel area and hydraulic
   diameter of the vessel, smaller sapwood area and smaller specific leaf area. The

relationship between mean vessel hydraulic diameter and mean vessel area vs
maximum height was positive, plateau species had higher values of mean vessel area
and mean vessel hydraulic diameter for the same maximum height. This species have
different investments in traits according to the water conditions in the soil.

- In conclusion, even in a fine scale, within few meters height separating contrasting soil
   texture and water table depth conditions, environmental filters may impose ecological
   restrictions on trees that could explain species complementary distribution in Central
   Amazonia. Thus, contrasting water table depth and soil texture may be important
   determinants of species composition and diversity.
- 372

#### 373 Introduction

374 Understand how environment influences the distribution of species is a central issue in 375 ecology (Jennifer L Baltzer et al. 2009; Condit et al. 2000; Russo et al. 2005). Environmental 376 factors such as water and nutrients work as filters that can alter the flora composition. In some 377 occasions they might prevent the establishment and the survival of species with physiological 378 restrictions (Engelbrecht et al. 2007; Fortunel et al. 2014). The variation in the physico-379 chemical properties of soil and water are related with the occurrence and distribution of different species of trees (Balvanera, Quijas, and Pérez-Jiménez 2011; Groom 2004; Lopez 380 381 and Kursar 2003). These factors are important for the maintenance of high diversity on a local 382 scale and is a major selection force generating diversity (Daws et al. 2002; Fine et al. 2006). In 383 tropical forests, various studies have shown that there is a high species *turnover* on space associated to the edaphic and hydric variations (Tuomisto & Dalberg, 2000; Jirka et al., 2007; 384 Drucker et al., 2008; Schietti et al., 2013). However, the mechanisms that explain this high 385 species turnover in space and their association with hydro-edaphic variations are still poorly 386 387 known.

In environments where resource availability is heterogeneous, niche partitioning can promote a high diversity, as it facilitates species coexistence (Chesson et al. 2004; Jackson et al. 1995; Meinzer et al. 1999; Stratton, Goldstein, and Meinzer 2000). The mechanism that structure plant communities along water gradients is the hydrological niche segregation (HNS) (Araya et al. 2011, 2012; Bartelheimer, Gowing, and Silvertown 2010; Silvertown, Araya, and Gowing 2015; Silvertown et al. 1999). The HNS is the result of biophysical constraints to tissues that transport water, leading to a safety vs. efficiency hydraulic trade-off (Silvertown, Araya, and Gowing 2015). Soil water conditions influence processes in the plant
anatomy, both dry and wet ecosystems (J. L. Baltzer et al. 2008; Davies and Zhang 1991;
Webb, Wallis, and Stewardson 2012), affecting species co-occurrence at the local scale by
filtering contrasting strategies in the use of water resources through investment in different
key hydraulic traits (P.-L. Fu et al. 2012; K. a McCulloh et al. 2012).

400 The hydraulic architecture (HA) is characterized as "the structure of the water conduction system in plants" (Melvin T. Tyree and Ewers 1991). HA influences the ascending transport 401 402 of water and nutrients from roots to leaves (Aiba and Nakashizuka 2009; K. A. McCulloh et 403 al. 2015; Poorter, Bongers, and Bongers 2006). It describes the xylem hydraulic relations and 404 determines the amount of leaves that can be supplied by the hydraulic system of the plant (Cruiziat, Cochard, and Am Illio 2002; M T Tyree and Sperry 1989; Melvin T. Tyree and 405 Ewers 1991). One important part of HA is the xylem anatomy because it provides greater 406 407 efficiency for the water transport or higher hydraulic safety and mechanical support, depending on the plant's investment strategy (Baas et al. 2004; Poorter, Bongers, and Bongers 408 409 2006) . Species occurring in environments with more humid soil usually invest in wider and 410 fewer vessels within the active xylem area (sapwood area), maximizing the efficiency of 411 water transport in these plants (Olson et al. 2014; Schuldt et al. 2013, 2015). If there is no 412 limitation of soil water, different allocation strategies in the plant architecture. Greater investment in leaf area with relation to the sapwood area (La:Sa) and in height, can also 413 414 confer competitive advantages allowing higher light uptake and maximizing tree growth 415 (Barnard and Ryan 2003; Gleason et al. 2012; Mokany et al. 2003; Phillips et al. 2003)

416 In dry environments, or in soils with lower water availability, plants must deal with the water deficit and prevent cavitation and death by hydraulic failure (Baas et al. 2004; Sperry, 417 418 Meinzer, and McCulloh 2008). Among the traits of xylem to minimize the risk of embolism is the reduction in the diameter of the vessel compensated by an increase in the number of 419 420 vessels in the sapwood area. Generally, narrower vessels are immersed in a matrix of 421 relatively high density wood, due to the greater proportion of xylem occupied by fibers 422 (Fortunel et al. 2014; Hacke et al. 2001; Jacobsen et al. 2007; Pratt et al. 2007). Changes in 423 hydraulic architecture, such as an increase in the allocation for the sapwood area instead of an 424 investment in leaf area (Choat, Sack, and Holbrook 2007; Gotsch et al. 2010) and height minimize the loss of water, but also reduce the rate of photosynthesis influencing growth rate 425 (Delzon et al. 2004; McDowell et al. 2002). 426

427 Climatic changes can have great impact on soil water conditions ultimately affecting 428 plant species distribution. There are strong indications that the El Niño-Southern Oscillation (ENSO) and anomalies from the tropical Atlantic, are increasing in frequency in the last 100 429 years (R. Fu et al. 2013; Jose A Marengo et al. 2011) and have caused extreme droughts, with 430 alarming decrease in the level of the big rivers, specially in Amazonia (J. A. Marengo and 431 432 Espinoza 2015). This scenario of climatic extreme events can have a great influence on belowground water conditions, enhancing the environmental filters acting over hydraulic 433 434 plant architecture. Terra-firme (non flooded) forests in Central Amazonia exhibit fine scale 435 variations in topography that control the belowground hydric conditions (Chauvel, Lucas, and 436 Boulet 1987) with seasonally saturated soils and well drained soils separated by a few dozen of meters. The areas vertically more distant from the water table (plateaus) would be more 437 438 susceptible to prolonged periods with lower soil water content, but soils in the plateau have finer texture and hence greater water retention capacity than valley sandy soils. However, 439 440 evolutionary may be more able to deal with shortage of water soil due historical events of drough. Therefore, it is crucial to know how hydraulic architecture traits affect species 441 distributions in the present to improve prediction of effects of global change on future 442 443 distribution and community composition.

444 This study investigates hydraulic architectural traits from at the tissue, to branchs and 445 whole plant level to understand the patterns of distribution of trees in a Central Amazon terra *firme* forest. A steep change in plant species composition occurs along a gradient of vertical 446 447 distance from the water table in a scale of few meters (Schietti et al., 2013), providing the 448 perfect setup to understand changes of hydraulic architecture on plants submitted to the same climatic conditions. Many congeneric species in different families present complementary 449 450 distribution along this gradient of water table depth. It is common to find species mostly 451 restricted to riparian areas (valleys), where the water table emerges, and species mostly 452 restricted to higher areas (plateaus) and slopes, where the water table is deep. These pairs of 453 species with complementary distribution and recently divergence in phylogeny offer a good 454 model to understand adaptive and functional relationships, because in this way the control of 455 phylogenetic relatedness is included in the sampling design, instead of a posteriori tests. Thus, the following questions were investigated: 456

457 (1) Do species restricted to contrasting hydro-edaphic environments have opposed458 hydraulic architecture strategies?

- 459 (2) Does the relationship among hydraulic architecture traits change according to the460 hydro-edaphic environment?
- 461 (3) What combination of hydraulic trait allows the establishment of species in different462 soil hydric conditions?

#### 463 Materials and Methods

#### 464 Study site

465 The study was conducted in the Reserva Florestal Ducke (hereafter Ducke Reserve),

located 26 km north of Manaus (2° 55'47.80''S; 59°58'30.34''W), in Central Amazonia. The

467 reserve covers 10.000 ha (10 x 10 km) of dense humid *terra-firme* tropical forest, with a

468 canopy height around 30-37 m, and emerging trees up to 45 m (Ribeiro et al. 1999). The

469 average annual precipitation between the years 1982 and 2011 was more 1,500 mm, and the

470 monthly average temperature was 26.8°C (Marques-Filho et al. 1981). The dry season

471 (months with precipitation <100mm) occurs from July to September.

The relief is well dissected, forming a gradient of soil water and soil texture, here called the

473 hydro-edaphic gradient. Plateaus and valleys represent the extreme opposite in this gradient.

474 The higher plateau areas have clayey, well-drained soils, and the valleys very sandy soils.

475 Plateaus are flat or gently sloped (< 7 degrees of inclination), the underground water table can

be more than 20 m deep, and the altitude a.s.l. ranges between 90 and 120 m. Valleys are also

477 mostly flat or gently sloped, underground water table is near the surface (up to 1 m depth)

and can be permanently waterlogged in some areas during the rainy season (Drucker, Costa,

and Magnusson 2008; Tomasella et al. 2008).

480

#### 481 Species and individual selection

482 The species were selected from the database of trees with  $DBH \ge 10$  cm marked by

483 Carolina V. Castilho in 72 permanent plots at Ducke Reserve between 2001 and 2009.

Fourteen pairs of congeneric species of dicotyledonous trees (Fig. 1) distributed in the more

abundant families at the Reserve (Chrysobalanaceae, Burseraceae, Fabaceae, Lecythidaceae,

486 Myristicaceae, Sapotaceae) and with distributions mostly restricted to one of the extremes of

the hydro-edaphic gradient were selected. We paired for each genus a species mostly

488 restricted to valleys (hereafter valley species) and a species mostly restricted to plateaus

(hereafter plateau species), totaling 28 species. Usually the selected species presented high
abundance in an environment and were rare in contrasting environment, suggesting
environmental constraint in its distributions in the area of study. We prioritized species
relatively well resolved taxonomically according to the description in the literature and the
opinion of specialists.

Five adult individuals of each species were selected based on data from the last census (2007-2009). They were selected from the larger diameter classes, for each species. For *Cariniana micranta* 4 individuals were collected, because during the collection period some individuals had no fully-expanded leaves. The largest individuals within each species were excluded from sampling, to avoid senescent trees. The samples were taken between October 2014 and September 2015 for a total of 163 individuals.

500

#### 501 Xylem anatomy and density

502

A core of stem xylem 5.15 mm diameter and length approximately equal to the radius of the trunk (thus including sapwood and heart) was collected from each individual below the point of tree diameter measurement (1,30 m of soil), with a Pressler's borer. Samples were stored in sealed PVC tubes (to prevent breakage and desiccation) and taken to the laboratory. The wood specific gravity was determined for the first 5 cm of the sample from bark to heart, in the remaining of the sample, and in the entire sample, to allow comparison with other studies.

Sun exposed branches, with well developed leaves and around 1m long were collected from
the upper canopy with the aid of an experienced climber. At the base of the branch a 5 cm

512 long sample was collected for determination of wood specific gravity, with and without bark.

513 Wood specific gravity was determined by the water displacement method (Hacke *et al.*,

514 2000). Weights were measured to the near 0.001g, the dry weight after drying 72h at  $105^{\circ}C$ .

Two individuals of each species were sampled for the wood anatomical measurements. The mean vessel area, mean vessel hydraulic diameter and vessel density were determined from samples of terminal branches. Sub-samples were removed from the base of the branch, stored in the FAA solution (Formalin, acetic acid and alcohol) for 72 hours and subsequently in alcohol 70%. These samples were taken to the laboratory, placed in glycerin and cross-sections 15-40 µm thick were cut with a rotation microtome (Precision sliding microtome American Optical 860). These cuts were clarified with 50% sodium hypochlorite
(for 30 seconds), stained with 1% aqueous safranin (2 minutes). An alcoholic dehydration
series from 30% to absolute ethanol 100% was then performed, cuts stayed 5 minutes in each
solution, then were transferred to pure xylene and mounted with permount.

525 The cross-section cuts were photographed with a digital camera (Axiocam Erc5s)

526 connected to a light microscope (Zeiss-Axio lab A1). Pictures were taken at the 5x

527 magnification, with a  $20\mu m$  reference scale, to allow capturing the maximum variability of

vessel size. A picture 352 cm<sup>2</sup> in area was selected for anatomical analyzes in the software
 ImageJ 1.48 (http://rsb.info.nih.gov/ij/), where the vessel elements were characterized in a

transverse plane in a semi-automated procedure (see details in Table 1). In each image, we

estimated only the average size of vessels and vessel density by their areas and numbers (*A*,

532 mean vessel area; *N*, number of vessel for unit of area). From these measures was estimated

some strategies related to specific conductivity of xylem. The mean vessel diameter (D=(A/

534 (FV=A\*N) and the ratio between size and number

of the vessel, S, (S=A/N) (Zanne et al. 2010), the mean vessel hydraulic diameter, Dh=( $\Sigma$ 

536  $D^4/n$ ), where *n* is the number of vessels (Scholz et al. 2013). Both circular and elliptical

537 vessels were treated as circles in diameter calculation. The conductivity index was estimated

as  $Ik=N*Dh^4$  (Fortunel et al. 2014). The xylem specific conductivity, Ks, was estimated using

the equation of Hagen-Poiseuille, Ks=( $\pi/128 \eta A$ ) x  $\Sigma D^4$ , where A is the cross-sectional area

of sapwood in the branch and  $\eta$  is the viscosity of water (1.002 x 10<sup>-9</sup> Mpa s<sup>-1</sup> in 20°C)

541 (Melvin T. Tyree et al. 1991).

In a 2 cm long sample taken from the base of each branch we measured heartwood depth,xylem depth and total diameter with a caliper, under a stereomicroscope.

544 Sapwood area (Sa= $\pi$ r<sup>2</sup>) was obtained from the subtraction of heartwood area from the total 545 branch area. For the stem, the measurement of sapwood area was performed in the same 546 cylinder collected with a Pressler's borer that was used to estimate the wood specific gravity. 547 We positioned the sample over a strong point light source (we used an Ipod) so that vessels 548 were parallel to the light beam, allowing the passage of light where these were open. This was 549 done under a estereomicroscope, and with a caliper we measured sapwood depth according to 550 the extension of the open vessels along the core. In this method we assume that active vessels 551 are open and inactive ones have been filled in the tylosis process. Tylosis occurs in 8 of the 12 genera studied, according to http://insidewood.lib.ncsu.edu/. We didn't find information on 552

tylosis formation\_for *Dipteryx*, *Pouteria*, e *Swartzia*.

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#### 557 Leaf area, specific leaf area and leaf area:sapwood area ratio

Branches used for leaf area determination were the same used for sapwood and other 558 559 anatomical measurements. Immediately after collection, branches were packed in closed 560 plastic bags containing a wet paper towel, and taken to the laboratory. Leaf area was measured by scanning all leaves of the branch (without petiole) and images were analyzed 561 562 with ImageJ software. To obtain specific leaf area (SLA) two leaves of the same branches 563 were scanned separatly and taken to the oven at 65°C, for obtaining the dry weight. The 564 specific leaf area was calculated as the ratio between leaf area and dry weight (cm<sup>2</sup> g-<sup>1</sup>). 565 We determined the ratio between leaf area and sapwood area (La:Sa) and the sapwood area in

branch (cm<sup>2</sup>)., the sapwood depth (cm) and sapwood area (cm<sup>2</sup>) on the stem. To make the
estimates of sapwood area of the trunk comparable between trees with different diameters, we

also calculated the proportion of sapwood area:basal area (Sa:Ba) on the trunk.

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#### 570 Mean height, maximum height, diameter at breast height

In all sampled species the height of the five individuals selected were measured, using a measurement tape uplift in the pole pruner by the climber and stretched vertically from top canopy to the ground. The maximum value among the five obtained for each species was adopted as the maximum height of the species, and the mean value wad adopted as mean height. All individuals had the DAP (diameter at breast height, 1.3 m from the floor) measured during sampling.

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#### 578 Data analyses

579 To evaluate if species in the same genus occurring in contrasting hydric conditions invest

differently in hydraulic architecture traits, we performed paired T tests using the mean valuesof species traits.

The influence of evolutionary history in these correlations was considered through analyses of
phylogenetic independent contrast (PIC). We built a phylogenetic tree using PhyloMatic v.3

584 (Webb & Donoghue, 2005), based on the maximum resolution of the phylogeny of

angiosperms (árvore R20120829). The phylogenetic correlations were calculated using

586 Phylocom 4.2. The PIC was calculated as the average difference in the trait value, for two

descendant species of the same node. For this analysis the length of the branch varies in scaleof 0 to 1.

To assess whether the relationship between the traits changes with the environment, we performed analyses of covariance (ANCOVA) between traits, considering valleys and

591 plateaus as factors.

592 To evaluate the patterns of covariation between multiple traits and hydraulic strategies of

species in different environments, we performed a principal components analysis (PCA)

including all attributes evaluated in this study. This analysis was performed considering either

the original values or those derived from the phylogenetic independent contrast analysis.

596 Traits that have not met the assumptions of normal distribution (vessel mean hydraulic

597 diameter, sapwood area (stem), specific leaf area, specific xylem conductivity, vessel size to

number ratio ) were log-transformed. All analyzes were performed using R 3.2.2 statistical

platform. Probabilities (P) below 0.1 were considered as marginally significant.

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#### 612 **Results**

Plateau species had higher values of wood specific gravity, while valley species had higher mean vessel hydraulic diameter, mean vessel area, specific leaf area and stem sapwood depth (Fig. 2). After accounting for the basal area of the tree (sapwood area: basal area), valley species presented higher proportions of conducting area in the stem. The other evaluated traits (mean height, maximum height, ratio La:Sa, Leaf area, ratio mumber:size, specific xylem condutivity, vessel density, vessel fraction) were not different between the sister species

619 occurring in contrasting hydro-edaphic conditions (results not shown). Species mean,

620 minimum and maximum values are presented to show the variability of seven functional traits

621 (Table 4).

Wood specific gravity in the stem was 8% higher (mean =  $0.78 \text{ g cm}^{-3}$ , range  $0.60 \text{ cm}^{-3}$  to

623  $0.95 \text{ cm}^{-3}$ ) in plateau species than in the sister valley species (mean=  $0.71 \text{ g cm}^{-3}$ ; range 0.47

 $cm^{-3}$  to 0.92 cm<sup>-3</sup>, paired test P=0.01, Fig.2a). Sapwood area: basal area ratio (Sa:Ba) in

valley species were 23% higher (mean = 0.6, range 0.28 to 0.90) than in the plateau sister

species (mean = 0.4 range 0.15 to 0.90; paired test, P=0.01, Fig.2b) and sapwood depth in

stems of valley species was 21% (mean = 6.51 cm, range 3.19 to 12.13) larger than for the

plateau sister species (mean = 4.75 cm, range 1.53 to 9.21; paired test, P = 0.01, Fig.2c).

629 Therefore, plateau species have denser wood, while valley species have higher area and depth

630 of conducting tissue in stem.

631 Three plateau species Cariniana micranta, Pouteria flavilatex and Licania heteromorpha had

high values of mean vessel hydraulic diameter and mean vessel area. We removed them from

the paired T-tests because they are the only deciduous species in our sample, shedding leaves

634 during the dry season, what provides a scape mechanism that allows the maintenance of wide

635 vessels without the risk of hydraulic failure in this environment. After removing these three

- species from the analyses, species occurring in the valleys had higher values of vessel area
- and mean vessel hydraulic diameter than their sister species in plateaus (paired test, P = 0.01,

Fig.2d, Fig.2e). Not only mean vessel size is higher on valleys but also a higher frequency of

639 large sizes is observed, as compared to plateau (Fig. 3).

Average and maximum adult height did not differ between valley and plateau species (resultsnot shown). Also, there was no difference between species in contrasting environments

considering the diameter at breast height, basal area, the height: diameter ratio and leaf area
and leaf area:sapwood area ratio (La:Sa) at the branch level. SLA did differ between
environments, being higher on valley species (paired test, p= 0.02, Fig.2f).

645 Positive correlations were observed between mean vessel area, the mean vessel hydraulic

646 diameter, hydraulic conductivity of the xylem and maximum height (Table 2, Fig. 4a, c,

Fig.6a). Vessel density and the sapwood area of the stem showed positive correlations with

648 maximum adult height (Table 2, Fig. 4e). Leaf area, specific leaf area, and La:Sa showed

649 negative correlation with mean height of species (Table 2, Fig.4 b,d,f). Cariniana micrantha

650 was outlier (showed high leaf area associated with high values of height, contrasting with the

651 general pattern of other species), therefore was removed from the analysis and is shown in

652 gray on graphs (Fig. 4b, d, f).

Most relationships between traits were the same in plateaus and valleys (Fig. 4, 5 and 6).

However, relationships between mean vessel hydraulic diameter, mean vessel area and the
species maximum height differed between environments. In plateaus, there is a higher
increment in the mean vessel area and in the mean vessel hydraulic diameter with the

657 increasing maximum height of species than in the valleys (Fig. 4a, c).

There was a negative relationship between Sa:Ba and stem wood specific gravity (Table 2,

Fig 5d). The relationship between wood specific gravity (stem) and maximum height was

only observed when the phylogenetic correction was done (Table 2). No correlation was

observed between wood specific gravity (branch) and vessel density, mean vessel hydraulic

diameter and vessel fraction (Table 2, Fig. 5c, e, f).

663 The relationship between specific conductivity of xylem and vessel density were differente

between environments, and also the relationship between vessel density and vessel mean

665 hydraulic diameter (Table 2, Fig. 6f, Fig.7). The relationship between specific xylem

666 condutivity and ratio number:size, vessel fraction, mean vessel hydraulic diameter, mean

667 vessel area and were positive in all the cases (Tabela 2, Fig. 6b, c, e).

Four components of the PCA analysis captured 77% of the trait variation among species. The
first two components explained 58% of total variation (Fig. 9, Fig. 8). The first PCA axis was
defined by the coordination between traits that confer higher water transport (higher values of

671 mean vessel hydraulic diameter, mean vessel area, and specific conductivity in the xylem) or

higher hydraulic safety (vessel density and specific leaf area). The second axis of PCA was

673 defined by the coordination of traits that may confer a higher mechanical resistance and

674 protection against attack from pathogens and herbivory (wood specific gravity) and sapwood

conductivity area (Sa:Ba, sapwood depth and sapwood area). In general, the results remained 675

consistent when phylogenetic relationships were included. (Fig. 9). 676

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#### **Discussion** 678

Species traits in contrasting environments 679

We investigated if pairs of congeneric tree species presented differences in hydraulic 680 architecture traits in response to different soil water conditions. We focus on two contrasting 681 682 environments (plateaus and valleys) that differ in water table depth and soil texture, but lie 683 few meters from each other on Central Amazonian forests. We found a different combination

684 of hydraulic architecture trait values for species associated to each environment that is

685 consistent with the hypothesis that soil hydrological conditions are filtering species in this

local scale. Plateau species specialize on hydraulic safety, having high wood density, lower 687 mean vessel hydraulic diameter, mean vessel area and smaller stem cross-sectional sapwood

688 area, while valley species specialize on hydraulic efficiency with opposed trait values.

689 Higher wood specific gravity on plateau species indicates that variations in the wood specific 690 gravity related with differences in soil water can emerge locally within the same genus. Higher values of wood specific gravity are associated with security against the hydraulic 691 692 failure (Hacke et al. 2001) and are usually found in drier environments where the xylem can 693 suffer negative pressures (Jennifer L Baltzer et al. 2009). With the reduction of water in the 694 soil the xylem vessels may suffer mechanical stress and risk of air seeding in the water 695 column, which may prevent transport (Jacobsen et al. 2005). A strategy reached by plants is the presence of a matrix of fibrous tissues, with wood of high-density and small-caliber 696 vessels (Jerome Chave et al. 2009). 697

698 In the valleys, species showed investments in traits that increase efficiency in water transport

as observed before in more humid conditions (Olson et al. 2014; Schuldt et al. 2013, 2015). 699

Tree species occurring in plateaus display narrower vessels on average, but a large variation 700

of size within plant, immersed in a relatively small sapwood area. The strategy observed in 701

these species allows them to achieve a good specific conductivity in the xylem and at the 702

703 same time prevent against hydraulic failure. These species invest in a wide range of vessel diameters with a few very wide vessels, which would reduce the number of vessels that are 704 705 lost in the case of a severe drought. Another strategy executed by plateau species, which also 706 prevents against the hydraulic failure, is investment in many narrow vessels possibly 707 aggregates. The higher specific conductivity in xylem gives support to the theory that the high 708 interconnectivity of the vessels would increase the hydraulic conductivity in the xylem (Loepfe et al. 2007; Martinez-Vilalta et al. 2012). With these strategies, plateaus species may 709 710 reduce the hydraulic damages during dry seasons and drought events kipping the water supply to leaves. This is why decidious species keeps large water supply to leaves without hydraulic 711 712 damage.

713 Leaf traits seem to show less differentiation than xylem traits between species in contrasting 714 hydro-edaphic habitats. Only the SLA differed between environments, plateau species having 715 lower mean values of SLA compared to sister species in the valleys. Lower SLA reflects 716 greater investment in leaf mass for a same leaf area, which is a typical strategy in dry environments or in soils with limitation of nutrients (Wright, Westoby, and Reich 2002). 717 718 Also, lower SLA may indicate a defense mechanism against herbivory and attack of pathogens (Fine et al. 2006). Fine et al. (2006) found that sandy soil specialists, which are 719 720 limited by nutrients, had lower SLA, which is associated to higher chemical and structural 721 protection against herbivory. In the present study, the species with lower SLA are associated 722 with clayey soil (plateau), which is the environment with higher hydric restriction, but not the higher nutrient limitation. Therefore, our results suggest that SLA of adult trees is more 723 724 associated to ground water conditions than with the restrictions of nutrients and related 725 pressure of herbivores. Other traits such as leaf longevity should be investigated to understand how investments in structural tissues change the strength and durability of leaves and how this 726 727 confers advantage in dry environments.

We found no difference in the mean height and in the maximum height of species in

contrasting environments. The valleys are vertically close the water table, which would give

trees unlimited access to water by roots or even conditions of excess of water in the soil,

- during the rainy seasons. The larger mean vessel area and in the mean vessel hydraulic
- diameter found in valleys (excluding 3 species) could minimize the costs associated with the

resistance in the transport system and enable higher statures (Enquist, West, and Brown 1999;

- Ryan, Yoder, and Mountain 1997). The reduction in investment in tissues that confer a higher
- wood specific gravity in the valleys could also enable species to achieve greater height. In the

more humid areas, higher values of SLA can be associated with higher photosynthetic
capacity, due to the low cost of production of structural leaf tissues, which could maximize
growth in height. However, the trees that occur in those habitats may suffer with frequent
disturbances caused by winds that could induce differential mortality (Toledo, Magnusson,
and Castilho 2013) preventing them to reach their full potential heights. Future studies should
consider both factors (water, soil and disturbance regimes) for better understanding of the
height potential of species occurring in different habitats.

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#### 744 Trait correlations in contrasting environments

745 We evaluated the correlation between 20 functional traits at the tissue, branch, and whole 746 plant level in 28 species of trees occurring in contrasting water table depth and soils texture 747 conditions. Part of these correlations differed between the two environments, suggesting 748 functional adjusts to contrasting soil water conditions. Mean vessel hydraulic diameter and mean vessel area showed a negative correlation with vessel density, and these relations 749 750 showed a tendency to differ between environments. Several studies have already shown a negative relationship between traits related to water transport evidencing a trade-off between 751 752 hydraulic efficiency and safety (Olson et al. 2014b; Poorter et al. 2010; Russo et al. 2010; 753 Schuldt et al. 2013b; Sperry, Meinzer, and McCulloh 2008b; Zanne et al. 2010). These 754 negative relationships are mainly due to a limitation of xylem biomechanics. However, our 755 results suggest that environmental conditions may adjust the trade-off relationships in order to 756 ensure higher efficiency or safety in water transport depending on wetter or drier conditions, respectively. For example, we found trees with larger hydraulic vessel diameter in plateau 757 758 reached larger heights compared to valleys. The influence of environmental conditions 759 changing these relationships shows that the hydro-edaphic conditions may work as 760 environmental filters selecting trees hydraulic responses.

The maximum height of trees showed a positive correlation with traits that increase the hydraulic efficiency. The mean vessels hydraulic diameter, the mean vessel area, the ratio between size and number of vessels, the specific conductivity of the xylem and the sapwood area in the stem co-varied positively with the maximum height in the species. Among these relations, as the species maximum height increase the mean vessel area, the mean vessel hydraulic diameter and the ratio between size and number of vessel increased at distinct increment rates in the two hydro-edaphic conditions. Unlike our expectations, across the species that occur in drier environment these relationships were more expressive, evidenced

by a higher beta coefficient. Wider vessels in taller species can compensate hydraulic

resistance imposed by a long system of water transport (Becker, Meinzer, and Wullschleger

2000; Fan et al. 2012; Martínez-Cabrera et al. 2011; Poorter et al. 2010; Preston, Cornwell,

and DeNoyer 2006; Zach et al. 2010). The positive relationship between the tree height and

traits that increase the water transport efficiency can be functionally suitable for the

competitive gain increasing light capture and photosynthetic rates and maximizing growth

(Scoffoni et al. 2015; Zhang et al. 2009). This strategy may ensure higher fitness in the driestenvironment, especially if the roots of these trees can reach the underground water table.

777 The height of the trees showed no relation with wood specific gravity. Other studies showed 778 that the carbon gain in trees has a controversial relationship with investment in tissues of 779 sustention. Some studies showed a positive relationship between height and wood specific 780 gravity (FALSTER and WESTOBY 2005; ter Steege and Hammond 2001), other studies 781 found a negative relationship (Martínez-Cabrera et al. 2011; Preston, Cornwell, and DeNoyer 2006; Thomas 1996), and many reported no relationship (Aiba and Nakashizuka 2009; Z.-X. 782 783 Fan et al. 2012; van Gelder, Poorter, and Sterck 2006; Poorter et al. 2010). The highest rates of height growth are more related with the hydraulic properties of xylem, a high specific leaf 784 785 conductivity, and with the photosynthetic capacity of the plants (Brodribb, Holbrook, and 786 Gutierrez 2002). Thus, it is expected a stronger relationship between height and xylem traits 787 and leaf traits than between height and wood specific gravity, as found in the present study.

788 The wood specific gravity showed no relation with the xylem traits. Some studies already 789 showed a positive relationship between the wood specific gravity and vessel density 790 (Martínez-Cabrera et al. 2011; Preston, Cornwell, and DeNoyer 2006). Higher values on these 791 characteristics prevent against hydraulic failure events and are usually seen in dry 792 environments. If vessel density presents negative relation with vessel diameter, we would expect also a negative relation between wood specific gravity and traits that increase the water 793 794 transport efficiency in the xylem (Anderegg and Meinzer 2015; Martínez-Cabrera et al. 2011; 795 K. A. McCulloh et al. 2015; Preston, Cornwell, and DeNoyer 2006). Thus, wetter locations would present less dense wood and wider vessel diameter, higher xylem specific conductivity 796 797 and a higher mean vessel area. However, the lack of relationship between the wood specific 798 gravity and xylem traits was already observed and is documented that the wood specific 799 gravity is decoupled from vessel traits (Fan et al. 2012; Hacke and Sperry 2001; Martínez-800 Cabrera et al. 2009; Poorter et al. 2010; Russo et al. 2010; Zanne et al. 2010) and leaf traits

(Baraloto et al. 2010). Wood specific gravity is a key trait and relates to several aspects of life
history, mechanical resistance, hydraulic safety, and with sustaining tissues (fiber) and storage
(parenchyma), which should be analyzed in future work.

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#### 806 Conservatism of wood traits

807 Our results showed that most part of the correlations between species hydraulic architecture 808 traits were consistent despite the phylogenetic relations among species, indicating that for 809 most traits exists evolutionary conservation. However, some correlations existed only when 810 phylogenetic contrast was not used (e.g. maximum height versus vessel density, mean height of the species versus leaf area) and some correlations existed only when phylogenetic 811 relations were considered (e.g. wood specific gravity versus maximum height, wood specific 812 gravity versus Sa:Ba, wood specific gravity versus sapwood area in the branch, wood specific 813 gravity versus mean vessel hydraulic diameter, wood specific gravity versus mean vessel area 814 815 and wood specific gravity versus leaf area). When a correlation is only seen when the 816 phylogenetic contrast is considered can be a signal of strong adaptive significance between 817 the characteristics, and that correlation between traits is not always mirror the cross-species 818 traits correlations (D. Y. Fan et al. 2011; Maherali and DeLucia 2000; Schafer, Oren, and 819 Tenhunen 2000). When correlations are only observed without phylogenetic contrast, means 820 low phylogenetic signal and higher lability in characteristics (Preston, Cornwell, and DeNoyer 2006). The principal components analysis (PCA) also showed that some attributes gain 821 822 strength (related more to the main axis of the analysis) while others become weaker, when the 823 phylogenetic relations were considered. It is already known that wood specific gravity is 824 phylogenetically conserved (Jerome Chave et al. 2009; Jérôme Chave et al. 2006; Swenson 825 and Enquist 2007), and that the xylem anatomy traits, such as vessel area and density, are 826 more plastic (von Arx, Archer, and Hughes 2012; Scoffoni et al. 2015). In the present study, 827 the wood specific gravity, the mean vessel area, the mean vessel hydraulic diameter showed 828 different responses of soil water conditions. The functional response of trees under different 829 environmental conditions may be the result of divergence of traits within the lineages. The 830 lack of consistency between the some correlations when phylogenetic contrast is used can be the result of traits that present higher plasticity according with the local water condition. 831

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### 837 Conclusion

This is the first study to our knowledge showing differences in hydraulic architecture 838 839 characteristics in tropical trees in a fine scale of few tens of meters between environments with contrasting water and edaphic conditions. Here, we show differences in hydraulic 840 841 architecture at the leaf, branch, stem and at the whole plant level of species with 842 complementary distributions associated with plateaus and valleys, environments with different water table depth and soil texture. These variations in local hydro-edaphic conditions 843 844 appear to be a strong environmental filter which leads to adjustments in the xylem, leaves, 845 stem and in the whole plant and may explain the distribution of closely related species in such diverse environments. In a scenario of climate changes, knowing the response of tree species 846 847 anatomical, physiological and morphological traits to soil water conditions allows predictions 848 about the establishment, survival and distribution of trees.

849

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- Table 1. List of 20 functional traits measured at the branch, stem and whole plant level for thisstudy with respective abbreviations and function

Trait	Abreviat	Organ	Function	Unit		
Diameter at breast	DBH	stem	Mechanical strength / Sap	m		
Height	Н	whole	Resource use	m		
Maximum height	Hmax	whole	Resource use	m		
Sapwood depth	DS	stem	Sap conduction	cm		
Sapwood area	Sa	stem	Sap conduction	cm <sup>2</sup>		
Sapwood area: Basal	Sa:Ba	whole	Mechanical strength / Sap			
Wood density	WD	stem	Mechanical strength	g cm <sup>-3</sup>		
Wood density	WD	branch	Mechanical strength	g cm <sup>-3</sup>		
Leaf area	La	branch	Resource use	m²		
Sapwood area	Sa	branch	Sap conduction	cm <sup>2</sup>		
Leaf area:Sapwood area	La:As	branch	Resource capture and			
Specific leaf area	SLA	leaf	Resouce capture	cm <sup>2</sup> g <sup>-</sup> 1		
Vessel density	VD	branch	Sap conduction	n μm-²		
Vessel diameter	Dm	branch	Sap conduction	μm-2		
Vessel size to number	S	branch	Sap conduction			
Mean vessel area	А	branch	Sap conduction	μm-2		
Vessel fraction	VF	branch	Sap conduction			
Xylem specific	Ks	branch	Sap conduction	kg m-1		
Vessel mean hydraulic	Dmh	branch	Sap conduction	μm-2		
Diameter hidraulic	Dh	branch	Sap conduction	μm-²		
Conductivity index	Ik	branch	Sap conduction	n μm-²		
	Trait Diameter at breast Height Maximum height Sapwood depth Sapwood area Sapwood area: Basal Wood density Wood density Leaf area Sapwood area Leaf area:Sapwood area Specific leaf area Vessel diameter Vessel diameter Vessel size to number Mean vessel area Vessel fraction Xylem specific Vessel mean hydraulic Diameter hidraulic Conductivity index	TraitAbreviatDiameter at breastDBHHeightHMaximum heightHmaxSapwood depthDSSapwood areaSaSapwood area:BasalSapwood area:BasalWood densityWDWood densityWDLeaf areaLaSapwood areaSaSapwood areaSaLeaf areaLaSapwood areaSaLeaf area:SaSpecific leaf areaSLAVessel densityVDVessel diameterDmVessel size to numberSMean vessel areaAVessel fractionVFXylem specificKsVessel mean hydraulicDmhDiameter hidraulicDhConductivity indexIk	TraitAbreviatOrganDiameter at breastDBHstemHeightHwholeMaximum heightHmaxwholeSapwood depthDSstemSapwood areaSastemSapwood area:BasalSa:BaWood densityWDstemWood densityWDbranchLeaf areaLabranchSapwood areaSabranchLeaf areaLabranchSapwood areaSabranchSecific leaf areaSLAleafVessel densityVDbranchVessel diameterDmbranchVessel size to numberSbranchVessel fractionVFbranchVessel fractionVFbranchVessel mean hydraulicDmhbranchDiameter hidraulicDhbranchConductivity indexIkbranch	TraitAbreviatOrganFunctionDiameter at breastDBHstemMechanical strength / SapHeightHwholeResource useMaximum heightHmaxwholeResource useSapwood depthDSstemSap conductionSapwood areaSastemSap conductionSapwood area:BasalSa:BawholeMechanical strength / SapWood densityWDstemMechanical strengthWood densityWDbranchMechanical strengthLeaf areaLabranchResource useSapwood areaSabranchResource captureSapwood areaSabranchResource capture andSpecific leaf areaSLAleafResource captureVessel densityVDbranchSap conductionVessel diameterDmbranchSap conductionVessel size to numberSbranchSap conductionVessel fractionVFbranchSap conductionVessel fractionVFbranchSap conductionVessel mean hydraulicDmhbranchSap conductionDiameter hidraulicDhbranchSap conductionDiameter hidraulicDhbranchSap conductionConductivity indexIkbranchSap conduction		

1233

**Table 2.** Relationships between hydraulic architecture traits of 28 species occurring in two contrasting environments (plateaus and valleys). Values of the effect relative magnitude (slope) of the trait, environment or the interaction between both in the relationships are showed followed by it the significance level (.,0.05 < P < 0.07; \*, P < 0.05; \*\*,P < 00.01; \*\*\*,P < 0.001). PIC, show the slope of the relationships using phylogenetic independent contrast

Trait relationships	Standardized beta coefficient								
	Trait	PIC	Environment	Interaction					
Maximum Height									
Vessel density	-0.33 **	-0.24	0.35	-0.27					
Vessel area	0.38 ***	0.60 ***	-0.22	0.59*					
Ratio size:number	0.29 ***	0.60 ***	-0.19	0.59.					
Xylem specific conductivity	0.53**	0.49**	-0.21	0.1					
Vessel mean hydraulic diameter	0.41 ***	0.62 ***	-0.23	0.57 *					
Sapwood area (Stem)	0.98 ***	0.63 ***	-0.56*	-0.35					
Height									
Leaf area	-0.76 *	0.14	0.03	0.72*					
Ratio leaf:sapwood area	-0.69*	-0.07	0.19	0.44					
Specific leaf area	-0.70**	-0.46 *	-0.46	0.43					
Wood density (stem)									
Maximum Height	-0.34	-0.42*	0.48	0.36					
Depth sapwood	-0.86 ***	-0.58 **	0.06	0.44					
Ratio sapwood:basal area	0.32	-0.39*	0.37	-0.34					
Leaf area	-0.33	-0.40*	0.49	0.05					
Specific leaf area	0.05	-0.27	0.53	0.16					
Wood density (branch)									
Vessel density	-0.62	0.13	0.56	0.51					
Vessel mean hydraulic diameter	0.31	-0.42*	0.47	-0.32					
Vessel area	0.29	-0.42*	0.47	-0.32					
Xylem specific conductivity	-0.73*	-0.24	0.4	0.45					
Sapwood area	-0.24	-0.41*	0.4	0.26					
Xylem specific conductivity									
Vessel mean hydraulic diameter	0.66 ***	0.71***	-0.03	0.04					
Fraction Vessel	0.61**	0.50**	-0.13	0.04					
Vessel area	0.57 ***	0.69***	-0.04	0.12					
Ratio size:number	-0.21	0.51***	-0.09	0.72					
Vessel density	0.4	-0.16	-0.12	-0.74.					
Vessel density									
Vessel mean hydraulic diameter	-0.25 ***	-0.64***	0.03	-0.59.					
Vessel area	-0.25***	-0.67***	0.04	-0.59.					
Fraction Vessel	0.71 **	0.49**	0.26	-0.24					
Ratio size:number	-1.28 *	-0.67***	0.17	0.49*					

	Н	Hmax	DS (stem)	Sa (Stem)	Sa:Ba	WD (stem)	WD	La	Sa (branch)	La:As	SLA	N	Dm	S	А	FV	Ks	Dmh	Dh	Ik
Н		0.624	0.197	0.396	-0.105	-0.094	-0.117	0.014	0.168	-0.168	-0.248	-0.191	0.481	0.350	0.487	0.265	0.470	0.533	0.493	0.481
Hmáx	0.681		0.197	0.350	-0.071	-0.208	-0.231	0.174	0.282	-0.202	-0.123	-0.157	0.493	0.350	0.499	0.311	0.504	0.544	0.459	0.516
DS (stem)	0.069	0.146		0.675	0.607	-0.464	-0.396	0.123	0.174	-0.151	-0.140	-0.003	0.179	0.048	0.151	0.077	0.100	0.197	0.020	0.088
Sa (Stem)	0.534	0.554	0.492		0.305	-0.356	-0.356	0.048	0.191	-0.236	-0.123	-0.009	0.299	0.111	0.282	0.197	0.231	0.316	0.185	0.231
Sa:Ba	-0.296	-0.199	0.603	0.106		-0.345	-0.265	0.071	0.031	-0.009	-0.031	0.242	-0.100	-0.197	-0.105	0.128	-0.066	-0.083	-0.191	-0.009
WD (stem)	0.085	-0.034	-0.466	-0.233	-0.460		0.556	-0.316	-0.345	0.128	-0.043	0.105	-0.134	-0.162	-0.117	-0.043	-0.134	-0.151	-0.020	-0.077
WD(branch)	0.087	0.005	-0.405	-0.199	-0.347	0.675		-0.157	-0.288	0.208	0.083	0.083	-0.168	-0.094	-0.151	-0.066	-0.179	-0.162	-0.043	-0.088
La	-0.169	0.034	0.180	-0.011	0.228	-0.175	-0.040		0.151	0.259	0.077	-0.048	0.214	0.174	0.162	-0.014	0.179	0.174	0.111	0.111
Sa (branch)	0.257	0.387	0.188	0.294	-0.040	-0.098	-0.138	0.019		-0.430	0.003	-0.100	0.254	0.214	0.282	0.037	0.299	0.305	0.208	0.151
La:As	-0.317	-0.209	-0.074	-0.243	0.153	-0.048	0.024	0.545	-0.352		-0.094	-0.026	0.043	-0.031	0.003	-0.014	-0.048	-0.031	0.031	0.009
SLA	-0.317	-0.236	-0.074	-0.265	0.164	0.090	0.183	0.365	-0.130	0.196		0.179	-0.162	-0.077	-0.145	0.077	-0.117	-0.191	-0.083	-0.083
Ν	-0.225	-0.255	0.125	-0.130	0.321	-0.193	-0.207	0.008	-0.154	0.029	0.199		-0.390	- 0.635	-0.350	0.407	-0.014	-0.362	-0.265	-0.037
Dm	0.519	0.517	0.063	0.360	-0.175	0.037	0.045	0.090	0.283	0.016	-0.249	-0.421		0.641	0.915	0.179	0.499	0.903	0.772	0.601
S	0.381	0.379	-0.053	0.254	-0.302	0.153	0.162	0.037	0.177	-0.069	-0.206	-0.792	0.630		0.590	-0.168	0.219	0.567	0.550	0.299
А	0.545	0.532	0.101	0.386	-0.159	0.021	0.040	0.085	0.268	-0.011	-0.243	-0.437	0.952	0.646		0.219	0.527	0.943	0.823	0.652
FV	0.190	0.114	0.180	0.148	0.111	-0.228	-0.193	0.058	0.061	0.079	-0.016	0.395	0.185	-0.185	0.169		0.430	0.219	0.236	0.487
Ks	0.397	0.395	0.259	0.376	0.063	-0.265	-0.225	0.021	0.374	-0.127	-0.265	-0.013	0.497	0.190	0.503	0.476		0.561	0.499	0.715
Dmh	0.529	0.527	0.074	0.370	-0.175	0.037	0.066	0.079	0.305	-0.037	-0.238	-0.432	0.894	0.640	0.942	0.175	0.497		0.766	0.652
Dh	0.519	0.517	0.063	0.360	-0.175	0.037	0.045	0.090	0.283	0.016	-0.249	-0.421	1.000	0.630	0.952	0.185	0.497	0.894		0.681
Ik	0.460	0.426	0.132	0.312	-0.021	-0.085	-0.061	0.074	0.257	-0.032	-0.243	-0.056	0.635	0.265	0.619	0.550	0.714	0.624	0.635	

Table 3. Matrix of correlations<sup>1</sup> between species mean values of all traits. Significant correlations (p < 0.05) are shown in bold. See Table 1 for trait abbreviations.

1 Table 4. Species mean (minimum – maximum) values are presented for seven functional traits measured at the branch, stem and whole plant level. See Table 1 for seven functional traits measured at the branch, stem and whole plant level.

		Η		Sa (St	tem)		WD			La				SLA		La	:Sa			Α	
	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
Carinianaintegrifolia	26	29	34	743	1296	1793	0.65	0.69	0.75	3956	4926	7435	47	61	81	0.28	0.44	0.83	296	1960	8234
Cariniana micrantha	35	40	42	283	752	964	0.56	0.61	0.66	6301	9006	11991	19	66	97	0.55	0.87	1.27	269	4873	14470
Chrysophyllum	20	23	27	253	608	988	0.62	0.67	0.74	3644	5996	8368	58	69	78	0.39	0.67	0.84	251	1368	4389
Chrysophyllumucuquirana	23	25	28	229	473	831	0.7	0.75	0.79	3678	4603	5377	43	54	60	0.41	0.45	0.5	150	1058	4743
Couratari guianensis	9	25	36	112	731	1854	0.53	0.54	0.56	4731	9348	15652	73	103	137	0.34	0.70	1.03	341	2362	9126
Couratari stellate	27	30	35	349	761	1257	0.7	0.73	0.78	4926	7712	12917	72	87	100	0.42	0.78	1.18	208	2360	10383
Dipteryx magnifica	22	26	29	106	221	320	0.92	0.97	1.03	1636	6551	9972	64	126	234	0.23	0.67	1.09	153	1126	4057
Dipteryx punctate	25	27	29	175	467	789	0.88	0.90	0.92	2934	6463	10492	51	162	467	0.31	0.63	1.02	432	3049	6682
Eschweilera laevicarpa	17	24	29	140	283	439	0.75	0.84	0.91	4824	7332	10882	51	68	81	0.42	1.09	3.25	316	2290	7231
Eschweilera truncate	20	24	30	174	365	717	0.8	0.87	0.95	4889	7103	11176	71	83	100	0.37	0.80	1.31	206	1736	4229
Lecythis pisonis	20	25	31	195	379	868	0.65	0.82	0.9	3803	5640	8352	56	95	159	0.19	0.50	1.12	250	1665	6151
Lecythis prance	25	27	28	130	256	400	0.82	0.88	0.96	2595	5356	9376	56	79	108	0.43	0.65	0.94	201	1236	3619
Licania heteromorpha	27	30	37	313	584	746	0.73	0.81	0.89	5467	7489	10408	68	77	86	0.52	0.72	0.95	745	3890	13350
Licania longistyla	16	20	23	53	211	429	0.77	0.87	0.94	3996	7395	12306	78	159	379	0.37	0.73	1.55	337	1466	5410
Licania macrophylla	14	17	26	54	117	192	0.88	0.93	0.99	3384	6793	9942	86	138	326	0.24	0.78	1.23	267	1382	6023
Licania octandra	16	23	31	89	377	840	0.72	0.80	0.92	4263	7564	13631	84	201	432	0.46	0.60	0.91	303	997	3264
Micropholis splendens	24	27	34	330	759	1141	0.62	0.68	0.73	3161	5373	8212	54	68	101	0.36	0.47	0.63	313	1995	7042
Micropholis williamii	18	21	27	45	169	366	0.71	0.81	0.89	3352	6313	8888	52	65	79	0.25	0.72	0.99	252	1356	4935
Pouteria flavilatex	22	28	33	72	176	311	0.78	0.82	0.91	2155	5177	8274	44	56	66	0.08	0.37	0.56	303	3818	14135
Pouteria williamii	28	29	30	338	525	701	0.68	0.77	0.89	2683	3511	4162	9	59	79	0.21	0.34	0.57	300	1884	9094
Protium klugii	14	17	22	73	250	549	0.43	0.52	0.62	4641	7550	10769	92	169	312	0.39	0.72	1.02	300	1360	7369
Protium nitidifolium	18	22	27	120	283	503	0.6	0.67	0.77	2548	6965	14425	50	71	88	0.33	0.82	1.21	302	1545	4549
Protium opacum	8	17	25	80	221	475	0.49	0.54	0.62	6972	8446	12199	115	133	186	0.62	0.84	1.01	303	1314	4441
Protium trifoliolatum	11	14	19	33	85	125	0.61	0.72	0.78	4204	6939	11662	103	117	124	0.52	0.82	1.5	256	748.9	2079
Swartzia lamellate	18	23	29	144	353	480	0.67	0.76	0.84	4260	7204	10741	73	96	134	0.25	0.69	1.23	308	1489	5250
Swartzia recurve	19	26	31	328	598	923	0.75	0.82	0.89	2154	7183	11587	60	85	167	0.36	0.73	1.71	303	1692	5801
Virola pavonis	26	29.40	36	1053	1277	1384	0.43	0.48	0.53	4219	6864	7968	75	97	149	0.43	0.62	0.87	253	1749	8076
Virolavenosa	15	20	22.6	136	234	395	0.54	0.62	0.71	3900	6657	12751	79	95	117	0.46	0.70	0.96	229	1190	4633

for 1	trait	abl	brev	iatio	ons.



- 3 **Figure 1**.Evolutionary relationship for 28 species of tropical trees selected for this study in the six most abundant families in the region. The
- 4 cladrogram is based in the maximum resolved angiosperm phylogeny (tree R20120829). Colors indicate the environment where the species is
- 5 more abundant (blue, valley; orange, plateau).



**Figure 2.** Wood density (a), sapwood area:Basal area (b), sapwood depth (c), vessel mean hydraulic diameter (d), mean vessel area (e) and specific leaf area (f) in 14 pairs of sister species associated with contrasting habitats (Valleys are lower areas vertically close to the water table with sandy soil and Plateaus are areas vertically distant to the water table with clayey soil). Lines connect the pair of congeneric species, and values of significance for the paired T-test are shown in the graphic. Colors indicate our six phylogenetic lineages (red, Sapotaceae; yellow, Leguminoseae; green, Burseraceae; blue, Lecythidaceae; purple, Myristicaceae; pink, Chrysobalanaceae). This specie in grays (*Cariniana micrantha, Licania heteromorpha* and *Pouteria flavilatex*) was remove of analysis because are outlier.



**Figure 3.** Frequency distribution of vessel area in 168 individuals of 28 tree species occurring in contrasting hydro-edaphic condition. Colors indicate the environment (plateau or valley) where the species are more abundant.



**Figure 4.**Relationships between tree height and other hydraulic architecture attributes of species associated to valleys (open circles) and to plateaus (closed circles). In the left panel are the relationships between (a) mean vessel area, (c) vessel mean hydraulic diameter, (e) sapwood area and maximum height; and in the right panel, the relationships between (b) leaf area, (d) specific leaf area, (f) Leaf area: Sapwood area and the mean height of species. Dashed lines show the adjusted model for the valleys and solid lines for the plateus . Points in grays are outliers. Correlation coefficients with phylogenetic independent contrast are given in Table 1 and the parameters of the regression models are given in Table 2.



Figure 5. Relationship between wood specific gravity and hydraulic architecture traits of species associated to valleys (open circles) and to plateaus (closed circles). The wood specific gravity in the branch was correlated with attributes of micro anatomy (xylem specific conductivity, vessel density, mean vessel hydraulic diameter and vessel fraction). The wood specific gravity in the stem was correlated with the attributes of the whole plant (Maximum adult stature and sapwood area:basal area). In the upper panel are the relationships with (a) maximum height; (b) Xylem specific conductivity and (c) Vessel density, and in the down panel the relationships with (d) Sapwood area: Basal area; (e) mean Vessel hydraulic diameter and (f) Fraction vessel area of species. Dashed lines show the adjusted model for the valleys and solid lines for the plateaus. Correlation coefficients with phylogenetic independent contrast are given in Table 1 and the parameters of the regression models are given in Table 2.



Figure 6. Relationships between xylem specific conductivity and other hydraulic architecture traits of species associated to valleys (open circles) and to plateaus (closed circles). In the upper
 panel are the relationships with (a) Maximum height; (b) Ratio size: number and (c) Vessel fraction; and in the down pannel the relationships with (d) Vessel mean hydraulic diameter; (e) Mean
 vessel area and (f) Vessel density of 28 species. Dashed lines show the adjusted model for the valleys and solid lines for the plateus. Correlation coefficients with phylogenetic independent
 contrast are given in Table 1 and the parameters of the regression models are given in Table 2



Figure 7. Relationship between the mean vessel hydraulic diameter and vessel density across
28 species associated to valleys (open circles) and to plateaus (closed circles). Solid and
dashed lines represent the model adjusted to plateau and valley respectively. Correlation
coefficients with phylogenetic independent contrast are given in Table 1 and the parameters of

the regression models are given in Table 2.

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38 Figure 8. Principal component analyses (PCA) on cross-species hydraulic architecture trait means (left) and phylogenetically independent contrasts (right) for sixteen traits among 28 39 tropical tree species. Colors show the gradient of relative contribution for each axis, with high 40 contribution in red, intermediate in blue and low contribution in green. Hmax, maximum 41 42 height; DBH, Diameter at breast height; DS, Sapwood depth; Sa (stem), Sapwood area (stem); Sa (branch), Sapwood area (branch); Sa:Ba, Sapwood area: Basal area; WD (stem), 43 44 Wood density (stem); La, Leaf area; La:Sa, Leaf area: Sapwood area; SLA, Specific leaf area; S, Vessel size to number ratio; A, Mean vessel area; Dmh, mean vessel hydraulic diameter; 45 VD, vessel density; VF, vessel fraction; Ks, xylem specific hydraulic conductivity. 46





48 Figure 9. Principal component analyses (PCA) on cross-species means without

49 phylogenetically independent contrasts, orange (plateau species) and blue (valley species)

62 Conclusão

64	Este é o primeiro estudo, no nosso conhecimento, que olha para as diferenças nas
65	características hidráulicas das plantas em uma escala tão refinada (de poucas dezenas de
66	metros entre ambientes) e mostra que as árvores respondem de forma diferente às condições
67	hídricas locais. Existe diferença na arquitetura hidráulica das espécies associadas a platôs e
68	baixios, ambientes com profundidades de lençol freático e textura de solo bastante distintos.
69	Essas variações nas condições hídro-edáficas locais parecem ser um forte filtro ambiental que
70	conduz a ajustes no xilema, nas folhas, e na planta inteira e podem explicar a distribuição de
71	espécies proximamente aparentadas em ambientes tão distintos. Em um cenário de mudanças
72	climáticas conheceras respostas anatômicas, fisiológicas e morfológicas das espécies que
73	permitirá predições sobre o crescimento, taxas demográficas, sobrevivência e distribuição
74	dessas espécies.
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Ministério da Iência, Tecnolog BRASIL

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

Aos 31 dias do mês de maio do ano de 2016, às 09h00min, no Auditório dos PPG's ATU/CFT/ECO, Campus III, INPA/V8, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Alberto Vicentini**, do Instituto Nacional de Pesquisas da Amazônia -INPA, o(a) Prof(a). Dr(a). **Jochen Schöngart**, do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). **Alberto de Assis**, do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). **Rafael Leandro de Assis**, do Instituto Nacional de Pesquisas da Amazônia - INPA, tendo como suplentes o(a) Prof(a). Dr(a). Carlos Alberto Nobre Quesada, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). Rafael do Nascimento Leite, do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de LUIZA HELENA MENEZES COSME, intitulado: "A IMPORTÂNCIA DA ARQUITETURA HIDRÁULICA PARA A COMPREENSÃO DO **PADRÃO DE DISTRIBUIÇÃO DE ÁRVORES EM UMA FLORESTA DE TERRA FIRME NA AMAZÔNIA CENTRAL**" Orientado pelo(a) Prof(a). Dr(a). Juliana Schietti de Almeida, 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)

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

Prof(a).Dr(a). Alberto Vicentini

Prof(a).Dr(a). Jochen Schöngart

Prof(a).Dr(a). Rafael Leandro de Assis

Prof(a).Dr(a). Carlos Alberto Nobre Quesada

Prof(a).Dr(a). Michael John Gilbert Hopkins

0 CAMILA CHEREM RIBAS

Coordenadora Substituta do Programa de Pós-Graduação em Ecologia / INPA PO 258/2014