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# Coordination and trade-offs among hydraulic safety, efficiency and drought avoidance traits in Amazonian rainforest canopy tree species

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## Summary

- Predicting responses of tropical forests to climate change-type drought is challenging because of high species diversity. Detailed characterization of tropical tree hydraulic physiology is necessary to evaluate community drought vulnerability and improve model parameterization.
- Here, we measured xylem hydraulic conductivity (hydraulic efficiency), xylem vulnerability curves (hydraulic safety), sapwood pressure–volume curves (drought avoidance) and wood density on emergent branches of 14 common species of Eastern Amazonian canopy trees in Paracou, French Guiana across species with the densest and lightest wood in the plot. Our objectives were to evaluate relationships among hydraulic traits to identify strategies and test the ability of easy-to-measure traits as proxies for hard-to-measure hydraulic traits.
- Xylem efficiency was related to capacitance, sapwood water content and turgor loss point, and other drought avoidance traits, but not to xylem safety ( $P_{50}$ ). Wood density was correlated ( $r = -0.57$  to  $-0.97$ ) with sapwood pressure–volume traits, forming an axis of hydraulic strategy variation.
- In contrast to drier sites where hydraulic safety plays a greater role, tropical trees in this humid tropical site varied along an axis with low wood density, high xylem efficiency and high capacitance at one end of the spectrum, and high wood density and low turgor loss point at the other.

## Introduction

The susceptibility of the Amazonian tropical rainforest to drought is of immense concern due to its critical role in regional hydrological cycles and moderation of climate, as well as its disproportionately large impact on global carbon cycles relative to other terrestrial ecosystems (Beer *et al.*, 2010; Saatchi *et al.*, 2011). A number of climate models predict increasing equatorial drought frequency and intensity in the near future (Fu *et al.*, 2013; Joetzjer *et al.*, 2013). Increasing drought due to increased vapour pressure deficit associated with climate change, El Niño Southern Oscillation or anomalous precipitation patterns has recently been linked to elevated rates of tree mortality at various locations across the globe (Allen *et al.*, 2010; Phillips *et al.*, 2010; Anderegg *et al.*, 2012; Bonal *et al.*, 2016). Thus, generating model parameterizations to predict the responses of Amazonia to climate change-type drought and its feedback to global climate forcing is a major research agenda. This effort is challenging

because of high tropical species diversity and limited data on how species diversity translates into functional diversity, with respect to physiological responses to water deficit. In laboratory studies, elevated atmospheric CO<sub>2</sub> reduces stomatal conductance and therefore increases leaf-scale photosynthetic water-use efficiency (Holtum & Winter, 2010), potentially reducing the impact of drought in a high CO<sub>2</sub> world. Yet, modelling Amazonian drought responses using only leaf-scale processes leads to divergences between model results and empirical data (Joetzjer *et al.*, 2014), suggesting that physiological parameterizations beyond the leaf, such as sapwood hydraulic properties, are necessary to estimate drought risk in tropical trees.

A major finding in plant hydraulics that links sapwood properties to drought susceptibility, and that can be applied to a diverse pool of tropical tree species, is the trade-off between xylem safety and efficiency (Gleason *et al.*, 2016). Current trends in plant hydraulics show that the ‘efficiency’ of xylem, characterized as water transport capacity per cross-sectional stem area, often

shows a trade-off against xylem 'safety', the ability to avoid cavitation and decline in function (Pockman & Sperry, 2000; Martínez-Vilalta *et al.*, 2002; Gleason *et al.*, 2016). The safety vs efficiency trade-off in plants is based on hydraulic theory and data demonstrating that wide vessels often cavitate at less negative water potentials than narrow vessels, whereas maximum rates of water transport through xylem vessels increase with vessel diameter (Pockman & Sperry, 2000; Martínez-Vilalta *et al.*, 2002; Wheeler *et al.*, 2005). Greater flow rates in large vessels are the result of fluid dynamics and can be modelled using the Poiseuille equation (Tyree & Ewers, 1991; Santiago *et al.*, 2004), whereas greater susceptibility to drought-induced xylem cavitation in large compared to small diameter vessels is thought to be the result of increasing probability of the seal of intervessel pits failing as the total area of pits increases (Wheeler *et al.*, 2005). Thus, there are very good biophysical and theoretical reasons why this trade-off should exist and constrain xylem function to a limited range of operation (Tyree *et al.*, 1994; Hacke *et al.*, 2006; Sperry *et al.*, 2008). However, there may also be very good reasons why this relationship might not apply across all taxa.

A recent global meta-analysis across 335 angiosperms and 89 gymnosperms illustrates how this relationship is significant, but weak; although there are no super-species with safe and efficient xylem, there are many species with low safety and low efficiency (Gleason *et al.*, 2016). The reasons why the safety vs efficiency trade-off may be weak globally or nonexistent locally include different ways in which efficiency may be expressed in sapwood (Preston *et al.*, 2006; Zanne *et al.*, 2010), or factors that reduce selection for safe xylem such as effective stomatal control or high water-availability climates (Maherali *et al.*, 2004; Mencuccini *et al.*, 2015). In fact, cavitation resistance is an important trait for plant responses to soil drought and might not be critical for survival in wet tropical forests without strong seasonality, but could increase in importance as seasonality increases. In essence, xylem safety calculated using vulnerability curves only tells us the water potential at which cavitation occurs, but not when a particular plant will reach that level (Pivovarov *et al.*, 2016; Santiago *et al.*, 2016). There may also be other traits that reduce the need for tolerance of low water potentials causing safety and efficiency to vary in isolation of one another. One trait that has been shown to trade off with xylem safety is capacitance, which reflects the stored water in stems that can temporarily supply the water for transpiration and protect xylem from precipitous drops in water potential (Meinzer *et al.*, 2008; Barnard *et al.*, 2011; Pivovarov *et al.*, 2016; De Guzman *et al.*, 2017). This is especially important in large and tall trees, where a large wood volume can potentially meet the water demands to sustain transpiration for several days (Scholz *et al.*, 2011). Indeed tropical tree species with high capacitance have been shown to survive drought even without high embolism resistance because they are buffered by stored water and are at lower risk of reaching the xylem tensions that cause hydraulic failure (Meinzer & Goldstein, 1996; Borchert & Pockman, 2005; Meinzer *et al.*, 2008, 2009; Sperry *et al.*, 2008). It was recently shown in a synthesis of tropical hydraulic trait data that the trade-off between drought avoidance, expressed as capacitance, and safety is more prominent than the trade-off

between xylem efficiency and safety (Christoffersen *et al.*, 2016). Thus, sapwood capacitance, along with other sapwood pressure-volume traits, may be emerging as a new axis of physiological variation that reflects drought avoidance, or the ability of sapwood to elude low xylem water potentials.

Clearly, xylem traits hold promise for better understanding the vulnerability of tropical trees to drought-induced mortality, as well as parameterizing models with increased robustness and realism. However, because comprehensive characterization of hydraulic physiology is tedious and time-consuming, relatively few data are available for parameterizing Earth system models with data on tropical tree species, so wood density is often used as an easy-to-measure surrogate (Chave *et al.*, 2009). We approached this problem through detailed physiological measures of hydraulic conductivity, sapwood vulnerability to drought-induced hydraulic failure and sapwood capacitance on emergent branches of 14 Amazonian canopy tree species in Paracou, French Guiana, that span the breadth of wood density found in the regional tree community. Our objectives were to: determine trade-offs among hydraulic traits to identify hydraulic strategies; evaluate coordination between xylem safety and efficiency with drought avoidance traits; and test the ability of wood density and easy-to-measure hydraulic traits as proxies for hard-to-measure hydraulic traits for more comprehensive inclusion in Earth system models.

## Materials and Methods

### Study site and species

The study was conducted in Paracou Research Station, French Guiana, South America (5°15'N, 52°55'W), a lowland seasonal tropical forest near Sinnamary (Gourlet-Fleury *et al.*, 2004). The site has a mean annual temperature of 25.6°C, and receives a mean annual precipitation of  $3041 \pm 259$  (1 SD) mm with a short dry season in March and a longer dry season in August–November. During the long dry season, precipitation can be < 50 mm per month (Bonafant *et al.*, 2008), and total precipitation during this period may not exceed 120 mm as in 2005, 2008 or 2012 (Supporting Information Fig. S1). Large interannual variation in precipitation at the site is caused by north/south movements of the Inter-Tropical Convergence Zone. The site is 40 m above sea level with an undulating topography of small hills surrounded by shallow swamps. Soils vary from relatively flat plateaus of white sand podzol or clay, to midslope clay soils with superficial drainage and seasonally inundated, low topography swamp soils (Baraloto *et al.*, 2005).

The site is typical of Amazonian rainforest of the Eastern Amazon (ter Steege *et al.*, 2006), with 160–180 species of trees  $\geq 10$  cm diameter per hectare, dominated by species in the Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae families (Baraloto *et al.*, 2012). Research was conducted within CIRAD permanent plots 6 and 15, each 6.25 ha and established in 1991 for studies in undisturbed forest. All trees  $\geq 10$  cm diameter within these plots have been tagged, mapped and identified to species, and are measured for diameter growth annually. We

selected 14 canopy tree species for study, focusing on plateau and slope species, but avoiding swamp species because our goal was to characterize the drought survival traits of upland species (Table 1). Our study species reflect the most common families at the site and sampling was stratified for phylogenetic robustness with replication in major groups including Fabaceae and Lecythidaceae. We also selected the species known to have among the densest wood (*Licania heteromorpha*  $0.80 \text{ g cm}^{-3}$ ) and the least dense wood (*Jacaranda copaia*  $0.34 \text{ g cm}^{-3}$ ), in an attempt to cover the complete range of vessel diameter and vulnerability to cavitation of upland trees at the site (Fortunel *et al.*, 2014). We did not exclude species with latex because our methods allowed us to circumvent their effect on trait measures. All of the Fabaceae we sampled have a thickening phloem exudate, and *Pradosia* and *Symphonia* have true laticifers producing latex (Table 1). Overall, we sampled 43 individual trees, with samples sizes between two and four individuals per species, depending on density and canopy exposure (Table 1).

### Hydraulic measurements

Tree climbers collected 3–4-m long upper canopy branches with clear sky exposure per species between 07:00 and 13:00 h in August–September 2013 and 2014, the peak of the dry season. The cut ends of sample branches were covered with parafilm to halt moisture loss and complete branches were double bagged in opaque heavy-duty plastic bags, sealed with waterproof tape. All branch samples were transported to the laboratory located in Kourou (45 min drive), by 14:00 h. Because many of our species have long xylem vessels, we used the bench dehydration technique to measure curves of xylem vulnerability to drought-induced cavitation. The bench dehydration technique is considered the most reliable technique for measuring species with long vessels (Choat *et al.*, 2010). Once in the laboratory, bags with sample branches were opened 1–2 times daily to sample small diameter (1–2 cm) 20–30 cm-long terminal stem segments and then sealed again to prevent

evaporation and allow the water potential to equilibrate throughout the sample branch. Sample stems were cut from the main sample branch underwater, cut ends were shaven with a razor blade, and the sample segment was fitted with tubing for the gravimetric measurement of hydraulic conductivity. For each sample stem cut from the main sample branch, two to three adjacent leaves were measured for leaf water potential ( $\Psi_l$ ) using a pressure chamber (Model 600; PMS Instruments, Albany, OR, USA) and a magnifying scope ( $\times 40$  Shop Microscope; Cole Parmer, Vernon Hills, IL, USA). For species with abundant gums or latex, cut stem segments were allowed to bleed out in water for 10 min before any measurements. Native stem hydraulic conductivity was determined by connecting stems to tubing filled with 20 mM KCl solution made with filtered ( $0.2 \mu\text{m}$ ) water flowing from an elevated source ( $< 2 \text{ kPa}$ ), through the stem, and into a graduated 1-ml pipette (Kimax-51; Kimble Chase, Vineland, NJ, USA) so that flow rates could be measured volumetrically, allowing the calculation of conductivity (Sperry *et al.*, 1988). During measurements, we maintained the meniscus upstream from the pipette tip such that no water droplet was able to form on the pipette tip and the pipette tip was occasionally dabbed with a kimwipe to ensure that no blockage occurred. Following the determination of native hydraulic conductivity, emboli were removed from stems by flushing with filtered ( $0.2 \mu\text{m}$ ) and degassed 20 mM KCl solution using a captive air tank to supply positive pressure (100 kPa) for 1 h, and measured for hydraulic conductivity as described above to determine maximum xylem hydraulic conductivity.

Cross-sectional sapwood area ( $A_s$ ;  $\text{cm}^2$ ) was determined for each conductivity sample by measuring sapwood diameter in two directions; distal leaf area ( $A_l$ ;  $\text{m}^2$ ) was determined by measuring the area of 10 representative leaves and multiplying by the total number of leaves on each sample. Stem hydraulic conductivity was divided by  $A_s$  to determine maximum xylem conductivity per unit sapwood area ( $k_{s,\text{max},x}$ ;  $\text{kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ), and by  $A_l$  to determine maximum xylem conductivity per unit leaf area

**Table 1** Study species, family, density, basal area and sample size for 14 Amazonian canopy rainforest tree species from Paracou, French Guiana

Species	Family	Density* (trees $\text{ha}^{-1}$ )	Basal area* ( $\text{m}^2 \text{ ha}^{-1}$ )	Trees sampled (no.)	Symbol (colour)
<i>Bocoa prouacensis</i>	Fabaceae	12.7	0.62	4	●
<i>Dicorynia guianensis</i>	Fabaceae	6.0	0.63	3	○
<i>Eperua falcata</i>	Fabaceae	38.6	3.93	3	●
<i>Eperua grandiflora</i>	Fabaceae	10.4	1.00	4	●
<i>Eschweilera sagotiana</i>	Lecythidaceae	39.3	2.60	3	●
<i>Jacaranda copaia</i>	Bignoniaceae	1.8	0.06	2	●
<i>Lecythis persistens</i>	Lecythidaceae	39.0	0.85	3	●
<i>Licania alba</i>	Chrysobalanaceae	27.1	1.20	4	●
<i>Licania heteromorpha</i>	Chrysobalanaceae	13.8	0.47	3	●
<i>Pradosia cochlearia</i>	Sapotaceae	7.6	0.79	3	●
<i>Sextonia rubra</i>	Lauraceae	2.1	0.34	3	●
<i>Symphonia globulifera</i>	Clusiaceae	2.2	0.34	3	●
<i>Tachigali melinonii</i>	Fabaceae	1.0	0.14	2	●
<i>Vouacapoua americana</i>	Fabaceae	9.7	0.87	3	●

\*Based on six 6.25-ha control plots at Paracou.

( $k_{l,max,x}$ ;  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ). We calculated leaf:sapwood area ratio ( $A_l:A_s$ ) on conductivity samples as a measure of hydraulic architecture.

Xylem conductivity was repeatedly measured on successive stems until the stem lost >90% conductivity (Fig. S2). Vulnerability curves were constructed by plotting  $\Psi_l$  vs the fraction of maximum conductivity (FMC) and fitting an inverse polynomial model (Manzoni *et al.*, 2013):

$$\text{FMC}(\Psi_x) = \left[ 1 + \frac{(\Psi_l)^{a_x}}{P_{50}} \right]^{-1} \quad \text{Eqn 1}$$

from which xylem water potential at 50% loss of conductivity ( $P_{50}$ ) and the slope of the vulnerability curve at  $P_{50}$  ( $a_x$ ) were determined for each species.

During collection of branches by tree climbers, strings were attached to fine twigs in the upper canopy so that they could later be pulled down at predawn and midday for the measurement of  $\Psi_l$ . Predawn  $\Psi_l$  was measured from 05:00 to 06:00 h and midday  $\Psi_l$  was measured between 12:00 and 13:00 h on clear days.

### Sapwood pressure–volume curves and wood density

Terminal stem samples 5–10 mm in diameter and 3–5 cm in length were collected from each sample branch upon arrival to the laboratory and were placed under degassed filtered water under light vacuum for rehydration overnight. We cut the sample to 10 mm in length, removed bark and pith to isolate xylem under filtered water, recorded volume, blotted to record saturated mass, and subsequently sealed them in psychrometer chambers. Xylem water potential ( $\Psi_x$ ) was measured with a thermocouple psychrometer (75-3VC Small Chamber Thermocouple Psychrometer; Merrill Instruments, Logan, UT, USA) connected to a water potential datalogger (Psypro; Wescor Inc., Logan, UT, USA) and placed inside an insulated chamber at 24°C. Values were logged every 0.5 h and  $\Psi_x$  was recorded when stable readings were achieved, alternated with measurements of fresh mass and a period of partial dehydration until a  $\Psi_x$  of  $-4$  MPa. Finally, samples were dried in an oven at 65°C for 48 h and weighed to determine dry mass and to calculate water released. Wood density (WD) was calculated as dry mass divided by fresh volume. Pressure–volume curve parameters were derived by plotting water potential against water released (Fig. S3), and extracting values for sapwood saturated water content ( $\theta_{s,x}$ ), sapwood osmotic potential at full turgor ( $\pi_{o,x}$ ), sapwood water potential at turgor loss point ( $\Psi_{tlp,x}$ ), total sapwood bulk elastic modulus ( $\epsilon_x$ ), total sapwood relative water content at turgor loss point ( $\text{RWC}_{tlp,x}$ ) and sapwood capacitance at full turgor ( $C_{ft,x}$ ) with the spreadsheet application by Sack & Pasquet-Kok (2011).

When interpreting sapwood pressure–volume traits, it is important to consider that this technique only measures parenchymal capacitance. Because our samples were fully hydrated when cut, xylem and fibre water were likely still present, and vessels cavitared as soon as water potentials became slightly negative. This differs from the water potential when vessel and fibre water are released in intact wood and likely generated steep

changes in the initial points of the pressure–volume curve. This potential artefact is important to consider because it should be proportional to the amount of vessels and therefore  $k_{s,max,x}$ . However, because it should only affect the initial points of the curve, this technique is still widely used for calculating  $C_{ft,x}$  (Meinzer *et al.*, 2008, 2009; Sperry *et al.*, 2008; Bucci *et al.*, 2016; De Guzman *et al.*, 2017).

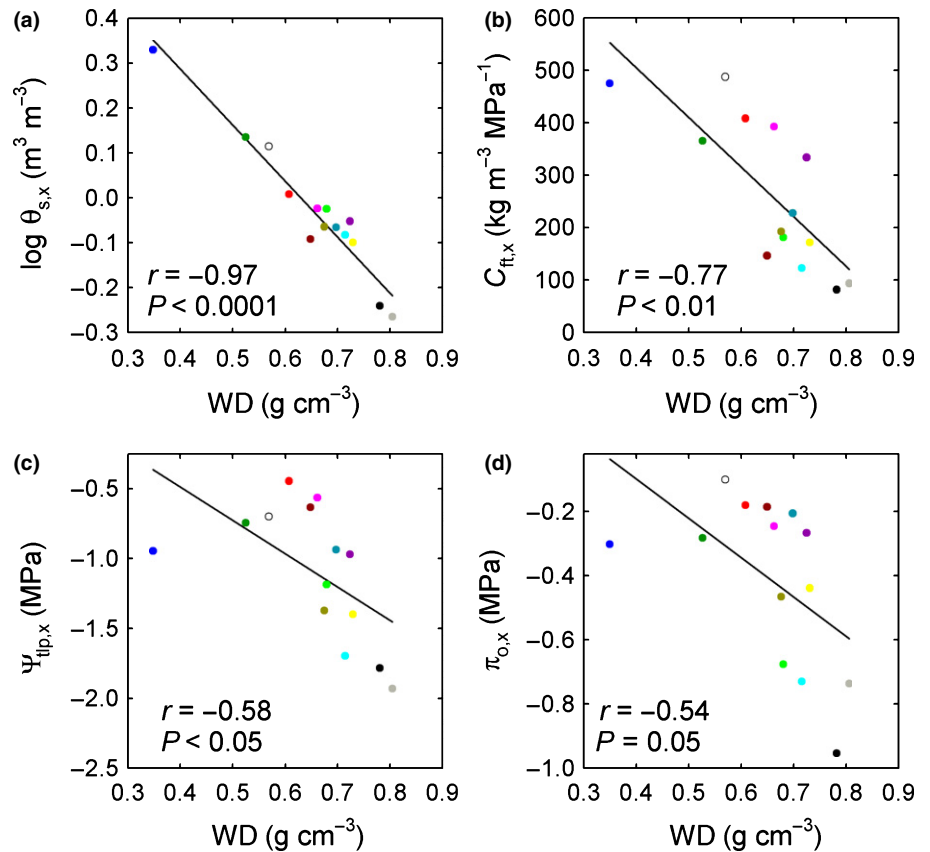
### Statistical analysis

Nonlinear curve fits for extracting vulnerability curve parameters were conducted using the NLS function in R (R Core Team, 2015). Data were tested for normality using the Shapiro–Wilk test in R. Log transformations were used to meet assumptions of normality for  $\theta_{s,x}$  and  $k_{l,max,x}$ . We evaluated bivariate trait relationships between mean values of species with Pearson product–moment correlation using the Hmisc package in R. Phylogenetic independent contrasts (PICs) were calculated using the PIC function in the APE package in R. The pruned tree (Fig. S4) was generated in phylocom (Webb & Donoghue, 2005), using the stored Angiosperm tree (Zanne *et al.*, 2014); alpha was set at 0.05 for all comparisons. Multiple comparisons were corrected using the False Discovery Rate (FDR) method to avoid inappropriately increasing the number of null hypotheses that are wrongly rejected (Pike, 2011). We used an FDR of 5% to calculate FDR-adjusted  $P$ -values using the Graphically Sharpened Method (Benjamini & Hochberg, 2000). FDR-adjusted  $P$ -values are reported in the Results section, Figs 1–4, and Table 2. We ran a Principal Component Analysis (PCA) of all measured traits using the `dudi.pca` function in the ADE4 package in R (Dray & Dufour, 2007). To better understand the global context of our data as compared to drier sites and to test whether there is declining cavitation resistance with increasing moisture availability, we also plotted our  $P_{50}$  data vs the Xylem Functional Trait (XFT) Database (Choat *et al.*, 2012) made available via the TRY Plant Trait Database (Kattge *et al.*, 2011).

### Results

Mean WD of sampled tissue across our study species ranged from  $0.34 \text{ g cm}^{-3}$  in *J. copaia* to  $0.80 \text{ g cm}^{-3}$  in *L. heteromorpha* (Table S1), and was highly related to sapwood pressure–volume parameters (Fig. 1). Values for  $\theta_{s,x}$ ,  $C_{ft,x}$ ,  $\Psi_{tlp,x}$  and  $\pi_{o,x}$  all showed negative correlation with WD (Fig. 1a–d), demonstrating a coordinated axis of physiological variation. We found no statistically significant correlations between WD and either  $\text{RWC}_{tlp,x}$  ( $r = 0.51$ ;  $P = 0.06$ ) or  $\epsilon_x$  ( $r = 0.48$ ;  $P = 0.08$ ). Vulnerability curve parameters did not show as strong of a relationship with WD as pressure–volume curve parameters.  $k_{l,max,x}$  strongly declined with increasing WD (Fig. 2a), but  $k_{s,max,x}$  and  $P_{50}$  did not show significant relationships with WD (Fig. 2b,c).

Predawn  $\Psi_l$  was always very near to 0 MPa, whereas midday  $\Psi_l$  varied from  $-0.97$  to  $-0.45$  MPa. Midday  $\Psi_l$  was always greater than  $P_{50}$ , which ranged from  $-3.46$  in *Bocoa prouacensis* to  $-1.03$  in *Eperua falcata* (Table S2), indicating that these trees maintained a pronounced hydraulic safety margin.  $P_{50}$  was



**Fig. 1** Relationship between species means of sapwood density (WD) and sapwood pressure–volume curve parameters: (a) sapwood saturated water content ( $\theta_{s,x}$ ); (b) sapwood capacitance at full turgor ( $C_{ft,x}$ ); (c) sapwood water potential at turgor loss point ( $\Psi_{tlp,x}$ ); (d) sapwood osmotic potential at full turgor ( $\pi_{o,x}$ ) for 14 species of Amazonian canopy rainforest trees from Paracou, French Guiana. Each point is the mean of a species;  $r$ -values indicate correlation coefficients; and solid lines indicate least squares regression lines. Symbol colours as in Table 1.

negatively correlated with  $\varepsilon_x$  ( $r = -0.59$ ;  $P < 0.05$ ), indicating that species with more resistant xylem showed a greater potential for elastic deformation of parenchyma. There were no other significant correlations involving  $P_{50}$  or  $a_x$ .

We measured significant correlations between  $C_{ft,x}$  and  $k_{l,max,x}$  (Fig. 3a) and  $k_{s,max,x}$  (Fig. 3b), indicating coordination between xylem efficiency and avoidance of low water potentials. There was significant correlation between  $k_{s,max,x}$  and  $RWC_{tlp,x}$  indicating a link between risk and xylem efficiency (Fig. 3c). We also found that  $k_{l,max,x}$  was correlated with  $\theta_{s,x}$  ( $r = 0.86$ ;  $P < 0.001$ ), whereas  $k_{s,max,x}$  was related to  $\theta_{s,x}$  ( $r = 0.61$ ;  $P < 0.05$ ),  $\pi_{o,x}$  ( $r = 0.57$ ;  $P < 0.05$ ) and  $\varepsilon_x$  ( $r = -0.77$ ;  $P < 0.01$ ).

Most of the cross-species correlations were within 0.10 of correlation coefficient values when evaluated as PICs (Table 2). Some relationships that occurred near the margin of significance gained or lost significance when evaluated as PICs, but overall there was a similar amount of significant relationships (25 in cross-species and 19 in PICs) across both types of analysis (Table 2), indicating that these correlations are the products of repeated evolutionary convergences in plant traits, as well as being functionally correlated among extant species.

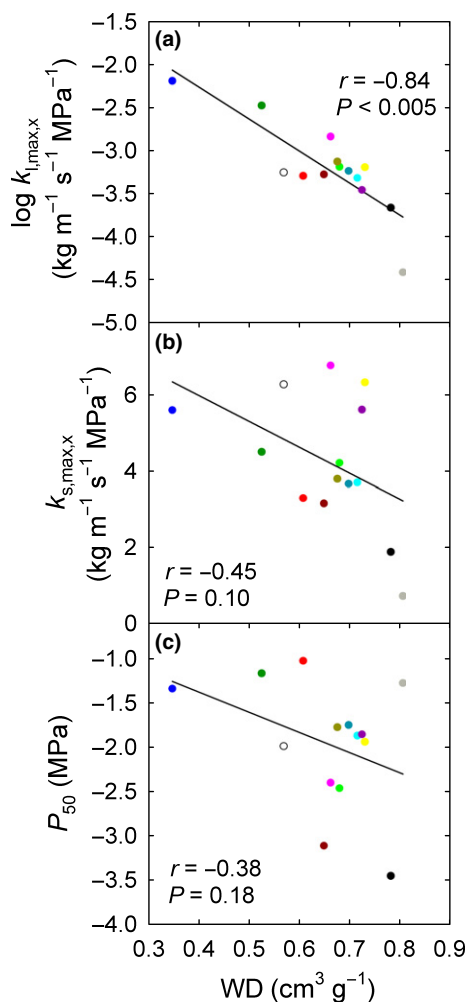
These correlations were reflected by PCA. The first axis accounted for 47.8% of all variation, and was dominated by WD,  $\theta_{s,x}$ ,  $\varepsilon_x$  and other sapwood pressure–volume curve parameters (Fig. 4). The second axis accounted for 17.6% more of the variation and was dominated by  $a_x$ ,  $A_1:A_s$  and midday  $\Psi_1$  (Fig. 4). Thus, the score of a species on the first axis is a

composite of sapwood pressure–volume curve parameters and WD where low scores indicate dense wood, low  $\theta_{s,x}$ , high  $\varepsilon_x$  and high  $RWC_{tlp,x}$  (*B. prouacensis*), and high scores indicate opposite traits (*J. copaia*) (Fig. 4). The second axis reflects several other traits that are orthogonal to the main axis of WD and sapwood pressure–volume curve parameters, and high scores indicate steep slopes of the xylem vulnerability curve (high  $a_x$ ) and high  $A_1:A_s$ .

Relative to the XFT Database, our  $P_{50}$  values showed relatively low cavitation resistance compared to drier sites, consistent with the overall trend of decreasing cavitation resistance with increasing mean annual precipitation (Fig. 5).

## Discussion

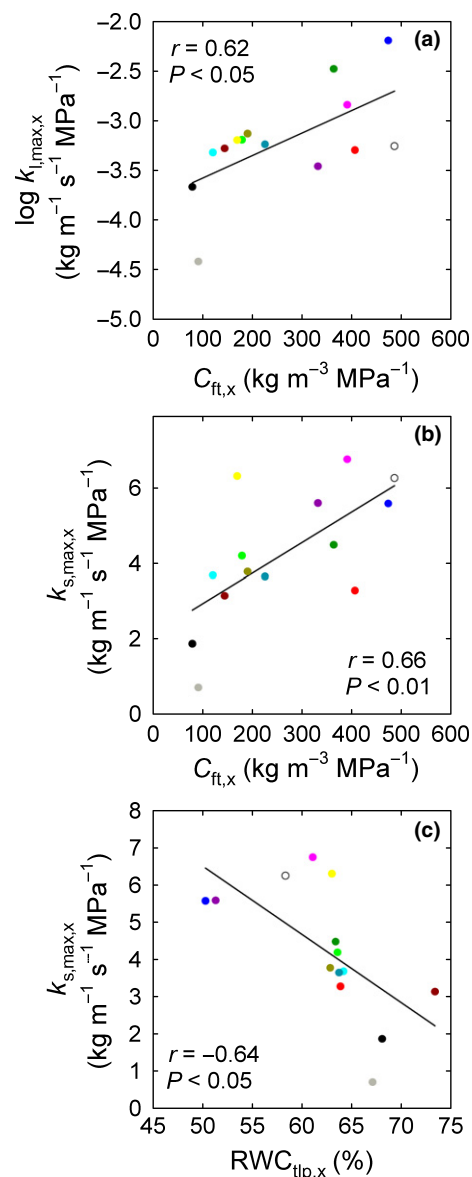
Our data demonstrate coordination among xylem hydraulic traits in terminal branches of some common and functionally diverse Eastern Amazonian canopy tree species. Sapwood pressure–volume traits were generally associated with wood density (WD), with dense wood related to low turgor loss points and low osmotic potential, traits that can prevent the negative effects of drought on xylem (Meinzer & Goldstein, 1996; Borchert & Pockman, 2005; Meinzer *et al.*, 2008, 2009; Sperry *et al.*, 2008). Yet it is important to note that dense wood also is related to low sapwood water content and low capacitance. There was little evidence that WD is related to xylem vulnerability curve parameters among these species, as only maximum xylem conductivity per unit leaf area ( $k_{l,max,x}$ ) showed a relationship with WD. Within



**Fig. 2** Relationship between species means of sapwood density (WD) and (a) maximum xylem conductivity per unit leaf area ( $k_{l,max,x}$ ); (b) maximum xylem conductivity per unit sapwood area ( $k_{s,max,x}$ ); (c) xylem water potential at 50% loss of stem hydraulic conductivity ( $P_{50}$ ) for 14 Amazonian canopy rainforest tree species from Paracou, French Guiana. Each point is the mean of a species;  $r$ -values indicate correlation coefficients; and solid lines indicate least squares regression lines. Symbol colours as in Table 1.

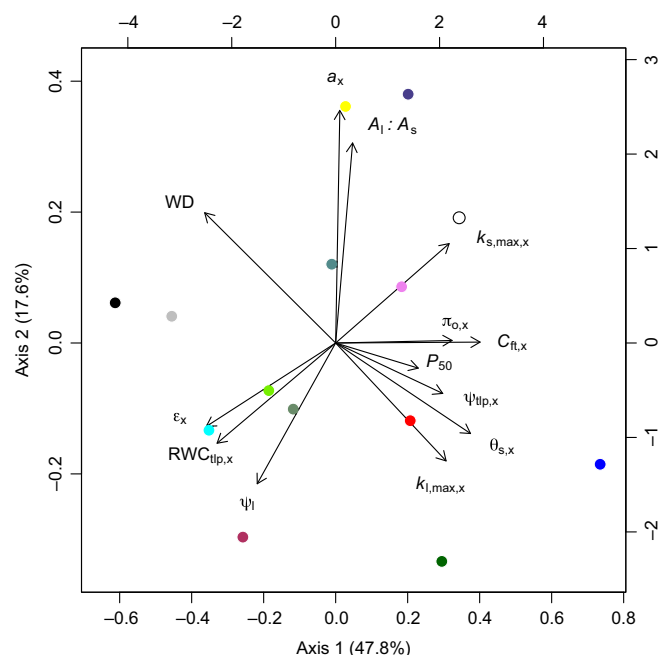
the context of the XFT Database, we also show reduced cavitation resistance as annual precipitation increases across the globe. We did not find evidence of a significant relationship between maximum xylem conductivity per unit sapwood area ( $k_{s,max,x}$ ) and xylem water potential at 50% loss of conductivity ( $P_{50}$ ), indicating that the safety vs efficiency trade-off is not a strong constraint at this site. Instead, much of the variation in hydraulic traits was related to PCA axis 1, demonstrating that these species vary along an axis with strategies marked by high xylem efficiency and high capacitance on one end of the spectrum and low water potential at turgor loss point on the other.

Our results show coordination between  $k_{l,max,x}$  and  $k_{s,max,x}$  with sapwood capacitance at full turgor ( $C_{ft,x}$ ), suggesting that greater connectivity of the xylem network provided by high specific hydraulic conductivity could allow greater recharge of capacitive water, a greater buffering capacity, or rapid rehydration

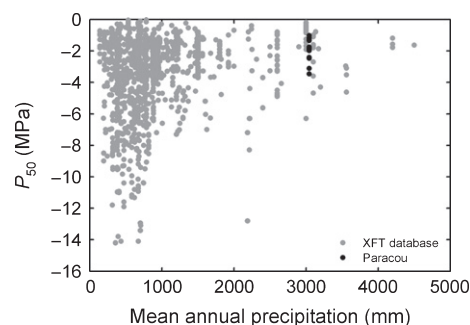


**Fig. 3** Relationships between species means of hydraulic conductivity and sapwood pressure–volume curve parameters: (a) maximum xylem conductivity per unit leaf area ( $k_{l,max,x}$ ) vs sapwood capacitance at full turgor ( $C_{ft,x}$ ); (b) maximum xylem conductivity per unit sapwood area ( $k_{s,max,x}$ ) vs  $C_{ft,x}$ ; (c)  $k_{s,max,x}$  vs sapwood relative water content at turgor loss point ( $RWC_{tlp,x}$ ) for 14 species of Amazonian canopy rainforest trees from Paracou, French Guiana. Each point is the mean of a species;  $r$ -values indicate correlation coefficients; and solid lines indicate least squares regression lines. Symbol colours as in Table 1.

during transient low vapour pressure deficit events, such as passing rain showers or clouds. Other studies of  $C_{ft,x}$  have found that although the water derived from capacitive processes may only comprise 10–30% of total daily transpiration, there can be a strong buffering effect of  $C_{ft,x}$  on plant water status (Sperry *et al.*, 2008). Daily minimum xylem water potential tends to increase with increasing capacitance across a range of tropical forest studies (Meinzer *et al.*, 2003, 2008; Scholz *et al.*, 2007), suggesting that the buffering effect of  $C_{ft,x}$  on daily fluctuations in xylem



**Fig. 4** Principal components analysis of hydraulic parameters for 13 traits and 14 Amazonian canopy rainforest tree species from Paracou, French Guiana. Each point represents data for a single species. The percentages in the axis labels indicate the variance explained by the axis. Traits: WD, sapwood density;  $k_{s,max,x}$ , maximum xylem conductivity per unit sapwood area;  $k_{l,max,x}$ , maximum xylem conductivity per unit leaf area;  $A_l : A_s$ , leaf : sapwood area ratio;  $\Psi_l$ , midday leaf water potential;  $P_{50}$ , water potential of leaf at 50% loss of stem hydraulic conductivity;  $a_x$ , slope of the xylem vulnerability curve at  $P_{50}$ ;  $\theta_{s,x}$ , sapwood saturated water content;  $\pi_{o,x}$ , sapwood osmotic potential at full turgor;  $\Psi_{tlp,x}$ , sapwood water potential at turgor loss point;  $\epsilon_x$ , total sapwood bulk elastic modulus;  $RWC_{tlp,x}$ , total sapwood relative water content at turgor loss point;  $C_{ft,x}$ , sapwood capacitance at full turgor. Symbol colours as in Table 1.



**Fig. 5** Relationship between mean annual precipitation and xylem water potential at 50% loss of stem hydraulic conductivity ( $P_{50}$ ) for 1230 species derived from the Xylem Functional Trait (XFT) Database (Choat *et al.*, 2012) and 14 Amazonian canopy rainforest tree species from Paracou, French Guiana, demonstrating declining cavitation resistance as moisture availability increases globally.

water potential can dampen the magnitude of the trade-off between xylem safety and efficiency (Sperry *et al.*, 2008; Bucci *et al.*, 2016). This appears to be the case in the humid lowland tropical forest of Paracou, where soil water deficit is relatively rare, relative humidity is usually above 85%, and  $C_{ft,x}$  shows greater coordination with other hydraulic traits than  $P_{50}$ . Moreover, the lack of the hydraulic safety vs efficiency trade-off in this study is consistent with our finding that within the context of the XFT Database, as annual precipitation increases across the globe there appears to be declining selection for physically resistant xylem (Fig. 5). Thus, the reduced importance of resistant  $P_{50}$  values in wet forests such as Paracou places weaker constraints on the coordination between safety vs efficiency, whereas drought avoidance traits such as  $C_{ft,x}$  show stronger coordination and play a large role in determining hydraulic strategies.

**Table 2** Correlation coefficients ( $r$ ) for traits and phylogenetic independent contrasts (PICs) for 14 species of Amazonian canopy rainforest trees from Paracou, French Guiana

	WD	$k_{s,max,x}$	$k_{l,max,x}$	$A_l : A_s$	Midday $\Psi_l$	$P_{50}$	$a_x$	$\theta_{s,x}$	$\pi_{o,x}$	$\Psi_{tlp,x}$	$\epsilon_x$	$RWC_{tlp,x}$	$C_{ft,x}$
WD	–	–0.45	<b>–0.84</b>	0.17	0.20	–0.38	0.31	<b>–0.97</b>	<b>–0.54</b>	<b>–0.58</b>	0.48	0.51	<b>–0.77</b>
$k_{s,max,x}$	–0.44	–	<b>0.65</b>	0.14	–0.26	0.08	0.46	<b>0.61</b>	<b>0.57</b>	0.53	<b>–0.77</b>	<b>–0.64</b>	<b>0.66</b>
$k_{l,max,x}$	<b>–0.86</b>	0.30	–	–0.39	–0.05	0.18	–0.07	<b>0.86</b>	0.47	0.57	–0.56	–0.46	<b>0.63</b>
$A_l : A_s$	0.16	0.07	–0.02	–	–0.46	–0.18	0.32	–0.10	–0.01	–0.17	–0.11	–0.49	0.12
Midday $\Psi_l$	0.15	–0.11	–0.24	–0.46	–	–0.43	–0.29	–0.24	–0.31	–0.20	0.56	0.46	–0.43
$P_{50}$	–0.46	0.24	0.42	0.11	<b>–0.64</b>	–	–0.05	0.42	0.33	0.15	<b>–0.59</b>	–0.43	0.45
$a_x$	0.29	0.47	–0.21	0.21	–0.22	–0.09	–	–0.17	0.05	–0.10	–0.24	–0.24	0.03
$\theta_{s,x}$	<b>–0.97</b>	0.51	<b>0.91</b>	0.02	–0.25	0.49	–0.16	–	0.59	<b>0.60</b>	<b>–0.61</b>	<b>–0.65</b>	<b>0.83</b>
$\pi_{o,x}$	–0.49	0.44	0.14	–0.07	–0.21	0.50	–0.02	0.39	–	<b>0.90</b>	<b>–0.67</b>	–0.33	<b>0.75</b>
$\Psi_{tlp,x}$	–0.55	0.41	0.19	–0.26	0.02	0.30	–0.23	0.40	<b>0.89</b>	–	–0.50	–0.21	<b>0.76</b>
$\epsilon_x$	0.44	<b>–0.71</b>	–0.36	–0.14	0.59	<b>–0.75</b>	–0.29	–0.50	<b>–0.62</b>	–0.42	–	<b>0.69</b>	<b>–0.68</b>
$RWC_{tlp,x}$	0.56	<b>–0.70</b>	<b>–0.63</b>	–0.44	0.43	–0.52	–0.25	<b>–0.71</b>	–0.27	–0.18	<b>0.71</b>	–	<b>–0.69</b>
$C_{ft,x}$	<b>–0.78</b>	<b>0.63</b>	0.57	0.08	–0.34	0.59	–0.03	<b>0.77</b>	<b>0.71</b>	<b>0.74</b>	<b>–0.65</b>	<b>–0.68</b>	–

Species trait correlation coefficients are given in the upper right section of the matrix ( $n = 14$ ). Correlation coefficients for PICs are given in the lower left section of the matrix ( $n = 13$ ). Bold type indicates significant correlations based on False Discovery Rate-adjusted  $P$ -values.

WD ( $\text{g cm}^{-3}$ ), sapwood density;  $k_{s,max,x}$  ( $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ), maximum xylem conductivity per unit sapwood area;  $k_{l,max,x}$  ( $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ), maximum xylem conductivity per unit leaf area;  $A_l : A_s$  ( $\text{m}^2 \text{cm}^{-2}$ ) leaf : sapwood area ratio; Midday  $\Psi_l$  (MPa) midday leaf water potential;  $P_{50}$  (MPa) water potential of leaf at 50% loss of stem hydraulic conductivity;  $a_x$  ( $\text{MPa}^{-1} \times 100$ ) slope of the xylem vulnerability curve at  $P_{50}$ ;  $\theta_{s,x}$  ( $\text{m}^3 \text{m}^{-3}$ ), sapwood saturated water content;  $\pi_{o,x}$  (MPa) sapwood osmotic potential at full turgor;  $\Psi_{tlp,x}$  (MPa), sapwood water potential at turgor loss point;  $\epsilon_x$  (MPa), total sapwood bulk elastic modulus;  $RWC_{tlp,x}$ , total sapwood relative water content at turgor loss point;  $C_{ft,x}$  ( $\text{kg m}^{-3} \text{MPa}^{-1}$ ), sapwood capacitance at full turgor.

Our finding that Eastern Amazonian canopy tree species exhibit high  $C_{\text{fit},x}$ , which functions as a benefit on the low wood density end of the spectrum, raises questions about the benefits of dense wood in this ecosystem, because dense wood is not correlated with greater cavitation resistance at this site. A low turgor loss point, in terms of both relative water content ( $\text{RWC}_{\text{tlp},x}$ ) and sapwood water potential ( $\Psi_{\text{tlp}}$ ), appears to be the major benefit for high-WD species. Turgor is a measure of the positive hydrostatic pressure in plant cells, and is required for maintaining cell growth, rigidity and general function (Taiz *et al.*, 2015). There also is evidence that living cells must have positive pressure (Tyree, 1976). Therefore, species with low sapwood turgor loss points can avoid the detrimental effects of water deficit on cells to lower limits of water potential and relative water content than species with high sapwood turgor loss points. This is potentially important for dense wooded species with low  $C_{\text{fit},x}$  and limited ability to buffer transient changes in sapwood water potential. Turgor loss point has been used extensively in leaves to characterize the drought resistance of contrasting species (Bartlett *et al.*, 2012; Maréchaux *et al.*, 2015; Anderegg *et al.*, 2016). Turgor loss point and other parameters derived from pressure–volume curves have not been used as extensively in sapwood as in leaves, but our results indicate that they describe aspects of drought resistance that are not described by  $P_{50}$ , including elastic deformation and osmotic regulation of living xylem parenchyma cells. Tropical trees typically have an axial parenchymal fraction that is three times higher than temperate trees, and thus have a greater proportion of living cells within their xylem than temperate trees (Morris *et al.*, 2016). This suggests that in tropical trees living in a relatively moist habitat without constant water deficit, the living aspects of xylem represented by sapwood pressure–volume curves may better represent axes of hydraulic strategy variation than the physical resistance of xylem.

The result that an easy-to-measure functional trait such as WD functions as a proxy for hard-to-measure hydraulic traits has potentially important implications for modelling drought responses in tropical forest, because our data indicate that among our 14 study species it is much easier to predict sapwood pressure–volume traits than  $P_{50}$  from WD. Numerous vegetation models characterize drought through simple routines based on soil moisture or coarse climatic variables and are unable to account for variation in drought resistance among species (Xu *et al.*, 2013; Medlyn *et al.*, 2016). However, newer models such as the hydraulic algorithm of the Trait Forest Simulator (TFS v2-Hydro), which can incorporate plant hydraulic processes with all parameters as measureable plant hydraulic traits (Christoffersen *et al.*, 2016), or the Ecosystem Demography model (ED2), which has been modified to incorporate hydraulic traits to predict leaf area dynamics and define plant functional types (Xu *et al.*, 2016), offer more direct ways to include detailed physiological data. We emphasize that incorporating hydraulic traits into predictive models in more direct ways than through correlations with WD will greatly improve the mechanistic realism of models and potentially add predictive power (Anderegg *et al.*, 2016).

Overall our results identify an axis of hydraulic strategy variation among Eastern Amazonian canopy tree species across the

range of wood density that exists at the site. We show for the first time that Amazonian tree species vary along an axis of hydraulic strategy variation with low wood density, high xylem efficiency and high capacitance at one end of the spectrum, and low turgor loss point at the other. This stands in contrast to findings in many other vegetation types that show hydraulic strategy variation along the safety vs efficiency spectrum (Pockman & Sperry, 2000; Martínez-Vilalta *et al.*, 2002; Wheeler *et al.*, 2005; De Guzman *et al.*, 2017). The lack of a safety vs efficiency trade-off among the Amazonian trees that we studied is noteworthy, and supports the idea of diminishing selection on xylem cavitation resistance as moisture availability increases (Fig. 5). Our analysis provides sufficient coverage of key hydraulic functions to increase our understanding of drought resistance in Amazonian canopy tree species. Although such understanding will help us model and predict the responses of Amazonian tree species to increasingly protracted drought, further challenges remain (Huntingford *et al.*, 2013; Joetzer *et al.*, 2014; Bonal *et al.*, 2016; Santiago *et al.*, 2016). First, for predicting the drought responses of what may be up to 50 000 unmeasured tree species in the tropics based on relationships with WD, constraining responses to a limited number of possible outcomes is likely to be our most realistic expectation. Second, linking a diverse set of responses with drought types that vary in intensity, duration and frequency propagates the complexity of our challenge. Finally, different sites containing species with contrasting evolutionary histories and environmental constraints will need to be considered to understand and predict the future of tropical forests under changing precipitation regimes. It is only through identification of axes of physiological strategy variation constrained by the physics of water transport and an improved understanding of interspecific trait variation that we can identify the limits of drought resistance and avoidance in tropical tree species, and predict realistic tipping points for the tropical forest biome.

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## Author contributions

L.S.S., M.E.D.G. and D.B. planned the hydraulic measurements; C.B., B.H., D.B., L.S.S., M.E.D.G. and J.E.V. selected the study species; M.E.D.G., L.S.S., J.E.V. and M.B. performed the hydraulic measurements; C.F., C.B. and D.B. provided preliminary data; M.E.D.G., C.F., B.H. and L.S.S. analysed the data; L.S.S. wrote the manuscript; and M.E.D.G., D.B., C.B., C.F. and B.H. provided edits.

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## Supporting Information

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

**Fig. S1** Annual precipitation at Paracou Research Station.

**Fig. S2** Vulnerability curves for all study species.

**Fig. S3** Sapwood pressure–volume curves for all study species.

**Fig. S4** Phylogenetic relationships among study species.

**Table S1** Mean sapwood pressure–volume curve parameters

**Table S2** Mean vulnerability curve parameters

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