Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients

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Summary

• Species distribution is strongly driven by local and global gradients in water availability but the underlying mechanisms are not clear. Vulnerability to xylem embolism (P_{50}) is a key trait that indicates how species cope with drought and might explain plant distribution patterns across environmental gradients. Here we address its role on species sorting along a hydro-topographical gradient in a central Amazonian rainforest and examine its variance at the community scale.

• We measured P_{50} for 28 tree species, soil properties and estimated the hydrological niche of each species using an indicator of distance to the water table (HAND).

• We found a large hydraulic diversity, covering as much as 44% of the global angiosperm variation in P_{50}. We show that P_{50}: contributes to species segregation across a hydro-topographic gradient in the Amazon, and thus to species coexistence; is the result of repeated evolutionary adaptation within closely related taxa; is associated with species tolerance to P-poor soils, suggesting the evolution of a stress-tolerance syndrome to nutrients and drought; and is higher for trees in the valleys than uplands.

• The large observed hydraulic diversity and its association with topography has important implications for modelling and predicting forest and species resilience to climate change.

Introduction

Global warming and more variable rainfall regimes have led to increased frequency and intensity of droughts, and to potentially large shifts in species distribution and ecosystem functioning (Malhi *et al.*, 2009; Phillips *et al.*, 2009). Global vegetation models predict, for example, high vulnerability of Amazonian forests to drought (Huntingford *et al.*, 2008), and sometimes even transition towards more open vegetation states (Cox *et al.*, 2004), whereas empirical and experimental plot studies have shown that, despite site specific vulnerability, drought triggers large-scale mortality of certain group of trees and specific species (Phillips *et al.*, 2009; Lewis *et al.*, 2011; Hilker *et al.*, 2014). However, the mechanisms underlying either forest resistance or vulnerability to predicted changes in rainfall are still not well understood.

Vulnerability to drought is determined by a suite of traits related to the water transport system (i.e. hydraulic system) of plants. Among these traits, the P_{50} (i.e. the water potential at which 50% loss of hydraulic conductivity occurs) is the most common index of xylem vulnerability to hydraulic failure and a

key determinant of tree drought tolerance (Rowland *et al.*, 2015; Anderegg *et al.*, 2016). Despite having the most vulnerable xylem tissue, tropical rainforests species are hypothesized to have the lowest within-biome variation in P_{50} and thus low resistance to drought-induced hydraulic failure compared with other biomes (Choat *et al.*, 2012). In this meta-analysis, P_{50} data have been reported for only 59 rainforest tree species mostly from sites with precipitation above 2400 mm. The Amazon, the largest and most biodiverse rainforest in the world, is still underrepresented in global plant hydraulic traits datasets (but see Rowland *et al.*, 2015; Santiago *et al.*, 2018).

Hydraulic traits might also be important for niche differentiation and species distribution across local moisture gradients (Engelbrecht *et al.*, 2008). Hydrological niche segregation occurs in a wide range of vegetation types and has been observed along topographic gradients in central Amazonia (Schietti *et al.*, 2014) but the underlying mechanisms are not clear (Silvertown *et al.*, 2015). P_{50} may be a key trait to understand hydrological niche segregation, because it determines the maintenance of water supply to leaves under water stress and hence, plant survival. Xylem

embolism vulnerability is also expected to be an important trait under selection across soils differing in water availability and water table depth, as soil water tension establishes the maximum xylem tension possible in an environment. This xylem tension is unavoidable even after stomatal closure and plants have to withstand by being resistant to embolism (Sperry & Love, 2015). Because of its strong predictive power of plant performance and distribution across environmental gradients, embolism resistance has recently been considered a mechanistic 'super-trait' (Brodribb, 2017; Larter et al., 2017).

In the Amazon basin, the seasonally inundated forests have recently been reported to be less resilient than upland forests and more susceptible to climate-driven transition to open vegetation states (Flores et al., 2017). Amazon floodplains occur around river basins, where forests can stay flooded for several months. Wetland forests are particularly susceptible to hydrological drought, i.e. abnormal decreases in the water table, and studies in the Amazon and in Borneo relate hydrological drought to increased fire occurrence and forest transition to alternative open vegetation states (Flores et al., 2017; Taufik et al., 2017). An overlooked type of wetland forest, the valley forests, occurs in Amazon micro-basins occupying c. 40–50% of the central Amazon area (Nobre et al., 2011). They occur in valley bottoms, are frequently waterlogged during rain events, and the water table is at or near surface, which may contribute to filtering of species composition towards species with waterlogging tolerance and high water demand, and potentially lower hydraulic safety, making valley forest trees likely to be more vulnerable to hydrological drought. From the valleys to the plateaus, the influence of the water table decreases progressively and plateaus are not affected by hydrological drought (here defined as below-normal water table level; see Van Loon, 2015), but by soil water deficits, commonly observed during meteorological droughts. This difference in abiotic drivers would suggest valley forests to strongly differ from plateau forests. In fact, species composition, forest structure and dominant functional traits are notably different between valley and plateau forests (Schietti et al., 2014; Cosme et al., 2017). Being close to the water table, it is expected that valley forest species evolved under higher water availability and have been selected for nonconservative traits and lower drought tolerance thresholds, making them more susceptible to hydrological drought than plateau species. In fact, recent evidence indicate four times higher drought mortality of western Amazon valley forest species compared with slope or plateau species (Zuleta et al., 2017), similar to the mortality patterns observed after the 1997–1998 El Niño drought in dipterocarp forests in Southeast Asia (Itoh et al., 2012). The vulnerability of valley forests depends not only on the traits of plants, but also on its interaction with hydrological conditions and how climatological drought can modify these conditions. However, if plant traits in valleys are predominantly hydraulically nonsafe, valleys could become more vulnerable than plateaus in the event of strong hydrological droughts.

In this study we analyze the P_{50} (i.e. the water potential at which 50% loss of conductivity occurs), the most common index of embolism resistance (Anderegg et al., 2016), and species'

hydrological niche, measured by their preferred position along a gradient of height above nearest drainage (HAND), an indicator of distance to water table. We test the hypotheses that: in this hyperdiverse rainforest, interspecific variation in a key drought vulnerability trait (P_{50}) represents a significant proportion of the global angiosperm species variation; xylem hydraulic resistance to embolism will vary according to the distance to the water table and valley forest trees have lower drought tolerance thresholds than plateau trees; and valley conditions favour the evolution of more embolism-vulnerable species while plateau conditions favour evolution of more embolism-resistant species and this divergence in drought adaptation has occurred repeatedly in distinct close phylogenetic lineages. Addressing these hypotheses and understanding the basis for local species segregation enable us to provide a strong basis for mechanistic models of plant hydraulics and projections of species distributions under climate change.

Our data greatly expand the knowledge of tropical rainforest trees' embolism resistance, which mostly comprises hyperhumid tropical forests (> 2400 mm annual rainfall). As topographical gradients (Tuomisto et al., 2003) and associated hydraulic diversity (Fortunel et al., 2014; Cosme et al., 2017) may be typical for large parts of the Amazon, although largely ignored in current dynamic global vegetation models, our results are pivotal for predicting Amazon resilience to drought.

Materials and Methods

Study site

The study was carried out at Reserva Florestal Adolpho Ducke, a 10 000 ha tropical rainforest reserve, 26 km north of Manaus, Brazil (59°52′40″W, 03°08′00″S) (Ribeiro, 1976). Reserva Ducke is a long-term ecological research site with 72 permanent plots for which data on topography, soil properties and species abundance are available (Costa et al., 2015). Average temperature is 26°C with a minimum of 19 and maximum of 39°C. Mean annual precipitation is c. 2200 mm (range 1900–3300 mm) with a wet season from November to June (Satyamurty et al., 2010).

The topography consists of a plateau incised by streams, forming small floodplains. This heterogeneity in topography has created a continuous gradient of soil properties and water availability, from the upland clay-rich and drier plateaus to clay–sandy slopes and the very sandy and seasonally waterlogged valleys. These hydrological environments can be described by their vertical height above the nearest drainage (HAND), which is a good proxy for the vertical distance of any point of the terrain to the water table (Nobre et al., 2011). The water table is very close to the surface in valleys, and can be 35 m deep on plateaus (Tomasella et al., 2008). HAND of the plots is positively correlated to soil clay content (Pearson $r = 0.88$, $P < 0.001$, $n = 72$, and concentration of exchangeable bases (sum of the bases – calcium, magnesium, potassium, and sodium) and of nitrogen ($r = 0.58$, $P < 0.001$, $n = 72$), but not to soil phosphorus (P) concentration ($r = 0.07$, $P = 0.58$, $n = 72$) (soil data from Costa et al., 2005). HAND values for the permanent plot locations were the

same used in (Schietti *et al.*, 2014), which were calculated using the HAND algorithm (Rennó *et al.*, 2008) based on SRTM digital elevation model (90 m of spatial resolution) with a minimum contribution area of 30 pixels (= 0.41 km^2). Soil P was extracted with the Mehlich1 solution and determined spectrophotometrically using ammonium molybdate and ascorbic acid (Donagema *et al.*, 2011).

Species selection

To evaluate species associations to the topographic and edaphic gradient, we selected 28 eudicotyledonous tree species that sort out along the topographic gradient (Table 1). To quantify the topographic and soil niches of the species, we weighted the HAND or P concentration of the plot by the abundance of the species in the plot (a) ($n = 72$ plots) and divided by the number of individuals of the species in all plots (a_t) using the following equation, where i is the plot:

$$\text{Species HAND or P} = \frac{\sum_{i=1}^{n}((\text{plot HAND or P})_i a_i)}{a_t}$$

We tested if species were restricted to some portion of the HAND gradient than expected by chance using a statistic that is independent of the number of sites occupied (Kinnup &

Magnusson, 2005). For each species, the test statistic was the observed SD over the mean value of the HAND gradient used by its individuals. Then we built a null model for each species, based on the variation in HAND expected to be found in occupied sites when the null hypothesis (no habitat specificity) is true, using a resampling procedure. This process was repeated 1000 times to obtain the distribution of random standard deviations for each species. The proportion of standard deviations in the 1000 random samples that were equal to, or less than, the observed standard deviation was used to test the null hypothesis of no habitat restriction for each species. Species with significant lower deviation from the average than expected by chance are restricted. Species with significant restriction were then classified as valley species (average HAND values < 17 m, $n = 10$ species), plateau/slope species, hereafter referred to as 'plateau species' (average HAND > 17 m, $n = 15$). Species not significantly restricted were classified as generalists. A previous study (Schietti *et al.*, 2014) has shown that 17 m is the level of the water table that defines the upper limit of the riparian zone.

To evaluate whether habitat-associated drought adaptation has occurred repeatedly in different phylogenetic lineages, we selected some species pairs that belonged to the same genus or family, in which one taxon was a plateau species, and the other a valley species (Supporting information Table S1). Some additional, unpaired species were included to sample species across the whole

Table 1 Selected species (28), their preferred habitat (P, plateau; V, valley; G, generalist), mean height above nearest drainage (HAND, with 10 and 90 percentiles in parenthesis), mean P$_{50}$ (MPa) and mean plant-available phosphorus concentration (P; mg kg^{-1}) at Reserva Ducke, Manaus, Brazil.

Family	Species	Habitat association	Mean HAND position (m)	Mean P$_{50}$ (MPa)	Mean P (mg kg^{-1})
Annonaceae	*Guatteria olivacea*[12]	G	20.4 (5.6–41.6)	−2.57	2.90
	Guatteria megalophylla[4]	V	3.3 (1.5–5.1)	−2.21	3.80
Burseraceae	*Protium gallosum*[19]	P	26.2 (6.2–37.9)	−2.54	3.43
	Protium nitidifolium[20]	P	25.7 (8.4–39.8)	−2.91	3.31
	Protium trifoliolatum[21]	P	23.2 (5.3–39.5)	−1.33	3.48
	Protium hebetatum[14]	G	19.49 (5.3–38.6)	−3.10	3.09
	Protium grandifolium[9]	V	10.80 (1.4–15.1)	−1.25	3.01
	Tetragastris panamensis[25]	P	25.7 (10.8–41.6)	−1.83	3.35
Chrysobalanaceae	*Licania heteromorfa*[18]	P	26.1 (6.2–39.8)	−3.33	3.24
	Licania longistyla[13]	G	15.2 (1.6–38.5)	−3.11	2.65
	Licania lata[7]	V	8.5 (1.7–21.1)	−1.71	3.16
Fabaceae	*Eperua duckeana*[3]	V	7.2 (1.6–14.4)	−0.88	3.12
	Swartzia recurva[23]	P	25.9 (5.8–43.6)	−3.66	3.18
	Swartzia tomentifera[24]	P	24.9 (5.3–39.3)	−3.64	3.44
	Swartzia ulei[10]	V	15.1 (1.7–34.7)	−2.20	3.69
	Zygia racemosa[27]	P	28.2 (8.5–41.6)	−4.10	3.28
	Zygia ramiflora[28]	P	29.8 (8.7–47.4)	−1.76	3.52
Lecythidaceae	*Eschweilera pseudodecolorans*[15]	P	29.7 (12.6–43.7)	−3.25	3.24
	Eschweilera truncata[16]	P	25.3 (8.0–41.4)	−2.43	3.22
	Eschweilera coriacea[11]	G	17.1 (2.8–37.5)	−1.72	3.32
Moraceae	*Helianthostylis sprucei*[17]	P	26.5 (8.4–41.6)	−4.04	3.07
Myristicaceae	*Virola venosa*[26]	P	27.68 (8.7–41.4)	−0.84	3.24
	Iryanthera juruensis[5]	V	14.3 (1.8–37.1)	−0.67	3.67
	Iryanthera ulei[6]	V	16.2 (2.3–38.2)	−0.56	4.15
Rutaceae	*Adiscanthus fusciflorus*[1]	V	2.2 (1.4–4.7)	−1.08	3.56
Sapotaceae	*Micropholis williamii*[8]	P	23.4 (6.2–42.8)	−1.78	3.22
	Chrysophyllum sanguinolentum[2]	V	9.5 (1.6–22.4)	−2.47	3.44
Violaceae	*Rinorea racemosa*[22]	P	26.2 (5.7–41.6)	−4.18	3.33

Numbers after species names indicate each species vulnerability curves as numbered in Supporting Information Fig. S1.

HAND gradient. Half of the selected species belong to the 50 most abundant species at Reserva Ducke, and 12 species belong to the 227 hyperdominant species in the Amazon (ter Steege *et al.*, 2013).

Xylem resistance to hydraulic failure

We used P_{50} as an indicator of xylem resistance to hydraulic failure; P_{50} is the xylem water potential at which 50% of hydraulic conductance is lost. We determined P_{50} for branches of juvenile trees, with stem diameter between 1 and 5 cm, and stem height between 2 and 10 m. We focused on juvenile trees, because it is logistically more feasible to access and collect the branches, and because the regeneration stage presents a crucial bottleneck in the life cycle of a tree; species adaptations to drought may be much more marked in the juvenile stage, when trees have a small root system compared with the adult stage when trees can partly avoid drought by having deeper roots and access to soil water (Engelbrecht & Kursar, 2003; Poorter & Markesteijn, 2008; Brum *et al.*, 2018).

For each species we collected one branch (longer than 1 m) from three to six individuals. Branches were collected early in the morning (when they were more hydrated). Hydraulic vulnerability curves were constructed using the pneumatic method (Pereira *et al.*, 2016; Zhang *et al.*, 2018). Branches were bench dried repeatedly to different water potentials, and had their air discharge and xylem water potential measured concurrently with a pressure chamber (PMS 1000; PMS Instruments Co., Albany, OR, USA). Before each xylem water potential measurement, branches were bagged for 1 h for leaf and xylem water potential to equilibrate. Percentage loss of conductance was estimated from percentage air discharge curves and P_{50} was calculated from a fitted sigmoidal curve relating percentage loss of conductance to xylem water potential. We fitted the curves at species level, combining the individuals per species. As we sampled only one branch per individual, this analysis was not possible at individual level.

Data analysis

For all statistical analysis, we used R v.3.3.0 with base packages (R Core Team, 2014). Global P_{50} data were obtained from (Choat *et al.*, 2012). Welch *T*-Test (default of 't.test' R base function) was used to determine if the global P_{50} dataset differed from our data collected at Ducke. To evaluate whether P_{50} was associated with species distribution across gradients in water availability and soil plant-available phosphorus concentration, we regressed species P_{50} with HAND and soil phosphorus concentration values, using simple and multiple linear regression. To evaluate whether species with different topographic niches (plateau, valley) also differed in P_{50} and whether this was because of repeated adaptation, we used a paired *t*-test on valley vs plateau species, by pairing species within genera or families or orders. Paired species are shown in Table S1. A subset including only family or genus level pairs is used to further evaluate the hypothesis. Pairing within clades allows for a phylogenetically independent contrast.

Nevertheless, we also tested for the existence of a phylogenetic signal in the hydrological niche of species and in the P_{50} metric. We built a phylogenetic tree for our species using the megaphylogeny of Zanne *et al.* (2014) available in Phylomatic v.3 (Webb & Donoghue, 2005) and calculated the Blomberg k (Blomberg *et al.*, 2003) and Pagel lambda (Pagel, 1999), with significance tested by 999 permutations. Blomberg k statistics compares the observed and expected variance to calculated independent contrasts. If relatives have similar trait values, then the variance of the independent contrasts will tend to be low. Pagel's lambda determines how much is needed to change the length of the original phylogenetic tree branches to eliminate the phylogenetic signal.

Results

In this Amazonian forest, valley forests (HAND <17 m) covers 46.1% of the area (Fig. 1). Xylem resistance to embolism formation (P_{50}) ranged from −0.56 to −4.2 MPa across species (Figs 2, S1). This local variation in P_{50} (3.7 MPa range) covers 44% of the global variation in P_{50} for angiosperms (−8.5 MPa, ranging from −0.1 to −8.6 MPa, Fig. 2). The mean P_{50} of the trees in this rainforest (−2.33 MPa) was more negative than the worldwide mean for tropical rainforest (−1.6 MPa), and similar to the worldwide mean of seasonal tropical forest (−2.4 MPa) (Fig. 2). Valley species had P_{50} values similar to tropical rainforest species ($t = 0.53$, df = 17, $P = 0.61$) and plateau species had a P_{50} 1.17 MPa lower than tropical rainforest species ($t = −3.62$, df = 25.0, $P = 0.001$) and similar to tropical seasonal forest species ($t = −1.1$, df = 21.6, $P = 0.28$).

The hydrological niche of the species (mean HAND) explained 22% of P_{50} variation ($F_{(1,26)} = 7.4$, $r^2 = 0.22$, $P = 0.01$; Fig. 3a), indicating that drought-resistant species (with low P_{50}) tended to occur preferentially in high and well-drained uplands with little access to the water table.

P_{50} also had a positive correlation with soil P concentration ($F_{(1,27)} = 5.2$, $r^2 = 0.16$, $P = 0.03$; Fig. 3b), indicating that drought-intolerant species (with high P_{50}) tended to occur on P-richer soils. Together, HAND, soil phosphorus and their interaction explained 45% of the variation in P_{50} across species ($F_{(3,24)} = 6.5$, $r^2 = 0.45$, $P = 0.002$).

The P_{50} of valley species was 1.32 MPa higher than that of plateau species ($t = 3.6$; df = 21.63; $P = 0.001$). A paired *t*-test between phylogenetic pairs indicated that the P_{50} of the plateau species was 1.28 MPa more negative than that of congeneric/confamilial/conorder valley species (Table S1; paired *T*-test $t = 4.2$; df = 8; $P = 0.0012$; Fig. 4). When only congeneric and confamilial pairs are considered, the patterns remain the same with plateau species −1.37 MPa more embolism resistant than valley species (paired *T*-test $t = 3.2$; df = 5; $P = 0.013$).
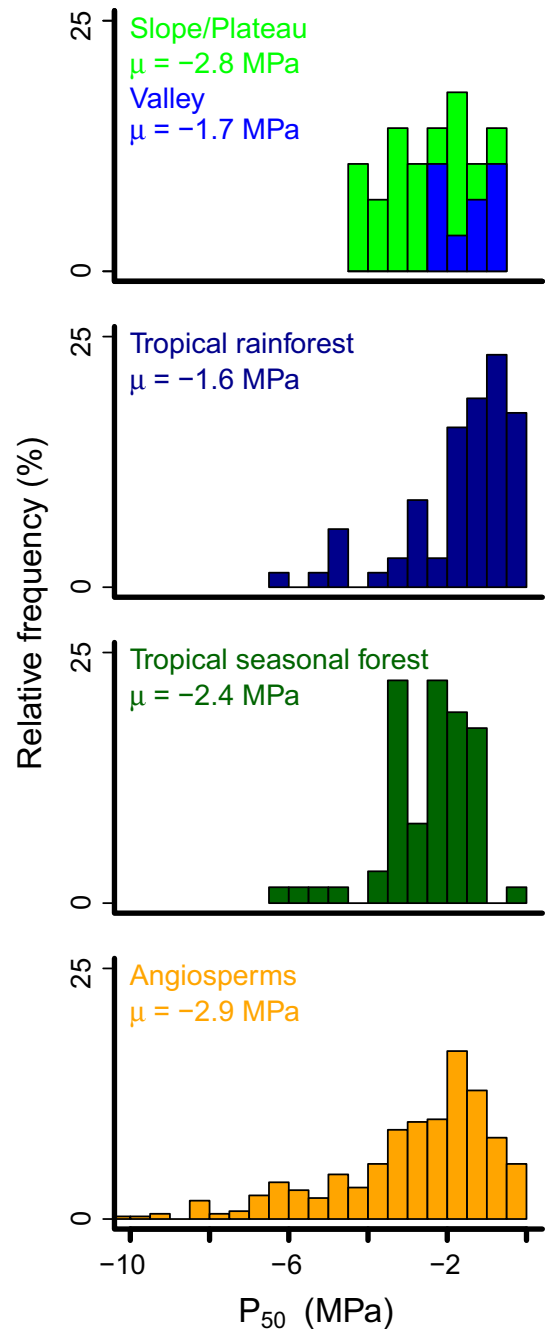
There was no phylogenetic signal for either the hydrological niche of species ($K = 0.26$, $P = 0.43$; $\lambda < 0.001$, $P = 1$) or species P_{50} ($K = 0.54$, $P = 0.06$; $\lambda = 0.99$, $P = 0.19$), and we can conclude that these traits are not conserved along phylogeny for the group of species evaluated here, that is, the hydrological niche of species within genus and even family have changed along evolution and the same for their resistance to embolism.
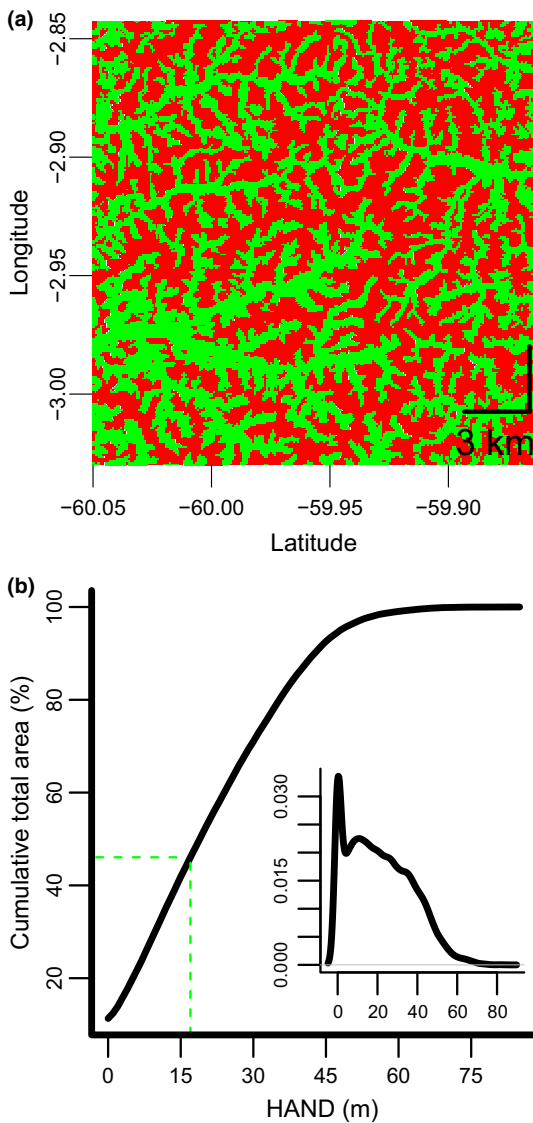
Fig. 1 Height above nearest drainage (HAND) of Ducke reserve. (a) Map of Ducke reserve highlighting valleys areas (HAND ≤ 17 m) in green and plateau areas (HAND > 17 m) in red. (b) Cumulative total area (%) of Ducke reserve according to HAND values (m). Green lines mark the 17 m threshold used for separating valley from plateau areas (Nobre *et al.*, 2011). The inset in (b) shows the probability distribution function of HAND values in Ducke reserve.


Fig. 2 Distribution of P_{50} (MPa) values from Amazon forest in Ducke's reserve in the valley (blue) and plateau (green), and global P_{50} data for tropical rainforest (dark blue), tropical seasonal forest (dark green), and all angiosperms (orange; data from Choat *et al.*, 2012).

Discussion

Our analysis revealed that xylem embolism resistance is highly variable at very small spatial scales within a hyperdiverse Amazonian forest, representing over 44% of the global variability for angiosperms. We show, for the first time, that: forest species in valleys are more drought vulnerable than plateau forest species, indicating that embolism resistance (P_{50}) contributes to species co-existence at very local scales within a single community and across a hydro-topographic gradient and not only at large scales (Choat *et al.*, 2012); P_{50} is the result of repeated evolutionary adaptation within closely related species across multiple Amazonian rainforest taxa; there is a link between P_{50} and species

tolerance and soil P availability, suggesting the evolution of a stress-tolerance syndrome to both nutrient and drought stress; and central Amazonian rainforest trees in the uplands have higher embolism resistance than previously observed for other rainforest trees (Choat *et al.*, 2012; Santiago *et al.*, 2018). The large observed hydraulic diversity and its association with topography have important implications for modelling (Christoffersen *et al.*, 2016) and predicting forest and species resilience to climate change.

(a) **(b)**
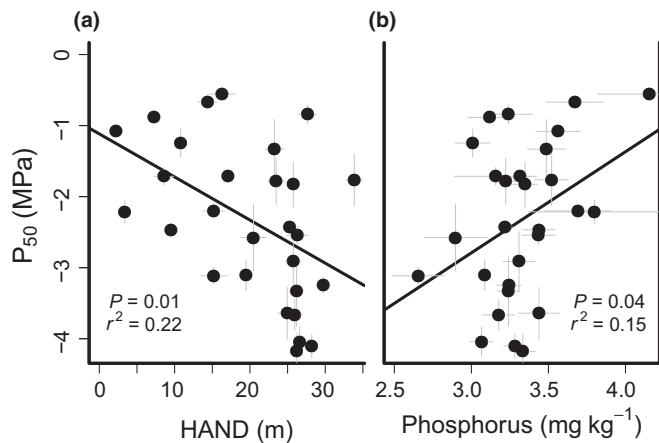
Fig. 3 P_{50} (MPa) of Amazon tree species as a function of (a) species mean height above nearest drainage (HAND, m), or (b) species mean soil phosphorus plant-available concentration (mg kg^{-1}). Horizontal and vertical grey lines over data indicate SE. Black lines are the best fit linear regressions with equations $\Psi_{50} = -1.12 - 0.06$HAND, $\Psi_{50} = -7.06 + 1.42$Phosphorus. Multiple regression of Ψ_{50} and HAND and phosphorus is $\Psi_{50} = -5.15 - 0.05$HAND $+ 1.17$Phosphorus ($r^2 = 0.32$, $P = 0.008$) and $\Psi_{50} = -7.2 - 0.84$HAND $- 2.42$Phosphorus $+ 0.23$Hand $\times$ Phosphorus ($r^2 = 0.45$, $P = 0.002$) with the interaction of P and HAND.
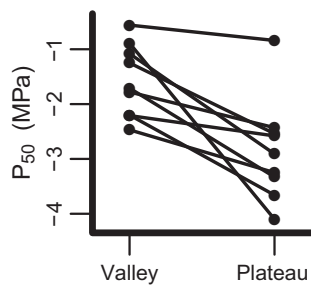
Fig. 4 Phylogenetic pairwise comparison of P_{50} (MPa) values of valley tree species with plateau tree species in a central Amazon forest. Paired species are shown in Supporting Information Table S1.

Higher xylem embolism vulnerability of valley tree species

P_{50} was related to the hydrological niche (mean HAND) of the species, indicating that hydraulic characteristics affect species distribution and partitioning of topographic gradients. Valley species occur close to the water table, which implies that water is readily available for these plants. Waterlogging occurs seasonally in valleys, and might represent a strong environmental filter for species that are not able to deal with hypoxic conditions. Valley species were shown to be less embolism resistant, which corroborates the contention that valley species evolved depending on water from the water table during drought periods. Plateau species, alternatively, are at least 17 m away from the water table, and have either invested in an embolism- resistant xylem or in deep roots to deal with seasonal soil water deficits (Brum et al., 2018). Clayey plateau soils hold more water at more negative water potentials, while sandy soils hold less water at less negative water potentials. However, during hydrological droughts, the

situation reverses and the sandy soils dry out more quickly than clay soils and to more negative water potentials. However, valley species presenting lower embolism resistance than plateau species suggests that severe hydrological drought in central Amazon may not be frequent under current climatic conditions because species with low P_{50} would be excluded from valley habitat. This hypothesis could be tested by evaluating if valley and plateau species in other forests subjected to strong hydrological droughts also differ in embolism resistance.

Higher drought vulnerability of valley forest species possibly explains the higher tree mortality found in the valley habitat in response to an extreme drought in a Colombian Amazon forest (Zuleta et al., 2017). Our results thus confirm valley species as particularly vulnerable to hydrological drought, while plateau species are mostly susceptible to meteorological drought. Plateau species having lower P_{50} than valley species (which is a necessary trait to deal with drier soils) suggest they can withstand the unavoidable tension caused in the xylem by the drying soil during the dry season. We also note that the hydraulic safety margin values (difference between P_{50} and minimum xylem water potential) for tropical forests is much more related to P_{50} ($r^2 = 0.40$; $P < 0.001$) than to minimum xylem water potential ($r^2 = 0.04$; $P = 0.002$) (dataset used in Choat et al., 2012). Finally, species hydrological niche (the species mean distance to the water table) explained 22% of the variation in P_{50}, and the same applied to other hydraulic traits (Cosme et al., 2017), suggesting that other factors, such as nutrient and waterlogging adaptations also influence species distribution along the topographic gradient, as has been demonstrated before (Fine et al., 2005). In fact, HAND, soil phosphorus and their interaction explained 45% of the variation in P_{50} across species. Therefore, a full understanding of niche partitioning along topographic gradients requires an integration of plant traits and all resources and stresses faced by plants, through empirical and modelling studies.

Drought tolerant species are more common in P-poor soils

Surprisingly, we found that plants with lower P_{50} occurred preferentially on P-poor soils. Phosphorus was not correlated to HAND, and therefore had an independent effect on P_{50}, being the only soil nutrient correlated with xylem embolism resistance. Soil phosphorus is an important predictor of tropical tree species distribution (Condit et al., 2013), but to our knowledge this is the first study showing a correlation between tree hydraulics and natural gradients in soil phosphorus. P_{50} might be related to soil phosphorus because they are part of the same evolutionary strategy or because of trait correlations. Plants require nutrients and energy to invest in water-transporting structures and maintain metabolic processes (Bittencourt et al., 2016), but the nutrient and energy costs of the water transport system have been neglected in the hydraulic literature (Bucci et al., 2006). Tolerance to nutrient and drought stress may be part of the same evolutionary strategy, as they require similar, conservative adaptive traits that enhance the efficiency of nutrient and water use and the residence time of these resources in the plant and lead to slow growth rates (Reich, 2014; Eller et al., 2018). Finally, P_{50} may be

correlated to soil P if both correlate to a common variable. For example, a low P_{50} can be simply a by-product of adaptation to P-poor soils, in which tough and dense wood with high lignin concentration, thick cell walls and small lumen area not only enhances stem longevity and the residence time of phosphorus in the plant (Thomas *et al.*, 2006), but also xylem embolism resistance. Additional studies are needed to evaluate if nutrient availability influence the chemical composition of plant vascular systems and thus xylem embolism resistance (Lima *et al.*, 2018; Pereira *et al.*, 2018). Alternatively, faster transpiration rates may be an important P-acquisition mechanism in phosphorus-poor soils (Cernusak *et al.*, 2011; Huang *et al.*, 2017) and a hydraulically resistant xylem would be required to sustain the low xylem water potentials developed in profligate water-using plants.

Embolism resistance is the result of repeated evolutionary adaptation

P_{50} may vary within an individual, between individuals and between populations (Sperry & Saliendra, 1994; Anderegg, 2015; Aranda *et al.*, 2015; Fichot *et al.*, 2015), and despite having a clear adaptive significance as a mechanism of drought tolerance in evergreen angiosperms, little is known about the role of phylogenetic history influencing the interspecific variation of this trait (Maherali *et al.*, 2004). The large (1.37 MPa) difference in P_{50} we found between closely related species and the absence of a phylogenetic signal suggest this trait is under strong divergent selection. Since this is a field study, the results might partially reflect plasticity. However, the strong association of specialized species of the congeneric pairs to each environment suggests that the interspecific variation of P_{50} reflects adaptation. A large part of the biodiversity of Amazonian trees (estimated as *c.* 16 000 species, ter Steege *et al.*, 2013) is found within *c.* 500 genera (Gentry, 1993), and our data suggest that recent drought adaptation may be one of the drivers of ecological speciation in the Amazon (Esquivel-Muelbert *et al.*, 2016). Future studies should investigate if topography affects intraspecific variability in P_{50} and if generalist species exhibit higher phenotypic plasticity in P_{50} than specialist species.

Are central Amazonian rainforest trees more drought resistant than elsewhere in the wet tropics?

The xylem vulnerability to hydraulic failure (P_{50}) of the central Amazonian rainforest species was more negative than that of other tropical rainforest species in a global meta-analysis (Choat *et al.*, 2012), and, in fact, very close to that of tropical seasonal forest. This suggests that species in central Amazon may be more drought resistant, possibly as a consequence of the nutrient-poor soils that select for slow-growing dense-wooded species, which invest in hydraulic safety (Reich *et al.*, 2003). For a full-picture of the drought resistance of Amazonian forests, we need to understand the interplay between stomatal regulation, xylem minimum water potentials, and xylem hydraulic properties, which will define the hydraulic safety margins of species. However, drought resistance is strongly linked to a species' hydrological

environment, so studies that assess how Amazonian forests will respond to future drier and hotter climates need therefore to take topographical heterogeneity and hydraulic and rooting depth diversity into account (Brum *et al.*, 2018). Floodplains of small rivers cover 1 million km^2, or 15% of the Amazon (Junk & Piedade, 1993), and 40–50% of central Amazon area (Nobre *et al.*, 2011) that may comprise drought-sensitive valley forests if water levels drop so much that trees experience drought, whereas the species in uplands may be more resistant to drought and climate change.

Our results have shown how little knowledge we have about the variation in hydraulic properties of rainforests. Our sampling of 28 species of central Amazonian trees almost doubled the mean P_{50} values known for tropical rainforests. Most strikingly, a high range of variation in P_{50} was found within a few metres of vertical distance in the same forest, associated with different hydrological habitats. Drought tolerance based on a low P_{50} value has evolved several times within genera or families, thus indicating that hydraulic traits contribute to both diversification and species co-existence within tropical forests. The low P_{50} values documented in plateau species suggest a larger potential to resist drought than other tropical forests studied so far, and the large local variation in hydraulic diversity suggest that topographically linked hydraulic traits should be part of models to understand climate change.

Author contributions

RSO, FRCC, LP designed research. RSO, FRCC, EvB, AdJ, PB, YA, FdVB, ECC, MVF, SG, ZTMG, MH, JS, JR-S, LP collected the hydraulics data. RSO, FRCC, EvB, AdJ, PRB, LP analysed the hydraulics data. FRCC performed the phylogenetic analyses. RSO and PRB wrote the first version of the manuscript with substantial input from FRCC and LP and all authors contributed to revisions.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Embolism resistance curves of all species.

Table S1 Species used in the pairwise comparisons.

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