Received: 15 September 2025 | Accepted: 13 April 2026

DOI: 10.1111/1365-2435.70381

BRITISH ECOLOGICAL SOCIETY Functional Ecology

RESEARCH ARTICLE

Wood anatomical trait correlations with hydraulic efficiency and safety in an aseasonal wet tropical forest

Julia Valentim Tavares[1,2] | Samuel L. Farrar[1] | Chris M. Smith-Martin[3] | Silvia Bibbo[1,4] | Kasia Ziemińska[1,5] | Farah Brenda Solis Petz[1] | María Uriarte[6] | Jess K. Zimmerman[7] | Robert Muscarella[1]

[1]Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden; [2]School of Geography, University of Leeds, Leeds, UK; [3]Department of Plant and Microbial Biology, University of Minnesota, Saint Paul, Minnesota, USA; [4]Division of Wood Science and Technology, SLU, Uppsala, Sweden; [5]Hawkesbury Institute for the Environment, University of Western Sydney, Richmond, New South Wales, Australia; [6]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York, USA and [7]Department of Environmental Sciences, University of Puerto Rico, San Juan, Puerto Rico, USA

Correspondence
Julia Valentim Tavares
Email: tavares.juliav@gmail.com

Funding information
National Science Foundation, Grant/Award Number: DEB-1753810; Vetenskapsrådet, Grant/Award Number: 2019-03758; Birgitta Sintring Foundation, Grant/Award Number: S2023-0009; Royal Swedish Academy of Sciences, Grant/Award Number: BS2025-0004

Handling Editor: Antonella Gori

Abstract

1. Xylem anatomy underpins the capacity of trees to transport water while avoiding hydraulic failure, shaping species performance and resilience to climate change. However, the specific ways anatomical traits underpin hydraulic trade-offs in tropical forests remain debated.
2. We investigated relationships between branch wood anatomical traits and their hydraulic properties across 78 individual trees, encompassing 13 species, in an aseasonal wet tropical forest in Puerto Rico. We combined metrics of vessel size, vessel grouping, and tissue fractions with key hydraulic traits, including theoretical hydraulic conductivity (K_{th}), embolism resistance (Ψ_{50}) and stem capacitance at full turgor (C_{ft}). This allowed us to address two questions. First, we tested whether species in an aseasonal wet forest exhibit a trade-off between xylem safety and efficiency. Second, we examined which anatomical traits are associated with hydraulic safety strategies, from drought tolerance to drought avoidance.
3. We found a high diversity of hydraulic strategies across species, with strong evidence of a trade-off between safety and efficiency: individuals with higher K_{th} and higher C_{ft} were more vulnerable to embolism (less negative Ψ_{50}). Contrary to the vessel diameter hypothesis, vessel size was not significantly related to embolism resistance. Instead, vessel connectivity emerged as a key determinant: species with a higher proportion of solitary vessels were significantly more vulnerable to embolism, supporting the vessel network hypothesis. Multivariate combinations of vessel traits also explained variation in Ψ_{50}, whereas tissue fractions, including total parenchyma and pith, did not predict variation in C_{ft}. These findings reveal that drought tolerance (low Ψ_{50}) and drought avoidance (high C_{ft}) are coordinated

with water transport efficiency (K_{th}), indicating that tropical tree species balance hydraulic strategies along complementary axes of safety-efficiency.
4. Together, this work advances understanding of the xylem structure–function link in tropical forests and emphasizes the importance of vessel network properties for predicting patterns of species co-existence and forest resilience under intensifying climatic extremes.

KEYWORDS
embolism resistance, hydraulic safety–efficiency trade-off, hydraulic traits, Puerto Rico, tropical forests, vessel connectivity, wood anatomy, xylem

1 | INTRODUCTION

Tropical forests house 50% of total terrestrial biodiversity on the planet (Jenkins et al., 2013; Kier et al., 2009) and play a fundamental role in global carbon and water cycles (Good et al., 2015; Pan et al., 2011; Wei et al., 2017). Over the past decades, changes in climatic conditions (e.g. increasing drought) have affected these ecosystems (Douville et al., 2023), resulting in changes in their floristic and functional composition (Aguirre-Gutiérrez et al., 2019, 2025; Esquivel-Muelbert et al., 2019), structure and dynamics (Bauman et al., 2022; Hubau et al., 2020; Tavares et al., 2023). Elucidating the mechanisms that confer species resistance to environmental stressors, including drought, are crucial to enable us to assess tropical forests' sensitivity to ongoing climate change.

Tree hydraulic and wood anatomical traits are associated with a variety of ecological strategies to deal with water stress, including both drought tolerance and drought avoidance (Table 1) (Santiago et al., 2018; Smith-Martin et al., 2023; Zimmermann, 1983). A commonly measured metric of tree drought tolerance is embolism resistance, defined as the xylem water potential at which 50% of the stem hydraulic conductivity is lost (Ψ_{50}). Ψ_{50} is related to species distributions across regional and local water availability gradients, where more negative values indicate a stronger resistance to embolism (Choat et al., 2012; Oliveira et al., 2019, 2021; Tavares et al., 2023; Tavares, Gloor, et al., 2026). Drought avoidance, often quantified by stem capacitance at full turgor (MPa), is the ability of stems to store water and to mobilize it under stressful conditions (Meinzer et al., 2009). Both drought tolerance and avoidance safeguard xylem integrity under water stress (Ziegler et al., 2023). Previous studies have suggested a trade-off between these strategies, although this relationship is not universal, with some evidence of partial decoupling (Meinzer et al., 2009; Santiago et al., 2018; Smith-Martin et al., 2023; Zimmermann, 1983).

In addition to driving hydraulic safety, xylem structure plays a critical role ensuring water transport from roots to leaves. Xylem

TABLE 1 List of species studied.

Family	Species	Code	Successional association[a]	Sample size	
				Anatomy *N*	Hydraulic *N*
Euphorbiaceae	*Alchornea latifolia*	ALCLAT	Fast	6	5
Flacourtiaceae	*Casearia arborea*	CASARB	Fast	4	4
Moraceae	*Cecropia schreberiana*	CECSCH	Fast	3	0
Cyrillaceae	*Cyrilla racemiflora*	CYRRAC	Fast	7	7
Lauraceae	*Ocotea leucoxylon*	OCOLEU	Fast	5	5
Araliaceae	*Schefflera morototoni*	SCHMOR	Fast	2	0
Boraginaceae	*Cordia borinquensis*	CORBOR	Intermediate	7	7
Elaeocarpaceae	*Sloanea berteroana*	SLOBER	Intermediate	8	6
Euphorbiaceae	*Drypetes glauca*	DRYGLA	SLB	6	5
Bignonaceae	*Tabebuia heterophylla*	TABHET	SLB	7	4
Burseraceae	*Dacryodes excelsa*	DACEXC	LLP	9	6
Fabaceae	*Inga laurina*	INGLAU	LLP	6	5
Sapotaceae	*Micropholis guyanensis*	MICGUY	Slow	8	8

[a]Successional associations are: LLP—long-lived pioneers; SLB—short-lived breeders with relatively fast demography; shade tolerance spectrum ranging from shade-intolerant with fast demographic strategies, intermediate tolerance and strategies, to shade-tolerant species with slow demographic strategies (Rüger et al., 2023). We note that demographic categories are used in our study as a descriptive framework rather than as formal groupings for hypothesis testing.

efficiency in water transport can be estimated based on the size and number of conducting vessels, which together determine the theoretical maximum amount of water transported per unit area (K_{th}, $m^4/MPa^{-1} \times s^{-1}$) (Zimmermann, 1983). There is a direct relationship between vessel size and hydraulic efficiency, whereby wider vessels exhibit higher hydraulic conductivity (Zimmermann, 1983). Due to its central role in plant carbon and water balance, the relationship between xylem efficiency and xylem safety (via drought tolerance or avoidance) is often considered a mechanistic basis for the 'growth-survival' trade-off (Argüelles-Marrón et al., 2023; Eller et al., 2018; Oliveira et al., 2021). High xylem efficiency supports elevated carbon assimilation and rapid growth but may increase vulnerability to hydraulic failure, whereas greater embolism resistance enhances survival under water stress, typically at the cost of reduced hydraulic efficiency. These physiological trade-offs are thought to scale up to species-level life-history variation, such that tree demographic strategies reflect contrasting allocations to growth versus persistence (Adler et al., 2014; Salguero-Gómez et al., 2016). Fast demographic strategies are generally associated with rapid growth and higher mortality risk, while slow strategies favour longevity and lower growth rates (Rüger et al., 2018, 2023; Wright et al., 2010). Increasing evidence suggests that these demographic patterns emerge from coordinated suites of functional traits governing resource acquisition, transport, and use, including xylem hydraulic and anatomical traits (Argüelles-Marrón et al., 2023; Rodríguez-Ramírez, Arroyo, et al., 2024; Rodríguez-Ramírez, Frei, et al., 2024). Organizing and quantifying the mechanistic basis for the xylem safety-efficiency relationship across individuals and species is thus crucial for advancing our understanding of species distributions, coexistence, and vegetation dynamics (Santiago et al., 2018). While the xylem safety-efficiency trade-off has been hypothesized and demonstrated by some studies (Isasa et al., 2023; Lobo et al., 2018; Pereira et al., 2023; Pratt et al., 2023; Sperry et al., 2006; Wheeler et al., 2005), its generality and underlying anatomical mechanisms remain under debate. A number of studies have reported weak (Gleason et al., 2016) or even absent relationships between safety and efficiency (Maherali et al., 2004; Trueba et al., 2019; Tyree et al., 1994), questioning the universality of this trade-off across multiple ecological contexts and the validity of metrics used to assess it (Meinzer et al., 2010).

One main hypothesis of the mechanism underlying the xylem safety-efficiency trade-off proposes a negative relationship between embolism resistance and the size of vessels (i.e. the 'vessel diameter' hypothesis) (Ellmore & Ewers, 1985; Gleason et al., 2016; Levionnois et al., 2021). In this hypothesis, large vessels, which have higher hydraulic efficiency, are less resistant to embolism. Under this framework, wood anatomical features cannot sustain both safety and efficiency simultaneously (Ellmore & Ewers, 1985; Gleason et al., 2016; Levionnois et al., 2021). In fact, studies investigating the long-standing discussion about the existence of a trade-off between xylem efficiency and safety, consistently show that no plants have both high embolism resistance and high hydraulic conductivity (Gleason et al., 2016). However, the opposite does not hold true, as several plant species present low safety and low efficiency. While some studies have found evidence of direct effects of vessel diameter on embolism resistance (Isasa et al., 2023; Lobo et al., 2018; Pratt et al., 2023; Sperry et al., 2006; Wheeler et al., 2005), other studies report the absence of a relationship between these variables (Maherali et al., 2004; Trueba et al., 2019; Tyree et al., 1994) or weak support for a global safety versus efficiency trade-off across tree species (Gleason et al., 2016).

One reason behind the lack of universality/generality of the vessel diameter hypothesis is that it does not consider that xylem conduits constitute a highly interconnected network. In contrast, the 'vessel network' hypothesis (Levionnois et al., 2021) suggests that the connectivity of the vascular network can affect both water transport properties as well as propagation of embolisms through the xylem. This 'vessel network' hypothesis encompasses two contrasting mechanisms: Greater vessel connectivity (i.e. vessel grouping) can improve embolism resistance by offering alternative pathways for water transport when some conduits become embolized, a possibility supported by experimental (Lens et al., 2011; Levionnois et al., 2021; Wason et al., 2021) and theoretical studies (Tyree et al., 1994). For instance, species growing under intense water stress tend to have more and larger groups of vessels than species associated with more mesic conditions, suggesting vessel grouping may provide hydraulic redundancy (Carlquist, 1984, 2009). On the other hand, high connectivity may facilitate the spread of gas bubbles between vessels, thereby increasing vulnerability to drought-induced embolism (Avila et al., 2023; Loepfe et al., 2007). Some studies have found that embolism resistance is positively associated with a higher proportion of solitary vessels, implying that greater vessel connectivity may facilitate the spread of embolism between neighbouring conduits (Loepfe et al., 2007; Martínez-Vilalta et al., 2012; Scholz et al., 2013).

A key anatomical feature underpinning these contrasting outcomes appears to be the intervessel pores (i.e. 'pits'), whose characteristics can prevent embolisms spreading between vessels (Jansen et al., 2009; Kaack et al., 2021; Levionnois et al., 2021, 2022; Smith-Martin, Jansen, et al., 2022). For example, thicker pit membranes are thought to inhibit embolism spread (Jansen et al., 2009; Kaack et al., 2021; Levionnois et al., 2021; Trueba et al., 2019), and dry forest species often have thicker membranes than their wet forest counterparts (Smith-Martin, Jansen, et al., 2022). The second mechanism under the vessel network hypothesis is that lower vessel connectivity may enhance embolism resistance, potentially because highly connected vessels are more likely to have leaky pit membranes that facilitate gas movement and trigger embolism propagation (Avila et al., 2023; Christman et al., 2009; Wheeler et al., 2005). The 'vessel diameter' and 'vessel network' hypotheses are likely not mutually exclusive, xylem safety is likely influenced by multiple factors resulting from a combination of various xylem characteristics rather than a single trait alone.

Other wood anatomical traits, apart from metrics of vessel size, grouping and intervessel properties, can also play a role in explaining xylem safety coordination and trade-offs (Kiorapostolou

et al., 2019). For instance, the fractional area occupied by different tissue types (e.g. xylem parenchyma) has, to date, received relatively less attention in xylem structure–function studies (Chen et al., 2020; Plavcová et al., 2016; Pratt & Jacobsen, 2017; Ziemińska et al., 2015). Beyond facilitating long-distance water transport from roots to leaves, wood traits provide other essential functions, including radial movement of water and nutrients through ray parenchyma, as well as the storage of water and nutrients in living fibres and both ray and axial parenchyma cells (Brodersen et al., 2018; Plavcová et al., 2016). Axial parenchyma fraction tends to correlate positively with mean vessel diameter, suggesting an important role in enhancing hydraulic conductivity (Chen et al., 2020; Morris et al., 2018), and has also been linked to stem water storage capacity (Borchert & Pockman, 2005; Michele Holbrook, 1995). Similarly, investment in pith tissue has also been shown to buffer water loss during dehydration (Borchert & Pockman, 2005; Michele Holbrook, 1995). A meta-analysis across tropical tree species revealed that higher specific hydraulic conductivity (*Ks*) is associated with high axial parenchyma investment and, contrary to expectation, found no evidence of a relationship between stem capacitance and investment in parenchyma (Janssen et al., 2020). Collectively, these findings underscore that tissue fractions, although less frequently studied, play important roles in xylem function (Aritsara et al., 2021).

Additionally, studies focusing on aseasonal tropical forests are relatively rare. These forests are typically not considered water-limited and harbour exceptionally high biodiversity. However, aseasonal wet conditions do not prevent episodes of hydraulic stress (e.g. during extreme drought events or hurricanes) (Smith-Martin et al., 2023; Smith-Martin, Muscarella, et al., 2022). It therefore remains unclear whether anatomical patterns identified in seasonal tropical forests also apply to aseasonal systems (Cosme et al., 2017; Zuleta et al., 2022). Here we explore the relationship between wood anatomical features and xylem function by integrating metrics of vessel size, grouping and tissue fractions with hydraulic traits (embolism resistance and stem capacitance) measured on the same individual branches of 78 individuals from 13 species in an aseasonal wet forest in Puerto Rico. We addressed the following research questions (Figure 1):

1. *Do species in an aseasonal wet tropical forest show evidence for a trade-off between xylem safety and efficiency?* We expect to find a xylem safety-efficiency trade-off as a negative relationship between embolism resistance and theoretical hydraulic conductivity (Isasa et al., 2023; Lobo et al., 2018; Pereira et al., 2023; Pratt et al., 2023; Sperry et al., 2006; Wheeler et al., 2005).
2. *Which wood anatomical traits are associated with different strategies of hydraulic safety, ranging from drought tolerance to drought avoidance?* We expect that species with larger vessels would have higher hydraulic efficiency but lower drought tolerance, in line with the 'vessel diameter' hypothesis (Ellmore & Ewers, 1985; Gleason et al., 2016; Levionnois et al., 2021). We also expect that species with higher vessel grouping would exhibit greater embolism resistance, supporting the 'vessel network' hypothesis (Levionnois et al., 2021). Alternatively, some studies suggest that species with more solitary vessels may be more resistant to embolism, as reduced connectivity might limit the spread of air between vessels (Avila et al., 2023; Loepfe et al., 2007). We also expect to observe a positive relationship between tissue fraction (pith and total parenchyma) and drought avoidance (Borchert & Pockman, 2005; Janssen et al., 2020; Michele Holbrook, 1995). Finally, because hydraulic function is likely governed by coordinated suites of traits, we hypothesise that a multivariate representation of wood anatomical traits may better describe variation in drought tolerance and avoidance than individual anatomical traits.

TABLE 2 Hydraulic and wood anatomical measurements.

Hydraulic traits	Stem embolism resistance (MPa)	Ψ_{50}
	Stem capacitance at full turgor (MPa)	C_{ft}
	Maximum theoretical hydraulic conductivity ($m^4/MPa^{-1} \times s^{-1}$)	K_{th}
Wood anatomical traits	Median vessel diameter (μm)	Vdiam
	Solitary vessel index	SVI
	Fractional area of vessel lumen	Vfrac
	Fractional area of pith	Pfrac
	Fractional area of axial parenchyma	Afrac
	Fractional area of ray parenchyma	Rfrac
	Fractional area of fibre	Ffrac
	Fractional area of total parenchyma (axial + ray)	RAPfrac

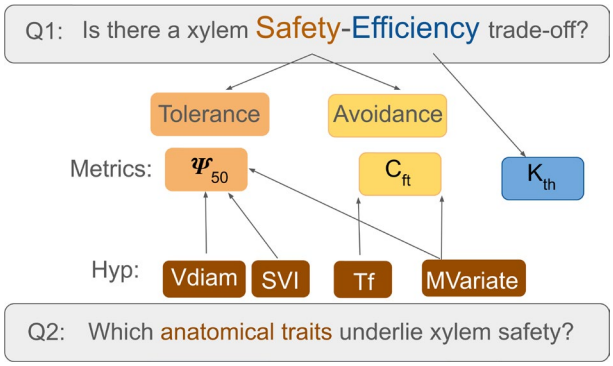

FIGURE 1 Conceptual diagram showing the key questions of this study (Q1 and Q2) and metrics evaluated to assess hydraulic efficiency (theoretical hydraulic conductance—K_{th}) and safety, on which we consider two different plant strategies: Drought tolerance (embolism resistance—Ψ_{50}) and drought avoidance (stem capacitance at full turgor—C_{ft}). We expect that species with higher embolism resistance will have lower vessel diameter (Vdiam) and higher solitary vessel index (SVI) or lower SVI, as an alternative hypothesis. We expect that species with high pith and total parenchyma fractions (Tf—tissue fractions) will have high C_{ft}. Additionally, we hypothesise that a multivariate representation of the evaluated wood anatomical traits, expressed as PC1, may be the best describer of Ψ_{50} and C_{ft} variation.

2 | METHODS

2.1 | Study site and focal species

We conducted this study in the Luquillo Experimental Forest (LEF) in El Yunque National Forest in northeast Puerto Rico (18°20′ N, 65°49′ W), with permission granted by the Luquillo LTER. The LEF is an aseasonal tropical wet forest that receives ca. 3500 mm of rainfall per year, with a minimum monthly average typically above 200 mm. Mean annual temperature of the LEF is 25°C (Thompson et al., 2002). We sampled 13 tree species that span a broad range of life-history strategies (Table 1).

2.2 | Sample collection

We measured branches for stem sapwood capacitance and stem resistance to embolism between July 2019 and December 2020 in one continuous campaign, with some interruptions in 2020 due to COVID-19 curfews when we were not able to sample. This is an ever-wet forest, and during the sampling period, no month received less than 100 mm of precipitation. To capture variation among individuals, our goal was to sample at least five healthy mature individuals representative of local populations per species from a range of elevations between 250 and 600 m. The sample size per species (Table 1) depended on their distribution across the elevation gradient and our ability to collect appropriate branch samples. Size of individual trees varied but all had a minimum DBH of 10 cm. For each individual, between 7 and 9 AM we sampled three sun-exposed canopy branches >1.5 m long using a pole cutter. We started the hydraulic trait measurements in the laboratory of all samples within 2 h of branch collection. To minimize branch drying during transport, we immediately sealed the cut ends in water bags while the whole branch was wrapped in black plastic bags with wet paper towels to reduce transpiration until the lab or vehicle was reached. Branches were stored in buckets of water as soon as possible with the cut end recut roughly 3 cm while under water, to reduce risk of air infiltration. Labs had climate controls to minimize the impact of temperature and humidity changes on measurements.

2.3 | Embolism resistance

Methods for estimating hydraulic parameters follow those reported in Smith-Martin, Jansen, et al. (2022) and Smith-Martin, Muscarella, et al. (2022). Briefly, we used the optical vulnerability (OV) technique to determine xylem embolism build-up in stems (Brodribb et al., 2016, 2017). We clamped distal stems (~3–6 mm) in custom-built three-dimensional printed clamps (OpenSourceOV—OSOV) with 8-megapixel Raspberry Pi camera and six bright light-emitting diodes operated by Raspberry Pi microcomputer. To place the stems in the clamps, we removed a ~2 cm^2 area of bark from distal branches with healthy foliage to expose the xylem. Adhesive hydrogel (Tensive, Fairfield, NJ, USA) was applied to the exposed xylem, covered with a coverslip, and clamped into OSOV clamps. The OSOV clamps were set to take a picture every 2 min until no more embolism events were observed for at least 12 h (~72–96 h depending on the species). Simultaneously, we used stem psychrometers to record water potential every 10 min. ImageJ software (National Institutes of Health, USA) was used to analyse the pictures of stem embolisms following Brodribb et al. (2016) and Brodribb et al. (2017). Embolism accumulation in stems was quantified as a cumulative total of embolized pixels in each image divided by the total number of embolized pixels. We used the fitted linear time and water potential relationship to find obtain the values at which 50% of the cumulative embolized pixels had occurred (Ψ_{50}). We were not able to measure OV curves on the stems of *Cecropia schreberiana* and *Schefflera morototoni* due to the large diameter of the distal stems of these species with hollow stems, which were too large to be clamped into our custom-made clamps and obtain clear images necessary for the OV curves. We did not estimate tissue fraction for these samples because of the lack of hydraulic data.

2.4 | Stem capacitance at full turgor

To measure stem capacitance (C_{ft}) we used stem psychrometric to construct pressure-volume curves while simultaneously measuring water loss. Full descriptions of the method are described in Smith-Martin, Jansen, et al. (2022) and Smith-Martin, Muscarella, et al. (2022). Briefly, leaves were removed to eliminate water loss through transpiration and the cut end of the branch was covered with parafilm. Water potential (Ψ, MPa) was measured with stem psychrometers (ICT International, Armidale, Australia) that were attached to the exposed stem xylem with an air-tight seal created with parafilm and set to log water potential every 10 min. Branches were air dried for at least 72 h and until Ψ measurements were stable for multiple hours. Simultaneously, branches were weighed periodically using a lab balance (precision to 0.01 g) and linear regressions were used to calculate mass water loss for a given Ψ. At the end measurement cycle, we dried the branches at 65°C for a minimum of 1 week to obtain dry mass. We used the Sack and Pasquet-Kok (2011) spreadsheet tool to calculate stem capacitance at full turgor, measured in MPa.

2.5 | Wood sample processing

Processing wood samples for anatomical analyses consisted of four steps: sampling, sectioning, staining and scanning; methods generally followed those presented in Ziemińska et al. (2023). Following the embolism resistance and sapwood capacitance measurements described above, we subsampled 7–10 cm of each branch using a hand pruner at 70 cm from the tip of the branch to account for vessel tapering towards the tip. We made sure that the sample was taken from a straight segment of branch without major branching,

deformation, or damage. We stored samples in 70% ethanol and transported them to Uppsala University for analysis. We used a WSL sledge microtome (www.wsl.ch/en/services-produkte/microtomes/) to cut 10–30 µm thick transverse sections. Thickness of the sections was determined by the properties of the wood, with some species or samples requiring thicker cutting to be of high quality. We stained cut sections for 10 min in an aqueous dye solution of 1% Safranin O and 1% Astra blue (Gärtner & Schweingruber, 2013), then rinsed in deionized H_2O before a successive dehydration in increasing concentration ethanol from 50%, 70%, 100%, 100%, 100% for 10 min each. Sections were then mounted with Euparal and dried at 60°C until Euparal was set.

We imaged the slides using a high-resolution slide scanner (Zeiss Axioscan 7) for digital analysis of anatomical features. To quantify vessel characteristics, we used a semi-automated threshold method in Qupath (Bankhead et al., 2017) to first identify features meeting certain criteria of colour, size, and roundness. We tuned this process manually for each species and, after using it to identify likely vessels, we cleaned and verified the annotations manually. The vessel annotations were then exported as .svg files for spatial analysis in R (v 4.1.3; R Core Team, 2020) using the 'sf' package (Pebesma, 2018) and custom scripts. We computed vessel area metrics (median vessel diameter and theoretical hydraulic conductivity K_{th}, as a metric of xylem efficiency, $m^4/MPa^{-1} \times s^{-1}$). The total K_{th} per sample was calculated as $\pi D^4/128\eta$, where D and η are vessel diameter and the viscosity index of water (1.002×10^{-9} MPa s at 20°C), respectively (Scholz et al., 2013).

We computed the solitary vessel index (SVI) to assess the vessel network hypothesis. Vessel connectivity was quantified from .svg-derived vessel polygons using custom R functions implemented in the open-source R package (https://github.com/bobmuscarella/qwar). These functions identify neighbouring vessel polygons and determine vessel group membership based on a minimum distance threshold derived from species-specific measurements of vessel double wall thickness. For this, we first measured the thickness of the double wall between two adjacent vessels on at least 70 vessels per species. The species mean values were then used as thresholds to detect vessel groups. Neighbour relationships among vessel polygons are identified using the poly2nb function from the spdep R package (Bivand, 2002). Two or more vessels were deemed a group when their double wall thickness was equal to or smaller than the threshold (von Arx et al., 2013). We used information on vessel groups to quantify the vessel grouping index (VGI) and the SVI. The VGI is computed as the total number of vessels divided by the total number of vessel groups; VGI values equal to 1 imply only solitary vessels are present, whereas values higher than 1 indicate more grouped vessels. The SVI was computed as the number of solitary vessels divided by the total number of vessel groups (a solitary vessel is considered as one group) (Scholz et al., 2013); higher values indicate a larger proportion of solitary vessels in the sample.

We used two approaches to measure tissue fraction. For vessels, we summed the area of all annotated vessels and divided by the total cross-sectional area of the sample. To quantify the fractional area of other tissue types, we used a grid sampling approach (Smith Jr et al., 1989; Ziemińska et al., 2015). Specifically, using Qupath software (Bankhead et al., 2017), we imposed a grid on each image with a mean of 368 ± 19.2 overlapping grid crosses per sample. We then manually identified the distinct tissue type (i.e. vessels, fibres, axial parenchyma, ray parenchyma and pith) at each grid intersection point. Tissue fractions were calculated for each sample by dividing the number of points in each specific tissue by the total number of intersection points for that sample (Ziemińska et al., 2015). Because hydraulic measurements were not available, fibre, axial, and ray parenchyma fractions were not computed for two species, *C. schreberiana* and *S. morototoni*. In total, we sampled three to nine individuals per species for anatomical analysis based on the amount of samples that were successfully tested for hydraulic traits and the quality of the available wood.

2.6 | Data analyses

To investigate xylem safety (drought tolerance and drought avoidance) and efficiency relationships, we used bivariate species centring linear mixed-effect models (Isasa et al., 2023), allowing slopes (β) and intercepts (α) to vary, and including species as a random effect (Figures 2c and 3a; Table S1). In this formulation (Equation 1), the predictor variable is decomposed into the species mean ($\overline{xj}$) and the deviation from that mean ($xi - \overline{xj}$), allowing us to estimate separate coefficients for across-species (β_{across}) and within-species (β_{within}) relationships (Isasa et al., 2023), explicitly partitioning trait–trait relationships into interspecific and intraspecific components. Size-related traits (Vdiam and K_{th}) were log-transformed prior to analysis due to their convex (nonlinear) relationship with xylem safety (Pereira et al., 2023).

$$y_i = (\alpha + u_j) + \beta_{across} \times \underline{x_j} + (\beta_{within} + v_j) \times \left(x_i - \underline{x_j}\right) + \epsilon_i \quad (1)$$

When random slopes for β_{within} were found to be redundant, which is when there was no evidence that species differed in their within-species response, we simplified the model by removing the random slope term (V_j). Redundancy was determined when the principal components of the random effects (rePCA) indicated the slope was close to zero, and model comparison using AIC showed no significant improvement in fit with the more complex model. For such cases (Figures 3b and 5; Table S3), we used Equation (2).

$$y_i = (\alpha + u_j) + \beta_{across} \times \underline{x_j} + \beta_{within} \times \left(x_i - \underline{x_j}\right) + \epsilon_i \quad (2)$$

We additionally tested for evidence supporting either the vessel diameter or network hypotheses (Table S2) by using multivariate species centring linear mixed-effect models (Isasa et al., 2023), where the fixed-effects part included two predictors, each decomposed

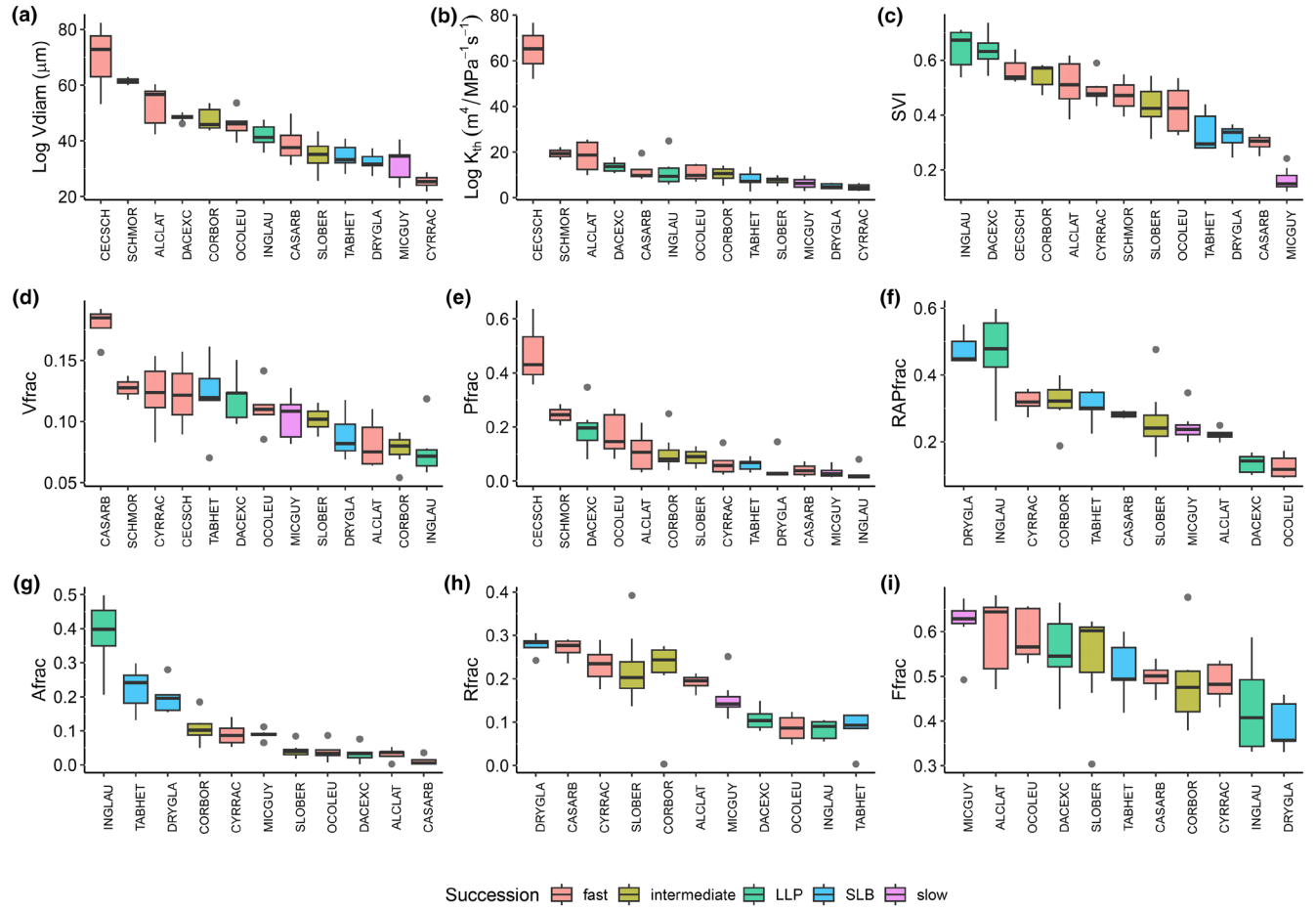

FIGURE 2 Wood anatomical trait variation across species in an aseasonal tropical forest. Panels show species variation in (a) log-transformed median vessel diameter, (b) log-transformed maximum theoretical hydraulic conductivity, (c) solitary vessel index, (d) fractional area of vessel lumen, (e) fractional area of pith, (f) fractional area of total parenchyma (axial + ray), (g) fractional area of axial parenchyma, (h) fractional area ray parenchyma, and (i) fractional area of fibre. Please see Tables 1 and 2 for species names and variable abbreviations, respectively. Successional associations are: LLP—long-lived pioneers; SLB—short-lived breeders; shade-intolerant species with fast, intermediate or slow demographic strategies (Rüger et al., 2023). We note that, in our study, demographic categories are used to provide descriptive context, rather than as explicit groupings for hypothesis testing. Tissue fractions of *Cecropia schreberiana* and *Schefflera morototoni* were not estimated due to the lack of embolism resistance measurements for those species.

into across and within species components, plus a random intercept for species, as follows:

$$y_i = (\alpha + u_j) + \beta_{1\text{across}} \times \underline{x_{1j}} + \beta_{1\text{within}} \times \left(x_{1i} - \underline{x_{1j}}\right) + \beta_{2\text{across}} \times \underline{x_{2j}} + \beta_{2\text{within}} \times \left(x_{2i} - \underline{x_{2j}}\right) + \epsilon_i \quad (3)$$

where variables are as described above except x_{1j} and x_{2j} are Vdiam and SVI for the j species, respectively. All variables in these models were scaled and centred prior to analysis.

We then performed bivariate species centring linear mixed-effect models (Isasa et al., 2023) to evaluate the extent to which pith and total parenchyma fractions are associated with stem capacitance at full turgor. Model fits of species centring linear mixed-effects models were performed by using package lme4 (Bates et al., 2014). We further investigated if a broad and multivariate representation of wood anatomical traits better describes variation in hydraulic safety (drought tolerance and drought avoidance) than univariate traits. To do so, we first computed the first and second principal component axes of all the wood anatomical features using a scaled and centred PCA. We then performed bivariate species centring linear mixed-effect models among wood anatomical traits, PC1 (vessel-related trait axis) and PC2 (tissue fraction-related axis) versus embolism resistance and stem capacitance at full turgor. The best model was assessed using AIC (Table S3).

3 | RESULTS

We found substantial interspecific variation in wood anatomical traits, reflecting a wide spectrum of hydraulic strategies in this aseasonal tropical forest (Figure 2). Median vessel diameter varied four-fold across species (22–82 μm). Shade-intolerant species with fast demographic strategies (e.g. *C. schreberiana*, *Alchornea latifolia*, *S. morototoni*) exhibited larger vessel diameters, whereas

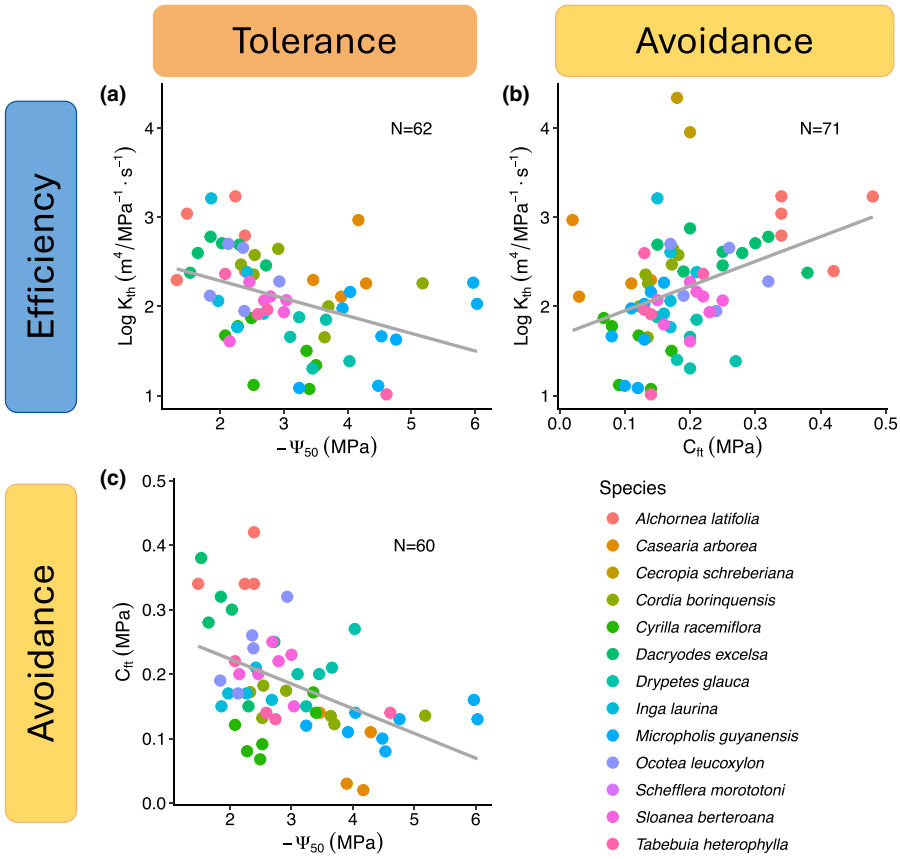

FIGURE 3 Relationship among hydraulic safety (drought tolerance and drought avoidance) and efficiency across individual trees in an aseasonal wet tropical forest. Panels show the relationships between (a) log-transformed maximum hydraulic conductivity and embolism resistance, (b) log-transformed maximum theoretical hydraulic conductivity and stem capacitance at full turgor and (c) stem capacitance at full turgor and embolism resistance. The regression line shows model prediction fitted by the LME within-species centring model, with species as random effect, and allowing slopes and intercepts to vary (Equations 1 and 2). We used a log scale for variables related to size/area (Vdiam and K_{th}). Each point represents an individual tree and colours denote species identity. There are no Ψ_{50} data for *Cecropia schreberiana* and *Schefflera morototoni* due to their hollow stems preventing optical measurements. Statistical results are shown in the Table S1.

shade-tolerant species with short-lived breeder strategies (Rüger et al., 2023) (*Tabebuia heterophylla*, *Drypetes glauca*) and slow demographic species (*Micropholis guyanensis*) tended to have much smaller vessels. This pattern across successional associations was also reflected in theoretical hydraulic conductivity, which spanned a 28-fold range (2.7–76.7 $m^4/MPa^{-1} \times s^{-1}$). Early successional species, including both fast growers and long-lived pioneers, had markedly higher potential water transport capacity than intermediate and late successional species. The SVI, a metric of vessel connectivity, also varied consistently with successional strategy. Long-lived pioneers had the highest SVI, followed by species with fast and intermediate strategies, while short-lived breeders showed lower values. The lowest SVI was observed in *M. guyanensis*, a shade-tolerant species with slow demography. The fractional areas of vessel lumen, axial parenchyma, ray parenchyma, fibre, and pith also exhibited high variation range across species. On average, fibres and ray parenchyma contributed with the highest tissue fraction across all species (0.52 ± 0.07 and 0.17 ± 0.04, respectively), followed by equal percentages of pith fraction (0.13 ± 0.05) and vessel and axial parenchyma fractions (0.11 each) (Table 3). In terms of tissue fraction variations, axial parenchyma presents the highest variation among species (Figure 2). The statistical summary of hydraulic traits analysed in this study, stem capacitance (C_{ft}) and embolism resistance (Ψ_{50}), which ranged from −0.02 to 0.48 and −1.3 to −6.0 MPa, respectively, are described in detail in Smith-Martin, Jansen, et al. (2022) and Smith-Martin, Muscarella, et al. (2022).

3.1 | Xylem safety (tolerance and avoidance) and efficiency relationships

We found evidence of a trade-off between xylem safety and log-efficiency across individuals (Figure 3; Table S1, linear mixed-effects model with within-species centring). Individuals with high theoretical hydraulic conductivity (K_{th}) generally had low embolism resistance, exhibiting less negative Ψ_{50} values ($p = 0.02$; Figure 3; Table S1). Drought avoidance, quantified as stem capacitance at full turgor

TABLE 3 Summary (mean and standard deviation) trait value per species.

Species	Succession	P50	C_{ft}	K_{th}	Vdiam	SVI	Vfrac	Pfrac	Afrac	Rfrac	Ffrac	RAPfrac
Alchornea latifolia	Fast	−1.96 ± 0.52	0.38 ± 0.06	18.16 ± 6.84	52.85 ± 7.91	0.51 ± 0.09	0.08 ± 0.02	0.11 ± 0.07	0.03 ± 0.02	0.19 ± 0.02	0.59 ± 0.09	0.22 ± 0.02
Casearia arborea	Fast	−3.96 ± 0.37	0.08 ± 0.06	11.81 ± 5.16	39.09 ± 7.83	0.30 ± 0.03	0.18 ± 0.02	0.04 ± 0.02	0.01 ± 0.02	0.27 ± 0.02	0.50 ± 0.04	0.28 ± 0.01
Cecropia schreberiana	Fast	NA	0.19 ± 0.01	64.72 ± 12.31	69.50 ± 14.91	0.57 ± 0.06	0.12 ± 0.03	0.47 ± 0.14	NA	NA	NA	NA
Cyrilla racemiflora	Fast	−2.80 ± 0.60	0.11 ± 0.04	4.58 ± 1.39	25.36 ± 2.32	0.49 ± 0.05	0.12 ± 0.02	0.06 ± 0.04	0.09 ± 0.03	0.23 ± 0.04	0.49 ± 0.04	0.32 ± 0.03
Ocotea leucoxylon	Fast	−2.33 ± 0.40	0.24 ± 0.06	10.86 ± 3.54	45.96 ± 5.20	0.42 ± 0.09	0.11 ± 0.02	0.17 ± 0.08	0.04 ± 0.03	0.09 ± 0.03	0.59 ± 0.06	0.13 ± 0.03
Schefflera morototoni	Fast	NA	NA	19.34 ± 3.88	61.48 ± 2.06	0.47 ± 0.11	0.13 ± 0.01	0.24 ± 0.06	NA	NA	NA	NA
Cordia borinquensis	Inter	−3.26 ± 1.00	0.15 ± 0.02	10.27 ± 3.16	47.82 ± 4.21	0.54 ± 0.05	0.08 ± 0.01	0.11 ± 0.07	0.11 ± 0.05	0.21 ± 0.10	0.49 ± 0.11	0.32 ± 0.07
Sloanea berteroana	Inter	−2.69 ± 0.34	0.20 ± 0.03	7.56 ± 1.52	34.80 ± 5.80	0.43 ± 0.08	0.10 ± 0.01	0.09 ± 0.03	0.04 ± 0.02	0.22 ± 0.08	0.54 ± 0.11	0.27 ± 0.10
Drypetes glauca	SLB	−3.50 ± 0.37	0.20 ± 0.04	4.99 ± 1.26	32.33 ± 3.48	0.32 ± 0.05	0.09 ± 0.02	0.05 ± 0.05	0.20 ± 0.05	0.28 ± 0.02	0.39 ± 0.06	0.48 ± 0.05
Tabebuia heterophylla	SLB	−3.01 ± 1.11	0.15 ± 0.04	8.21 ± 3.44	34.51 ± 4.52	0.34 ± 0.07	0.12 ± 0.03	0.06 ± 0.02	0.22 ± 0.07	0.08 ± 0.05	0.51 ± 0.07	0.31 ± 0.05
Dacryodes excelsa	LLP	−2.01 ± 0.44	0.26 ± 0.07	13.80 ± 2.38	48.47 ± 1.30	0.63 ± 0.06	0.12 ± 0.02	0.19 ± 0.07	0.03 ± 0.02	0.11 ± 0.02	0.55 ± 0.07	0.14 ± 0.03
Inga laurina	LLP	−2.24 ± 0.33	0.17 ± 0.02	11.64 ± 7.07	41.82 ± 4.36	0.64 ± 0.08	0.08 ± 0.02	0.03 ± 0.03	0.38 ± 0.10	0.08 ± 0.02	0.43 ± 0.10	0.47 ± 0.12
Micropholis guyanensis	Slow	−4.62 ± 0.97	0.12 ± 0.02	6.20 ± 2.50	31.92 ± 6.04	0.16 ± 0.04	0.10 ± 0.02	0.03 ± 0.02	0.09 ± 0.01	0.16 ± 0.04	0.62 ± 0.05	0.24 ± 0.05

(C_{ft}), was negatively associated with embolism resistance ($p = 0.01$; Figure 3; Table S1) and positively related to K_{th} ($p = 0.02$; Figure 3; Table S1), as individuals more vulnerable to embolism also had higher values of C_{ft} and higher theoretical hydraulic conductivity.

3.2 | Wood anatomical traits and their relationship with xylem safety

Contrary to expectations for the vessel diameter hypothesis, we did not find a significant relationship between embolism resistance (Ψ_{50}) and median vessel diameter (Linear mixed-effects model with within-species centring; $p = 0.11$; Table S3). In contrast, and consistent with the vessel network hypothesis, the SVI was a strong predictor of embolism resistance, with individuals exhibiting a higher proportion of solitary vessels being significantly more vulnerable to embolism (Linear mixed-effects model with within-species centring; $p < 0.001$; Table S3). The multivariate mixed-effect model (Equation 3) has also revealed a stronger contribution of SVI ($p = 0.01$; standardized $\beta = 0.62$) than Vdiam ($p = 0.64$; standardized $\beta = 0.09$) in predicting Ψ_{50} (Table S2). Stem capacitance at full turgor (StemC_{ft}) varied from 0 to 0.5 MPa across our dataset and was not significantly associated with pith fraction, total parenchyma fraction (Figure 5; Table S3), or with the individual tissue fractions of axial and radial parenchyma (Figure S1).

To assess whether multivariate combinations of wood anatomical traits were better predictors of hydraulic safety strategies (drought tolerance and drought avoidance) than univariate traits, we conducted a principal component analysis of anatomical traits (PCA; Figure 4). The first two principal components explained 38.3% (PC1) and 20.0% (PC2) of the total trait variation, respectively. PC1 captured variation mainly in vessel-related traits, including vessel density, VGI, vessel fraction and theoretical vessel conductivity. In contrast, PC2 was primarily associated with variation in tissue fractions, such as parenchyma and fibre fractions (Figure 4). The model including PC1 to predict Ψ_{50} provided the best fit (AIC = 137.18), with both across-species ($p = 0.01$) and within-species ($p = 0.04$) effects significant. The SVI model also performed well (AIC = 143.85), with a strong positive across-species effect ($p < 0.001$) but no within-species relationship ($p = 0.69$). PC2 showed no significant effects and an intermediate fit (AIC = 146.92). Vessel diameter was the weakest predictor (AIC = 154.41), with neither across- nor within-species effects significant ($p > 0.10$).

For drought avoidance, among the predictors tested for stem capacitance at full turgor (C_{ft}), only PC1 showed a significant relationship (Figure 5; Table S3). The best-fitting model (AIC = −163.05) included a negative across-species effect ($p = 0.01$), indicating that species with higher PC1 scores, which are associated with higher VGI and higher vessel density, tend to have lower capacitance. No within-species effect was detected ($p = 0.83$). Models including RAP, Pfrac, or PC2 showed no significant effects for either across- or within-species components ($p > 0.29$) and had higher AIC values, suggesting lower explanatory power.

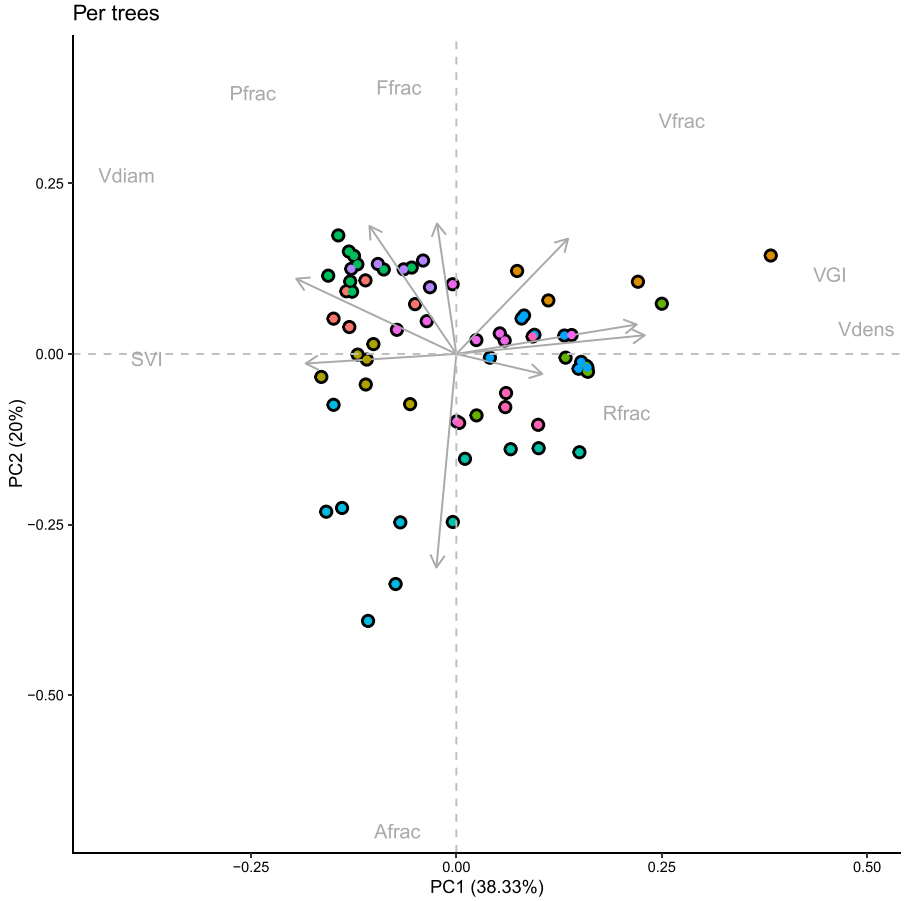

FIGURE 4 Multivariate representation of anatomical traits variation (PCA). Points represent 67 individuals of 11 species (different colours). Please see Table 1 for the variables' abbreviations. The first two principal components explained 38.3% (PC1—vessel-related trait axis) and 20.0% (PC2—tissue fraction-related axis) of the total trait variation. Tissue fractions of *Cecropia schreberiana* and *Schefflera morototoni* were not estimated due to the lack of embolism resistance measurements for those species.

4 | DISCUSSION

Our study investigates the relationship between xylem function and multiple wood anatomical traits across 78 adult trees in an aseasonal tropical forest, encompassing 13 species with diverse life-history strategies. We evaluated relationships between hydraulic safety (drought tolerance and avoidance) and wood anatomical traits related to vessel size, vessel grouping, and tissue fractions. Our main findings show (1) a high diversity of hydraulic and anatomical traits among species in an aseasonal wet environment, emphasizing the role of xylem function for species life-history strategies; and (2) a key role of vessel network structure (as the proportion of solitary vessels) on species' embolism resistance.

4.1 | Evidence of trade-off between xylem safety and efficiency

The xylem safety-efficiency trade-off has been a central hypothesis in plant hydraulics, positing that greater embolism resistance often comes at the cost of reduced hydraulic conductivity (Gleason et al., 2016; Isasa et al., 2023; Levionnois et al., 2021; Lobo et al., 2018; Pratt et al., 2023; Sperry et al., 2006; Wheeler et al., 2005). Consistent with this framework, we found a negative relationship between embolism resistance (Ψ_{50}) and log-transformed theoretical hydraulic conductivity (K_{th}), as well as between Ψ_{50} and stem capacitance at full turgor (C_{ft}). However, we found no support for the vessel diameter hypothesis, suggesting that other anatomical traits, such as vessel connectivity and intervessel characteristics, may also modulate this trade-off.

A trade-off between drought resistance and avoidance has previously been observed across species (Liang & Ye, 2024; Santiago et al., 2018; Smith-Martin, Muscarella, et al., 2022). In our study, we also found a negative relationship between embolism resistance and stem capacitance at full turgor across individual trees. C_{ft} varied substantially among species (total variation = 0.5 MPa), reflecting contrasting drought avoidance strategies even within an aseasonal wet forest. Individuals with higher C_{ft} were generally more vulnerable to embolism (less negative Ψ_{50}), but could maintain higher K_{th}, potentially enabling greater water transport under favourable conditions. This coordination suggests that individuals with reduced embolism resistance may maximize their xylem safety by increasing their capacity to store and release water, potentially buffering short-term water deficits. Such buffering may be particularly relevant in

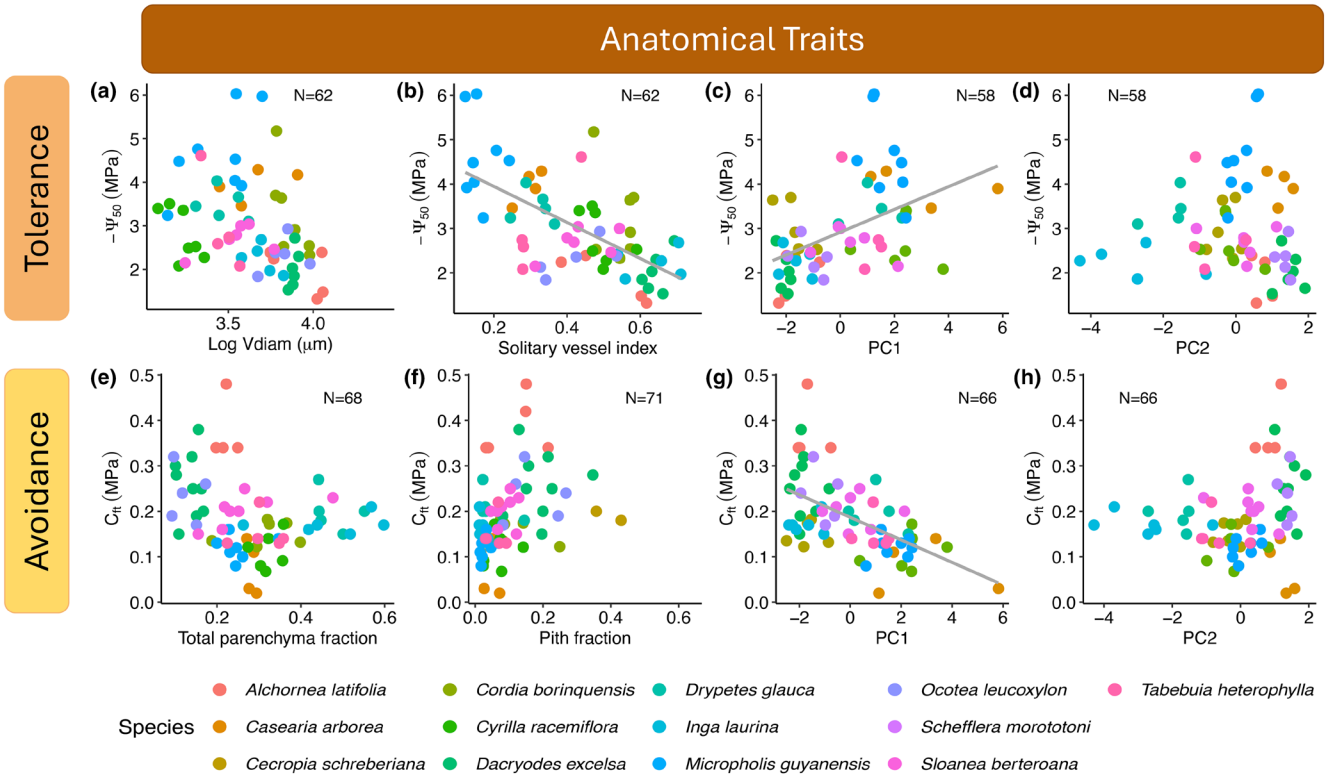

FIGURE 5 Relationship between wood anatomical traits and xylem safety (drought avoidance and tolerance). Top panels (a–d) display wood anatomical traits versus drought tolerance (Ψ_{50} = embolism resistance). Bottom panels (e–h) display drought avoidance (C_{ft} = stem capacitance at full turgor) versus wood anatomical traits. Each point represent an individual tree and colours denote species identity. Tissue fractions of *Cecropia schreberiana* and *Schefflera morototoni* were not estimated due to the lack of Ψ_{50} data for those species, as hollow stems prevented optical measurements. Statistical results are displayed in the Table S3.

aseasonal forests like Luquillo, where hydraulic stress is often associated with episodic disturbances (e.g. hurricanes and drought events) rather than prolonged drought (Smith-Martin, Muscarella, et al., 2022; Ziemińska et al., 2023). Overall, our results indicate that individuals balance water transport efficiency and safety through complementary drought tolerance and avoidance strategies, thereby contributing to the observed diversity of hydraulic strategies and niche partitioning (Andrés-Hernández & Rodríguez-Ramírez, 2025; Brum et al., 2019; Penha et al., 2024).

4.2 | SVI is a strong describer of embolism resistance variation

Previous studies demonstrated that the vessel diameter and network hypotheses are not mutually exclusive, as they emphasize different structural mechanisms—conduit size versus vessel connectivity—by which xylem architecture can influence hydraulic safety (Levionnois et al., 2021). In our study, we did not find a statistically significant relationship between vessel diameter and embolism resistance (Ψ_{50}) across individual trees, suggesting that vessel size alone may not be the strongest predictor of xylem safety, in agreement with several studies (Gleason et al., 2016; Maherali et al., 2004; Trueba et al., 2019; Tyree et al., 1994). However, it is important to notice that we did observe a trend in the expected direction (Figure 5), and importantly, Ψ_{50} was significantly correlated with theoretical conductivity (K_{th}; Figure 3), which itself is strongly related to vessel diameter. This suggests that vessel size likely contributes to embolism resistance, although not statistically detected in our study (Isasa et al., 2023; Lens et al., 2022).

Our findings strongly support the vessel network hypothesis, which posits that the spatial arrangement and connectivity of vessels play a critical role in hydraulic function and vulnerability to embolism. Specifically, we found that species with a higher proportion of solitary vessels were more vulnerable to embolism, suggesting that vessel grouping enhances xylem safety. A high degree of vessel connectivity may limit the spread of embolism, potentially by reducing the likelihood of air entry through pit membranes (Jansen et al., 2009; Kaack et al., 2021; Levionnois et al., 2021; Smith-Martin, Jansen, et al., 2022). As suggested by previous studies, this effect likely arises from pit membrane properties, such as membrane thickness and pore constrictions (Kaack et al., 2021), which regulate gas diffusion among adjacent vessels (Pereira et al., 2023). Together, these mechanisms provide a structural explanation for the close association between embolism resistance and pit membrane traits, highlighting the central role of vessel network architecture in conferring hydraulic safety in angiosperm xylem (Kaack et al., 2021).

Our result contrasts with the expectation that solitary vessels, by reducing connectivity, would confer greater embolism resistance

(Loepfe et al., 2007), and instead aligns with previous findings that vessel grouping improves resistance (Lens et al., 2011; Levionnois et al., 2021; Tyree et al., 1994). However, alternative interpretations should also be considered. Carlquist (1984) proposed that species with more solitary vessels often possess a background matrix of imperforate tracheary elements (ITEs), which may contribute to hydraulic function by serving as conductive bridges or providing limited water transport. It is therefore possible that species classified as less embolism resistant based on optical methods may, in fact, maintain some degree of conductivity through these ITEs. This idea is supported by recent work revisiting 'Carlquist's Law', which argues that the functional role of ITEs in hydraulic architecture has been historically underappreciated (Olson, 2023; Johnson et al., 2023). Incorporating these anatomical perspectives may help refine our understanding of how vessel spatial arrangement interacts with other xylem components to influence embolism resistance.

We expected that species with high pith and total parenchyma fractions would have high stem capacitance. While tissue fractions, such as living parenchyma cells, are often implicated in water storage and transport (Carlquist, 2001; Morris et al., 2018), their influence on drought avoidance was not significant in our study. This finding contrasts with studies that have emphasized the role of parenchyma in water storage (Carlquist, 2001) and drought resilience (Janssen et al., 2020). Although we observed substantial variation in stem capacitance among individuals (0.02–0.48 MPa) within this aseasonal forest, the absence of a clear relationship with tissue fractions suggests that stem capacitance may be governed by additional anatomical or physiological features not captured in our analyses. These may include fibre lumen (Janssen et al., 2020), tissue connectivity, cell wall properties, and the spatial integration of water storage tissues within the vessel network (Pratt & Jacobsen, 2017). Importantly, the lack of association between tissue fractions and drought avoidance should not be interpreted as evidence of limited functional importance of these tissues. Rather, it indicates that tissue fractions alone may be insufficient proxies for estimating capacitance at the branch scale in this environment. The absence of data on parenchyma and fibre fractions for two early successional species in our dataset could also obscure potential relationships. Another potential explanation, as highlighted by (Jupa et al., 2016) and (Janssen et al., 2020), is that the total amount of parenchyma tissue may not directly determine the initial release of stored water. Instead, species may differ in the rate at which capacitance is released, with some exhibiting rapid and others slower water release as reflected in moisture release curves. This is particularly relevant given that parenchyma may act as a water storage reservoir and transport pathway (Borchert & Pockman, 2005; Plavcová et al., 2016).

We hypothesized a superior predictive power of multivariate representations of anatomical traits over univariate metrics on explaining embolism resistance variation. Indeed, PC1, which integrated multiple aspects of vessel architecture, was the most informative predictor, capturing both interspecific and intraspecific variation in embolism resistance. The SVI alone also emerged as a very strong predictor, but no within-species variation was detected, consistent with the idea that species with more solitary vessels are more vulnerable to embolism. This finding underscores the importance of vessel connectivity in determining embolism resistance and also highlights the value of partitioning trait effects into across- and within-species components to disentangle the mechanisms underpinning xylem safety.

Surprisingly, when evaluating the multivariate representation of wood anatomical traits and drought avoidance, we found that vessel-related trait axis (PC1) was the only predictor of C_{ft}, suggesting that multivariate vessel metrics influence capacitance. Our results suggest that while tissue fractions may contribute to overall hydraulic function, their influence may be overshadowed by vessel-related traits in aseasonal tropical forests, which could reflect the unique ecological conditions of these forests compared to their seasonal counterparts (Cosme et al., 2017; Zuleta et al., 2022). This finding suggests that other anatomical features, particularly vessel-related traits, may play a more dominant role in shaping hydraulic strategies in aseasonal tropical forests. Further investigations across other aseasonal tropical forests and also across forests under other climatic conditions are needed to investigate the generalization of this finding (González-Melo et al., 2025).

It is worth considering potential methodological sources of variation in the observed relationships between xylem anatomy and hydraulic function. Because anatomical traits and functional measurements (such as K_{th} and Ψ_{50}) were not obtained from the exact same location along the stem, discrepancies in vessel diameter due to longitudinal or radial variation within twigs could weaken the observed anatomical–functional relationships. For example, theoretical conductivity was measured on stem segments further from the tip than those used for Ψ_{50} determination via the optical method. Since vessel diameters tend to increase with stem age and distance from the apex (Anfodillo et al., 2006), this spatial mismatch may lead to an overestimation of average vessel size relative to the segments where embolism resistance was assessed.

In contrast, vessel network properties such as the SVI, which capture the spatial arrangement and connectivity of vessels rather than their absolute dimensions, may be comparatively more stable along both the longitudinal and radial axes of branches. This relative spatial stability likely reduces sensitivity to within-branch anatomical gradients, helping to explain why SVI emerged as a stronger and more consistent predictor of embolism resistance than vessel diameter. These considerations highlight the challenges of linking structure and function in xylem, especially when anatomical and physiological measurements cannot be made simultaneously or on exactly the same tissue. Nevertheless, since all samples were processed consistently across individuals and species, we do not expect this to introduce systematic bias into our comparative analysis.

5 | CONCLUSIONS

Our findings offer a comprehensive view of the interplay between wood anatomical traits and xylem function in an aseasonal tropical forest. Overall, our findings suggest significant evidence of xylem safety-efficiency trade-offs, in which trees with xylem more

vulnerable to embolism formation generally have higher theoretical hydraulic conductivity and higher stem capacitance at full turgor. By demonstrating the diversity of hydraulic strategies and the fundamental role of vessel connectivity in influencing embolism resistance, our study provides a deeper understanding of how trees allocate resources into different wood tissues and their relationship with xylem function in an aseasonal wet tropical forest. Our findings may also have potential relevance for predicting species-specific responses to climatic extremes (e.g. drought, hurricanes) in these systems. Further broad-scale analyses across tropical forests under different climatic envelopes, as well as, currently rare, studies evaluating intervessel characteristics of tropical tree species are needed to assess the generality of these patterns. Incorporating such trait-based insights into dynamic vegetation models and trait-based Earth system models may offer important contributions for the understanding and modelling of the complexity and nuances of tropical forests' resistance and resilience to ongoing climatic changes.

AUTHOR CONTRIBUTIONS

Julia Valentim Tavares and Robert Muscarella design the study. Samuel L. Farrar and Chris M. Smith-Martin collected all botanical material and measured hydraulic traits. Samuel L. Farrar processed all wood anatomical samples, with assistance from Kasia Ziemińska. Silvia Bibbo and Farah Brenda Solis Petz analysed the anatomical images. María Uriarte and Jess K. Zimmerman maintained long term monitoring of the field site. Julia Valentim Tavares performed data analyses with inputs from Robert Muscarella and María Uriarte. Julia Valentim Tavares led the manuscript writing with inputs from Robert Muscarella, Kasia Ziemińska, Chris M. Smith-Martin, Samuel L. Farrar, María Uriarte, and Jess K. Zimmerman. All authors contributed to revising and editing the final text.

ACKNOWLEDGEMENTS

The authors thank the support from the Swedish Research Council (Vetenskapsrådet, grant 2019-03758 to RM), the Birgitta Sintring Foundation (Sweden, grant S2023-0009 to JVT), The Royal Swedish Academy of Sciences (Kungl.Vetenskapsakademien, grant BS2025-0004 to JVT) and the US National Science Foundation (NSF, grant DEB-1753810 to MU and RM).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used to produce the main figures and analyses of this paper are available at Dryad Digital Repository, DOI: 10.5061/dryad.t4b-8gtjhp (Tavares, Farrar, et al., 2026).

ORCID

Julia Valentim Tavares https://orcid.org/0000-0003-3784-5720
Chris M. Smith-Martin https://orcid.org/0000-0002-6557-1432
María Uriarte https://orcid.org/0000-0002-0484-0758
Robert Muscarella https://orcid.org/0000-0003-3039-1076

REFERENCES

Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(2), 740–745. https://doi.org/10.1073/pnas.1315179111

Aguirre-Gutiérrez, J., Díaz, S., Rifai, S. W., Corral-Rivas, J. J., Nava-Miranda, M. G., González, R., Hurtado, A. B., Revilla, N. S., Vilanova, E., Almeida, E., de Oliveira, E. A., Alvarez-Davila, E., Alves, L. F., de Andrade, A. C. S., Lola da Costa, A. C., Vieira, S. A., Aragão, L., Arets, E., Aymard, G. A., … Malhi, Y. (2025). Tropical forests in the Americas are changing too slowly to track climate change. *Science (New York, N.Y.)*, *387*(6738), eadl5414. https://doi.org/10.1126/science.adl5414

Aguirre-Gutiérrez, J., Oliveras, I., Rifai, S., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T. R., Feldpausch, T. R., Gvozdevaite, A., Hubau, W., Kraft, N. J. B., Lewis, S. L., Moore, S., Niinemets, Ü., Peprah, T., Phillips, O. L., Ziemińska, K., Enquist, B., & Malhi, Y. (2019). Drier tropical forests are susceptible to functional changes in response to a long-term drought. *Ecology Letters*, *22*(5), 855–865. https://doi.org/10.1111/ele.13243

Andrés-Hernández, A. R., & Rodríguez-Ramírez, E. C. (2025). Does climatic variation drive the adjustment of functional traits? An assessment of tropical montane cloud forest tree species. *Frontiers in Plant Science*, *16*, 1555607. https://doi.org/10.3389/fpls.2025.1555607

Anfodillo, T., Carraro, V., Carrer, M., Fior, C., & Rossi, S. (2006). Convergent tapering of xylem conduits in different woody species. *The New Phytologist*, *169*(2), 279–290. https://doi.org/10.1111/j.1469-8137.2005.01587.x

Argüelles-Marrón, B., Meave, J. A., Luna-Vega, I., Crispin-DelaCruz, D. B., Szejner, P., Ames-Martínez, F. N., & Rodríguez-Ramírez, E. C. (2023). Adaptation potential of neotropical montane oaks to drought events: Wood anatomy sensitivity in *Quercus delgadoana* and *Quercus meavei*. *Functional Ecology*, *37*(7), 2040–2055. https://doi.org/10.1111/1365-2435.14362

Aritsara, A. N. A., Razakandraibe, V. M., Ramananantoandro, T., Gleason, S. M., & Cao, K.-F. (2021). Increasing axial parenchyma fraction in the Malagasy Magnoliids facilitated the co-optimisation of hydraulic efficiency and safety. *The New Phytologist*, *229*(3), 1467–1480. https://doi.org/10.1111/nph.16969

Avila, R. T., Kane, C. N., Batz, T. A., Trabi, C., Damatta, F. M., Jansen, S., & McAdam, S. A. M. (2023). The relative area of vessels in xylem correlates with stem embolism resistance within and between genera. *Tree Physiology*, *43*(1), 75–87. https://doi.org/10.1093/treephys/tpac110

Bankhead, P., Loughrey, M. B., Fernández, J. A., Dombrowski, Y., McArt, D. G., Dunne, P. D., McQuaid, S., Gray, R. T., Murray, L. J., Coleman, H. G., James, J. A., Salto-Tellez, M., & Hamilton, P. W. (2017). QuPath: Open source software for digital pathology image analysis. *Scientific Reports*, *7*(1), 16878. https://doi.org/10.1038/s41598-017-17204-5

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv*. http://arxiv.org/abs/1406.5823

Bauman, D., Fortunel, C., Delhaye, G., Malhi, Y., Cernusak, L. A., Bentley, L. P., Rifai, S. W., Aguirre-Gutiérrez, J., Menor, I. O., Phillips, O. L., McNellis, B. E., Bradford, M., Laurance, S. G. W., Hutchinson, M. F., Dempsey, R., Santos-Andrade, P. E., Ninantay-Rivera, H. R., Chambi Paucar, J. R., & McMahon, S. M. (2022). Tropical tree mortality has increased with rising atmospheric water stress. *Nature*, *608*(7923), 528–533. https://doi.org/10.1038/s41586-022-04737-7

Bivand, R. (2002). *Spdep: Spatial dependence: Weighting schemes, statistics [Dataset]. CRAN: Contributed packages*. The R Foundation. https://doi.org/10.32614/cran.package.spdep

Borchert, R., & Pockman, W. T. (2005). Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiology*, *25*(4), 457–466. https://doi.org/10.1093/treephys/25.4.457

Brodersen, C. R., Knipfer, T., & McElrone, A. J. (2018). In vivo visualization of the final stages of xylem vessel refilling in grapevine (*Vitis vinifera*) stems. *The New Phytologist*, *217*(1), 117–126. https://doi.org/10.1111/nph.14811

Brodribb, T. J., Carriqui, M., Delzon, S., & Lucani, C. (2017). Optical measurement of stem xylem vulnerability. *Plant Physiology*, *174*(4), 2054–2061. https://doi.org/10.1104/pp.17.00552

Brodribb, T. J., Skelton, R. P., McAdam, S. A. M., Bienaimé, D., Lucani, C. J., & Marmottant, P. (2016). Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. *The New Phytologist*, *209*(4), 1403–1409. https://doi.org/10.1111/nph.13846

Brum, M., Vadeboncoeur, M. A., Ivanov, V., Asbjornsen, H., Saleska, S., Alves, L. F., Penha, D., Dias, J. D., Aragão, L. E. O. C., Barros, F., Bittencourt, P., Pereira, L., & Oliveira, R. S. (2019). Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. *The Journal of Ecology*, *107*(1), 318–333. https://doi.org/10.1111/1365-2745.13022

Carlquist, S. (1984). Vessel grouping in dicotyledon wood. *Aliso*, *10*(4), 505–525. https://doi.org/10.5642/aliso.19841004.03

Carlquist, S. (2001). Evolution in wood: An ecological/functional synthesis. In *Comparative wood anatomy* (pp. 335–379). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-04578-7_11

Carlquist, S. (2009). Xylem heterochrony: an unappreciated key to angiosperm origin and diversifications. *Botanical Journal of the Linnean Society*, *161*(1), 26–65. https://doi.org/10.1111/j.1095-8339.2009.00991.x

Chen, Z., Zhu, S., Zhang, Y., Luan, J., Li, S., Sun, P., Wan, X., & Liu, S. (2020). Tradeoff between storage capacity and embolism resistance in the xylem of temperate broadleaf tree species. *Tree Physiology*, *40*(8), 1029–1042. https://doi.org/10.1093/treephys/tpaa046

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., … Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, *491*(7426), 752–755. https://doi.org/10.1038/nature11688

Christman, M. A., Sperry, J. S., & Adler, F. R. (2009). Testing the "rare pit" hypothesis for xylem cavitation resistance in three species of acer. *The New Phytologist*, *182*(3), 664–674. https://doi.org/10.1111/j.1469-8137.2009.02776.x

Cosme, L. H. M., Schietti, J., Costa, F. R. C., & Oliveira, R. S. (2017). The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *The New Phytologist*, *215*(1), 113–125. https://doi.org/10.1111/nph.14508

Douville, H., Raghavan, K., Renwick, J., Allan, R. P., Arias, P. A., Barlow, M., Cerezo-Mota, R., Cherchi, A., Gan, T. Y., Gergis, J., Jiang, D., Khan, A., Mba, W. P., Rosenfeld, D., Tierney, J., & Zolina, O. (2023). Water cycle changes. In *Climate change 2021 – The physical science basis* (pp. 1055–1210). Cambridge University Press. https://doi.org/10.1017/9781009157896.010

Eller, C. B., De Barros, F., Bittencourt, P. R. L., Rowland, L., Mencuccini, M., & Oliveira, R. S. (2018). Xylem hydraulic safety and construction costs determine tropical tree growth. *Plant, Cell & Environment*, *41*(3), 548–562. https://doi.org/10.1111/pce.13106

Ellmore, G. S., & Ewers, F. W. (1985). Hydraulic conductivity in trunk xylem of elm, *Ulmus americana*. *IAWA Journal*, *6*(4), 303–307. https://doi.org/10.1163/22941932-90000958

Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J. W., Feldpausch, T. R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B. S., Marimon-Junior, B. H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., … Phillips, O. L. (2019). Compositional response of Amazon forests to climate change. *Global Change Biology*, *25*(1), 39–56. https://doi.org/10.1111/gcb.14413

Gärtner, H., & Schweingruber, F. H. (2013). *Microscopic preparation techniques for plant stem analysis*. Verlag Dr. Kessel.

Gleason, S. M., Westoby, M., Jansen, S., Choat, B., Hacke, U. G., Pratt, R. B., Bhaskar, R., Brodribb, T. J., Bucci, S. J., Cao, K.-F., Cochard, H., Delzon, S., Domec, J.-C., Fan, Z.-X., Feild, T. S., Jacobsen, A. L., Johnson, D. M., Lens, F., Maherali, H., … Zanne, A. E. (2016). Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *The New Phytologist*, *209*(1), 123–136. https://doi.org/10.1111/nph.13646

González-Melo, A., Salgado-Negret, B., Norden, N., González-M, R., Benavides, J. P., Cely, J. M., Abad Ferrer, J., Idárraga, Á., Moreno, E., Pizano, C., Puentes-Marín, J., Pulido, N., Rivera, K., Rojas-Bautista, F., Solorzano, J. F., & Umaña, M. N. (2025). Linking seedling wood anatomical trade-offs with drought and seedling growth and survival in tropical dry forests. *The New Phytologist*, *245*(1), 117–129. https://doi.org/10.1111/nph.20222

Good, S. P., Noone, D., & Bowen, G. (2015). WATER RESOURCES. Hydrologic connectivity constrains partitioning of global terrestrial water fluxes. *Science (New York, N.Y.)*, *349*(6244), 175–177. https://doi.org/10.1126/science.aaa5931

Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A. K., Ewango, C. E. N., Fauset, S., Mukinzi, J. M., Sheil, D., Sonké, B., Sullivan, M. J. P., Sunderland, T. C. H., Taedoumg, H., Thomas, S. C., White, L. J. T., Abernethy, K. A., Adu-Bredu, S., … Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, *579*(7797), 80–87. https://doi.org/10.1038/s41586-020-2035-0

Isasa, E., Link, R. M., Jansen, S., Tezeh, F. R., Kaack, L., Sarmento Cabral, J., & Schuldt, B. (2023). Addressing controversies in the xylem embolism resistance-vessel diameter relationship. *The New Phytologist*, *238*(1), 283–296. https://doi.org/10.1111/nph.18731

Jansen, S., Choat, B., & Pletsers, A. (2009). Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. *American Journal of Botany*, *96*(2), 409–419. https://doi.org/10.3732/ajb.0800248

Janssen, T. A. J., Hölttä, T., Fleischer, K., Naudts, K., & Dolman, H. (2020). Wood allocation trade-offs between fiber wall, fiber lumen, and axial parenchyma drive drought resistance in neotropical trees. *Plant, Cell & Environment*, *43*(4), 965–980. https://doi.org/10.1111/pce.13687

Jenkins, C. N., Pimm, S. L., & Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(28), E2602–E2610. https://doi.org/10.1073/pnas.1302251110

Johnson, K. M., Everbach, S. R., Holbrook, N. M., & Olson, M. E. (2023). Evaluating Carlquist's Law from a physiological perspective. *IAWA Journal*, *44*(3-4), 429–438. https://doi.org/10.1163/22941932-bja10134

Jupa, R., Plavcová, L., Gloser, V., & Jansen, S. (2016). Linking xylem water storage with anatomical parameters in five temperate tree species. *Tree Physiology*, *36*(6), 756–769. https://doi.org/10.1093/treephys/tpw020

Kaack, L., Weber, M., Isasa, E., Karimi, Z., Li, S., Pereira, L., Trabi, C. L., Zhang, Y., Schenk, H. J., Schuldt, B., Schmidt, V., & Jansen, S. (2021). Pore constrictions in intervessel pit membranes provide a mechanistic explanation for xylem embolism resistance in angiosperms. *The New Phytologist*, *230*(5), 1829–1843. https://doi.org/10.1111/nph.17282

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across Island and mainland regions. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(23), 9322–9327. https://doi.org/10.1073/pnas.0810306106

Kiorapostolou, N., Da Sois, L., Petruzzellis, F., Savi, T., Trifilò, P., Nardini, A., & Petit, G. (2019). Vulnerability to xylem embolism correlates

to wood parenchyma fraction in angiosperms but not in gymnosperms. *Tree Physiology*, *39*(10), 1675–1684. https://doi.org/10.1093/treephys/tpz068

Lens, F., Gleason, S. M., Bortolami, G., Brodersen, C., Delzon, S., & Jansen, S. (2022). Functional xylem characteristics associated with drought-induced embolism in angiosperms. *The New Phytologist*, *236*(6), 2019–2036. https://doi.org/10.1111/nph.18447

Lens, F., Sperry, J. S., Christman, M. A., Choat, B., Rabaey, D., & Jansen, S. (2011). Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus acer. *The New Phytologist*, *190*(3), 709–723. https://doi.org/10.1111/j.1469-8137.2010.03518.x

Levionnois, S., Jansen, S., Wandji, R. T., Beauchêne, J., Ziegler, C., Coste, S., Stahl, C., Delzon, S., Authier, L., & Heuret, P. (2021). Linking drought-induced xylem embolism resistance to wood anatomical traits in neotropical trees. *The New Phytologist*, *229*(3), 1453–1466. https://doi.org/10.1111/nph.16942

Levionnois, S., Kaack, L., Heuret, P., Abel, N., Ziegler, C., Coste, S., Stahl, C., & Jansen, S. (2022). Pit characters determine drought-induced embolism resistance of leaf xylem across 18 neotropical tree species. *Plant Physiology*, *190*(1), 371–386. https://doi.org/10.1093/plphys/kiac223

Liang, X., & Ye, Q. (2024). Integrating dehydration tolerance and avoidance in drought adaptation. *Journal of Plant Ecology*, *17*(6), rtae073. https://doi.org/10.1093/jpe/rtae073

Lobo, A., Torres-Ruiz, J. M., Burlett, R., Lemaire, C., Parise, C., Francioni, C., Truffaut, L., Tomášková, I., Hansen, J. K., Kjær, E. D., Kremer, A., & Delzon, S. (2018). Assessing inter- and intraspecific variability of xylem vulnerability to embolism in oaks. *Forest Ecology and Management*, *424*, 53–61. https://doi.org/10.1016/j.foreco.2018.04.031

Loepfe, L., Martinez-Vilalta, J., Piñol, J., & Mencuccini, M. (2007). The relevance of xylem network structure for plant hydraulic efficiency and safety. *Journal of Theoretical Biology*, *247*(4), 788–803. https://doi.org/10.1016/j.jtbi.2007.03.036

Maherali, H., Pockman, W. T., & Jackson, R. B. (2004). Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, *85*(8), 2184–2199. https://doi.org/10.1890/02-0538

Martínez-Vilalta, J., Mencuccini, M., Alvarez, X., Camacho, J., Loepfe, L., & Piñol, J. (2012). Spatial distribution and packing of xylem conduits. *American Journal of Botany*, *99*(7), 1189–1196. https://doi.org/10.3732/ajb.1100384

Meinzer, F. C., Johnson, D. M., Lachenbruch, B., McCulloh, K. A., & Woodruff, D. R. (2009). Xylem hydraulic safety margins in woody plants: Coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology*, *23*(5), 922–930. https://doi.org/10.1111/j.1365-2435.2009.01577.x

Meinzer, F. C., McCulloh, K. A., Lachenbruch, B., Woodruff, D. R., & Johnson, D. M. (2010). The blind men and the elephant: The impact of context and scale in evaluating conflicts between plant hydraulic safety and efficiency. *Oecologia*, *164*(2), 287–296. https://doi.org/10.1007/s00442-010-1734-x

Michele Holbrook, N. (1995). Stem water storage. In *Plant stems* (pp. 151–174). Elsevier. https://doi.org/10.1016/b978-012276460-8/50009-6

Morris, H., Gillingham, M. A. F., Plavcová, L., Gleason, S. M., Olson, M. E., Coomes, D. A., Fichtler, E., Klepsch, M. M., Martínez-Cabrera, H. I., McGlinn, D. J., Wheeler, E. A., Zheng, J., Ziemińska, K., & Jansen, S. (2018). Vessel diameter is related to amount and spatial arrangement of axial parenchyma in woody angiosperms. *Plant, Cell & Environment*, *41*(1), 245–260. https://doi.org/10.1111/pce.13091

Oliveira, R. S., Costa, F. R. C., van Baalen, E., de Jonge, A., Bittencourt, P. R., Almanza, Y., Barros, F., Cordoba, E. C., Fagundes, M. V., Garcia, S., Guimaraes, Z. T. M., Hertel, M., Schietti, J., Rodrigues-Souza, J., & Poorter, L. (2019). Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. *The New Phytologist*, *221*(3), 1457–1465. https://doi.org/10.1111/nph.15463

Oliveira, R. S., Eller, C. B., Barros, F., Hirota, M., Brum, M., & Bittencourt, P. (2021). Linking plant hydraulics and the fast-slow continuum to understand resilience to drought in tropical ecosystems. *The New Phytologist*, *230*(3), 904–923. https://doi.org/10.1111/nph.17266

Olson, M. E. (2023). Imperforate tracheary element classification for studies of xylem structure-function relations. *IAWA Journal*, *44*(3-4), 439–464. https://doi.org/10.1163/22941932-bja10125

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science (New York, N.Y.)*, *333*(6045), 988–993. https://doi.org/10.1126/science.1201609

Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal*, *10*(1), 439. https://doi.org/10.32614/rj-2018-009

Penha, D., Brum, M., Alves, L. F., Domingues, T. F., Meneses, A., Branches, R., Restrepo-Coupe, N., Oliveira, R. S., Moura, J. M. S., Pequeno, P. A. C. L. A., Prohaska, N., & Saleska, S. R. (2024). Preserving isohydricity: Vertical environmental variability explains Amazon forest water-use strategies. *Tree Physiology*, *44*(8), tpae088. https://doi.org/10.1093/treephys/tpae088

Pereira, L., Kaack, L., Guan, X., de Silva, M., Miranda, M. T., Pires, G. S., Ribeiro, R. V., Schenk, H. J., & Jansen, S. (2023). Angiosperms follow a convex trade-off to optimize hydraulic safety and efficiency. *The New Phytologist*, *240*(5), 1788–1801. https://doi.org/10.1111/nph.19253

Plavcová, L., Hoch, G., Morris, H., Ghiasi, S., & Jansen, S. (2016). The amount of parenchyma and living fibers affects storage of non-structural carbohydrates in young stems and roots of temperate trees. *American Journal of Botany*, *103*(4), 603–612. https://doi.org/10.3732/ajb.1500489

Pratt, R. B., Castro, V., & Jacobsen, A. L. (2023). The functional significance of tracheids co-occurring with vessels in xylem of eudicots suggests a role in embolism tolerance. *IAWA Journal*, *44*(3–4), 477–494. https://doi.org/10.1163/22941932-bja10111

Pratt, R. B., & Jacobsen, A. L. (2017). Conflicting demands on angiosperm xylem: Tradeoffs among storage, transport and biomechanics. *Plant, Cell & Environment*, *40*(6), 897–913. https://doi.org/10.1111/pce.12862

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rodríguez-Ramírez, E. C., Arroyo, F., Ames-Martínez, F. N., & Andrés-Hernández, A. R. (2024). Tracking climate vulnerability across spatial distribution and functional traits in *Magnolia gentryi* in the Peruvian tropical montane cloud forest. *American Journal of Botany*, *111*(9), e16400. https://doi.org/10.1002/ajb2.16400

Rodríguez-Ramírez, E. C., Frei, J., Ames-Martínez, F. N., Guerra, A., & Andrés-Hernández, A. R. (2024). Ecological stress memory in wood architecture of two neotropical hickory species from central-eastern Mexico. *BMC Plant Biology*, *24*(1), 638. https://doi.org/10.1186/s12870-024-05348-2

Rüger, N., Comita, L. S., Condit, R., Purves, D., Rosenbaum, B., Visser, M. D., Wright, S. J., & Wirth, C. (2018). Beyond the fast-slow continuum: Demographic dimensions structuring a tropical tree community. *Ecology Letters*, *21*(7), 1075–1084. https://doi.org/10.1111/ele.12974

Rüger, N., Schorn, M. E., Kambach, S., Chazdon, R. L., Farrior, C. E., Meave, J. A., Muñoz, R., van Breugel, M., Amissah, L., Bongers, F., Craven, D., Hérault, B., Jakovac, C. C., Norden, N., Poorter, L., van der Sande, M. T., Wirth, C., Delgado, D., Dent, D. H., … Lopez, O. R. (2023). Successional shifts in tree demographic strategies in wet and dry neotropical forests. *Global Ecology and Biogeography:*

A Journal of Macroecology, *32*, 1002–1014. https://doi.org/10.1111/geb.13669

Sack, L., & Pasquet-Kok, J. (2011). Leaf pressure–volume curve parameters. *Prometheus: Protocols in Ecological & Environmental Science*. https://prometheusprotocols.net/function/water-relations/pressure-volume-curves/leaf-pressure-volume-curve-parameters/

Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., Zuidema, P. A., de Kroon, H., & Buckley, Y. M. (2016). Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(1), 230–235. https://doi.org/10.1073/pnas.1506215112

Santiago, L. S., De Guzman, M. E., Baraloto, C., Vogenberg, J. E., Brodie, M., Hérault, B., Fortunel, C., & Bonal, D. (2018). Coordination and trade-offs among hydraulic safety, efficiency and drought avoidance traits in Amazonian rainforest canopy tree species. *The New Phytologist*, *218*(3), 1015–1024. https://doi.org/10.1111/nph.15058

Scholz, A., Klepsch, M., Karimi, Z., & Jansen, S. (2013). How to quantify conduits in wood? *Frontiers in Plant Science*, *4*, 56. https://doi.org/10.3389/fpls.2013.00056

Smith, T. G., Jr., Marks, W. B., Lange, G. D., Sheriff, W. H., Jr., & Neale, E. A. (1989). A fractal analysis of cell images. *Journal of Neuroscience Methods*, *27*(2), 173–180. https://doi.org/10.1016/0165-0270(89)90100-3

Smith-Martin, C. M., Jansen, S., Brodribb, T. J., Medina-Vega, J. A., Lucani, C., Huppenberger, A., & Powers, J. S. (2022). Lianas and trees from a seasonally dry and a wet tropical forest did not differ in embolism resistance but did differ in xylem anatomical traits in the dry forest. *Frontiers in Forests and Global Change*, *5*, 1–14. https://doi.org/10.3389/ffgc.2022.834891

Smith-Martin, C. M., Muscarella, R., Ankori-Karlinsky, R., Delzon, S., Farrar, S. L., Salva-Sauri, M., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2022). Hurricanes increase tropical forest vulnerability to drought. *The New Phytologist*, *235*(3), 1005–1017. https://doi.org/10.1111/nph.18175

Smith-Martin, C. M., Muscarella, R., Ankori-Karlinsky, R., Delzon, S., Farrar, S. L., Salva-Sauri, M., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2023). Hydraulic traits are not robust predictors of tree species stem growth during a severe drought in a wet tropical forest. *Functional Ecology*, *37*(2), 447–460. https://doi.org/10.1111/1365-2435.14235

Sperry, J. S., Hacke, U. G., & Pittermann, J. (2006). Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany*, *93*(10), 1490–1500. https://doi.org/10.3732/ajb.93.10.1490

Tavares, J. V., Farrar, S. L., Smith-Martin, C. M., Bibbo, S., Ziemińska, K., Petz, S., Brenda, F., Uriarte, M., Zimmerman, J. K., & Muscarella, R. (2026). *Wood anatomical trait correlations with hydraulic efficiency and safety in an aseasonal wet tropical forest* [Dataset]. Dryad. https://doi.org/10.5061/dryad.t4b8gtjhp

Tavares, J. V., Gloor, E., Silva, T. S. F., Oliveira, R. S., Coelho de Souza, F., Signori-Müller, C., Diniz, F. C., Pereira, L., Acosta, M., Gilpin, M., Marca Zevallos, M. J., Salas Yupayccana, C. A., Perez-Mullisaca, F. M., Jancoski, H., Scalon, M. C., Schwantes Marimon, B., Marimon Junior, B. H., Malhi, Y., Oliveras Menor, I., … Galbraith, D. (2026). Family imprint reveals basin-wide patterns of Amazon forest embolism resistance. *Nature Communications*, *17*(1), 2073. https://doi.org/10.1038/s41467-026-69892-1

Tavares, J. V., Oliveira, R. S., Mencuccini, M., Signori-Müller, C., Pereira, L., Diniz, F. C., Gilpin, M., Marca Zevallos, M. J., Salas Yupayccana, C. A., Acosta, M., Pérez Mullisaca, F. M., Barros, F. d. V., Bittencourt, P., Jancoski, H., Scalon, M. C., Marimon, B. S., Oliveras Menor, I., Marimon, B. H., Jr., Fancourt, M., … Galbraith, D. R. (2023). Basin-wide variation in tree hydraulic safety margins predicts the carbon balance of Amazon forests. *Nature*, *617*(7959), 111–117. https://doi.org/10.1038/s41586-023-05971-3

Thompson, J., Brokaw, N., Zimmerman, J. K., Waide, R. B., Everham, E. M., Lodge, D. J., Taylor, C. M., García-Montiel, D., & Fluet, M. (2002). Land use history, environment, and tree composition in a tropical Forest. *Ecological Applications: A Publication of the Ecological Society of America*, *12*(5), 1344–1363. https://doi.org/10.2307/3099976

Trueba, S., Delzon, S., Isnard, S., & Lens, F. (2019). Similar hydraulic efficiency and safety across vesselless angiosperms and vessel-bearing species with scalariform perforation plates. *Journal of Experimental Botany*, *70*(12), 3227–3240. https://doi.org/10.1093/jxb/erz133

Tyree, M. T., Davis, S. D., & Cochard, H. (1994). Biophysical perspectives of xylem evolution: Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA Journal*, *15*(4), 335–360. https://doi.org/10.1163/22941932-90001369

von Arx, G., Kueffer, C., & Fonti, P. (2013). Quantifying plasticity in vessel grouping – Added value from the image analysis tool ROXAS. *IAWA Journal/International Association of Wood Anatomists*, *34*(4), 433–445. https://doi.org/10.1163/22941932-00000035

Wason, J., Bouda, M., Lee, E. F., McElrone, A. J., Phillips, R. J., Shackel, K. A., Matthews, M. A., & Brodersen, C. (2021). Xylem network connectivity and embolism spread in grapevine (*Vitis vinifera* L.). *Plant Physiology*, *186*(1), 373–387. https://doi.org/10.1093/plphys/kiab045

Wei, Z., Yoshimura, K., Wang, L., Miralles, D. G., Jasechko, S., & Lee, X. (2017). Revisiting the contribution of transpiration to global terrestrial evapotranspiration. *Geophysical Research Letters*, *44*(6), 2792–2801. https://doi.org/10.1002/2016GL072235

Wheeler, J. K., Sperry, J. S., Hacke, U. G., & Hoang, N. (2005). Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: A basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment*, *28*(6), 800–812. https://doi.org/10.1111/j.1365-3040.2005.01330.x

Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2010). Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, *91*(12), 3664–3674. https://doi.org/10.1890/09-2335

Ziegler, C., Levionnois, S., Bonal, D., Heuret, P., Stahl, C., & Coste, S. (2023). Large leaf hydraulic safety margins limit the risk of drought-induced leaf hydraulic dysfunction in neotropical rainforest canopy tree species. *Functional Ecology*, *37*(6), 1717–1731. https://doi.org/10.1111/1365-2435.14325

Ziemińska, K., Bibbo, S., Farrar, S., Thompson, J., Uriarte, M., Ziaco, E., Zimmerman, J. K., & Muscarella, R. (2023). Shifts in wood anatomical traits after a major hurricane. *Functional Ecology*, *37*(12), 3000–3014. https://doi.org/10.1111/1365-2435.14451

Ziemińska, K., Westoby, M., & Wright, I. J. (2015). Broad anatomical variation within a narrow wood density range – A study of twig wood across 69 Australian angiosperms. *PLoS One*, *10*, e0124892.

Zimmermann, M. H. (1983). *Xylem structure and the ascent of sap*. Springer. https://doi.org/10.1007/978-3-662-22627-8

Zuleta, D., Muller-Landau, H. C., Duque, A., Caro, N., Cardenas, D., Castaño, N., León-Peláez, J. D., & Feeley, K. J. (2022). Interspecific and intraspecific variation of tree branch, leaf and stomatal traits in relation to topography in an aseasonal Amazon forest. *Functional Ecology*, *36*(12), 2955–2968. https://doi.org/10.1111/1365-2435.14199

SUPPORTING INFORMATION

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

Figure S1. Relationship between stem capacitance at full turgor (C_{ft}) and parenchyma fractions. Colours denote species. Statistical results are displayed in Table S4. Tissue fractions of *Cecropia*

schreberiana and *Schefflera morototoni* were not estimated due to the lack of Ψ_{50} data for those species, as hollow stems prevented optical measurements.

Table S1. Results of bivariate species-centred linear mixed-effects models (Isasa et al., 2023) testing relationships between xylem safety (drought tolerance and avoidance) and efficiency. Please see Section 2 for further model details.

Table S2. Results of multivariate species-centred linear mixed-effects models (modified from Isasa et al. (2023)) testing the vessel diameter and vessel network hypotheses (dependent variable = Ψ_{50}). Models include fixed effects decomposed into across- and within-species components, with species fitted as a random intercept.

Table S3. Species-centred linear mixed-effects models comparing multivariate (PC1 and PC2) versus individual wood anatomical traits in predicting embolism resistance and stem capacitance at full turgor. Model selection was based on AIC.

How to cite this article: Tavares, J. V., Farrar, S. L., Smith-Martin, C. M., Bibbo, S., Ziemińska, K., Solis Petz, F. B., Uriarte, M., Zimmerman, J. K., & Muscarella, R. (2026). Wood anatomical trait correlations with hydraulic efficiency and safety in an aseasonal wet tropical forest. *Functional Ecology*, *00*, 1–17. https://doi.org/10.1111/1365-2435.70381