

## LETTER

# Leaf habit affects the distribution of drought sensitivity but not water transport efficiency in the tropics

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**Abstract**

Considering the global intensification of aridity in tropical biomes due to climate change, we need to understand what shapes the distribution of drought sensitivity in tropical plants. We conducted a pantropical data synthesis representing 1117 species to test whether xylem-specific hydraulic conductivity ( $K_S$ ), water potential at leaf turgor loss ( $\Psi_{TLP}$ ) and water potential at 50% loss of  $K_S$  ( $\Psi_{P50}$ ) varied along climate gradients. The  $\Psi_{TLP}$  and  $\Psi_{P50}$  increased with climatic moisture only for evergreen species, but  $K_S$  did not. Species with high  $\Psi_{TLP}$  and  $\Psi_{P50}$  values were associated with both dry and wet environments. However, drought-deciduous species showed high  $\Psi_{TLP}$  and  $\Psi_{P50}$  values regardless of water availability, whereas evergreen species only in wet environments. All three traits showed a weak phylogenetic signal and a short half-life. These results suggest strong environmental controls on trait variance, which in turn is modulated by leaf habit along climatic moisture gradients in the tropics.

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**KEY WORDS**

aridity, pantropical, rainfall seasonality, turgor loss point, xylem hydraulic conductivity, xylem vulnerability to embolism

**INTRODUCTION**

As tropical ecosystems face novel drier climatic conditions (Cai et al., 2018; Feng et al., 2013; McDowell et al., 2020), there is an urgent need to understand which plant species and ecosystems are most vulnerable to changes in water availability (Brodribb et al., 2020). Water availability determines tropical vegetation associations (Holdridge, 1947) by influencing plant species distributions (Condit et al., 2013), patterns of leaf flushing and leaf shedding (Borchert et al., 2002) and variation in primary productivity among plant communities (Muller-Landau et al., 2021). It follows that species occurrences along water availability gradients should reflect the physiological characteristics that allow plants to cope with drought stress (hereafter drought sensitivity) (Esquivel-Muelbert et al., 2017).

Plant sensitivity to drought can be characterised by the physiological characteristics that describe plant water status, water transport and drought resistance along water availability gradients (Anderegg et al., 2016; Bartlett et al., 2012; Choat et al., 2012; Gleason et al., 2013). We focused on three key traits that influence such physiological processes: maximum xylem-specific hydraulic conductivity ( $K_s$ ), water potential at leaf turgor loss ( $\Psi_{TLP}$ ) and the water potential at 50% loss of  $K_s$  or accumulation of embolism in the xylem ( $\Psi_{P50}$ ) (Table 1). Plant hydraulic traits provide insight into the

physiological thresholds to damage during drought, from the cells to the tissues (e.g. leaves), and when water transport becomes impaired due to drought stress.  $\Psi_{P50}$  is correlated with tropical plant species mortality rates during drought stress periods (Berry et al., 2019; Kursar et al., 2009; Powers et al., 2020), and  $\Psi_{TLP}$  provides information on variation in species' stomatal control and is linked to demographic differences between plants from wet and dry tropical environments (Maréchaux et al., 2018; Medeiros et al., 2019; Meinzer et al., 2016). As a whole, plant hydraulic traits provide empirically measured assessments of plant drought sensitivity; hence, understanding how these traits vary across environmental gradients has promising potential to represent tropical plant function in dynamic vegetation models and earth system models (Mencuccini et al., 2019).

Globally, plant species from wet environments tend to show less negative values of  $\Psi_{TLP}$ ,  $\Psi_{P50}$  and higher  $K_s$  than species from drier environments (Bartlett et al., 2012; Liu et al., 2019). Values of these traits are also linked to the local climatic regime in which species grow and reproduce (Li et al., 2018), and local topographical variations in soil water content (Baltzer et al., 2008). For instance, less negative  $\Psi_{TLP}$  values (higher drought sensitivity) are found in species associated with overall high soil moisture content or growing in close proximity to the water table (Bartlett, Zhang, et al., 2016; Maréchaux et al., 2015; McFadden et al., 2019). This

**TABLE 1** Definitions and the associated physiological process of the three hydraulic traits involved in the present study

Trait	Units	Definition	References
$K_s$	$\text{Kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$	Characterises the hydraulic conductance of the xylem in a branch segment, that is the water flux per driving force, normalised by the branch length and the xylem cross-sectional area. It informs on water transport efficiency, tends to be higher in fast-growing species and links the fast-slow plant economic spectrum	Melcher et al. (2012); Reich (2014)
$\Psi_{TLP}$	MPa	Represents the value when the pressure potential ( $\Psi_p$ ) is zero and the leaf bulk water potential ( $\Psi_w$ ) is determined by the leaf cell osmotic potential ( $\Psi_s$ ), in other words, leaves are at their wilting point. It provides an estimate of the threshold for which leaves can maintain photosynthetic function under drought stress, the minimum soil water potential for water uptake, seedling survival under drought and the stomatal closure water potential	Tyree and Hammel (1972); Brodribb and Holbrook (2003b); Bartlett et al. (2012); Álvarez-Cansino et al. (2022)
$\Psi_{P50}$	MPa	Usually, the steepest point in the non-linear relationship between a measure of cavitation (i.e. loss of conductivity or accumulation of embolism events in xylem vessels) and water potential in the xylem. It describes xylem water transport impairment because of drought stress and increased tension in the xylem, and it is linked to high mortality rates in trees during drought events	Tyree and Sperry (1989); Choat et al. (2012); Anderegg et al. (2016)

$\Psi_{\text{TLP}}$ -environment relationship appears to be stronger in evergreen species than in drought-deciduous tropical species (Kunert et al., 2021), suggesting a decoupling of  $\Psi_{\text{TLP}}$  variation from response to local water availability for drought-deciduous plants. However, whether these patterns hold at a pan-tropical scale is yet to be tested.

Phenological leaf habits are associated with contrasting physiological strategies to cope with drought: avoidance versus tolerance (Delzon, 2015; Levitt, 1980). Drought-avoidant species tend to maximise productivity when water is available, whereas drought-tolerant species can maintain physiological function even under low water supply (Brodribb et al., 2002; Brodribb & Holbrook, 2003a). Plant species' values of  $\Psi_{\text{TLP}}$ ,  $\Psi_{\text{P50}}$  and  $K_s$  may vary along this drought tolerance-avoidance continuum regardless of their leaf habit (Vargas et al. 2021), such independent variation would support the decoupling of traits related to maximum water and carbon transport through the plant from traits that describe sensitivity to drought (Sack et al., 2003). Indeed, both leaf habit types co-exist along gradients of water availability in the tropics, underscoring the need to clarify how leaf habits may modulate other traits in driving forest responses to drought (Wu et al., 2022).

It has been difficult to disentangle the extent to which plant hydraulic trait variation is related to site-specific environmental conditions or species' evolutionary history (Laughlin et al., 2020). To understand how these factors might shape plant sensitivity to drought at the pantropical scale, we propose that species' evolutionary histories constrain plant hydraulic traits and drought sensitivity differently for contrasting leaf habit strategies (Figure 1), which in turn vary as a function of the climatic conditions at which a species is most likely to occur (i.e. a species climatic affiliation) (Esquivel-Muelbert et al., 2017). We predict that the differences in plant hydraulic trait values between evergreen and drought-deciduous species will decrease in wetter environments. This is because drought-deciduous plants are expected to tend to demonstrate drought avoidance regardless of their climatic affiliation, while evergreen species will span the tolerance vs. avoidance trait continuum, with their physiology coupled to water availability.

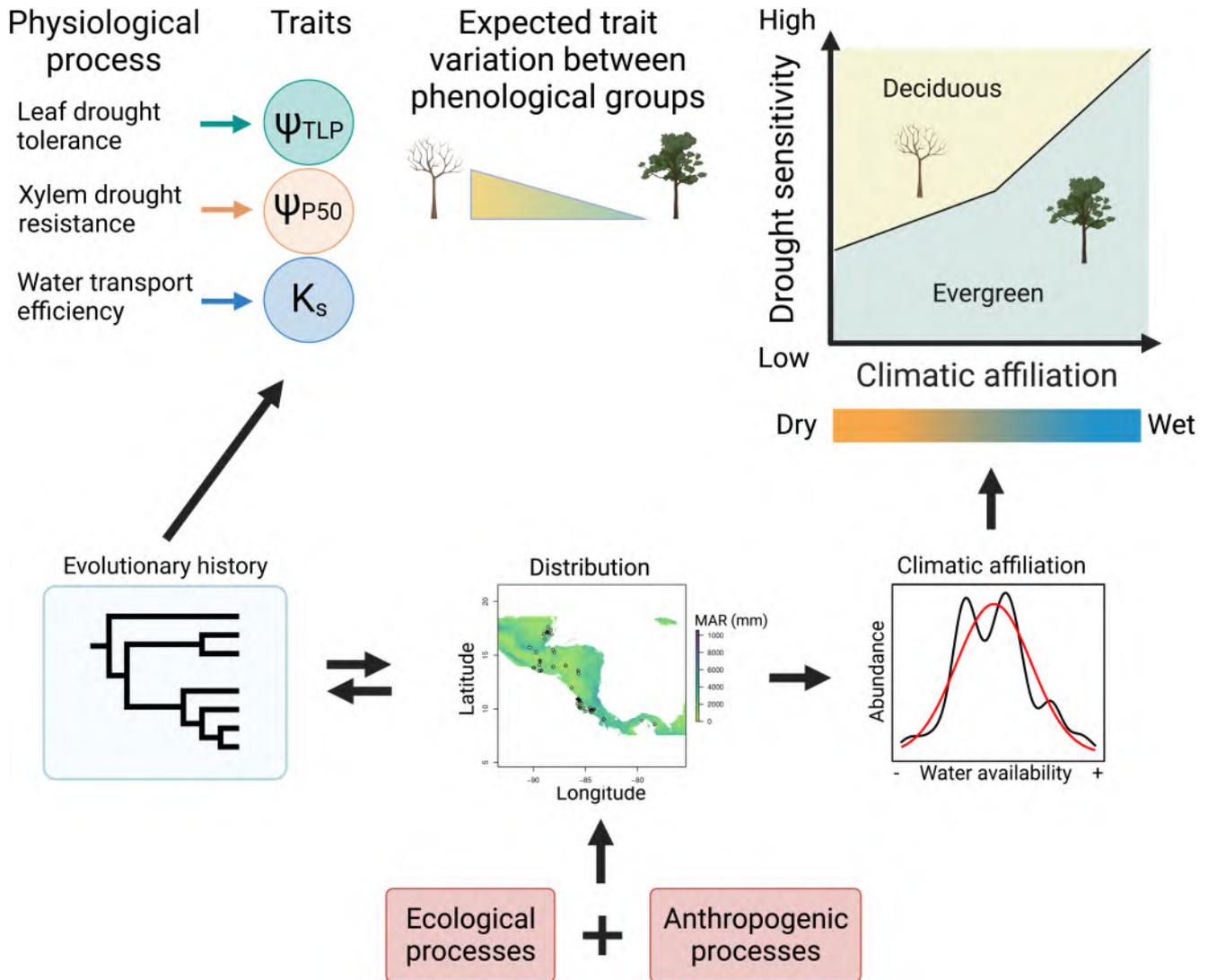
We performed the most comprehensive data synthesis on plant hydraulic traits to date for tropical species, with the objective of understanding how water availability and evolutionary history shape the distribution of drought tolerance and water transport in tropical plant species. We expanded the work in previous data syntheses of plant hydraulic traits (Anderegg et al., 2016; Bartlett et al., 2012; Bartlett, Klein, et al., 2016; Choat et al., 2012; Gleason et al., 2016; Johnson et al., 2012; Liu et al., 2019) by adding new observations spanning 1117 tropical species. Furthermore, we proposed that plant hydraulic traits are shaped by an environmental-evolutionary constraint space, wherein species' performance depends upon both adaptations to withstand

drought and whether these represent a disadvantage in specific environmental conditions. Low  $\Psi_{\text{TLP}}$  and low  $\Psi_{\text{P50}}$  may incur costs in growth (e.g. dense wood and low chemical defence), and thus would not be advantageous in wet environments where natural enemies and shade impose a greater selection (Brenes-Arguedas et al., 2009; Niinemets & Valladares, 2006; Spear et al., 2015). In contrast to  $\Psi_{\text{TLP}}$  and  $\Psi_{\text{P50}}$ , which are linked mainly to drought tolerance, low  $K_s$  can also be linked to adaptations useful in wet environments (e.g. shade tolerance) (Brenes-Arguedas et al., 2013). We hypothesised that these three traits are important to species' performance and therefore will be labile. We tested the following specific predictions: (1) There will be greater variance in  $\Psi_{\text{TLP}}$  and  $\Psi_{\text{P50}}$  in dry environments, representing drought-sensitive (i.e. high  $\Psi_{\text{TLP}}$  and  $\Psi_{\text{P50}}$ ) and drought-resistant traits (i.e. low  $\Psi_{\text{TLP}}$  and  $\Psi_{\text{P50}}$ ), whereas in wet environments drought-sensitive traits are typical. By contrast,  $K_s$  can be low or high across the spectrum of climates (Gleason et al., 2016). (2) In dry environments, drought-sensitive trait values will be mostly represented by plants with a drought avoidance strategy (i.e. drought-deciduous). (3) Plant hydraulic traits will show weak phylogenetic signals (Guillemot et al., 2022), indicating great diversification across the phylogenetically diverse species within the communities sampled.

## MATERIAL AND METHODS

### Plant hydraulic traits

We performed a data synthesis of stem xylem-specific hydraulic conductivity ( $K_s$ ), leaf water potential at turgor loss point ( $\Psi_{\text{TLP}}$ ) and xylem vulnerability to embolism ( $\Psi_{\text{P50}}$ ). We compiled trait data from unpublished contributions, the xylem functional trait database (<https://xylemfunctionaltraits.org/>), and published and freely available data. We performed our web search in Google Scholar (<http://scholar.google.com>, accessed February 2020), ISI Web of Knowledge (<http://webofknowledge.com>, accessed February 2020), and Data Dryad (<http://datadryad.org>, accessed February 2020), using the keywords: “turgor loss point”, “tropical”, “hydraulic conductivity”, “p50” and “xylem vulnerability”. We only included data collected within the Tropic of Cancer (23.44° N) and the Tropic of Capricorn (23.44° S) (Figure 2). Our final database consisted of  $K_s$  ( $n = 870$ ),  $\Psi_{\text{TLP}}$  ( $n = 1089$ ) and  $\Psi_{\text{P50}}$  ( $n = 1254$ ). This dataset included  $K_s$  and  $\Psi_{\text{P50}}$  observations in stems, leaves and roots, which were later analysed separately and together. For the analyses, we filtered out duplicated observations across data sources, and we excluded  $\Psi_{\text{P50}} > -0.5$  MPa as these might indicate artefacts in the measurements (Cochard et al., 2013). We also recorded whether species were drought-deciduous or evergreen in leaf habit. Given that in tropical forests water availability and atmospheric



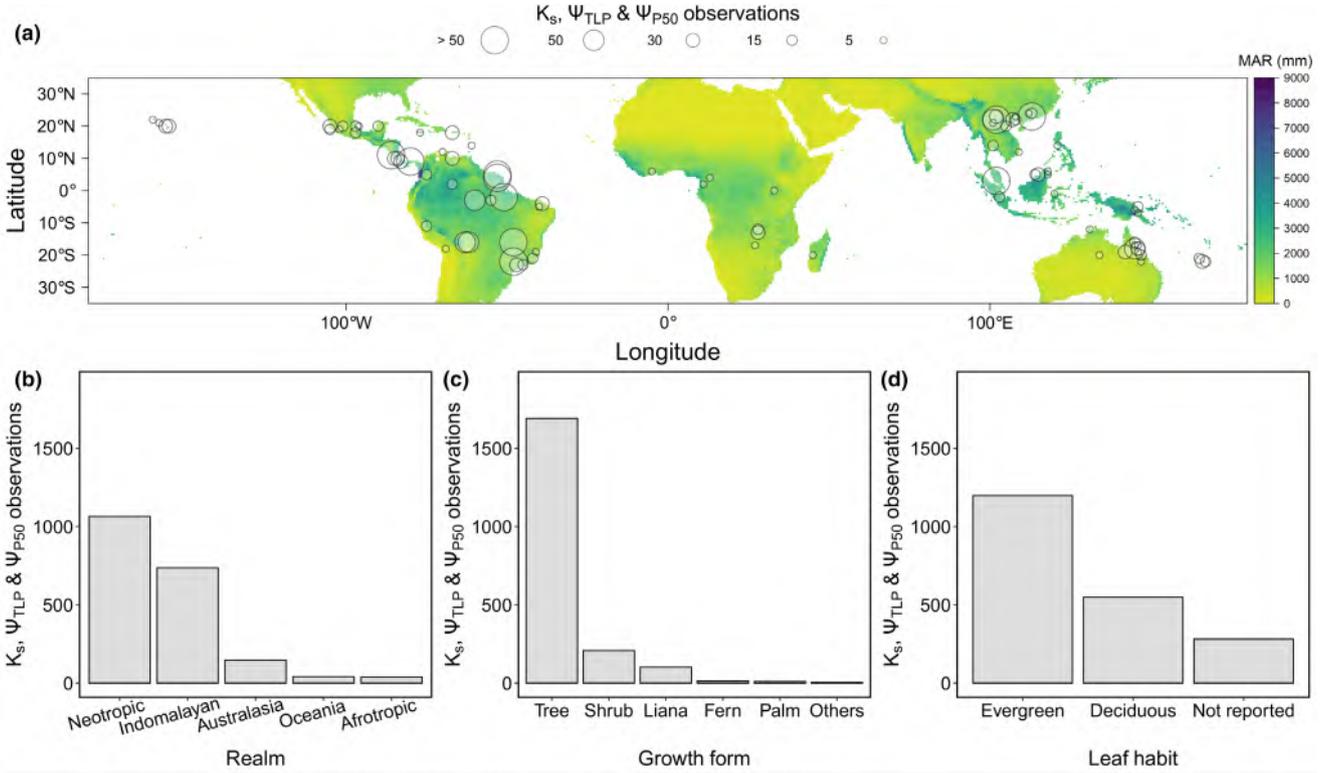
**FIGURE 1** A framework describing the variation of plant hydraulic trait values in tropical evergreen and tropical drought-deciduous species as a function of species' climatic affiliation to water availability. In general, drought-deciduous plants will show traits indicative of drought sensitivity and exploitative water use when compared to evergreen species across the range of climatic affiliations. This translates into higher values of xylem-specific hydraulic conductivity ( $K_s$ ), leaf water potential at turgor loss point ( $\Psi_{TLP}$ ) and the water potential at 50% loss of conductivity or 50% accumulation of embolism events in the xylem ( $\Psi_{P50}$ ). Plant hydraulic trait variation may be affected by species' evolutionary history. Climatic affiliations are defined as a function of species distributions depending on several factors including evolutionary history, ecological processes and anthropogenic processes. Black arrows indicate directionality on how evolutionary and ecological processes affect trait values and climatic affiliations. Coloured arrows indicate which physiological process is linked with empirically measured plant hydraulic traits.

water demand are the main controls on patterns of leaf flushing and leaf shedding (Borchert, 1994; Frankie et al., 1974; Wright & van Schaik, 1994), for simplicity, we binned observations from semi-deciduous ( $n = 34$ ), facultative deciduous ( $n = 4$ ) and brevi-deciduous ( $n = 6$ ) in the deciduous leaf habit. However, we acknowledge that other processes also affect leaf phenology such as irradiance or competition for resources (Chen et al., 2020; Sapijanskas et al., 2014). When species' leafing phenology was not available from the primary source, we based the leaf habit classification on online digital flora repositories from the region where the traits were collected, when available, or treated them as missing data.

Species nomenclature was then confirmed and updated (Notes S1).

### Species occurrences

For each species, we used occurrence records to estimate their climatic affiliations along water availability gradients (Esquivel-Muelbert et al., 2017; Feeley et al., 2020; Laughlin et al., 2020). To do this, we downloaded occurrence records using the BIEN data portal (<https://bien.nceas.ucsb.edu/bien/>) (accessed in July 2021). We chose the BIEN data portal as it encompasses curated



**FIGURE 2** Geographical distribution of studies with data for three plant hydraulic traits: Xylem-specific hydraulic conductivity ( $K_s$ ), the water potential at turgor loss point ( $\Psi_{TLP}$ ) and the water potential at 50% loss of conductivity or 50% accumulation of embolism events in the xylem ( $\Psi_{P50}$ ) (a). The colour gradient represents the mean annual rainfall (MAR) across the world tropics, and the circles' size is the number of observations. The number of observations of plant hydraulic traits for each biological realm (Olson et al., 2001) (b), growth form (c) and species leaf habit (d).

records from different data sources including the Global Biodiversity Information Facility (GBIF), SpeciesLink, inventory plot networks and functional trait data geolocations (Maitner et al., 2018). After downloading occurrence records, we performed a quality assessment of the data. First, we removed any duplicate records from the same pair of geographical coordinates. Second, we excluded any record from citizen science platforms, as they might contain taxonomic misidentifications. Third, we removed any occurrence record based on geographical centroids.

## Climate data

We characterised climate using two datasets: one associated with the geolocation of the plant hydraulic trait measurements (more than one observation per species), another one using the median and extreme climatic values (maximum and minimum) of species occurrence data obtained from BIEN (one observation per species). The water supply was characterised by obtaining monthly precipitation records from 1981 to 2020 for each geographical coordinates pair using gridded CHIRPS data with a spatial resolution of  $\sim 5.4$  km ( $0.05^\circ$ ) (Funk et al., 2015). First, we calculated the mean annual precipitation (MAP) as the sum of the total annual rainfall

for each hydrological year divided by the number of years. We defined the hydrological year as the 12 months after the lowest precipitation record in a month from a calendar year (Schwartz et al., 2020). To characterise the variability in water supply, we calculated the seasonality index (S) as:

$$S = D \cdot \frac{\text{MAP}}{\text{MAP}_{\max}} \quad (1)$$

where D is the relative entropy and quantifies the rainfall concentration during the wet season, calculated as  $D = \sum_{m=1}^{12} p_m \log_2(p_m/q_m)$ , where for a given month m there is a probability of precipitation ( $p_m$ ) given MAP ( $p_m = \text{rain}_m/\text{MAP}$ ) and a uniform distribution that assumes rainfall to be distributed equally ( $q_m = 1/12$ ) (Feng et al., 2013).  $\text{MAP}_{\max}$  is the observed maximum mean annual rainfall in the dataset (Feng et al., 2013). S varies in such a way that when rainfall is equally distributed during the year the value is 0 and maximised when  $\text{MAP}_{\max}$  is concentrated in a single month (Feng et al., 2013). To characterise the atmospheric water demand, we used gridded potential evapotranspiration data at  $\sim 1$  km ( $0.01^\circ$ ) resolution from the Global Aridity and Potential Evapotranspiration (PET) database (<http://www.cgiar-csi.org>) (Zomer et al., 2008). We acknowledge different resolutions in the climatic products used, however, evidence

suggests that analyses using resolutions with a grid cell size between 5 and 1 km produce almost identical results (Pinto-Ledezma & Cavender-Bares, 2021). We calculated the aridity index (AI) as the ratio between MAP and PET. Greater values of AI indicate wetter environments in which the water supply exceeds the atmospheric water demand (Zomer et al., 2008). Furthermore, we obtained the maximum climatological deficit (MCWD) defined as the most negative value of the cumulative difference between monthly precipitation and PET, and the dry season length defined as the number of consecutive months in which monthly precipitation is less than PET (Schwartz et al., 2020). We then overlaid the geographical coordinates for species with >15 unique occurrences with the climate data to obtain the median, minimum and maximum values of each climatic variable. In summary, we obtained three sets of climatic values: two at the species level, using the median from BIEN-derived occurrences and using extreme values of BIEN-derived occurrences (minimum and maximum), and one at the observation level, using values obtained from the trait sampling localities. While these indices ignore differences among sites that result from edaphic variability, they provide insight into the water supply and atmospheric demand.

## Phylogeny

We constructed a phylogenetic tree of all species using the V.PhyloMaker package in the R software (Jin & Qian, 2019). This package uses a mega-tree as a backbone, derived from two extensive phylogenies that include 74,533 species and all families of extant vascular plants (Smith & Brown, 2018; Zanne et al., 2014). The species not included in the mega-tree were bound to the half point of the genus branch, and similarly, missing genera were placed at the midpoint of the branch of its family (Qian & Jin, 2016). Branch lengths were estimated using the BLADJ approach as implemented in V.PhyloMaker. The resulting tree had 1084 terminals with each terminal corresponding to one species. This number of species is fewer than the total number of species in our database ( $n = 1117$ ) because we limited our phylogenetic tree to the species with resolved taxonomic classification. We then pruned the tree tips according to the species we had leaf habit information and >15 occurrence records for each trait:  $K_s$  ( $n_{SP} = 443$ ),  $\Psi_{TLP}$  ( $n_{SP} = 463$ ) and  $\Psi_{P50}$  ( $n_{SP} = 499$ ).

## Statistical analysis

We fitted a series of phylogenetic multilevel models (BMLMs) to study the effects of climate and leaf habit on  $K_s$ ,  $\Psi_{TLP}$  and  $\Psi_{P50}$ . These models allowed us to test whether in wet environments only drought-sensitive traits are possible and that drought-sensitive species in dry environments are mostly represented by drought-deciduous

plants. First, we fitted BMLMs with individual climatic predictors and leaf habits. After assessing collinearity among climatic predictors (Table S1), we fitted another set of BMLMs in which traits varied as a function of the linear of AI and S, including an interaction between leaf habit and each climatic predictor (Notes S2). In this second set of models, we used AI and S as our main climatic predictors because they were not strongly correlated (Pearson's rho <0.75). Considering that the geographical distribution of our data may not fully represent the full range of species occurrences across their climate range, we test whether climatic affiliations are stronger predictors of observed trait variation than the climate in which the traits were sampled. For this, we fitted the same BMLM three times: using median climatic affiliation values ( $AI_{med}$  and  $S_{med}$ ), using the values linked to the driest and more seasonal environment where the species occurs ( $AI_{min}$  and  $S_{max}$ ), and using climatic values obtained from the trait sampling localities ( $AI_{site}$  and  $S_{site}$ ). Additionally, we further explored the quantile variation of the predictor coefficients in the BMLM (Cade & Noon, 2003). To do so, we fitted the BMLM using the 10, 30, 50, 70 and 90 percentiles of the three plant hydraulic traits.

In the BMLMs, we accounted for methodological differences and species-specific sources of variation by including a random intercept of the sampling method nested within species. Additionally, we included a random intercept for the phylogeny with a specific variance structure defined by a phylogenetic distance matrix among taxa (Notes S2). By having species-specific random effects in addition to the phylogeny, we parameterised the uncertainty associated with ecological processes independent of species evolutionary history (Garland et al., 2000; Hadfield & Nakagawa, 2010). We used these models to estimate phylogenetic signals for each trait. To do so, we calculated Lynch's phylogenetic trait heritability:

$$\lambda = \frac{\sigma_P^2}{\sigma_P^2 + \sigma_R^2} \quad (2)$$

where  $\sigma_P^2$  represents the variance of the phylogeny and  $\sigma_R^2$  represents the variance of the residuals (Garamszegi, 2014). In other words, we assessed the intra-class correlation for trait values within the phylogeny. Equivalent to Pagel's lambda, a  $\lambda$  value approaching zero indicates a weak phylogenetic signal under the Brownian motion model of evolution, while a value approaching one indicates a strong phylogenetic signal (Freckleton et al., 2002; Housworth et al., 2004). We complemented this analysis by calculating the trait rate of adaptation ( $\alpha$ ) (i.e. rate of change in trait values towards the primary optimum) through an Ornstein–Uhlenbeck model as implemented in the R package *geiger* (Harmon et al., 2008). The  $\alpha$  parameter was then used to calculate trait phylogenetic

half-life as  $t_{1/2} = \frac{\ln(2)}{\alpha}$  (Hansen et al., 2008). In this context,  $t_{1/2}$  is defined as the time it takes for the trait values to reach the trait optimum (Hansen, 1997). A low  $t_{1/2}$  value relative to the phylogeny's earliest split indicates that most of the trait variation in the data comes from other processes not explained by the phylogenetic distance (Hansen et al., 2008).

In all models, we performed hypothesis testing by assessing whether the posterior 95% high-density intervals (HDI) intersect with the region of practical equivalence (ROPE) (Kruschke & Liddell, 2018). We defined the ROPE based on the variability of the response variable in question as  $[-0.1 * SD_y, 0.1 * SD_y]$  (Kruschke, 2018), where  $SD_y$  is the standard deviation of either  $K_S$ ,  $\Psi_{TLP}$  or  $\Psi_{P50}$ . We performed probability sampling using a Hamiltonian Monte-Carlo algorithm over four Markov-chains Monte-Carlo (MCMC) with 15,000 iterations and a burn-in period of 3000 iterations. We visually inspected for convergence in the MCMC and the Gelman–Rubin ( $\hat{R}$ ) statistic approaching 1.00 (Gelman & Rubin, 1992). Whenever  $\hat{R}$  values were higher than 1.01, we increased the number of iterations. Additionally, we inspected model fit through a visual inspection of the empirical cumulative distribution function (ECDF) overlay of predicted and observed responses, a visual assessment of the fitted versus predicted values for the response variable, and by calculating a Bayesian ‘ $R^2$ ’ in which the variance of predicted values is divided by the variance of predicted values plus the expected variance of the errors (Gelman et al., 2019). Data management and statistical analyses were conducted in R Version 4.1.0 (R Core Team, 2021) with the packages *ape* (Paradis & Schliep, 2019), *bayestestR* (Makowski et al., 2019), *BIEN* (Maitner et al., 2018), *geiger* (Harmon et al., 2008), *raster* (Hijmans, 2021), *tidyverse* (Wickham et al., 2019), *V.Phylomaker* (Jin & Qian, 2019) and *zoo* (Zeileis & Grothendieck, 2005). BLMMs were implemented using the probabilistic programming language Stan (Carpenter et al., 2017) through the R package *brms* (Bürkner, 2017, 2018).

## RESULTS

### Patterns of pantropical drought tolerance

Our dataset included a total of 3159 observations spanning 1117 species from 134 families, with Fabaceae as the most well-sampled with 149 species. More than half of the observations were of plant species with evergreen leaf habits (Figure 2) and ~50% of the observations were collected in the Neotropics (Figure 2). Plant hydraulic traits were associated with AI (Figure 3) but not with S (Figure S1). Evergreen species distributed in wetter environments (higher AI) had less negative  $\Psi_{TLP}$  and  $\Psi_{P50}$  than those in drier environments (Figure 3). Moreover, evergreen species showed less negative  $\Psi_{TLP}$  and  $\Psi_{P50}$  in climates with a short dry season and with higher mean

annual rainfall (Figures S2 and S3). By contrast, neither  $AI_{med}$  nor  $AI_{min}$  was correlated with  $\Psi_{TLP}$  or  $\Psi_{P50}$  for drought-deciduous species. Neither  $AI_{med}$  nor  $AI_{min}$  was correlated with  $K_S$  regardless of species leaf habit (Figure 3; Figure S1). For  $K_S$  and  $\Psi_{TLP}$ , these patterns changed when using  $AI_{site}$ . Specifically,  $K_S$  and  $\Psi_{TLP}$  values increased as a function of  $AI_{site}$  for drought-deciduous and for both leaf habit types respectively (Figure 3). Interestingly, the dry season length for the site at which traits were sampled also had a negative effect on  $K_S$ , which decreased in places with longer dry seasons in drought-deciduous species (Figure S4). Using data only from branches for  $K_S$  and  $\Psi_{P50}$  yielded weaker effects by climatic predictors than when combining observations from branches, roots and leaves (Figures S1 and S5).

### Unequal variation of plant hydraulic traits

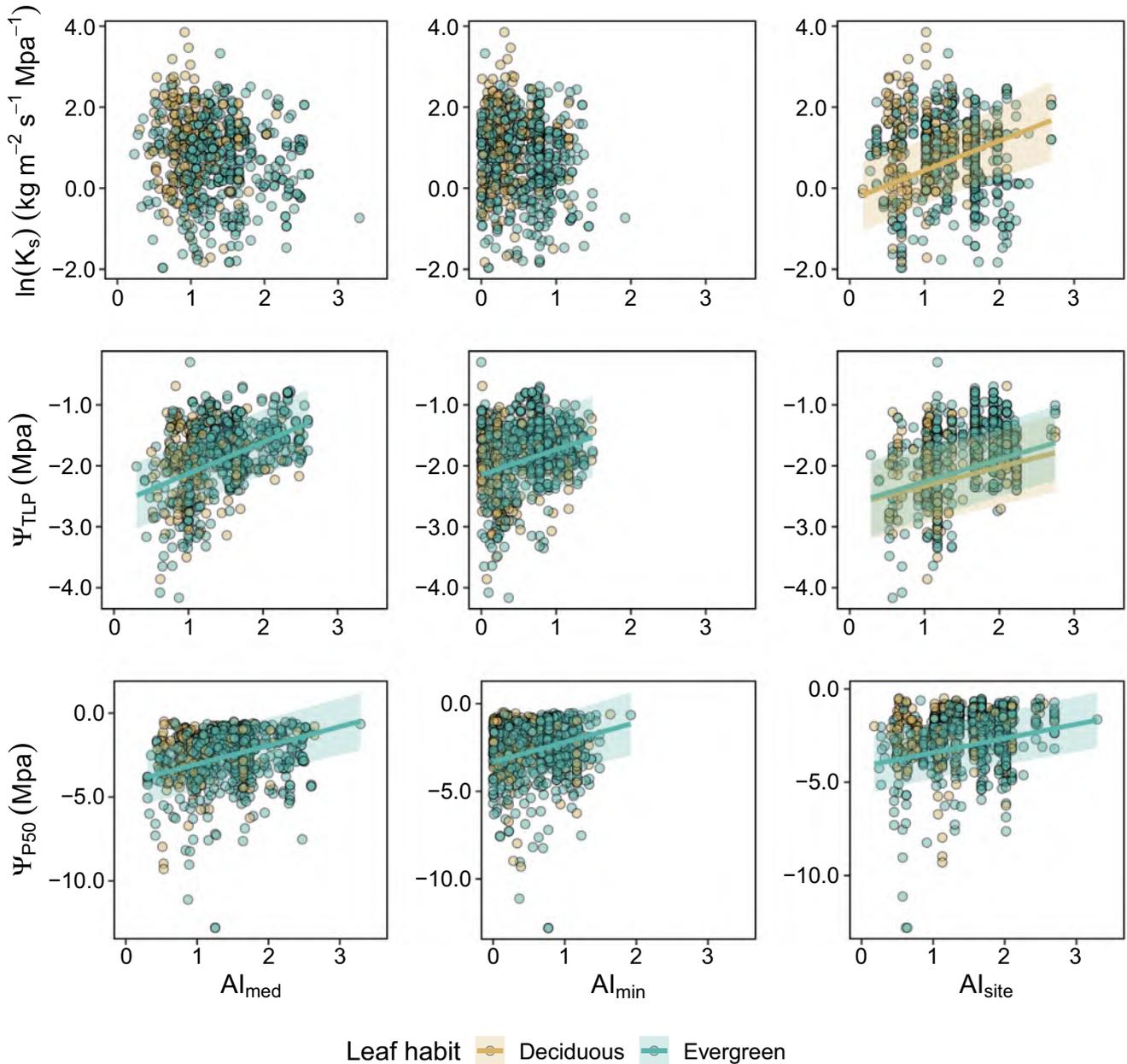
The quantile regression analysis showed that for evergreen species the  $\beta$  coefficients of  $\Psi_{TLP}$  and  $\Psi_{P50}$  as a function of  $AI_{med}$  affiliation were  $>0.20$  and  $>0.35$ , respectively, across all quantiles (Figure 4). On the other hand, drought-deciduous species showed  $\beta$  coefficients with negligible differences from 0 across all quantiles, except for the upper 10% (90th percentile) for  $\Psi_{P50}$  (Figure 4). However, for  $AI_{site}$  the results were quite different. First, the  $\beta$  coefficients of  $K_S$  for drought-deciduous species were  $>0.15$  in the lower quantiles (Figure 4). Second, the overall effect of  $AI_{site}$  on  $\Psi_{TLP}$  and  $\Psi_{P50}$  showed  $\beta$  coefficients  $<0.2$ . In the case of  $\Psi_{TLP}$  drought-deciduous species showed greater  $\beta$  coefficients across quantiles than evergreen species. Neither  $S_{med}$ ,  $S_{site}$ , nor the plant organ influenced the plant hydraulic traits' quantile-specific variation (Figure S6 and S7).

### Phylogenetic signal

Traits showed a low phylogenetic signal ( $\lambda$ ) under the Brownian motion model of evolution, but  $\lambda$  was always greater than 0 (null hypothesis of no phylogenetic signal) (Table 2). These patterns can be explained by the short trait phylogenetic half-life ( $<10$  MY) for all hydraulic traits with respect to the earliest split in the phylogenetic trees ( $>300$  MY) (Table 2). Moreover, the amount of variance in the traits associated with the phylogeny was relatively low when compared to the variance associated with species-specific sources of variation other than phylogenetic relatedness or methodological differences in data collection (Figure S8).

## DISCUSSION

Our extensive data synthesis on plant hydraulics in the tropics maps hydraulic traits onto the climatic



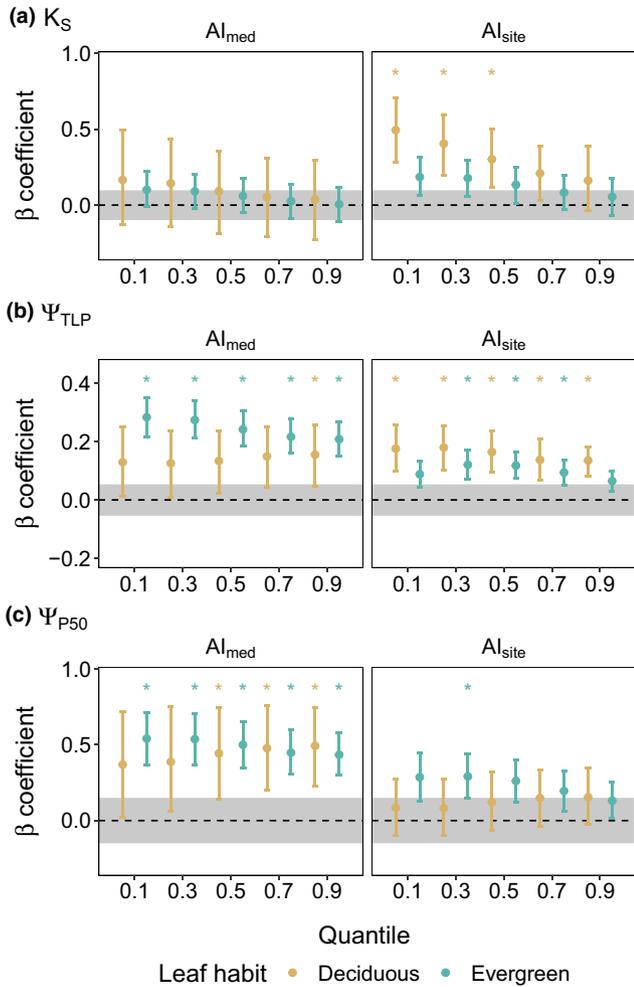
**FIGURE 3** Scatter plots showing the effects of aridity index (AI) on plant hydraulic traits: Xylem-specific hydraulic conductivity ( $K_S$ ), the water potential at leaf turgor loss ( $\Psi_{TLP}$ ) and the water potential at 50%  $K_S$  loss or 50% accumulation of embolism events in the xylem ( $\Psi_{P50}$ ). Regression coefficients ( $\beta$ ) were obtained by fitting three independent phylogenetic Bayesian multilevel linear models using as climatic predictors the median climatic affiliation values ( $AI_{med}$ ), the extreme climatic affiliation values ( $AI_{min}$ ) and the trait sampling localities climate ( $AI_{site}$ ). Regression lines and their associated 95% high-density credible intervals indicate strong evidence ( $\beta \neq 0$ ) of a given climatic predictor's effect on plant hydraulic traits.

constraints of species occurrences. We found four key patterns. First, species aridity climatic affiliation—which essentially describes the median climatic moisture conditions of species occurrences—is related to variation in  $\Psi_{TLP}$  and  $\Psi_{P50}$ , but not  $K_S$ . Second, environmental conditions in the sampling localities are related to variation in all three plant hydraulic traits. Third, the relationship between  $\Psi_{P50}$  and aridity is weaker in drought-deciduous than evergreen species, as predicted. Fourth, trait variation is more linked to environmental variability than evolutionary history.

Below, we further explore these results in the context of how these traits link to adaptations that allow species to survive drought stress and influence their performance along water availability gradients.

### Pantropical variation in plant hydraulic traits

At the pantropical scale, species affiliated with arid environments showed low  $\Psi_{TLP}$  and  $\Psi_{P50}$  (Figure 3). It is well known that aridity gradients affect variation in these two



**FIGURE 4** Phylogenetic Bayesian multilevel quantile regression estimates (0.10, 0.30, 0.50, 0.70 and 0.90) of slope coefficients ( $\beta$ ) using aridity index (AI) obtained from species' median climatic affiliations (a) and the trait sampling localities (b). Each point represents the median  $\beta$  with its associated 95% high-density credible interval (HDI). The grey shade around 0 represents the region of practical equivalence based on the variability of the response variable in question as  $[-0.1*sdy, 0.1*sdy]$ , if intersected by the HDI indicates that there is weak to little evidence that  $\beta$  differs from zero.

traits (Bartlett et al., 2012; Blackman et al., 2014; Choat et al., 2012; Li et al., 2018; Peters et al., 2021), which we confirmed in our analyses (Figure 3). When using the climatic affiliations,  $AI_{med}$  and  $AI_{min}$ , we showed that the variation in  $\Psi_{TLP}$  and  $\Psi_{P50}$  reflect the environmental constraints of species occurrences for evergreen taxa (Figure S7). On the other hand, the analysis using the environmental conditions where traits were sampled suggests that all three hydraulic traits vary as a function of water availability. Together, these analyses suggest that the ecological processes that select plant hydraulic trait variation towards drought tolerance along water availability gradients are the same processes that define species' habitat occurrences (Rosenzweig, 1987). This adds an underlying physiological mechanism to observations that plant species affiliated with wetter environments

**TABLE 2** Phylogenetic metrics derived from the phylogenetic Bayesian multilevel linear models (BMLMs) using each climatic predictor and the Ornstein–Uhlenbeck model (OUM) for each plant hydraulic trait: Xylem specific hydraulic conductivity ( $K_S$ ), the water potential at turgor loss point ( $\Psi_{TLP}$ ) and the water potential at 50% loss of conductive or 50% accumulation of embolism events in the xylem ( $\Psi_{P50}$ ). Where we show Lynch's phylogenetic trait heritability for the BMLMs using the median climatic affiliation values ( $\lambda_{median}$ ), using the extreme climatic affiliation values ( $\lambda_{extreme}$ ), and the trait sampling localities climate ( $\lambda_{site}$ ); in addition to the trait rate of adaptation ( $\alpha$ ) and the trait phylogenetic half-life ( $t_{1/2}$ ) obtained from the OUM

Metrics	$K_S$	$\Psi_{TLP}$	$\Psi_{P50}$
$\lambda_{median}$	0.003 [0.001, 0.006]	0.009 [0.004, 0.018]	0.017 [0.008, 0.030]
$\lambda_{extreme}$	0.003 [0.001, 0.006]	0.015 [0.006, 0.026]	0.019 [0.009, 0.031]
$\lambda_{site}$	0.004 [0.001, 0.008]	0.012 [0.006, 0.021]	0.012 [0.005, 0.022]
$\alpha$	0.0996	0.0874	0.0848
$t_{1/2}$ (MY)	6.96	7.93	8.18
Tree length (MY)	325.05	390.70	390.70

often experience higher mortality rates during drought (Esquivel-Muelbert et al., 2017; Zuleta et al., 2017). This evidence also suggests that plant hydraulic traits play an important role in regulating species occurrences along water availability gradients, as they define species' ability to withstand drought stress but also reduce species' performance in environments with pests and shade tolerance as filtering factors (Baltzer et al., 2008; Brenes-Arguedas et al., 2009; Spear et al., 2015). A more detailed approach including metrics of fitness, community-level interactions and intra-specific trait variation is needed to fully explain species niches more thoroughly (Bohner & Diez, 2020; Kearney & Porter, 2009), as all these aspects define the species niche (Treurnicht et al., 2020). As such, integrating plant hydraulic traits into fitness-based ecological niche modelling should be a priority.

We found that  $S_{med}$  and  $S_{site}$  showed no effect on traits, but  $S_{max}$  did affect  $K_S$  variation for evergreen species (Figure S1). Seasonal variation in water availability is an important driver of species hydraulic strategies, with species optimising their  $K_S$  for a given  $\Psi_{P50}$  (Liu et al., 2020).  $S_{max}$  is defined as the maximum value of seasonality observed in the species occurrence records, with seasonality defined as the distribution of rainfall within a year and the contrast to the wettest month (Feng et al., 2013). Thus, highly seasonal places ( $S > 0.3$ ) receive most of the rain in less than 6 months regardless of their total rainfall. As  $K_S$  increases as a function of the wet season water availability (Gleason et al., 2013), our results suggest a tight coupling between water transport efficiency and local water availability more so than the environmental constraints that limit tropical plant species occurrences at coarser scales. It is also possible that the observed patterns

link to adaptations in wood structural anatomy (e.g. narrower vessels) and wood density, which are common in slow-growing species across water availability gradients (Bittencourt et al., 2016).

### Is drought deciduousness uncoupled from water availability?

Our data do not allow us to make inferences about the relative abundances of drought-deciduous versus evergreen taxa along water availability gradients; however, they clearly suggest that evergreen and drought-deciduous species differ in three main aspects: (1) drought-deciduous species are affiliated with drier and more seasonal environments than evergreen species (Figure S9), (2) the plant hydraulic trait values of drought-deciduous species do not vary as a function of their climatic affiliations while evergreen species showed increasing drought tolerance with decreasing climatic water availability (Figure 3) and (3) trait variation converges in both groups for drought-sensitive species in wet environments (Figure 4). Oliveira et al. (2021) hypothesised that regardless of leaf habit both groups will follow environmental variability, and dry environments will favour trait values indicative of drought resistance. To some extent our data support such a hypothesis (e.g. evergreen plants); however, we also found that regardless of the environment drought-deciduous species have  $\Psi_{TLP}$  and  $\Psi_{P50}$  values indicative of higher vulnerability to drought compared to evergreen species. Moreover, on a global scale, without considering climatic moisture, drought-deciduous and evergreen species seem to have similar  $\Psi_{TLP}$  and  $\Psi_{P50}$  (Figure S10). This highlights the importance of aridity in defining plant hydraulic trait variation and differences between phenological strategies.

Drought-deciduous leaf habit implies a physiological strategy of drought avoidance with plant hydraulic trait values indicative of profligate water use and tissues poorly adapted to resist long periods of drought stress (Eamus, 1999; Levitt, 1980). This was evident when looking at the inter-quantile variation of  $K_s$  in response to  $AI_{site}$ , where drought-deciduous species in the lower quartiles showed greater responsiveness to water availability (Figure 4). This links to the fact that tropical drought-deciduous plant species will maximise metabolic rates during a shorter period without water limitation when compared to evergreen species (Brodribb et al., 2002), which grants success in environments with shorter growing seasons (Vico et al., 2017). By contrast, the environmental pressures that select evergreen species in dry environments are likely different from the ones that select evergreen species in wet environments (Steege & Hammond, 2001). In other words, there is one way to be a tropical drought-deciduous species, but many ways to be a tropical evergreen species, from the perspective of plant hydraulic traits (Vargas et al. 2021). These patterns

hold up at global to regional scales, as the  $\Psi_{TLP}$  of evergreen species is coupled with topographical water availability while the opposite occurs in drought-deciduous species (Bartlett, Zhang, et al., 2016; Kunert et al., 2021; McFadden et al., 2019), limiting evergreen species to areas close to water bodies or shallow water tables in dry tropical environments (Hartshorn, 1983). Regardless of leaf habit, species affiliated with wet environments will show greater vulnerability to drought, and in dry environments, drought-sensitive species will be largely represented by a drought-deciduous leaf habit.

### Plant hydraulic traits are labile

For all hydraulic traits, we found a low phylogenetic signal and short trait phylogenetic half-life (Table 2), indicating that plant hydraulic traits are likely under strong selective pressures (Guillemot et al., 2022). For instance,  $\Psi_{P50}$  varies more strongly as a function of water availability than species evolutionary history within monophyletic groups (Skelton et al., 2021). Suggesting that adaptation to the local environment may be the main source of plant hydraulic trait variability (Ramírez-Valiente & Cavender-Bares, 2017; Rosas et al., 2019). More studies are needed to document the magnitude of plasticity in plant hydraulic traits, but the evidence to date suggests that across species there is great trait diversification that does not necessarily follow species phylogenetic relatedness. One example could be plant organs with differentiated sensitivity to drought (Johnson et al., 2012), as the effect size by climatic predictors varied when using data only from stems (Figures S1 and S5). Although it is hard to disentangle if such a pattern is due to differences between sampling climate and climatic affiliations (Figure S11), or different thresholds to drought in stems, leaves and roots as comparative data among plant organs using standard methods are yet to be collected. This warns against using species mean values based on a handful of observations to represent species optimum phenotype across environmental gradients (Gauzere et al., 2020), or the use of lineage-based frameworks to resolve plant functional types when it comes to including plant hydraulic traits in dynamic vegetation models.

## CONCLUSIONS

Our geographically extensive dataset reflects how the sampling of plant hydraulic traits has accelerated in the last 30 years in tropical regions providing an unprecedented insight into how species' habitat preference relates to their physiological characteristics. These relationships advance our understanding of why species thrive in certain environments and why wet tropical environments may harbour greater physiological diversity (Steege & Hammond, 2001). By linking plant hydraulic

trait variation with species' evolutionary history and species leaf habit, we provide mechanistic insight into the possible drivers of observed changes in dominance between evergreen and drought-deciduous species in tropical forests (Aguirre-Gutiérrez et al., 2020; Swenson et al., 2020). As it is evident that a drought-deciduous strategy might be favoured by increases in seasonality and aridity (Feng et al., 2013; McDowell et al., 2020; Vico et al., 2017), the consequences of these changes on ecosystem function remain unexplored.

### AUTHOR CONTRIBUTIONS

GVG, NK, KAT and JSP conceptualised the study. GVG, NK, WMH, ZCB, LKW, CMSM, BTW and LT assembled the trait database. GVG and AMB assembled species phylogeny. GVG and NBS extracted and managed environmental data. GVG and JPL performed statistical analyses with input from LS. GVG wrote the first draft of the manuscript with inputs from JSP. All authors provided input and rigorous feedback in subsequent drafts of the manuscript.

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### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.14128>.

### DATA AVAILABILITY STATEMENT

The compiled pantropical database on plant hydraulics, phylogenetic tree and climatic affiliations could be found here: <https://doi.org/10.5061/dryad.1ns1rn8x4>. The R code used in the statistical analyses could be found here: <https://doi.org/10.5281/zenodo.7089603>. Additionally, the plant hydraulic traits data are also archived as part of the xylem functional trait database: <https://xylemfunctionaltraits.org/>. All data will be freely available after a 1-year embargo, for earlier access please contact the corresponding author.

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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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