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LETTER

Hydraulic variability of tropical forests is largely independent of water availability

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Abstract

Tropical rainforest woody plants have been thought to have uniformly low resistance to hydraulic failure and to function near the edge of their hydraulic safety margin (HSM), making these ecosystems vulnerable to drought; however, this may not be the case. Using data collected at 30 tropical forest sites for three key traits associated with drought tolerance, we show that site-level hydraulic diversity of leaf turgor loss point, resistance to embolism (P_{50}), and HSMs is high across tropical forests and largely independent of water availability. Species with high HSMs (>1 MPa) and low P_{50} values (< -2 MPa) are common across the wet and dry tropics. This high site-level hydraulic diversity, largely decoupled from water stress, could influence which species are favoured and become dominant under a drying climate. High hydraulic diversity could also make these ecosystems more resilient to variable rainfall regimes.

KEYWORDS

cavitation, tropical dry forest, tropical lianas, tropical trees, tropical wet forest, xylem vulnerability

INTRODUCTION

Water availability patterns and sensitivity to drought shape the geographic distribution of plant species and community composition (Bunker & Carson, 2005; Engelbrecht et al., 2007; Holdridge et al., 1971; Richards, 1952; Slik, 2004). Traits associated with the plant water transport system (i.e. hydraulic traits) are robust indicators

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of species-level drought tolerance (Esquivel-Muelbert et al., 2019; Liang et al., 2021; Powers et al., 2020; Shao et al., 2023; Trugman et al., 2020). Vascular plants transport water under negative pressure from the soil to their leaves through their hydraulic vascular system (Angeles et al., 2004; Dixon & Joly, 1895) and the failure of this transport system is a key cause of drought-induced mortality (Choat et al., 2018; Hammond et al., 2019; Johnson et al., 2022; Losso et al., 2022; Nardini et al., 2013; Nolan et al., 2021; Urli et al., 2013). The failure of the plant hydraulic system during drought is caused by the formation of air bubbles in the xylem conduits. Under low soil moisture and/or increased evaporative demand during drought, increasing tension in the xylem water column leads to the formation and propagation of embolisms through the xylem network, restricting the movement of water from the soil to the leaves (Sperry et al., 1988; Sperry & Saliendra, 1994; Zimmermann, 1983). If water transport is restricted below the minimum required threshold to ensure survival, the hydraulic system fails and the plant may, in part or in whole, die. Hydraulic traits reflect at which point during a drought event an individual plant will lose the function of a sufficient proportion of its xylem network, due to embolism accumulation and propagation, to reach hydraulic failure, and ultimately death. Interspecific variation in these traits determines which species within a site will be more susceptible to severe drought events and how site-level composition might change with a changing climate (Anderegg et al., 2015, 2016; Esquivel-Muelbert et al., 2019; Trugman et al., 2020).

Tropical forests account for the majority of global terrestrial aboveground biomass (Pan et al., 2011) contain more than half of global woody plant diversity (Slik et al., 2015), and are experiencing an increase in the frequency and severity of drought events. However, there is limited consensus on the degree of variation in hydraulic vulnerability to drought among tropical tree species. Although some studies have found that most species live close to the edge of their hydraulic limit to maximize carbon capture capacity (Barros et al., 2019; Choat et al., 2012; Fontes et al., 2020; Tyree & Sperry, 1988; Wolf et al., 2016), others have shown that many species operate with wider hydraulic safety margins (HSMs) and that the size of these margins varies greatly within a site (Oliveira et al., 2019; Peters et al., 2021; Powers et al., 2020; Ziegler et al., 2019). Over time, such differences could favour drought-tolerant taxa leading to shifts in species composition (Engelbrecht et al., 2007), as has been observed in some regions (Fauset et al., 2012; Trugman et al., 2020). However, only a handful of studies have explored site-level hydraulic diversity in tropical forests, and how particular tropical forests may shift in composition under more frequent extreme drought events remains uncertain.

Drought tolerance may hinge on water availability. In drier environments, there is a selection pressure for all species to be relatively drought-tolerant; however, even in such environments, studies have shown that some species have hydraulic traits associated with greater drought tolerance than others within the same site (Larter et al., 2017; Powers et al., 2020; Skelton et al., 2017; Smith-Martin, Jansen, et al., 2022; Smith-Martin, Skelton, et al., 2020; Vargas et al., 2021). This variation in drought tolerance observed in drier environments may be due in part to species having different drought resistance strategies (i.e. drought tolerance and drought avoidance). Studies have found that in some wet environments, there is also a range of drought tolerance among species based on their hydraulic traits (Oliveira et al., 2019; Santiago et al., 2018; Smith-Martin et al., 2023; Smith-Martin, Jansen, et al., 2022; Smith-Martin, Muscarella, et al., 2022; Ziegler et al., 2019). This variation in drought tolerance across species in these wet environments, where there is less environmental pressure to withstand aridity, and where we would expect all species would be uniformly drought vulnerable, could be the product of historic climatic conditions, the biogeographical origin of the species, or reflect other past or present environmental factors (Baker et al., 2020; Blackman et al., 2012; Dick & Pennington, 2019). In a global synthesis, Choat et al. (2012) found that most tropical tree species had uniformly high xylem vulnerability to embolism (less negative P_{50} values) and very narrow HSMs, implying that most species function close to the edge of their hydraulic capacity, potentially making tropical forest biomes very vulnerable to drought. However, this study only included 59 tropical tree species from mostly wet environments (>2400 mm mean annual rainfall) as data from tropical forests were limited at the time. Several recent studies have observed a wide range in P_{50} values within wet (Barros et al., 2019; Fontes et al., 2020; Oliveira et al., 2019; Santiago et al., 2018; Smith-Martin et al., 2023; Smith-Martin, Jansen, et al., 2022; Smith-Martin, Muscarella, et al., 2022; Ziegler et al., 2019) and dry (Barros et al., 2019; Powers et al., 2020; Smith-Martin, Jansen, et al., 2022; Vargas et al., 2021) tropical forest sites and a growing number of studies have found that high HSMs (>1 MPa) are common within wet and dry tropical forest sites (Barros et al., 2019; Martin-StPaul et al., 2017; Powers et al., 2020; Smith-Martin et al., 2023; Smith-Martin, Jansen, et al., 2022; Smith-Martin, Muscarella, et al., 2022; Vargas et al., 2021; Ziegler et al., 2019).

Mean annual precipitation (MAP) is the main climatic variable considered in studies of tropical species distribution and hydraulic trait variation across environmental gradients (Condit et al., 2002, 2013; Engelbrecht et al., 2007; Gaviria et al., 2017; Swaine, 1996). Yet, intra-annual rainfall seasonality and the availability of water relative to evaporative losses may be even more important factors than MAP in driving the evolution of species' hydraulic traits (Ledo et al., 2018; Liu et al., 2021; Schwartz et al., 2020; Serra-Maluquer et al., 2022; Sperry et al., 2016). Previous studies have found rainfall seasonality index (SI), climatic water deficit (CWD) and maximum monthly cumulative water deficit

(MCWD)—of which the latter two are exacerbated by hotter droughts—are related to species' hydraulic traits (Barros et al., 2019; Liu et al., 2019; Peters et al., 2021; Serra-Maluquer et al., 2022). However, few studies have examined the association between diversity of hydraulic traits within sites and these climate variables.

The number of studies that have measured water-stress tolerance traits such as turgor loss point (Ψ_{tlp}), P_{50} and HSMs in tropical forests over the last decade have increased significantly and data at the site-level are now accumulating. However, these studies have not been synthesized to paint a pantropical picture of the variability in hydraulic traits within and among tropical forest sites. As a result, the scale of variation in these hydraulic traits in the tropics, and how it changes across water availability gradients, is not well understood. Addressing this knowledge gap is important because temperate and boreal forest communities with greater hydraulic diversity are more resilient to drought (Anderegg et al., 2018), a finding which may also apply to tropical forests. Here, we leverage the increasing number of studies over the last decade that have measured Ψ_{tlp}, P_{50} and HSMs at tropical forest sites, together with additional unpublished data, to address the following question: (1) How much variation in Ψ_{tlp}, P_{50} and HSMs exists among species within a tropical forest site? We anticipate that tropical forests at different sites will be hydraulically diverse with a wide range of values in Ψ_{tlp}, P_{50} and HSMs across species. (2) What is the association between climatic drivers of water stress and site-level mean (SLM), range (SLR), and coefficient of variation (SLCV) of Ψ_{tlp}, P_{50} and HSMs? We expect that SLM Ψ_{tlp} and SLM P_{50} will become more negative, SLM HSMs will become larger, and the SLR and SLCV of these values will become narrower with increases in CWD, MCWD and SI, and lower MAP as species converge towards greater drought tolerance traits under greater water stress.

METHODS

Hydraulic trait data

We compiled published and unpublished hydraulic trait data related to drought tolerance for 30 sites, including multiple species of adult woody plants (lianas, trees and one palm) (Table S1). The unpublished data consist of Ψ_{tlp} measured with the bench dehydration method (Tyree & Hammel, 1972) and P_{50} measured on leaves with the optical vulnerability technique (Brodribb et al., 2016) (Table S1). These unpublished measurements were conducted at the same time and location as the data for Powers et al. (2020) but on co-occurring lianas. To get a sense of site-level hydraulic diversity, we only included studies where five or more co-occurring species had been measured at the same site. Specifically, we compiled data of Ψ_{tlp}, water potential at which 50% of hydraulic conductivity has been lost (P_{50}), and minimum leaf water potential recorded in the field (Ψ_{min}). We only included studies for which P_{50} was available. The published data were obtained from a previously collated plant hydraulics data in the xylem functional trait database (https://xylemfunctionaltraits.org/, accessed September 2020), and our web search in Google Scholar (http://scholar.google.com, accessed August 2021), ISI Web of Knowledge (http://webofknowledge.com, accessed August 2021), and Data Dryad (http://datadryad.org, accessed August 2021), using the keywords: "p50" and "xylem vulnerability". We only included data collected between the Tropics of Cancer (23°44′ N) and Capricorn (23°44′ S). HSMs are commonly calculated as the difference between (1) Ψ_{min} and P_{50}; and, (2) Ψ_{tlp} and P_{50}, with both methods rendering similar results (Guillemot et al., 2022; Martin-StPaul et al., 2017). Thus, we calculated HSMs as $\Psi_{min} - P_{50,}$ and when Ψ_{min} was not available, then we used $\Psi_{tlp} - P_{50}$.

The final compiled data set included information from 30 tropical forest sites across 10 countries: Ψ_{tlp} from 16 sites, P_{50} from 30 sites and HSMs from 24 sites (Table S2). The number of species measured at each site ranged from 5 to 46 with an average of 14 species per site (Table S2) representing a total of 368 naturally occurring woody species. To decrease the possibility of including measurements that had been affected by artefacts caused by open vessels, we excluded studies that met all of the following three criteria: xylem vulnerability was measured with the air injection or the centrifuge method, maximum vessel length was not taken into account, and more than half of the species in the study had very high P_{50} values ($P_{50} \geq -0.50$ MPa), suggesting R-Shaped vulnerability curves (Lamarque et al., 2018; Martin-StPaul et al., 2017). Because our compiled data set is extracted from many different studies with different methods, it is to be expected that some degree of variation exists due to sampling differences. Despite this limitation, we believe our large compiled data set is a powerful tool for shedding light on pantropical patterns in hydraulic trait diversity and their association with climate.

Climate data

For each site, we computed several climatic variables based on data from CHELSA (Brun et al., 2022; Karger et al., 2017). First, we calculated annual potential evapotranspiration (PET; mm year^{-1}) by summing monthly mean values of PET. We also computed CWD (mm) as the difference between annual PET and MAP (Skelton et al., 2021), and MCWD as the minimum monthly value of water deficit across the 12 months for each site (Aragão et al., 2007; Phillips et al., 2010). Specifically, we first computed the water deficit at each site based on an average monthly transpiration rate of 100 mm during the wettest month. We then calculated the cumulative water deficit for each subsequent month and took the negative value of the month with the minimum water deficit value as the MCWD. Lastly, we calculated a SI (Feng et al., 2013). This metric quantifies rainfall concentration during the year as $\mathrm{SI} = \sum_{m=1}^{12} p_m \log_2 (p_m / q_m)$, where p_m is the proportion of annual rainfall that occurs in a given month m and q_m is a uniform distribution that assumes rainfall is equally distributed across all months of the year (i.e. $q_m = 1/12$). SI ranges between 0 when rainfall is equally distributed during the year to a maximum value when all annual rainfall occurs in a single month.

Data analysis

To evaluate within-site hydraulic trait variation (Question 1), we calculated SLM, SLR and SLCV of Ψ_{tlp}, P_{50} and HSMs. To assess the association between climatic variables, namely CWD, MCWD, SI and MAP with SLM, SLR and SLCV for Ψ_{tlp}, P_{50} and HSMs (Question 2), we used linear regression. Because the number of species measured in each site varied widely (from 5 to 46 species per site), we used weighted linear regression based on the number of species measured per site. We also fitted a second set of unweighted regressions to determine if the results were different. Additionally, we fit linear mixed models with the species level hydraulic traits (Ψ_{tlp}, P_{50}, HSMs) and climatic variables (CWD, MCWD, SI, MAP) as fixed effects and the unique site ID as a random effect using the *nlme* R package (Pinheiro & Bates, 2023). To assess how observed variation among species could be explained by climate versus site factors, we extracted marginal R^2 and conditional R^2 from the mixed models using the *MuMIn* R package (Barton, 2023). The compiled data set we used for this study only includes one mean trait value per species per site, thus we were unable to include uncertainty in the analyses. We performed all analyses using R statistical software (Version 4.2.3).

RESULTS

Overall, there was a large range in hydraulic trait values across the 368 woody tropical species we included in the study: Ψ_{tlp} varied from −4.17 to −0.93 MPa, P_{50} from −10.98 to −0.80 MPa, and HSMs from −0.78 to 6.81 MPa. Across the 30 tropical forest sites considered, mean SLM Ψ_{tlp} was −1.90 MPa, P_{50} was −2.76 MPa, and mean HSMs was 1.41 MPa (Figure 1a; Table S2). There was substantial variation among sites in average values for all three traits: SLM Ψ_{tlp} varied between −2.40 and −1.25 MPa, P_{50} between −5.91 and −1.38 Pa, and HSMs between −0.13 and 3.51 MPa (Table S2). Mean SLR of P_{50} and HSMs was more than two times higher than for Ψ_{tlp}: mean SLR of Ψ_{tlp} was 1.41 MPa, whereas for P_{50} it was 3.28 MPa, and for HSMs 2.95 MPa (Figure 1b; Table S2). Mean SLCV of HSMs was more than two times higher than for Ψ_{tlp} and P_{50}: mean SLCV of Ψ_{tlp} was 0.23 MPa, P_{50} was 0.35 MPa, and HSMs was 1.04 MPa (Figure 1c; Table S2). There also was substantial variation among sites in the range of values for all three traits: SLR Ψ_{tlp} varied between 0.54 and 3.05 MPa, P_{50} between 0.88 and 9.73 MPa, and HSMs between 1.00 and 7.34 MPa (Table S2).

In general, site-level hydraulic diversity was independent of water availability. SLM, SLR, SLCV of hydraulic traits were variable across climatic conditions without clear patterns. Nevertheless, sites under high CWD conditions had a narrower range of P_{50} values (Figure 2c) and HSMs values (Figure 2d). There was also a decrease in SLCV Ψ_{tlp} with an increase in MAP (Figure 2a) and SLM P_{50} became

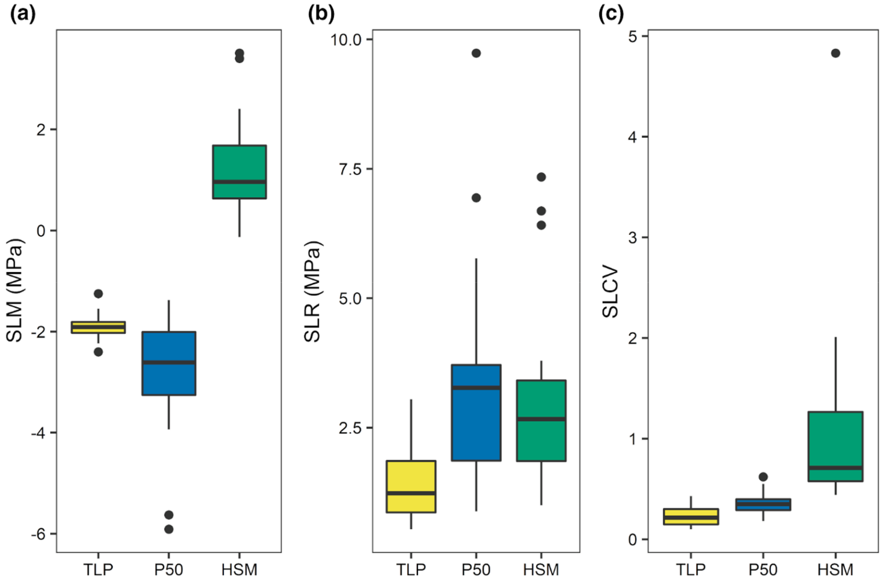

FIGURE 1 Site-level mean (SLM; a), site-level range (SLR; b) and site-level coefficient of variance (SLCV; c) of leaf turgor loss point (TLP), resistance to embolisms (P_{50}) and hydraulic safety margins (HSM). Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers.

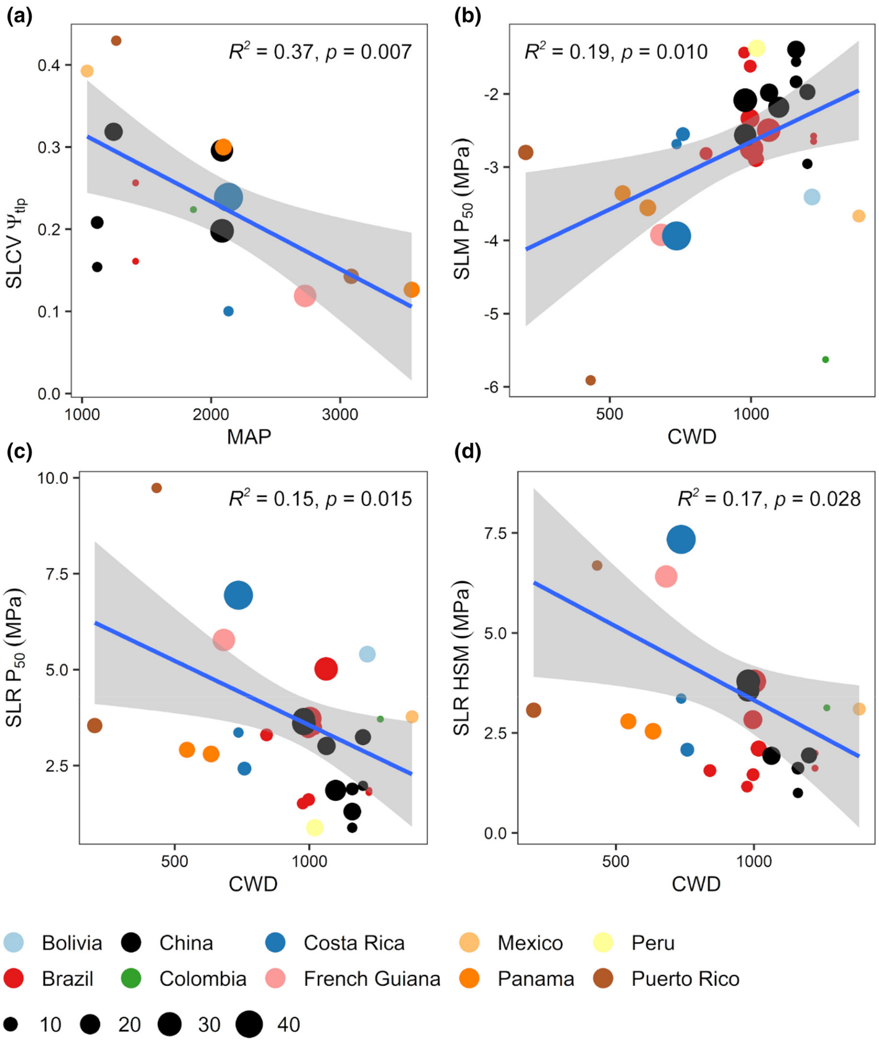

FIGURE 2 Weighted linear regressions of site-level mean (SLM), range (SLR) and coefficient of variance (SLCV) of leaf turgor loss point (Ψtlp; a), resistance to embolisms (P_{50}; b, c), and hydraulic safety margins (HSM; d) and mean annual precipitation (MAP) and climatic water deficit (CWD) extracted from CHELSA. Regressions were weighted by the number of species measured at each site—represented by circle size. See method for details. Blue lines depict parameters of linear regressions and shaded areas 95% confidence intervals.

less negative with an increase in CWD (Figure 2b). None of the other weighted linear regressions were statistically significant (Figures S1–S3; Table S3). Based on the results from the unweighted linear regressions, there was only a significant association between SLR for P_{50} and HSMs with CWD (Table S4). None of the fixed effects in the mixed models were statistically significant and most of the variance was explained by the random site effect (Table S5).

DISCUSSION

Site-level hydraulic traits across the 30 sites considered revealed that tropical forests are more hydraulically diverse than previously thought (Choat et al., 2012), with large ranges in hydraulic trait values among species within the same site. Many species had high drought tolerance traits even in locations with high rainfall, suggesting that tropical forest ecosystems may be more resilient to drought than previously thought. Overall, there was more variation in xylem vulnerability to embolism than leaf turgor loss point. Site-level hydraulic diversity, based on SLR, was variable and largely independent of rainfall and aridity gradients and seasonality patterns. As expected, the range in P_{50} and HSMs became narrower with an increase in CWD, as variability in drought tolerance traits among species was lower at sites with higher CWD. However, contrary to what we expected, site-level mean P_{50} became less negative as CWD increased, perhaps because some species in drier sites have drought avoidance strategies such as deep roots, higher water storage capacity in tissues, or drought deciduousness. MCWD, rainfall SI, and mean annual precipitation (MAP) largely were not associated with site-level hydraulic diversity. With this study, we show that at a pantropical level, species with wide HSMs (>1 MPa) and more negative P_{50} values (< −2 MPa) are common within and across both wet and dry tropical forests.

Large site-level variation in hydraulic traits

Our data set showed that within a site, species exhibited a large range in traits associated with drought tolerance. Overall, we found that variation among species in any given site was high, with a mean SLR of 3.28 MPa in P_{50} and HSMs of 2.95 Mpa. Across sites, there was an 11-fold difference in SLR of P_{50} values and a sevenfold difference in SLR of HSMs values. The wide range in HSMs indicates that not all the species within these tropical forests function at the edge of their hydraulic capacity, a fact that does not support the expectation that species should operate with narrow HSMs to sustain CO_2 assimilation for as long as possible before closing their stomata to limit xylem embolism formation as water becomes more limited (Barros et al., 2019; Choat et al., 2012; Fontes et al., 2020; Tyree & Sperry, 1988). Studies in temperate forests also had similar SLRs in P_{50} and HSMs independent of rainfall. For example, across Australia, the SLR of P_{50} and HSMs (respectively) were 3.13 and 2.88 MPa in Daintree (wet tropical rainforest, MAP=5180 mm), 2.68 and 2.79 MPa in Warra (temperate wet forest, MAP=1500 mm), and 3.45 and 3.81 MPa in Swansea (dry sclerophyll woodland, MAP=650 mm) (Peters et al., 2021; Smith-Martin, Skelton, et al., 2020). These results indicate that large SLRs in hydraulic traits associated with drought tolerance are not restricted to the tropics.

Site-wide variation in turgor loss point was not as marked as for P_{50} and HSMs. We found that the mean SLR in Ψ_{tlp} was 1.41 MPa and we found a fivefold difference in SLR across sites suggesting greater convergence in this trait than embolism resistance (11-fold difference in SLR P_{50}). Although some research has suggested stomatal closure and the onset of xylem cavitation are closely associated (Jones & Sutherland, 1991), recent studies have found that this might not be the case (Creek et al., 2020; Martin-StPaul et al., 2017; Mencuccini et al., 2015; Wolf et al., 2016). Martin-StPaul et al. (2017) propose that P_{50} is independent of stomatal closure, and its proxy Ψ_{tlp}, and that there is a threshold of leaf water potential at ~−3 MPa beyond which most plants will need to close their stomata or risk mortality. Among the 216 Ψ_{tlp} values in our data set, only two species had values of Ψ_{tlp} more negative than ~−3 MPa (−4.16 and −3.76 MPa), supporting the threshold proposed by Martin-StPaul et al. (2017). Guillemot et al. (2022) found the size of HSMs is driven by P_{50} and not Ψ_{tlp}, supporting our finding that the range in Ψ_{tlp} values is lower than in P_{50} and HSMs. A caveat is that we only obtained Ψ_{tlp} from 16 sites and sampling a larger number of sites may reveal a larger SLR in Ψ_{tlp}. The higher observed site-level coefficient of variance (SLCV) of HSMs than that of Ψ_{tlp} and P_{50} may in part reflect the two methods we used to calculate HSMs, although previous studies found the two methods yield similar results (Guillemot et al., 2022; Martin-StPaul et al., 2017), or variation in Ψ_{min} measurements among studies (Martínez-Vilalta et al., 2021).

The observed high site-level hydraulic diversity in drier and wetter environments may reflect species differences in water use and drought resistance strategies (avoidance and tolerance) within sites, fostering species coexistence. In a theoretical paper modelling water competition among plant species in a Mediterranean environment, Levine et al. (2022) showed that differences in phenology and growing season length, due to varying abilities among species to grow under progressively drier conditions, lead to the coexistence and maintenance of higher diversity. Empirical studies also found that species with greater growth rates are less drought tolerant (Eller et al., 2018; Oliveira et al., 2021), further supporting the trade-off between higher growth and greater drought tolerance. For example, Phillips et al. (2010) found higher drought-induced mortality of tree species with low wood density, a trait often associated with higher P_{50} values (Liang et al., 2021) and likely higher growth rates (Oliva Carrasco et al., 2014). Similarly, Smith-Martin, Muscarella, et al. (2022) found a trade-off between growth and drought tolerance traits—species with the highest growth rates had less negative P_{50} values and smaller HSMs. Trade-offs between drought avoidance (tissue water storage capacity) and drought tolerance (embolism resistance) may also result in high hydraulic diversity (Oliveira et al., 2021; Smith-Martin et al., 2023). Species with greater drought tolerance would be favoured during times when water is limited, whereas fast-growing drought-avoiding species would perform better under non-drought conditions, potentially fostering coexistence of species with different strategies.

Rooting depth is another important drought resistance strategy. For example, using stable isotopes during a drought to estimate where co-occurring trees were obtaining their water from to estimate maximum rooting depth, Brum et al. (2018) found that shallow-rooted species had hydraulic traits associated with higher drought tolerance than the deeper-rooted species that could access deeper water. Excavation of root systems of mature deciduous and evergreen trees in a highly seasonal tropical forest showed that evergreen trees had deeper roots than the deciduous species, presumably so that evergreen trees could access deeper sources of water to maintain leaf function during the dry season (Smith-Martin, Xu, et al., 2020). Drought deciduousness is yet another drought avoidance strategy that is often employed by species growing in drier sites. For example, Choat et al. (2005) found that two drought-deciduous tree species from a seasonally dry rainforest were more vulnerable to embolisms than two co-occurring evergreen tree species. This trade-off between drought tolerance and drought deciduousness has also been discussed by Oliveira et al. (2021).

Ontogeny likely also plays a role in drought resistance within species. Although our data set is composed of measurements from adult individuals, a few studies have measured hydraulic traits on juveniles and mature individuals of the same species. Juvenile leaves were more vulnerable to drought than the leaves of mature trees of two heteroblastic tree species, the temperate Australian *Eucalyptus globulus* and the endemic Hawaiian *Acacia koa*, (Lucani et al., 2019; Pasquet-Kok et al., 2010). This may be the case for other species, meaning that seedlings and saplings would be more vulnerable to drought than their mature counterparts. However, other studies found adults to be more susceptible to drought-induced mortality than seedlings and saplings (Esquivel-Muelbert et al., 2017). Ultimately, which ontogenetic stage is more susceptible to drought may be species- and site-specific.

Patterns across environmental gradients

Tropical forest site-level variation in hydraulic traits seems to be largely decoupled from mean annual rainfall, water deficit and rainfall seasonality patterns. Across the 30 sites in our data set, we only found an association between lower SLM embolisms resistance (less negative P_{50}), smaller SLR in P_{50} and HSMs with an increase in CWD, and a decrease in SLCV of Ψ_{tlp} with a decrease in MAP. When we did not take sample size into account, we only found narrower SLR of P_{50} and HSMs in sites with high CWD. Aside from these patterns, hydraulic trait SLMs, CLRs and CLCVs did not reflect site water stress using the climate variables considered. What we show at a pantropical level can be observed in some of the site-level studies we include in our compiled data set. For example, two studies conducted in a lowland tropical rainforest of the Guiana Shield (MAP = 2728 mm year^{-1}, CWD = 683, MCWD = 77, SI = 0.21) found a large range of variation in P_{50} (−7.63 to −1.86 MPa) and HSMs values (−0.09 to 5.64 MPa) across 26 species (Santiago et al., 2018; Ziegler et al., 2019). Furthermore, across the 26 species measured in these two studies, 15 had P_{50} values below −3 MPa and 17 had HSMs greater than 1 MPa, potentially allowing these species to withstand severe drought despite this site having high rainfall, low water deficit and being relatively aseasonal (Santiago et al., 2018; Ziegler et al., 2019). Working in a drier Central Amazonian rainforest, with lower MAP, MCWD, and SI, but a higher CWD (MAP = 2294 mm year^{-1}, CWD = 1062, MCWD = 39, SI = 0.13) than the forest in French Guiana, Oliveira et al. (2019), found high variation in P_{50} values among 28 tree species (P_{50} ranged from −4.18 to −0.88 MPa) and nine species had P_{50} values lower than −3 MPa. A second study at a different location in Central Amazonian forests with similar water availability patterns (MAP = 2365 mm year^{-1}, CWD = 975, MCWD = 29, SI = 0.15) and using a largely different set of species, found a range in P_{50} values of only −2.59 to −0.59 MPa across 16 species with the majority of P_{50} values above −2 MPa suggesting that species in this community are not very embolism resistant despite the similar climatic conditions (Fontes et al., 2020). Yet another study conducted in two different Amazonian forests with contrasting MAP, MCWD and CWD, found similar patterns in P_{50} and HSMs in both forests despite the substantial difference in water availability (Barros et al., 2019). Oliveira et al. (2019) noted that Central Amazonian rainforest species were more embolism resistant than expected for tropical rainforests based on a global analysis (Choat et al., 2012) and hypothesized that such variation had arisen from species adaptations to the local topographic and low nutrient conditions. Other studies have also highlighted the importance of soil depth, topography and water table depth in driving hydraulic diversity and drought resistance (both drought tolerance and avoidance strategies) of Amazonian forests (Brum et al., 2019; Cosme et al., 2017; Costa et al., 2023; Marca-Zevallos et al., 2022; Sousa et al., 2020). However, this level of hydraulic diversity seems to also be common outside of Amazonian forests.

Studies in Central America and the Caribbean, included in our data set, also illustrate similar patterns. For example, studies conducted at two sites with contrasting environmental conditions in Puerto Rico found large site-level variation in P_{50} and HSMs. The first site which is largely aseasonal with high rainfall and low water deficit (MAP = 3086 mm year^{-1}, CWD = 202, MCWD = 0, SI = 0.04), had a range in P_{50} values of −4.40 to −0.86 MPa and HSMs of −0.44 to 2.60 MPa (Smith-Martin et al., 2023; Smith-Martin, Muscarella, et al., 2022). The second site in a seasonal tropical dry forest (MAP = 1265, CWD = 432, MCWD = 267, SI = 0.18), had P_{50} values between −10.98 to −1.25 MPa and HSMs between 0.13 to 6.81 MPa (Vargas et al., 2021), showing that although some species in this dry forest had higher drought-tolerant traits than those found in the much wetter Puerto Rican forest, there were also species with similar levels of drought tolerance traits despite the large difference in water availability between the sites. Studies conducted in a very seasonal tropical dry forest in Costa Rica, (MAP = 2135, CWD = 736, MCWD = 425, SI = 0.66), including 46 species of woody plants (trees and lianas), found P_{50} values ranging from −8.49 to −1.55 MPa and HSMs from −0.78 to 6.56 MPa (Powers et al., 2020; Vargas et al., 2021). Combined, the findings emerging from all these recent studies reveal that tropical environments have a greater range in levels of embolism resistance and vulnerability to hydraulic failure than previously thought based on the Choat et al. (2012) global synthesis. Our study shows that the site-level hydraulic diversity largely cannot be explained by differences in water availability.

In tropical wet forests, divergent biogeographical histories (Baker et al., 2020; Dick & Pennington, 2019) coupled with the lack of selective pressure from climate may be leading to this high range in levels of drought tolerance traits among forest species. This variation could lead to pantropical changes in community composition. However, there is also great variation among wet rainforest communities in the preponderance of drought-resistant strategies with some forests dominated by drought-tolerant species (e.g. some forests in Central and Eastern Amazonia, French Guiana, and a wet forest in

Panama (Barros et al., 2019; Oliveira et al., 2019; Santiago et al., 2018; Smith-Martin, Jansen, et al., 2022; Ziegler et al., 2019)) and others by drought vulnerable ones (e.g. Puerto Rico (Smith-Martin et al., 2023; Smith-Martin, Muscarella, et al., 2022), other forests near Manaus (Fontes et al., 2020)). In drier forests, where there is a strong selective pressure to be drought resistant, it is to be expected that species would converge towards high levels of drought tolerance with a more limited range in hydraulic traits within communities than those found in wetter forests. However, our compiled data set revealed that that was not the case. Drier forests with higher rainfall SI in Puerto Rico, Mexico, Panama, Colombia and Amazonian all had a high range of hydraulic trait values, with some species having high drought-tolerance traits but others having more drought-vulnerable traits (Barros et al., 2019; Oliveira et al., 2019; Powers et al., 2020; Smith-Martin, Jansen, et al., 2022; Vargas et al., 2021).

The origins and causes of this variation offer an interesting research avenue. Some species are in the middle of their ranges at a certain location while others may be at their limits; thus, some of the species with hydraulic traits that do not closely match the climatic condition in terms of drought tolerance of a given site may be at the edge of their climatic range (Changenet et al., 2021). Esquivel-Muelbert et al. (2017) found that water deficit affiliation or the precipitation conditions where each genus had the highest relative abundance was a good predictor of drought-induced mortality. Genera that were wet-affiliated had higher drought-induced mortality than genera that were dry-affiliated (Esquivel-Muelbert et al., 2017), supporting the idea that species with hydraulic traits that do not align with local water availability regimes are likely not in the most favourable portion of their distribution range. Biogeographical histories may also explain the occurrence of species in locations with climatic conditions that do not align with their hydraulic traits, as these hydraulic traits may represent past water availability patterns that have since changed, leaving these species and/or populations particularly susceptible to any further changes in rainfall variability (Baker et al., 2020; Dick & Pennington, 2019). It is also likely that some species with low drought tolerance growing at drier sites are relying on drought avoidance strategies such as deep roots, drought deciduousness or high water storage capacity as we discussed above.

Conclusions

Our compiled data set reveals that within-site variation in P_{50} and HSMs is widespread in the tropics. The available site-level studies are, of course, far from comprehensive, but they give us a sense of existing variability. The fact that this variation in xylem vulnerability and risk of hydraulic failure appears to mostly be decoupled from CWD, rainfall and rainfall seasonality patterns at the annual timescale could make some species within these sites disproportionately vulnerable to punctuated extreme drought events, and may also determine which species will become dominant under a further warming and drying climate, leading to changes in community composition. However, the high level of hydraulic diversity found within these tropical forest sites could also mean that tropical forests at the ecosystem level are better suited to withstand expected increases in rainfall variability than forests with lower hydraulic diversity.

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AUTHOR CONTRIBUTIONS

Chris M. Smith-Marin and María Uriarte conceptualized the project. All authors collected the data. Chris M. Smith-Marin, Robert Muscarella and María Uriarte analysed the data. Chris M. Smith-Marin and María Uriarte wrote the manuscript and all co-authors contributed to the final draft.

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SUPPORTING INFORMATION

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

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