

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

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Summary

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- Species distributions and assemblage composition may be the result of trait selection through environmental filters. Here, we ask whether filtering of species at the local scale could be attributed to their hydraulic architectural traits, revealing the basis of hydrological micro-habitat partitioning in a Central Amazonian forest.
- We analyzed the hydraulic characteristics at tissue (anatomical traits, wood specific gravity (WSG)), organ (leaf area, specific leaf area (SLA), leaf area : sapwood area ratio) and whole-plant (height) levels for 28 pairs of congeneric species from 14 genera restricted to either valleys or plateaus of a *terra-firme* forest in Central Amazonia.
- On plateaus, species had higher WSG, but lower mean vessel area, mean vessel hydraulic diameter, sapwood area and SLA than in valleys; traits commonly associated with hydraulic safety. Mean vessel hydraulic diameter and mean vessel area increased with height for both habitats, but leaf area and leaf area : sapwood area ratio investments with tree height declined in valley vs plateau species. [Correction added after online publication 29 March 2017: the preceding sentence has been reworded.] Two strategies for either efficiency or safety were detected, based on vessel size or allocation to sapwood.
- In conclusion, contrasting hydrological conditions act as environmental filters, generating differences in species composition at the local scale. This has important implications for the prediction of species distributions under future climate change scenarios.

Introduction

An understanding of how environment influences the distribution of species is a central issue in ecology (Condit *et al.*, 2000; Russo *et al.*, 2005; Baltzer *et al.*, 2009). Environmental factors, such as water availability and soil physico-chemical properties, can work as filters that shape the functional and floristic composition of plant communities (Jackson *et al.*, 1999; Groom, 2004; Engelbrecht *et al.*, 2007; Moeslund *et al.*, 2013). Droughts and flooding events can prevent the establishment and survival of species with physiological restrictions (Engelbrecht *et al.*, 2007; Fortunel *et al.*, 2014), consequently influencing tree species distributions (Lopez & Kursar, 2003; Groom, 2004; Balvanera *et al.*, 2011). In tropical forests, various studies have shown that there is a high plant species turnover in space associated with edaphic and hydrological variation (Tuomisto & Dalberg, 2000; Jirka *et al.*, 2007; Drucker *et al.*, 2008; Schiatti *et al.*, 2014). However, the mechanisms that explain this turnover in space and

their association with hydro-edaphic variation are still poorly known.

In environments in which resource availability is heterogeneous, niche partitioning can promote high diversity, as it facilitates the spatial segregation of plant species (Silvertown *et al.*, 1999; Araya *et al.*, 2010, 2012; Bartelheimer *et al.*, 2010). The spatial and temporal variation of water availability in tropical forests is a key feature that potentially selects for contrasting hydraulic architecture of trees and may explain plant distribution patterns (Meinzer *et al.*, 1999; Tomasella *et al.*, 2008; Apgaua *et al.*, 2015). Here, we use the definition of hydraulic architecture (HA) of a plant as ‘the structure of the water conductance system in plants’ (Tyree & Ewers, 1991), which is given by the combination of xylem vessel size and density, the ratio of sapwood area to basal area ($A_s : B_a$), leaf area to sapwood area ratio ($A_l : A_s(\text{branch})$) and tree height. Wood specific gravity (WSG) and specific leaf area (SLA) were not originally described as part of HA, but WSG is partially a result of vessel size, number and conduit wall span and thickness, and higher WSG tends to support higher tensions in the xylem pipeline (Hacke & Sperry, 2001; Hacke *et al.*, 2001; Jacobsen *et al.*, 2005; Pratt *et al.*, 2007), whereas SLA tends to be lower in drier conditions (Cunningham *et al.*, 1999; Fonseca

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et al., 2000), and so they were included here to provide an integrative perspective. HA describes the xylem hydraulic relationships and determines the amount of leaves that can have water supplied by the hydraulic system of the plant (Tyree & Sperry, 1989; Tyree & Ewers, 1991; Cruiziat *et al.*, 2002). Each species exhibits a combination of HA traits given the hydraulic constraints posed by the environment (Shumway *et al.*, 1991; von Arx *et al.*, 2012), which can be linked to the plant's ability to tolerate drought or waterlogging. The combination of traits follows biophysical rules, such that there cannot be many interconnected, large, lengthy, grouped (conferring hydraulic efficiency) and isolated, narrow, smaller (hydraulic safety) vessels at the same time (Fan *et al.*, 2011; Pineda-García *et al.*, 2015), leading to a theoretical trade-off between hydraulic safety vs efficiency (Tyree *et al.*, 1994). However, a recent meta-analysis provided only weak support for this expectation (Gleason *et al.*, 2016; Schuldt *et al.*, 2015), raising a debate about the need to re-evaluate the concepts and interpretation of some metrics in plant hydraulics (Bittencourt *et al.*, 2016; Brodersen, 2016). The range of combinations of hydraulic traits for species occurring in different sets of environmental conditions, which result in viable ecological strategies, is largely unknown.

In dry environments, or in soils with lower water availability, plants must invest in traits that confer hydraulic resistance to be able to deal with recurrent water deficits without suffering significant cavitation and/or increased risk of death by hydraulic failure (Baas *et al.*, 2004; Sperry *et al.*, 2008; Rowland *et al.* 2015). Among the adjustments in xylem traits to minimize the risk of embolism is the reduction in the diameter of the vessel, compensated by an increase in the number of vessels in the sapwood area. Generally, narrower vessels are immersed in a matrix of relatively high-density wood, because of the greater proportion of xylem occupied by fibers (Hacke *et al.*, 2001; Jacobsen *et al.*, 2007; Pratt *et al.*, 2007; Fortunel *et al.*, 2014) and thicker conduit walls relative to lumen area, which increase the resistance to implosion. Changes in HA, such as an increase in the allocation for sapwood area in relation to investment in leaf area (Choat *et al.*, 2007; Gotsch *et al.*, 2010) and height, minimize the loss of water, but also reduce the rate of photosynthesis and growth (McDowell *et al.*, 2002; Delzon *et al.*, 2004).

By contrast, mesic environments may select species that usually invest in a set of traits that confer higher hydraulic efficiency (i.e. to conduct water with minimum energy expenditure). Xylem hydraulic efficiency can be achieved by investing in large vessels, as these reduce the resistance to water flow (Hacke *et al.*, 2006, 2007; Fan *et al.*, 2011) and increase conductivity, because hydraulic conductance efficiency is proportional to the sum of the vessel diameters to the fourth power (Poiseuille's law; Zimmermann (1983)). The HA of plants in mesic environments should exhibit a combination of wide vessels in low-density wood and leaves with high SLA, maximizing the investment in photosynthetic area with low production cost of supporting tissues, which could maximize growth and confer a competitive advantage in the acquisition of light. We hypothesize that the safety vs efficiency trade-off affects species co-occurrence at the local scale

by filtering different trait values (and HAs) in contrasting environments.

Some HA traits, such as tree height and WSG, are known to integrate aspects of plant performance and correlate with other plant traits in different environmental conditions (Poorter, 2008; Poorter *et al.*, 2010; Hoeber *et al.*, 2014). Tree height, for instance, is closely related to light competition and carbon gain (Iwasa *et al.*, 1985; Westoby *et al.*, 2002; Falster & Westoby, 2003, 2005; Poorter *et al.*, 2003), and reflects characteristics of plant life history, such as longevity and time to reproduction (Thomas, 1996; Moles *et al.*, 2004). Tree height has been shown to be negatively correlated to the total leaf area to sapwood area ratio ($A_l : A_s$) in several studies in temperate climatic regions (Magnani *et al.*, 2000; Schafer *et al.*, 2000; McDowell *et al.*, 2002; Delzon *et al.*, 2004; Sellin & Kupper, 2006). However, a positive correlation between tree height and $A_l : A_s$ in angiosperms seems to be more common in tropical humid climates (Gerrish, 1990; Vertessy *et al.*, 1995; Mokany *et al.*, 2003; Calvo-Alvarado *et al.*, 2008). These results indicate that relationships between HA traits can change according to environmental conditions at the regional scale. However, it is unknown whether different environmental conditions at the local scale could also drive changes in the correlations between HA traits.

Climatic changes impact soil water conditions, ultimately affecting plant species distribution. There are strong indications that the El Niño-Southern Oscillation (ENSO) has increased in frequency in the last 100 yr (Marengo *et al.*, 2011; Fu *et al.*, 2013; Cai *et al.*, 2014) and that there has been an intensification in the hydrological cycle of the Amazon basin with a trend to wetter, but more variable, conditions in the last two decades (Gloor *et al.*, 2013). The higher ENSO frequency and greater variance in rainfall have caused extreme droughts, with an alarming decrease in the level of the large rivers (Marengo & Espinoza, 2016) and an increase in the annual amplitude of the discharge of the Amazon River (Gloor *et al.*, 2013). Climatic changes influence below-ground water conditions, enhancing the environmental filters acting on plant HA. *Terra-firme* forests in Central Amazonia show fine-scale variation in topography that controls the below-ground hydrological conditions (Chauvel *et al.*, 1987), with soils that are frequently saturated during the rainy season (valleys) and well-drained soils (plateaus) separated by a few meters. Plateaus are vertically more distant from the water table, and are more susceptible to prolonged periods with lower soil water content. It might therefore be expected that plant species restricted to plateaus would be naturally selected over evolutionary time to be able to deal with soil water shortage, and would be less affected by more frequent droughts. Therefore, it is crucial to determine how hydraulic architectural traits are related to species distributions in the present to improve predictions of the effects of climate change on future species distributions and assemblage compositions.

This study investigates hydraulic architectural traits at the tissue, organ and whole-plant levels in order to understand the patterns of distribution of trees in a Central Amazonian *terra-firme* forest. In a recent study, Schiatti *et al.* (2014) found a steep change in plant species composition along a terrain gradient of

vertical distance to the water table at a scale of a few meters in central Amazonia, providing an opportunity to study changes in HA of plants in different hydro-edaphic conditions that are subjected to the same climate. Many congeneric species in different families have complementary distributions along the gradient of water table depth. It is common to find species mostly restricted to riparian areas (valleys), and species mostly restricted to higher areas (plateaus and higher slopes). Congeneric pairs of species with a complementary distribution and recent divergence in phylogeny allow the evaluation of adaptive and functional relationships, because the control of phylogenetic relatedness is included in the sampling design, instead of using a posteriori tests (Ackery, 2003; Fine *et al.*, 2006; Baraloto *et al.*, 2007). We investigated the following questions. Do species that are restricted to contrasting hydro-edaphic environments have divergent HA traits? Do the relationships among hydraulic architectural traits change according to the hydro-edaphic environment? How do hydraulic traits combine into ecological strategies and are there different strategies for each soil hydrological condition?

Materials and Methods

Study site

The study was conducted in the Reserva Florestal Adolpho Ducke (hereafter Ducke Reserve), located 26 km north of Manaus (2°55'47.80"S, 59°58'30.34"W), in Central Amazonia. The Reserve covers 10 000 ha (10 × 10 km²) of dense humid *terra-firme* tropical forest, with a canopy height of 30–37 m and emergent trees reaching up to 45 m (Ribeiro *et al.*, 1999). The average annual precipitation between 1965 and 1980 was 2300 mm, and the monthly average temperature was 26°C (Marques-Filho *et al.*, 1981). The dry season (months with precipitation of <100 mm) usually occurs from July to September.

The relief is well dissected, forming a gradient of soil water and soil texture, here called the hydro-edaphic gradient. Plateaus and valleys represent the extremes in this gradient. The plateaus are higher areas (elevation above sea level between 90 and 120 m) with clayey and generally more fertile soils, and the valleys are the lower riparian areas with sandy and generally less fertile soils. Plateaus are flat or gently sloped (<7° of inclination) with the water table *c.* 20 m deep and have well-drained soils. Valleys are also mostly flat or gently sloping with the water table close to the surface (up to 1 m depth), and soils can be seasonally waterlogged in some areas during the rainy season (Drucker *et al.*, 2008; Tomasella *et al.*, 2008).

Species and individual selection

The species were selected from the database of 72 permanent plots of trees (diameter at breast height (DBH) ≥ 10 cm) inventoried between 2001 and 2009 in Ducke Reserve. Fourteen pairs of congeneric dicotyledonous tree species were selected (Fig. 1). These 28 species are included in the six most abundant families in the Reserve (Chrysobalanaceae, Burseraceae, Fabaceae, Lecythidaceae, Myristicaceae, Sapotaceae) and have distributions

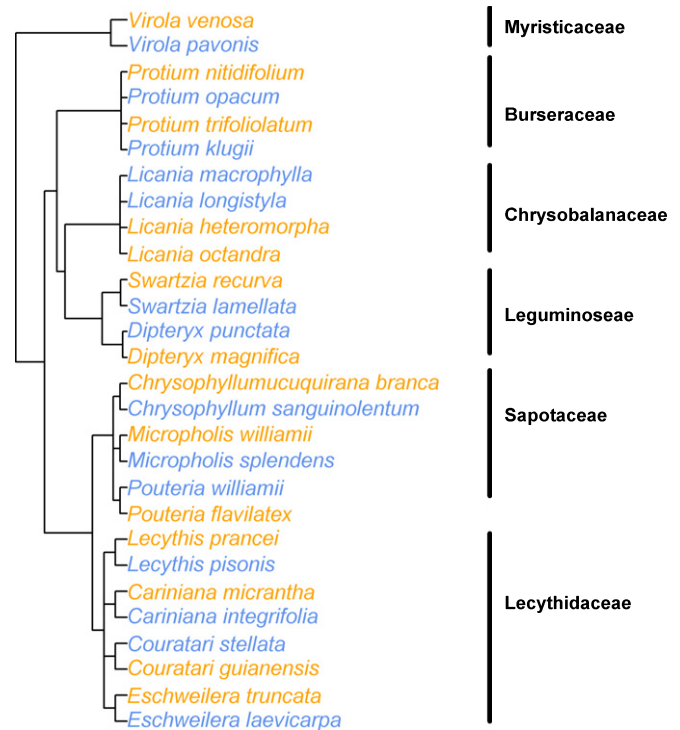


Fig. 1 Evolutionary relationship for 28 species of tropical trees selected for this study in the six most abundant families in the region. The cladogram is based on the maximum resolved angiosperm phylogeny (tree R20120829). Colors indicate the environment in which the species is more abundant (blue, valley; orange, plateau).

mostly restricted to one of the extremes of the hydro-edaphic gradient. For each genus, we paired a species mostly restricted to valleys (hereafter valley species) and a species mostly restricted to plateaus and higher slope areas (hereafter plateau species). We prioritized species relatively well resolved taxonomically according to the description in the literature and the opinion of specialists. Five to eight adult individuals from the larger diameter classes of each species were selected based on data from the last census (2007–2009), except for *Cariniana micrantha*, for which only four individuals were sampled, because some individuals had no fully expanded leaves during the sampling period. The largest individuals within each species were excluded from sampling, because field observations indicated that many of them were senescent. The samples were taken between October 2014 and September 2015 on a total of 163 individuals, and we measured 17 functional traits at the leaf, branch, stem and whole-plant levels (Table 1).

Xylem anatomy and specific gravity

Xylem specific gravity (dry weight per fresh mass) was estimated for stems and branches of all individuals. A core of the stem xylem with a diameter of 5.15 mm and length approximately equal to the radius of the stem (thus including sap and heartwood in the sample) was taken from each individual with a Pressler borer. Samples were taken *c.* 1.20 m above the ground (below the point of tree diameter measurement) and stored in sealed PVC tubes to prevent breakage and desiccation. In the laboratory, the stem bark

Table 1 List of 17 functional traits measured at the branch, stem and whole-plant level for this study with corresponding abbreviations and function

Trait	Abbreviation	Organ	Unit
Height	H	Whole plant	m
Sapwood area : basal area	$A_s : B_a$	Stem	
Diameter at breast height	DBH	Stem	m
Sapwood depth	D_s	Stem	cm
Sapwood area	A_s	Stem	cm ²
Wood specific gravity	$WSG_{(stem)}$	Stem	g cm ⁻³
Wood specific gravity	$WSG_{(branch)}$	Stem	g cm ⁻³
Specific leaf area	SLA	Leaf	cm ² g ⁻¹
Leaf area	$A_{l(branch)}$	Branch	m ²
Leaf area : sapwood area	$A_l : A_{s(branch)}$	Branch	
Vessel density	VD	Branch	$n \mu\text{m}^{-2}$
Vessel fraction	VF	Branch	
Vessel size to number ratio	S	Branch	
Mean vessel area	A	Branch	μm^2
Vessel mean hydraulic diameter	D_{mh}	Branch	μm^2
Theoretical specific conductivity	K_{theo}	Branch	kg m ⁻¹ MPa ⁻¹ s ⁻¹
Conductivity index	I_k	Branch	$n \mu\text{m}^{-2}$

n , number of vessels.

was removed. We evaluated WSG for the first 5 cm of the core sample (predominantly sapwood), starting from bark to pith.

Branches exposed to the sun of *c.* 1 m in length with well-developed leaves were sampled from the upper canopy by an experienced climber. A 5-cm-long sample was taken from the base of the sampled branch to estimate WSG. WSG was determined without bark by water displacement. Mass was measured on a balance with a limit of reading of 0.001 g after drying the wood for 72 h at 105°C.

Two individuals of each species were sampled for xylem anatomical measurements. The mean vessel area, mean vessel hydraulic diameter and vessel density were determined from the terminal branches used for WSG estimates. Subsamples of 2 cm in length (~1 cm in diameter) were taken from the base of the branch, stored in FAA solution (formalin, acetic acid and alcohol) for 72 h, and subsequently in alcohol 70%. These samples were immersed for a few seconds in glycerin and cross-sections, 15–40 μm thick, were cut with a sliding microtome (Precision sliding microtome American Optical 860[®]; American Optical, Buffalo, NY, USA). These cuts were cleared in 50% sodium hypochlorite for 30 s and stained with 1% aqueous safranin for 2 min. The sections were then dehydrated in an alcoholic dehydration series from 30% to absolute ethanol 100%, with 5 min in each solution. They were subsequently transferred to pure xylene and mounted on slides with Permount[®].

The cross-section cuts were photographed with a digital camera (Axiocam Erc5s; Zeiss, Göttingen, Germany) connected to a light microscope (Zeiss-Axio lab A1). Photographs were taken at $\times 5$ magnification, with a 20- μm reference scale, to allow

the estimation of the variability in vessel size. A photograph of 352 cm² in area was selected for anatomical analyses using 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. For images with good contrast, we performed an automated delimitation of the vessels with a threshold function in ImageJ. For those with lower contrast, we manually filled the vessel areas. In each image, we measured individual vessel areas and counted the total number of vessels to estimate the mean vessel area (A) and number of vessels per unit area (vessel density, VD). Counts of individual vessels and measures of their area were used to estimate other traits related to water transport efficiency, such as the vessel fraction (VF), defined as the fraction of sapwood occupied by vessels ($VF = A * N$), the ratio between the size and number of vessels (S), where $S = A/N$ (Zanne *et al.*, 2010), and the mean vessel hydraulic diameter $D_{mh} = (\sum D^4/n)^{1/4}$, where n is the number of vessels in an image (Scholz *et al.*, 2013) and D is the diameter of the vessel calculated from the individual vessel area ($D = (4A/\pi)^{1/2}$). The mean vessel hydraulic diameter reflects the capacitance based on the Hagen–Poiseuille law, which postulates that a few large vessels could contribute to water transport similarly to many narrow vessels (Cavender-Bares *et al.*, 2005; Anfodillo *et al.*, 2006; Beikircher & Mayr, 2009; Gea-Izquierdo *et al.*, 2012). Both circular and elliptical vessels were treated as circles in diameter calculation. For elliptical vessels, the smallest width of cross-section was used as D . The conductivity index (I_k) was estimated as $I_k = N * D_{mh}^4$ (Fortunel *et al.*, 2014). The theoretical specific conductivity (a measure of xylem porosity) K_{theo} was estimated using the equation of Hagen–Poiseuille.

$$K_{theo} = \left(\frac{\pi}{128\eta A_s} \right) \times \sum D^4 \quad \text{Eqn 1}$$

where A_s is the cross-sectional area of sapwood in the branch and η is the viscosity of water (1.002×10^{-9} MPa s⁻¹ at 20°C) (Tyree & Ewers, 1991; Santiago *et al.*, 2004). The vessel diameter and A_s were expressed in micrometers for K_{theo} calculations.

Specific leaf area, leaf area of the branch and sapwood area

Branches used for the estimates of leaf area (A_l , total leaf area of the branch) were the same as used for sapwood area estimates and anatomical measurements. Immediately after sampling, the branches were packed in plastic bags containing a wet paper towel and were taken to the laboratory. Leaf area was estimated by scanning all leaves of the branch (without petiole), and the leaf areas on the images were analyzed with ImageJ software. SLA was estimated from two leaves of the same branches that were scanned separately and dried in an oven for 48 h at 65°C. SLA was calculated as the ratio between fresh leaf area and dry weight (cm² g⁻¹).

We determined the ratio between leaf area and sapwood area ($A_l : A_{s(branch)}$) in the branch, sapwood depth (D_s , in cm) and sapwood area (cm²) in the stem. In order to compare stem sapwood

area in trees with different stem diameters, we calculated the proportion of the stem basal area occupied by sapwood ($A_s : B_a$).

We measured sapwood and heartwood (including pith) depths and the diameter of the branch in a 2-cm-long sample taken from the base of each branch with a Vernier caliper under a stereomicroscope. Sapwood area ($A_s = \pi r^2$) was obtained by subtraction of heartwood and pith areas from the branch cross-sectional area. For the stem, sapwood area was estimated in the same core sample taken with the Pressler borer that was used to estimate WSG. The core sample was placed over a strong light source (an iPhone light) in a position in which vessels were parallel to the light beam, allowing the passage of light where the vessels were open. We measured D_s as the extension of the open vessels along the core (Pfausch *et al.*, 2012), measured with Vernier calipers under a stereomicroscope. This method assumes that active vessels are open and inactive ones have been filled by tylosis. Tylosis occurs in eight of the 12 genera studied, according to the Inside Wood Database (<http://insidewood.lib.ncsu.edu/>). We did not find information on tylosis formation for *Dipteryx*, *Pouteria* and *Swartzia*.

Tree height and diameter

We estimated the total height of all trees included in the sample. Estimates were taken by climbing the tree or a neighboring tree and stretching a measuring tape vertically from the top of the canopy, using the pruner head, to the ground. The mean height per species was the average of the five individuals sampled for that species. The DBH (1.3 m above the ground) of all individuals was measured with diameter tape graduated in millimeters.

Data analyses

To evaluate whether species in the same genus occurring in contrasting hydrological conditions invest differently in hydraulic architectural traits, we used paired *t*-tests with the mean values of species traits.

We also undertook phylogenetically independent contrast (PIC) analyses as an alternative method of controlling for phylogenetic autocorrelation in the analyses of trait correlation. We reconstructed phylogenetic relationships among our species using PhyloMatic v.3 (Webb & Donoghue, 2005), based on the maximum resolution of the phylogeny of angiosperms (tree R20120829). Phylogenetic trees were built in PHYLOCOM 4.2 and then used to calculate phylogenetically independent contrasts with the R package APE. An independent phylogenetic contrast is the difference in the trait values between two congeneric species. Each contrast is scaled by the branch length representing the time divergence between congeneric species, multiplied by the standard deviation of the trait mean for that pair. The trait mean for the pair is assumed to be the ancestral condition. Contrasts for all pairs were then compared among traits with regression models, including an interaction term to test for the effect of environment.

To assess whether the relationship between traits changed with the environment, we used analyses of covariance (ANCOVA), considering valleys and plateaus as treatments. A principal components analysis (PCA) was used to evaluate the patterns of covariation between traits (all attributes evaluated in this study) and to describe hydraulic strategies of species in different environments. Traits that did not meet the assumptions of normal distribution (mean vessel hydraulic diameter, sapwood area (stem), SLA, specific xylem conductivity and vessel size to number ratio) were log-transformed. All analyses were performed using the R 3.2.2 statistical platform.

Results

Plateau and valley species differ in their hydraulic traits

Plateau species had higher values of WSG, and valley species had higher values of mean vessel hydraulic diameter, mean vessel area, SLA and stem D_s (Fig. 2). In plateau species, narrow vessels appeared more frequently (Supporting Information Fig. S1). After accounting for tree basal area (sapwood area : basal area), valley species had higher proportions of conducting area in the stem. There was no significant difference in DBH between valley and plateau trees (Fig. S2), and so the difference in the ratio of sapwood to basal area was not caused by a difference in tree size between the two topographic positions.

Tree height, $A_1 : A_{s(\text{branch})}$ ratio, theoretical specific conductivity, VD, VF and vessel size to number ratio did not differ significantly between the congeneric species occurring in the contrasting hydro-edaphic conditions (Fig. S3). Species mean, minimum and maximum values of the six functional traits are presented in Table S1.

Stem WSG was, on average, 9% higher (mean, 0.78 g cm⁻³; range, 0.60–0.95 cm⁻³) in plateau species than in congeneric valley species (mean, 0.71 g cm⁻³; range, 0.47–0.92 cm⁻³; paired *t*-test, $P = 0.03$, Fig. 2a). The sapwood area : basal area ratio ($A_s : B_a$) in valley species was 50% higher (mean, 0.6; range, 0.28–0.90) than in congeneric plateau species (mean, 0.4; range, 0.15–0.90; paired *t*-test, $P = 0.01$, Fig. 2b), and D_s in stems of valley species was 37% larger (mean, 6.51 cm; range, 3.19–12.13 cm) than for congeneric plateau species (mean, 4.75 cm; range, 1.53–9.21 cm; paired *t*-test, $P = 0.04$, Fig. 2c).

Three plateau species, *C. micrantha*, *Pouteria flavilata* and *Licania heteromorpha*, had high values of mean vessel hydraulic diameter and mean vessel area that were outliers in relation to those of the other species. Two of these species are deciduous (*C. micrantha*, *P. flavilata*), shedding leaves during the dry season. 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 congeneric species on plateaus (paired *t*-test, $P = 0.002$, Fig. 2d, and $P = 0.02$, Fig. 2e). Mean species-specific vessel area was larger in valleys than on plateaus, but some plateau species also had large vessels (Fig. 3c). SLA was higher in valley species than in plateau species (paired *t*-test, $P = 0.02$, Fig. 2f).

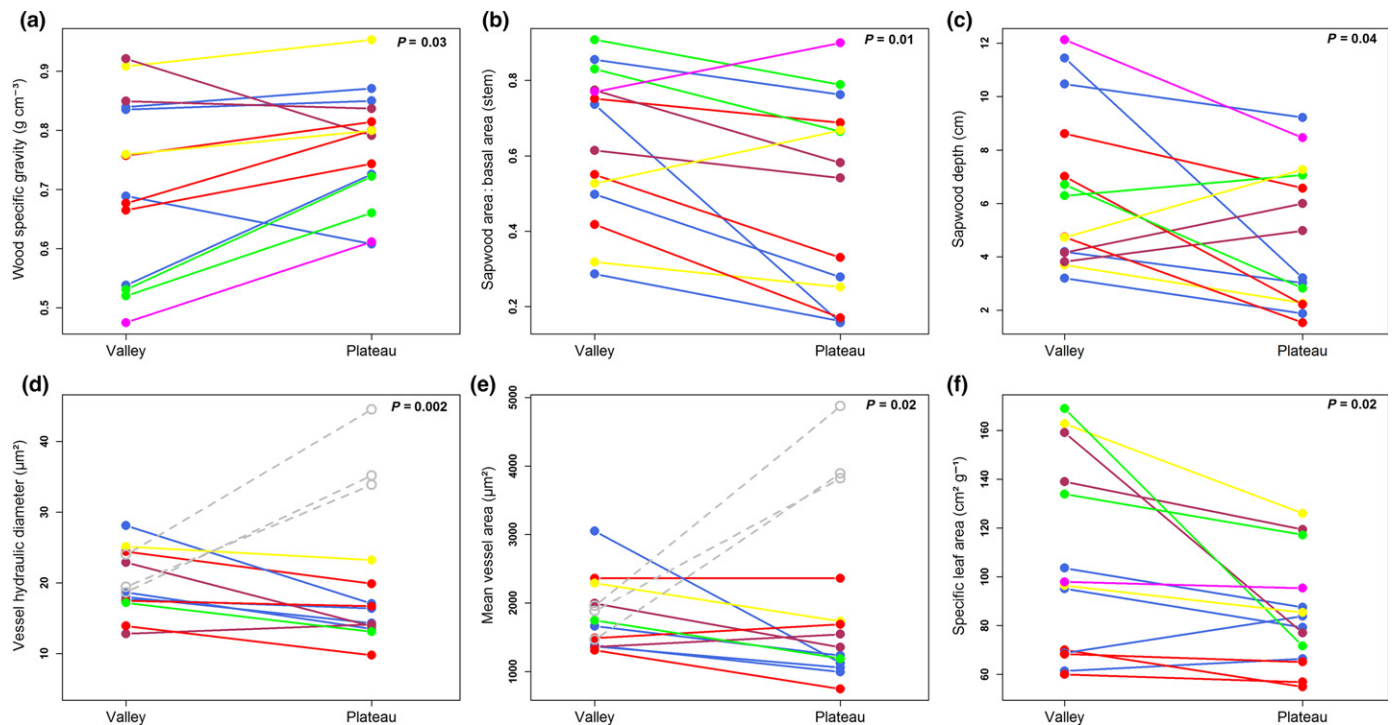


Fig. 2 Wood specific gravity (a), sapwood area : basal area (b), sapwood depth (c), mean vessel hydraulic diameter (d), mean vessel area (e) and specific leaf area (f) for 14 pairs of congeneric species associated with contrasting habitats ('Valleys' are lower areas vertically close to the water table with sandy soil, and 'Plateaus' are areas vertically distant from the water table with clayey soil). Lines connect pairs of congeneric species, and values of significance for the paired *t*-test are shown for each comparison. All relationships are shown in original measurement units, but *t*-tests for mean vessel hydraulic diameter, mean vessel area and specific leaf area use log-transformed values to achieve normality. Colors indicate our six phylogenetic lineages (red, Sapotaceae; yellow, Leguminosae; green, Burseraceae; blue, Lecythidaceae; purple, Myristicaceae; pink, Chrysobalanaceae). Species in gray and their congeneric pairs (*Cariniana micrantha* and *Cariniana integrifolia*; *Licania heteromorpha* and *Licania longistyla*; *Pouteria flavilata* and *Pouteria williamii*) were outliers removed from the analyses. Two of these species are deciduous (*Cariniana micrantha*, *Pouteria flavilata*), shedding leaves during the dry season, an escape mechanism that allows the maintenance of wide vessels without the risk of hydraulic failure in this environment.

All trait values estimated for the 28 species evaluated in this study are presented in Table S3.

Covariation among traits

Mean vessel hydraulic diameter, theoretical specific conductivity and $A_s : B_a$ were all positively correlated with tree height (Table 2; Fig. 3c,e). There was significant correlation of leaf area and SLA with tree height (Table 2; Fig. 3b,d).

$WSG_{(stem)}$ and $A_s : B_a$ were negatively correlated (Table 2; Fig. 4d), and $WSG_{(branch)}$ was also negatively related to the theoretical specific conductivity, VD and VF (Table 2; Fig. 4b,c,f). There was no correlation between $WSG_{(stem)}$ and tree height, and $WSG_{(branch)}$ and mean vessel hydraulic diameter (Table 2; Fig. 4a,e).

The relationships between the theoretical specific conductivity and vessel size to number ratio, VF, VD, mean vessel hydraulic diameter, mean vessel area and height are shown in Fig. S4.

The vessel size to number ratio, $A_s : B_a$ and leaf area were correlated with tree height only in the analysis with phylogenetic correction. Also, VD, theoretical specific conductivity and VF were correlated with WSG only in the analysis with phylogenetic correction (Table 2). Correlations between all traits are shown in Table S2.

Some trait relationships differ between environments

Most relationships between traits did not differ between plateaus and valleys (Table 2; Figs 3–5). However, in plateau species, there was a positive relationship between leaf area and tree height, and this relationship was negative in the valleys (Fig. 3b). Also, the relationship between $A_l : A_{s(branch)}$ and tree height was negative for valley species, but no relationship was found on plateaus (Fig. 3f). [Correction added after online publication 29 March 2017: in the preceding text 'positive' was replaced by 'negative'.]

In plateaus, there was a trend of higher proportional increment in mean vessel hydraulic diameter ($P = 0.08$) and mean vessel area ($P = 0.08$) with increments in tree height; however, only an overall relationship between these vessel traits and tree height was significant ($P < 0.05$; Table 2; Fig. 3). Also, the relationship between mean vessel hydraulic diameter and VD seemed different in plateaus and valleys ($P = 0.07$), but only the model including both environments was significant (Table 2; Fig. 5).

A tendency for a negative correlation was also observed between WSG and $A_s : B_a$ (Table 2; Fig. 4d; $P = 0.07$). Also, there was no correlation between mean vessel hydraulic diameter and WSG (Table 2; Fig. 4e; $P = 0.06$). For plateau species, the higher the increment in sapwood area relative to the basal area, the lower the investment in WSG. In plateaus, there was a trend of higher

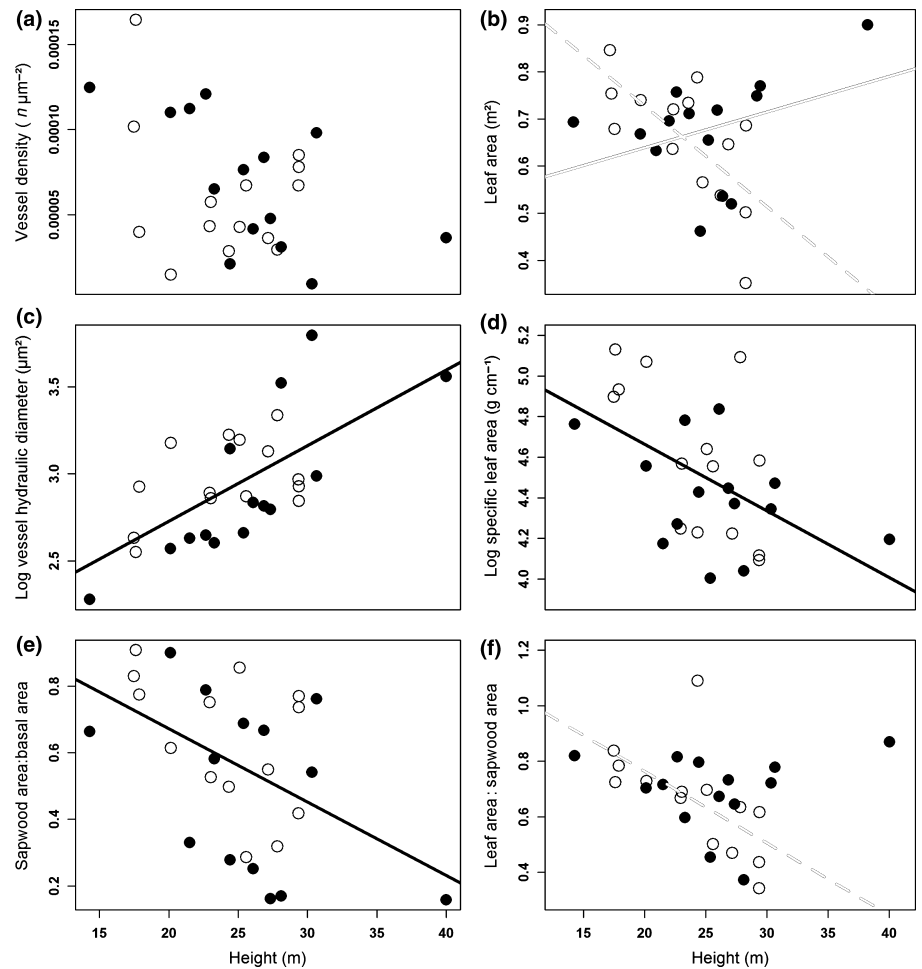


Fig. 3 Relationships between tree height and other hydraulic architectural attributes of species associated with valleys (open circles) and plateaus (closed circles). Black lines show the global model for all species (plateau and valleys). Gray lines show the relations within each environment, when a difference between them was detected. Dashed lines show the adjusted model for the valleys and solid lines show the same for the plateaus. In the left panels are the relationships between (a) mean vessel density, (c) mean vessel hydraulic diameter and (e) sapwood area : basal area, and the mean height of the species; in the right panels are the relationships between (b) leaf area, (d) specific leaf area and (f) leaf area : sapwood area, and the mean height of the species. Parameters of regression models with phylogenetic independent contrasts are given in Table 2.

proportional increment in vessel mean hydraulic diameter ($P=0.08$) and in mean vessel area ($P=0.08$) with increments in tree height; however, only an overall relationship between these vessel traits and tree height was significant ($P<0.05$; Table 2; Fig. 4). The relationship between vessel mean hydraulic diameter and VD tended to differ in plateaus and valleys ($P=0.07$), but only the model including both environments was significant (Table 2; Fig. 5). Also, a tendency for higher magnitude in the negative relationship between WSG and $A_s : B_a$ (Table 2; Fig. 4d; $P=0.07$) was observed for valley species.

Hydraulic strategies

The first component of the PCA captured 36% of the trait variation among species. The second component explained 22% of the total variation (Fig. 6). Species with higher values of mean vessel hydraulic diameter, mean vessel area, vessel size to number ratio, height and DBH are found on the right side of PCA1, and species with higher density of small vessels and larger proportional investment in sapwood area ($A_s : B_a$) are found on the left side. The second PCA axis was associated with higher wood specific density on the lower side and with higher VF and theoretical specific conductivity on the upper side. Valley and plateau species were spread across the PCA space, with no clear grouping to any side of the main axes.

Discussion

Do species restricted to contrasting hydro-edaphic environments have divergent hydraulic architectural strategies?

We investigated whether pairs of congeneric tree species showed differences in HA traits associated with different soil water conditions. We focused on two contrasting environments (plateaus and valleys) that differ in water table depth and soil texture, but occur within a few meters of each other in central Amazonian forests. We found a different combination of hydraulic architectural trait values for species associated with each environment, which is consistent with the hypothesis that soil hydrological conditions filter species at this local scale. Plateau species had higher WSG, lower mean vessel hydraulic diameter, lower mean vessel area and smaller stem cross-sectional sapwood area, suggesting that these species sacrifice hydraulic efficiency and invest in higher hydraulic safety, whereas valley species had contrasting trait values, suggesting more investment in water transport efficiency. Schuldt *et al.* (2013, 2015) and Olson *et al.* (2014) also found greater investment in traits associated with water transport efficiency in humid environments. [Correction added after online publication 29 March 2017: in the preceding text ‘valley’ was replaced with

Table 2 Relationships between hydraulic architectural traits of 28 species occurring in two contrasting environments (plateaus and valleys)

Trait relationships	Standardized regression coefficients			
	Trait	PIC	Environment	Interaction
Height				
Mean vessel area	0.47***	0.65***	−0.33	0.47
Vessel mean hydraulic diameter	0.34***	0.60***	−0.34	0.53
Theoretical specific conductivity	0.41*	0.61***	−0.07	0.21
Vessel density	−0.30	0.10	0.36	−0.24
Ratio size : number	0.25***	−0.18	−0.30	0.51
$A_s : A_a$	−0.47**	−0.26	−0.41	0.05
Wood specific gravity	0.02	−0.24	0.45	−0.05
Leaf area	−0.86*	0.11	0.26	1.16**
$A_l : A_s(\text{branch})$	−0.82	−0.09	0.33	0.85*
Specific leaf area	−0.84**	−0.53**	−0.39	0.56
WSG_(stem)				
Depth sapwood	−0.86***	−0.54**	0.06	0.44
Ratio sapwood : basal area	−0.96**	−0.40*	0.08	−0.60
Leaf area	−0.30	−0.40*	0.50	0.01
WSG_(branch)				
Vessel density	−0.73**	−0.29	0.59	0.30
Vessel fraction	−0.80**	−0.37	0.54	0.36
Vessel mean hydraulic diameter	0.28	−0.10	0.77	−0.24
Theoretical specific conductivity	−0.10**	−0.26	−1.20	0.05
K_{theo}				
Mean vessel area	0.58**	0.77***	0.16	0.05
Vessel fraction	0.69***	0.78***	−0.01	0.22
Ratio size : number	−0.45	−0.21	0.08	0.71
Mean vessel hydraulic diameter	−0.26	0.54**	0.10	0.66
Vessel density	0.45	0.12	0.02	−0.32
Vessel density				
Vessel mean hydraulic diameter	−0.56**	−0.68***	0.26	−0.01*

Standardized regression coefficients indicate the relative strength of the independent variable effect on the dependent variable. Values of standardized regression coefficients for each trait, environment or their interaction are followed by significance level (*, $0.05 < P < 0.07$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). PIC indicates the standardized regression coefficients of the relationships using phylogenetic independent contrasts. Values in bold indicate relationships with $P < 0.05$.

‘humid’.] Plateau species also invest in a wider range of vessel diameters with a few very wide vessels, which increase hydraulic redundancy and probably reduce the number of vessels that are lost in the case of a severe drought. However, direct measurements of hydraulic safety (e.g. P_{50} values) and/or xylem anatomical characteristics that are directly linked to embolism resistance (e.g. intervessel pit membrane thickness) are still needed to confirm the hypothesis that plateau species are more drought resistant (Lens *et al.*, 2011; Li *et al.*, 2016).

Higher WSG in plateau species indicates that there can be within-genus variation in WSG related to local differences in soil water. Higher values of WSG are commonly associated with

security against hydraulic failure (Hacke *et al.*, 2001), and are sometimes found in drier environments in which xylem needs to withstand very negative pressures (Baltzer *et al.*, 2009). With the reduction of water in the soil and increasing atmospheric demand, xylem vessels have to withstand not only high tensions, but also mechanical stress and the risk of air seeding into the water column, which may impair water transport (Jacobsen *et al.*, 2005). The presence of a matrix of fibrous tissues, with high-density wood and small-caliber vessels, may be a functional solution to withstand these conditions (Chave *et al.*, 2009). High WSG may also be selected in low-resource environments because of its low respiratory maintenance cost (Larjavaara & Muller-Landau, 2010, 2012). Therefore, selective pressures, other than those associated with water transport, may affect wood traits.

SLA differed between environments, plateau species having lower mean values of SLA than congeneric species in the valleys. Lower SLA reflects greater investment in leaf mass for a given leaf area, which is a common strategy in low-resource environments (dry and/or nutrient-poor soils) (Wright *et al.*, 2002). Plateau soils are drier, but have higher concentrations of nitrogen and exchangeable bases. If nutrients were the main driver of SLA, we should expect higher SLA on plateaus. Our results suggest that SLA of adult trees in this Amazonian forest is more strongly associated with soil moisture which indirectly controls mass-flow nutrient uptake (Wright *et al.*, 2001; Hoffmann *et al.*, 2005). Other traits, such as leaf longevity, should be investigated to understand how investment in structural tissues changes the strength and durability of leaves, and how this confers advantage in drier environments.

We found no difference in the height of species in contrasting environments. The valleys are vertically close to the water table, which would give trees unlimited access to water by roots, or even conditions of excess water in the soil during the rainy season. The larger mean vessel area and mean vessel hydraulic diameter found in valleys could minimize the costs associated with the resistance in the transport system and enable higher stature (Ryan & Yoder, 1997; Enquist *et al.*, 1999). The observed reduction in investment in tissues that confer a higher WSG in the valley species could enable them to achieve greater height. Higher values of SLA in valley species are associated with higher photosynthetic capacity, because of the low cost of production of structural leaf tissues, which maximizes growth in height. However, the trees that occur in valleys suffer more severely from disturbances caused by winds that may kill trees, because of soil instability in this environment (de Toledo *et al.*, 2013), preventing them from reaching their potential heights. Future studies should consider both soil water and disturbance regimes to better understand the height potential of species occurring in different habitats.

In the present study, we found strong evidence that environmental filters select divergent species traits of plant HA on a local scale. This finding has important implications for predictions of drought-induced tree mortality and future species distribution, because current land surface models assessing the impact of climate change disregard the role of microtopography as a key factor selecting for species with contrasting hydraulic traits. Some of

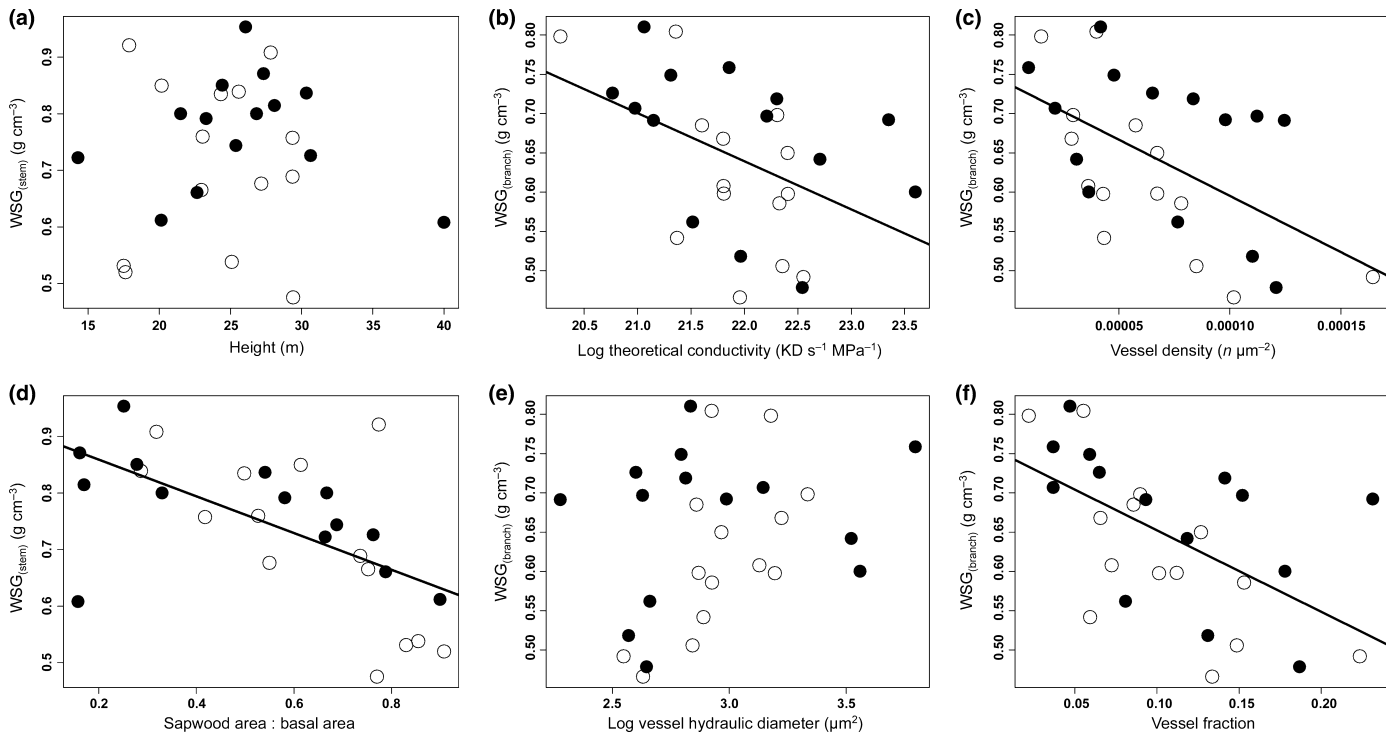


Fig. 4 Relationships between wood specific gravity (WSG) and hydraulic architectural traits of species associated with valleys (open circles) and plateaus (closed circles). WSG in the branch was correlated with attributes of micro-anatomy (theoretical specific conductivity, vessel density, mean vessel hydraulic diameter and vessel fraction). WSG in the stem was correlated with attributes of the whole plant (mean height and sapwood area : basal area). In the upper panels are the relationships with (a) mean height, (b) theoretical specific conductivity and (c) vessel density, and in the lower panels are the relationships with (d) sapwood area : basal area, (e) mean vessel hydraulic diameter and (f) vessel fraction of species. No differences in these relationships were found for plateau and valley species. The parameters of the regression models are given in Table 2.

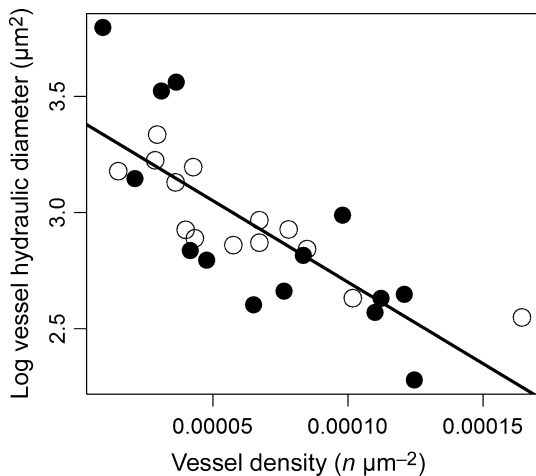


Fig. 5 Relationship between the mean vessel hydraulic diameter and vessel density across 28 species associated with valleys (open circles) and plateaus (closed circles). The parameters of the regression model are given in Table 2.

the traits measured here have been shown to improve significantly the predictions of models simulating responses of tropical forests to drought (Christoffersen *et al.*, 2016). Our results indicate the importance of field-based surveys of species HA traits along environmental gradients at the local scale to improve model predictions.

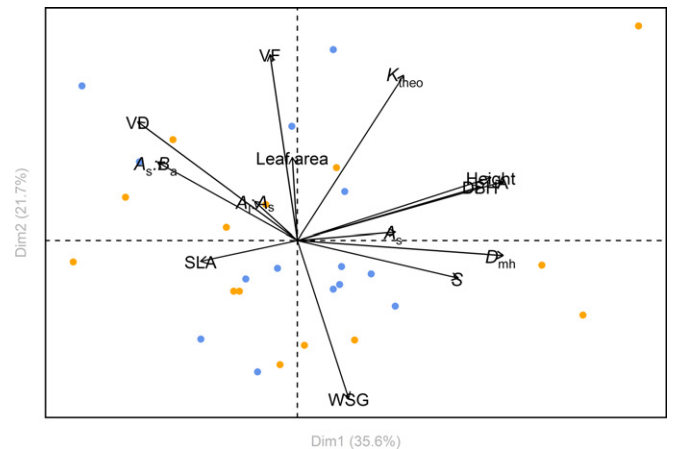


Fig. 6 Principal component analysis (PCA) on cross-species means without phylogenetically independent contrasts among 28 tropical tree species. Orange, plateau species; blue, valley species. Fourteen hydraulic architectural traits were included: A, mean vessel area; DBH, diameter at breast height; D_{mh} , mean vessel hydraulic diameter; Height; K_{theo} , xylem theoretical specific conductivity; Leaf area; A_s , leaf area; $A_s : B_a$, sapwood area ratio in the branch; S, vessel size to number ratio; A_s , sapwood area; $A_s : B_a$, sapwood area : basal area ratio; SLA, specific leaf area; VD, vessel density; VF, vessel fraction; WSG, wood specific gravity.

The hydraulic traits examined here differ between valley and plateau species, but may not represent the whole set of traits underlying the habitat segregation between them. Given our

focus on hydraulic safety vs hydraulic efficiency, we were able to detect suites of traits that would prevent valley species from establishing in plateaus. Valley species tended to have trait values associated with higher efficiency (greater vessel hydraulic diameter, mean vessel area and sapwood area), but not hydraulic safety (narrow and isolated vessels, greater WSG). By contrast, what prevents plateau species from establishing in valleys may be the absence of traits that enable plants to withstand the hypoxia or anoxia imposed by waterlogging, such as aerenchyma, aerial roots, lenticels and metabolic changes in the respiration pathway (Parolin, 2001; Parent *et al.*, 2008). We focused on traits at the adult stage, but segregation could have been defined much earlier if seeds were unable to germinate and develop given the water constraints (seasonally dry or waterlogged) of each habitat (Pérez-Ramos & Marañón, 2009). Therefore, the full understanding of habitat segregation in central Amazonian forests would benefit from integrative studies linking traits that affect survival under water stress conditions (waterlogging and drought) at different life stages of trees. Moreover, traits related to nutrient acquisition and defense against herbivores and pathogens may also be implicated in this habitat segregation (e.g. Fine *et al.*, 2006), and experimental studies of the relative importance of traits for dealing with water or nutrients would be an important step towards a full comprehension of habitat filtering.

Do the relationships among hydraulic architectural traits change according to the hydro-edaphic environment?

Some correlations differed between the two environments for the 28 species of trees, suggesting adjustments to contrasting soil water conditions among the 20 functional traits analyzed. Leaf area and $A_l : A_{s(\text{branch})}$ were negatively correlated with height, and this relationship differed between the two habitats. Lower allocation to leaf area (lower $A_l : A_{s(\text{branch})}$) compensates for the increase in resistance associated with a longer hydraulic pathway. Taller species in the valley showed a greater proportional investment in sapwood area than leaf area. The higher investment in sapwood area rather than vessel area to a given leaf area increases hydraulic efficiency without compromising safety, transporting water efficiently through narrow vessels. This might be favored because the water transport during waterlogged periods in the valleys might be limited by higher resistance in root water uptake. Narrow vessels in a wider sapwood area may be a solution to maintain both hydraulic safety (at the tissue level) and efficiency (at the individual level through a greater number of vessels per stem) in an environment that is very dynamic hydrologically.

The strength of the relationships between species height and mean vessel area, mean vessel hydraulic diameter and the ratio between the size and number of vessels differed ($P = 0.08$) between species in the two hydro-edaphic conditions. [Correction added after online publication 29 March 2019: in the preceding text the probability has been added.] Wider vessels in taller species can compensate for hydraulic resistance imposed by a long water transport system (Becker *et al.*, 2000; Preston

et al., 2006; Poorter *et al.*, 2010; Zach *et al.*, 2010; Martínez-Cabrera *et al.*, 2011; Fan *et al.*, 2012). However, this observation of higher investment in larger vessels in taller trees is counter-intuitive, as this can increase the risk of cavitation. [Correction added after online publication 29 March 2019: in the preceding text 'tall plateau' has been replaced with 'taller'.] Two of the tallest trees in the plateau are deciduous species (*C. micrantha* and *P. flavilata*), a strategy that prevents hydraulic failure during periods of high atmospheric demand and low water availability and allows higher carbon gain and growth during favorable periods because of higher hydraulic efficiency. Therefore, deciduousness may be a key characteristic that allows investment in height for plateau trees, and the prevalence of this trait should be investigated further for this community.

How do hydraulic traits combine into ecological strategies and is there a single strategy for each soil hydrological condition?

There is no single strategy for valley or plateau plants that could be associated with their success in each habitat. Our comparisons of valley vs plateau species showed that valley species had lower WSG, and higher vessel hydraulic diameter (D_{mh}), vessel area (A), SLA, sapwood area : basal area ratio ($A_s : B_a$) and D_s . Using PCA, we can see that D_{mh} and A group together with height, DBH and vessel size to ratio number (S) to the right side of axis 1, whereas $A_s : B_a$ and SLA group with VD and $A_l : A_s$ to the left side. Therefore, two main hydraulic strategies can be distinguished: one that aligns better with the classical 'efficient type', associated with large vessels in smaller numbers, and another that may also confer efficient conductivity, given by higher allocation of stem tissues to active sapwood. Given that valley plants had average higher D_{mh} , A and $A_s : B_a$ (and the contrary for plateau species), they are spread along this main axis, instead of grouped together on a single one of these strategies. We may conclude that there is more than one way to attain higher efficiency or safety that is used by plants of both habitats.

Conclusion

This study shows differences in hydraulic architectural characteristics in Amazonian tropical trees on a fine scale of a few meters between environments with contrasting water and edaphic conditions. Here, we show differences in HA at the leaf, branch, stem and whole-plant level of species with complementary distributions associated with plateaus and valleys, environments with different water table depth and soil texture. These variations in local hydro-edaphic conditions appear to be a strong environmental filter which leads to adjustments in the xylem, leaves, stem and whole plant, and may explain the distribution of closely related species in such diverse environments. In a scenario of climate change, a knowledge of the response of the anatomical, physiological and morphological traits of tree species to soil water conditions allows predictions to be made about the establishment, survival and distribution of Amazonian trees in the future.

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Author contributions

J.S. designed the study. L.H.M.C. conducted field sampling, laboratory and statistical analyses, and wrote the first draft of the manuscript. All authors contributed to the final version. J.S., F.R.C.C. and R.S.O. contributed to the interpretation of the results.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Frequency distribution of vessel area.

Fig. S2 Frequency distribution of height and diameter at breast height (DBH).

Fig. S3 Relationship between 14 pairs of congeneric species associated with contrasting habitats.

Fig. S4 Relationships between theoretical specific conductivity and other hydraulic architectural traits of species associated with contrasting habitats.

Table S1 Species mean (minimum–maximum) values for seven functional traits measured at the branch, stem and whole-plant level

Table S2 Matrix of correlations between species mean values of all traits

Table S3 Trait values estimated for the 28 species

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