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# Beyond leaf habit: generalities in plant function across 97 tropical dry forest tree species

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## Summary

- Leaf habit has been hypothesized to define a linkage between the slow-fast plant economic spectrum and the drought resistance-avoidance trade-off in tropical forests ('slow-safe vs fast-risky'). However, variation in hydraulic traits as a function of leaf habit has rarely been explored for a large number of species.
- We sampled leaf and branch functional traits of 97 tropical dry forest tree species from four sites to investigate whether patterns of trait variation varied consistently in relation to leaf habit along the 'slow-safe vs fast-risky' trade-off.
- Leaf habit explained from 0% to 43.69% of individual trait variation. We found that evergreen and semi-deciduous species differed in their location along the multivariate trait ordination when compared to deciduous species. While deciduous species showed consistent trait values, evergreen species trait values varied as a function of the site. Last, trait values varied in relation to the proportion of deciduous species in the plant community.
- We found that leaf habit describes the strategies that define drought avoidance and plant economics in tropical trees. However, leaf habit alone does not explain patterns of trait variation, which suggests quantifying site-specific or species-specific uncertainty in trait variation as the way forward.

## Introduction

Ecologists have long been interested in the physiological variation inherent to leaf habit of plant species. Leaf habit classifications link directly to leaf life span (Reich, 1995), ranging from species with long-lived leaves, i.e. evergreen leaf habit, to species with short leaf lifespans that flush and drop cohorts of leaves within a year, i.e. deciduous leaf habit. It has been hypothesized that nutrient-poor environments favor evergreen leaf habits, given the high nutrient use efficiency of evergreen plants and high leaf construction costs (Aerts, 1995). At the same time, the presence of seasonal drought is thought to favor a deciduous leaf habit (Vico *et al.*, 2017). However, leaf construction costs, nutrient use efficiency and drought regimes alone do not explain the dominance of evergreen or deciduous species in certain environments (Givnish, 2002). An integrative approach by Oliveira *et al.* (2021) lays out distinct leaf habits as strategies that arise from

environmental pressures, i.e. water and nutrient limitation. In this scheme, dry-nutrient rich habitats favor deciduousness and the evergreen leaf habit is restricted to nutrient poor environments or environments with little drought stress.

Leaf habits define two strategies: one that avoids and one that resists drought stress (Levitt, 1980; Delzon, 2015). Earlier work has shown that generally drought-deciduous species present profligate water use and are poorly adapted to function during drought stress (Eamus, 1999; Pineda-García *et al.*, 2015). Some of the traits usually found in drought deciduous plants include a low modulus of elasticity and a high (i.e. less negative) turgor loss point (Sobrado, 1986; Fanjul & Barradas, 1987; Bartlett *et al.*, 2012), high values of hydraulic conductivity, photosynthetic rates and specific leaf area (Choat *et al.*, 2006; Fu *et al.*, 2012), but a larger decline in conductivity and leaf water potentials during dry periods compared to evergreen species (Sobrado, 1993; Brodribb *et al.*, 2002). In other words, deciduous species maximize water

use when conditions are optimal. By contrast, evergreen species tolerate seasonal water shortages through minimizing water loss and/or ensuring access to deep water sources (Brodribb *et al.*, 2002; Hasselquist *et al.*, 2010; Smith-Martin *et al.*, 2020). Collectively, this body of knowledge suggests a trade-off between hydraulic safety and drought avoidance (Christoffersen *et al.*, 2016), which also positions evergreen and deciduous species along opposite axis of the 'fast-slow' plant economic spectrum (Wright *et al.*, 2004; Reich, 2014); i.e. evergreen species show a slow-hydraulically safe growing strategy and deciduous species a fast-hydraulically risky approach (Oliveira *et al.*, 2021). However, studies comparing physiological function in relation to leaf habit typically rely on comparisons between a handful of species, which hinders broad generalizations.

Many studies of leaf habit have taken place in tropical dry forests (TDFs), as these environments harbor a range of leaf phenological strategies (Murphy & Lugo, 1986; Eamus, 1999; Eamus & Prior, 2001). In contrast to wetter tropical forests, water availability (i.e. soil moisture, relative humidity and stem water potential) are the main environmental cues controlling leaf shedding and leaf flushing in the TDF (Frankie *et al.*, 1974; Reich & Borchert, 1984; Wright & Cornejo, 1990). Besides evergreen and deciduous leaf habits, other strategies are found in TDFs, such as species that partially shed their leaf area during the dry season (i.e. semi-deciduous) and species that briefly shed their entire leaf area (i.e. brevi-deciduous) (Borchert, 1994; Eamus, 1999; Borchert *et al.*, 2002). Some plant species are facultative deciduous such that patterns of leaf shedding depend on local microclimate and access to water (Reich & Borchert, 1984). This complexity may stymie attempts to use leaf habit to bin species and their traits into plant functional types (PFTs) that can be used in simulation models (Powers & Tiffin, 2010). Resolving the extent to which leaf habit predicts physiological function is imperative, as tropical forests have a disproportionate effect on the global carbon cycle relative to their areal extent and hence the global climate system (Hubau *et al.*, 2020; McDowell *et al.*, 2020).

There is now abundant evidence that tropical climates are changing, and in particular, rainfall seasonality and drought intensity have increased in more arid tropical regions (Feng *et al.*, 2013). More intense droughts trigger changes in forest composition due to increased mortality (Phillips *et al.*, 2010; Powers *et al.*, 2020; Swenson *et al.*, 2020). Also, shifts to a more arid and seasonal climate are coincident with increasing abundance of drought-deciduous tree species in tropical forests (Fauset *et al.*, 2012; 2019; 2020). Understanding how these changes in forest composition and leaf habit affect productivity and ecosystem resilience to drought has implications for modeling forest dynamics and forecasting primary productivity. Moreover, leaf habit is amenable to remote sensing (Huechacona-Ruiz *et al.*, 2020) and is a common way to differentiate PFTs in ecosystem simulation models (Table 1). The implicit assumption of either mapping or modeling leaf habits is that this reflects underlying physiological differences among species. However, the use of plant hydraulics in understanding the functional differences among leaf habit has rarely been tested for a large number of species.

**Table 1** Most recent earth system models that incorporate leaf habit classifications to define some plant functional types in their vegetation dynamics modules.

| Model | Leaf habits | Reference |
|---|---|---|
| Community Land Model v.4 – CLM4 | Evergreen, seasonal-deciduous and stress-deciduous | Lawrence *et al.* (2011); Dahlin *et al.* (2015) |
| Ecosystem Demography v.2 – ED2 | Cold-deciduous, drought-deciduous and evergreen | Medvigy *et al.* (2009) |
| Functionally Assembled Terrestrial Ecosystem Simulator – FATES | Broadleaf evergreen tropical, needleleaf evergreen extratropical, broadleaf evergreen extratropical, broadleaf hydrodeciduous tropical tree, broadleaf cold-deciduous extratropical tree, broadleaf evergreen extratropical shrub and broadleaf hydrodeciduous extratropical shrub | Fisher *et al.* (2015) |
| Joint UK Land Environment Simulator – JULES | Cold-deciduous and drought-deciduous | Clark *et al.* (2011) |

In these models, leaf habit is used to define some plant functional types (PFTs) but they are not the sole defining characteristic of PFTs; other features such as size, life-form (shrub, moss, tree, liana), reproductive strategy, photosynthetic pathway and architecture are commonly used (Prentice & Cowling, 2013; Wullschleger *et al.*, 2014).

The main objective of this study was to test whether leaf habit explains hydraulic trait variation under the 'slow-safe vs fast-risky' framework (Oliveira *et al.*, 2021), in order to determine the physiological generalities that can be drawn from leaf habit in diverse ecosystems. We sampled a large suite of plant functional traits in 97 species of four study sites that spanned much of the climatic, edaphic, and biogeographic diversity of TDFs in the Americas. Our first question was whether patterns of trait variation varied consistently in relation to leaf habit. We supported our first question by exploring whether leaf habit arrayed species in opposite axis of the 'slow-safe vs fast-risky' multivariate trait ordination. Our second goal was to test for possible site effects on trait variation. For this, we explored the sources of variability in our data and then tested if traits of evergreen and deciduous species vary among sites. For our third goal, we explored whether these leaf habit classifications provided insight into plant community function by relating community weighted mean (CWM) trait values to the proportion of deciduous species present in replicated forest plots across the sites.

## Materials and Methods

### Study sites

Tropical dry forests experience warm temperatures year-round with a mean > 19°C. Mean annual rainfall ranges from 600 to 2500 mm, with a period of decreased precipitation lasting up to

10 months (Murphy & Lugo, 1986; Allen *et al.*, 2017). TDF often has high species turnover among sites, resulting in areas of unique species composition (Dryflor *et al.*, 2016). Within this context of broad climatic, edaphic (Waring *et al.*, 2021), and biological diversity, we selected four sites in public and private protected land that encompassed the breadth of this variation (Fig. 1): the Área de Conservación Guanacaste in north-western Costa Rica (CR: 10°43′31.39″N, 85°35′46.99″W), the Kaxil Kiuic Reserva Biocultural in the Yucatán peninsula (MX: 20°5′26.73″N, 89°33′47.66″W), the Bosque Estatal de Guánica in Puerto Rico (PR: 17°58′2.17″N, 66°53′17.54″W), and a private farm in Tolima, Colombia (CO: 5°3′36.00″N, 74°49′48.00″W). We worked in secondary successional stands (i.e. *c.* 40–100 yr old), which represent the predominant status of TDF in the Americas (Hoekstra *et al.*, 2005; Miles *et al.*, 2006). Most sites (CO, CR and PR) have a similar land-use history of forest regeneration from timber extraction, clear cutting for agriculture, cattle pasture, charcoal pits and human settlements (Molina-Colón & Lugo, 2006; Calvo-Alvarado *et al.*, 2009; Pizano & García, 2014; González-M *et al.*, 2019), with the

exception of MX that has been under a Mayan swidden cultivation regime for *c.* 2000 yr (Rico-Gray & Garcia-Franco, 1991).

These sites encompass the breath of variation in rainfall regimes for TDF in the Americas (Supporting Information Table S1; Notes S1). The CO forest has the highest mean annual rainfall (MAR, in millimeters) but the lowest seasonality, and a short 4-month dry season (Fig. 1). The CR climate has high rainfall seasonality, MAR of *c.* 1750 mm, and a 7-month dry season (Fig. 1). In MX precipitation has a low seasonality, with a MAR of *c.* 1200 mm and a 9-month dry season (Fig. 1). Puerto Rico has the driest conditions with a dry season of > 10 months, MAR < 1000 mm and low seasonality (Fig. 1).

The sites also differ in soil properties (Fig. 1). Soils in CR are clays derived from recent volcanic depositions (Waring *et al.*, 2019). In CO, soils are sandy clay loams influenced by the Andes mountain range sedimentary deposits with high concentrations of phosphorus (Duenas & Castro, 1981). In MX, the soils are clays developed from limestone and sedimentary depositions (Dupuy *et al.*, 2012). Last, the plots in PR have shallow clay loams developed on a limestone bedrock, with low extractable
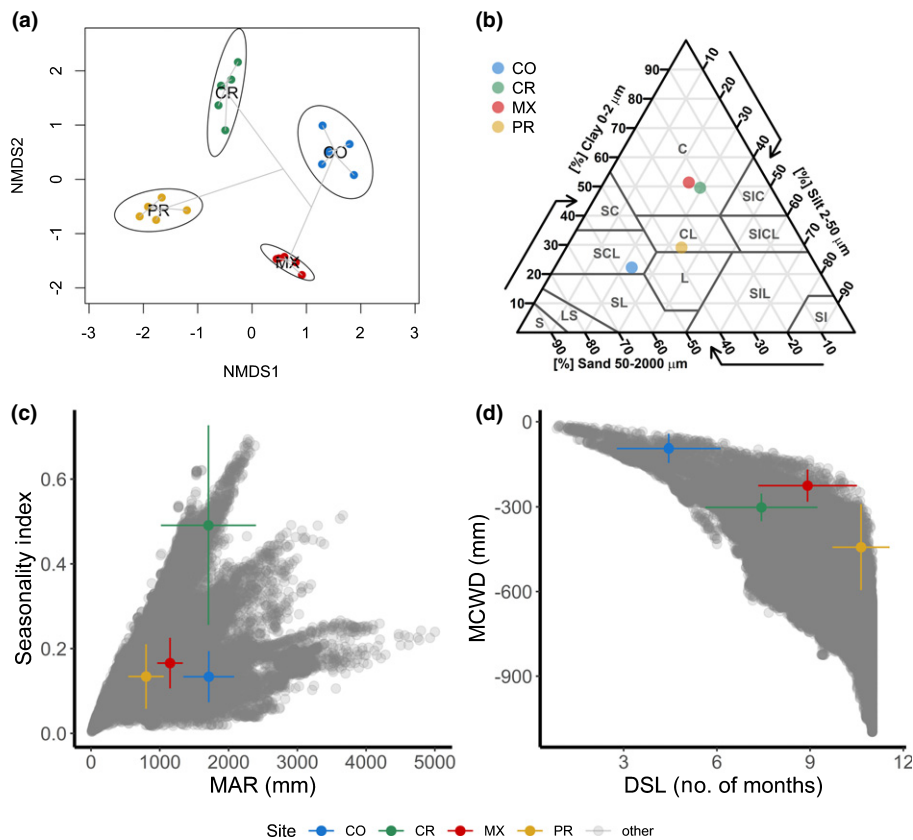


**Fig. 1** Site specific characteristics that could determine trait variation. (a) Results from a nonmetric multidimensional scaling (NMDS) using Bray–Curtis distance matrix on forest composition data. (b) Mean soil texture (colored dots) at each tropical dry forest site in this study. Classification triangle according to the United States Department of Agriculture: clay (C), silty clay (SIC), sandy clay (SC), clay loam (CL), silty clay loam (SICL), sandy clay loam (SCL), loam (L), silty loam (SIL), sandy loam (SL), silty (SI), loamy sand (LS) and sand (S). (c, d) Rainfall regime properties for the tropical dry forest biome (gray points) and the sites in this study (colored points). Includes the seasonality index, mean annual rainfall (MAR), maximum climatological water deficit (MCWD) and the dry season length (DSL). Site specific data and error bars represent the mean (colored points) and temporal standard deviation (error bars) of the rainfall properties obtained from meteorological stations. Gray points are data from the CHIRSP dataset (Funk *et al.*, 2015). Sites coded as: Colombia (CO), Costa Rica (CR), Mexico (MX) and Puerto Rico (PR).

nutrient availability (Lugo & Murphy, 1986). We used data on soil particle-size distribution collected in the plots described later (Waring *et al.*, 2021).

## Species selection and plant community characterization

At each site, we used five previously established vegetation plots that varied in shape and size across sites (Table S2). In each plot, all stems ≥ 2.5 cm in diameter breast height (DBH) were measured and identified to species. We used the plot data to quantify total tree basal area per hectare (BA, in $m^2 ha^{-1}$) and the proportion of deciduous tree species (%). A nonmetric dimensional scaling (NDMS) on species abundance per plot showed that sites have distinct floristic composition (Fig. 1). We selected 10–59 of the most abundant species per site for physiological trait measurements. Collectively, these species accounted for *c.* 85% of the total BA of each plot (Table S2). We obtained leaf habit information for some species from previous studies (Frankie *et al.*, 1974; Reich & Borchert, 1984; Van Bloem *et al.*, 2005; Powers & Tiffin, 2010; González-M *et al.*, 2021). Whenever this information was not available, we relied on direct observation from local taxonomists and plant collectors in these sites. Deciduous species are defined as remaining leafless for several months during the dry season. Evergreen species include the species that retain a full canopy during the entire year. Semi-deciduous encompasses species that partially shed their crown or synchronously drop their entire canopy with a rapid flushing during the dry season.

## Plant traits

Our trait data included previously published data from two studies performed in the CR site (Powers & Tiffin, 2010; Powers *et al.*, 2020), which we complemented with newly collected data for 61 additional species from the four sites. The total number of species with trait data was 97. Some species were reported to have a different leaf habit for two given sites, which yielded the following species distribution per leaf habit was: 31 evergreen, 53 deciduous and 15 semi-deciduous. New data collection occurred in 2017 and 2018 with field campaigns timed to coincide with the rainy season at each site: September–October 2017 for MX, November–December 2017 for CO, June–July 2018 for CR and September–October 2018 for PR. Our trait selection is based on the plant characteristics that best describe the axes of variation in the 'fast-risky vs slow-safe' trade-off (Oliveira *et al.*, 2021). We measured six functional traits that describe the variation associated with the fast-slow plant economics axis (Reich, 2014): wood density (WD, in $g cm^{-3}$), leaf area (LA, in $cm^2$), specific leaf area (SLA, in $cm^2 g^{-1}$), foliar nitrogen concentration ($N_{leaf}$, %), foliar carbon concentration ($C_{leaf}$, %) and foliar phosphorus concentration ($P_{leaf}$, %). For SLA and LA, we selected 5–10 individuals per species-level with a DBH > 10 cm (5 cm for PR) and sampled two fully expanded sunlit leaves from each tree (usually the third one down the apex) (Pérez-Harguindeguy *et al.*, 2013). LA measurements included petioles, and these were also used to calculate SLA. For $N_{leaf}$ and $C_{leaf}$, we collected 10–15 leaves in the same

conditions from five individuals, and leaves were bulked by individual, dried at 65°C for 72 h, shipped to the University of Minnesota and finely ground. $C_{leaf}$ and $N_{leaf}$ were analyzed on an ESC 410 Costech CN Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). For $P_{leaf}$, we composited samples from three to five individuals per species. Samples for $P_{leaf}$ were predigested for 60 min with 2 ml of hydrogen peroxide ($H_2O_2$) and 0.5 ml of nitric acid ($HNO_3$) at the University of Minnesota Research Analytical Laboratory. Samples were digested using the wet ash microwave Miller Digest method followed by elemental quantification with an iCAP™ 7600 ICP-OES (inductively coupled argon plasma optical emission spectroscopy) analyzer (ThermoFisher Scientific, Waltham, MA, USA). WD was collected on three to five individuals per species and measured using the water displacement method on wood cores that were soaked in water overnight without their bark, then fresh volume was quantified as the change in water weight needed to displace the core. The wood cores were then dried at 60°C for 72 h and weighed again (Pérez-Harguindeguy *et al.*, 2013).

We measured five hydraulic traits to characterize the hydraulic safety and drought avoidance axis (Christoffersen *et al.*, 2016; Oliveira *et al.*, 2021): the water potential at turgor loss point ($\Psi_{TLP}$, in MPa), leaf vulnerability to embolism ($\Psi_{P50-leaf}$, in MPa), Huber value (HV), stem xylem specific hydraulic conductivity ($K_S$, in $kg m^{-1} s^{-1} MPa^{-1}$), and the hydraulic safety margin (HSM, in MPa). For each hydraulic trait, we collected samples during pre-dawn hours to ensure minimal water loss through open stomata and leaf water potentials ($\Psi_{leaf}$, in MPa) between −0.020 and −0.200 MPa. We measured HV on one sunlit terminal branch with a diameter *c.* 0.5 cm from five individuals per species by measuring the xylem area at the base of the branch with a Mitutoyo Absolute Digimatic (Mitutoyo America, Aurora, IL, USA) digital caliper and then dividing it to the total LA of the branch measured from photographs using IMAGEJ (Schneider *et al.*, 2012). To obtain $\Psi_{TLP}$, we performed pressure–volume (PV) curves on two leaves from three to five individuals per species by measuring $\Psi_{leaf}$ continuously on leaves while they were bench-dehydrating inside air sealed bags at ambient temperature. Simultaneously, we measured leaf fresh mass ($LF_{mass}$, in g) and, after recording none or minimal changes (< 0.020 MPa) in $\Psi_{leaf}$ along with changes in $LF_{mass}$, leaves were dried at 65°C for 72 h before weighing to quantify leaf dry mass ($LD_{mass}$, in g). Leaf water mass ($H_2O_{mass}$, in g) was calculated as: $H_2O_{mass} = LF_{mass} - LD_{mass}$. To analyze the PV curves, we obtained the saturated water content (SWC, in grams) as the intercept in the regression between $\Psi_{leaf}$ in response to $H_2O_{mass}$. We estimated the relative water content (RWC) of a given leaf as: RWC = ($H_2O_{mass}$/SWC). We used the $-1/\Psi$ in response to $100 - RWC$ to obtain $\Psi_{TLP}$, which is the point when the regression slope changes (Bartlett *et al.*, 2012). The slope change represents the value when the pressure potential is zero and the leaf cell osmotic potential is higher and equilibrates with the leaf bulk water potential (Tyree & Hammel, 1972). PV-curves were analyzed using the R script available in the following code repository: https://github.com/gevargu/Plant_Ecophysiology_Tools.

On three individuals from five to six species per site, we collected > 1 m long canopy branches to construct optical vulnerability curves and measure $\Psi_{P50\text{-leaf}}$ as the water potential value at which 50% embolism events occur in leaf xylem (Brodribb *et al.*, 2016). To construct the vulnerability curves, we used an Epson Perfection V800 Photo Color Scanner (Epson America Inc., Long Beach, CA, USA) and took high-resolution images of leaves dehydrating while attached to their respective branches. Simultaneously, we measured $\Psi_{leaf}$ on each branch using two leaves in a similar position to the scanned leaf. We measured $\Psi_{leaf}$ initially every 30 min during the first 6 h, then every 90 min from 06:00 h to 21:00 h during the days it took branches to be completely dehydrated (i.e. leaves with a crispy dry appearance). We quantified $\Psi_{P50\text{-leaf}}$ as the water potential for which the accumulation of embolisms in leaf midrib vein (first order), the veins that come directly from the midrib vein (second order), and all the other minor veins (third order) reached 50% of the maximum cumulative number of embolism events counted (Fig. S1). IMAGEJ software was used (Schneider *et al.*, 2012) to analyze the image sequences with the implementation of an image difference macro as described in OpenSourceOV (http://www.opensourceov.org/). We then fitted a sigmoidal function to the vulnerability curve to estimate the $\Psi_{leaf}$ at which 50% occurred (Duursma & Choat, 2017) (Fig. S2). Logistical constraints and the time involved in making these measurements restricted us to sampling a smaller number of species at each site. Lower (more negative) values of $\Psi_{P50\text{-leaf}}$ indicate species that can withstand substantial drought stress before suffering 50% embolism in their leaf's vascular bundles. We then used the difference between $\Psi_{P50\text{-leaf}}$ and $\Psi_{TLP}$ to calculate the HSM (HSM = $\Psi_{TLP} - \Psi_{P50\text{-leaf}}$) because when $\Psi_{leaf}$ approaches $\Psi_{TLP}$ it triggers stomatal closure in the tropical dry forest trees (Brodribb *et al.*, 2003; Brodribb & Holbrook, 2003). We acknowledge this definition of HSM is different from the original quantification using minimum water potential in the field (Meinzer *et al.*, 2009). However, by calculating the HSM based on leaf function we were able to characterize the threshold for cavitation and the capacity of avoiding such limit (Choat *et al.*, 2018). For both vulnerability curves and PV curves, we used a 1505D Pressure Chamber Instrument (PMS Instrument Company, Albany, OR, USA).

We measured native $K_S$, which represents the efficiency of water transport through the stem xylem at field capacity (Sperry *et al.*, 1988) on five individuals per species after first estimating vessel length for each species using the air injection method (Pérez-Harguindeguy *et al.*, 2013). Then we collected separate > 1 m long current year stems from canopy branches with diameters between 1 and 2 cm before dawn to obtain a measure of maximum native conductance. During sampling we placed the branch cut ends underwater immediately after cutting and let them rehydrate for 2 h in the laboratory before any measurement. We cut and connected the branch segments underwater to a custom-built flow meter with a high precision pipette (1 ml in 1/100) attached to the end, filled with a degassed solution of potassium chloride (KCl, 0.01 mmol) (Melcher *et al.*, 2012). Flow rate through the xylem was calculated as follows: $Q_s = 0.05/t_{0.05\,ml}$, where $t_{0.05\,ml}$ is the time in seconds that the meniscus moves

through 0.05 ml. For each sample we performed 3–4 pressure/flow measurements at different heights of the water column (30, 60, 90 and/or 120 cm). The different heights provided the pressure head value obtained through the following equation: $P = (rgh)/(\rho)$, where $r$ is the solution viscosity adjusted to temperature, $g$ represent the gravity corrected by latitude, $h$ the water column height and $\rho$ the solution density. Then we fitted a linear relationship: $Q_s = \alpha + \beta P$, with hydraulic conductivity ($K$) determined as $\beta P$. We calculated $K_S$ by dividing $K$ by xylem area and branch segment length. Code for these calculations is available at: https://mcculloh.botany.wisc.edu/methods/. For several species, we had branch segments smaller than the observed maximum vessel length (Fig. S3). Despite the possible effects of using branch segments with open vessels (Melcher *et al.*, 2012), we did not find any effect of segment length on $K_S$ for those species. To identify possible outliers due to branch segment artifact, we regressed the $K_S$ as a function of the percent difference between the branch segment and the maximum vessel length (Fig. S4). Variation of orders of magnitude within the same species was considered due to artifacts (i.e. open vessels, hollow pit) and hence removed from the data.

## Statistical analysis

Our first objective was to determine the role of leaf habit classification on species trait values. For this we used linear models for species-level mean values of each trait as response variables and leaf habit as the categorical explanatory variable. We obtained the $F$-value of a one-way analysis of variance (ANOVA) among leaf habits and performed multiple comparisons using a Tukey's HSD (honestly significant difference) correction. For each trait we performed a bootstrap with 5000 replicates to estimate 95% confidence intervals of the standardized differences. We complemented this analysis by determining if leaf habit spanned contrasting physiological trait strategies in the 'safe-slow vs fast-risky' trade-off. For this, we performed a principal component analysis (PCA) to quantify the multivariate trait space ordination among species. Then, we selected the components of the PCA that together accounted for > 60% trait variation and constructed a Euclidean distance matrix among species. Finally, we performed a permutation multivariate analysis of variance (PERMANOVA) to test the null hypothesis that leaf habit does not separate species along the multidimensional trait space. We complemented the PERMANOVA with multiple comparison tests among leaf habit groups with a Bonferroni correction. In this PCA we included only LA, SLA, WD, $N_{leaf}$, $K_S$, HV and $\Psi_{TLP}$, to account for collinearity and maximize the number of species for which we have a complete data set of the mentioned traits ($n = 53$). It is worth noticing that if a species was sampled in various sites we calculated a single mean value per species, with the exception of *Luehea candida* (DC.) Mart. and *Casearia corymbosa* Kunth, which were reported to have distinct leaf habit at different sites.

Our second aim was to determine the role of site in trait variation within leaf habits. We first performed a variance partitioning analysis to understand the relative importance of leaf habit on

trait variation when compared to other sources of variation including site, taxonomic family, and species identity. In this analysis, we used a restricted maximum likelihood approach with a nested linear model for each trait (Messier *et al.*, 2010). Then we built two linear models for each trait, one comparing deciduous species values for sites in which we had > 5 deciduous tree species (MX, CR and PR), and one comparing evergreen species values for sites in which we had > 5 evergreen species (CO, CR and PR). For both deciduous and evergreen species, we performed an ANOVA and performed multiple comparisons among sites using a Tukey's HSD correction. In this case we used the values for each species in the site the measurements were taken.

Last, we explored the implications of community-level patterns of deciduousness on forest function. We compared three approaches: (1) species-specific trait values measured from each site, (2) site-level mean trait values for species with different leaf habits, or (3) the biome-level mean trait values for the entire dataset. We calculated CWM trait values for each plot defined as $CWM = \sum_{i=1}^{S} a_{ip} \times t_i$, where $a_{ip}$ is the relative contribution of the species $i$ to the total basal area in plot $p$, and $t_i$ is the mean trait value of species $i$ based on species-specific values, leaf habit-specific values for each site, or leaf habit-specific values for the biome (i.e. mean trait value per leaf habit for the entire dataset). Then, we examined whether community weighted trait values varied consistently as a function of the proportion of deciduous species in the community using a simple regression approach. For these regression models we explored the presence of nonlinear relationships between the CWMs and the proportion of deciduous species. We visually tested for normal distribution of the residuals, the presence of homoscedasticity and linearity for all the analyses that involved a linear model approach. All data management, physiological data processing and statistical analyses were done using R software for statistical computing v.3.6.1 (R Core Team, 2019) and the following packages: NLME (Pinheiro *et al.*, 2019), ADE4 (Dray & Dufour, 2007; Bougeard & Dray, 2018), CAR (Fox & Weisberg, 2019), VEGAN (Oksanen *et al.*, 2019), STATS (R Core Team, 2019) and FD (Laliberté & Legendre, 2010; Laliberté *et al.*, 2014).

## Results

### Traits as a function of leaf habit

For most of the traits, deciduous plant species differed from evergreen plant species, while semi-deciduous showed intermediate values that were more similar to those of evergreen species (Fig. 2). In general, deciduous plant species had significantly 30% larger leaves, 16% higher SLA, 18% higher $N_{leaf}$, 67% higher $K_s$, 17% higher $\Psi_{TLP}$ and 18% higher $\Psi_{P50\text{-}leaf}$ than evergreen species (Fig. 2). However, evergreens had 14% higher WD and 20% greater HV than deciduous species but similar values to those shown by semi-deciduous trees (Fig. 2). The values of $G_{leaf}$, $P_{leaf}$ and HSM did not differ among groups. Despite these significant differences in traits among leaf habits, in most cases trait variation was large for all three leaf habit groups, with sample size corrected coefficient of variations (CVs) > 30% for most traits with the

exception of $G_{leaf}$, suggesting that the range of values within any leaf habit group is large.

The PCA aligned deciduous species in the trait space of a fast-risky strategy, while evergreen and semi-deciduous species showed more slow-safe strategy (Fig. 3). The first principal component (PC1) of the PCA explained 39.93% of the data variance and arrayed species along an axis of water transport efficiency, drought avoidance and photosynthetic demand. Higher values in the PC1 were related to higher $N_{leaf}$ ($\rho = 0.79$), higher $K_S$ ($\rho = 0.67$) and higher $\Psi_{TLP}$ ($\rho = 0.72$), while lower values were occupied by species with high WD ($\rho = -0.73$) (Fig. 4). The second principal component (PC2) explained 16.54% of the variance and aligned species along an axis of water demand by photosynthetic tissues, with high values in the PC2 related to high SLA ($\rho = 0.73$) and low HV ($\rho = -0.64$) (Fig. 3). The third principal component (PC3) of the PCA was related to the variation in HV ($\rho = 0.70$) and explained 13.11% of the variance. The PERMANOVA showed a significant effect of leaf habit in multivariate trait space ($F = 4.30$; $R^2 = 0.15$; $P < 0.01$) in which the centroid of deciduous species occupied a different multivariate trait space when compared to evergreens ($P < 0.05$) and semi-deciduous ($P < 0.01$), while evergreen and semi-deciduous shared a similar position of the centroid ($P > 0.05$).

### Variation within leaf habits among sites

Site accounted for c. 36% of the variance across all traits, taxonomic family c. 15%, leaf habit c. 11% and species identity c. 36%. However, the importance of each source of variation differed among traits. Site differences were most important for LA (46%), $N_{leaf}$ (47%), $P_{leaf}$ (64%) and $K_S$ (56%) (Fig. 4). Family differences contributed for most of the variance for WD (46%), while species identity was the dominant source of variation for SLA (69%), $G_{leaf}$ (34%), $\Psi_{P50\text{-}leaf}$ (40%) and HSM (43%) (Fig. 4). Site and species accounted for 37% of HV variation each. Leaf habit was the dominant source of variation only for $\Psi_{TLP}$ (46%), and accounted 25% for HV (Fig. 4). Unaccounted variance was c. 2%.

We had sufficient data to test for site effects on evergreen species at three sites (CO, CR and PR). The traits of evergreen species differed among sites for LA ($F = 13.27$; df = 26; $P < 0.001$), SLA ($F = 4.65$; df = 26; $P < 0.05$), $N_{leaf}$ ($F = 20.32$; df = 26; $P < 0.001$), $P_{leaf}$ ($F = 33.48$; df = 26; $P < 0.001$), WD ($F = 7.09$; df = 26, $P < 0.01$), HV ($F = 6.06$; df = 13, $P < 0.05$), $\Psi_{P50\text{-}leaf}$ ($F = 7.82$; df = 14; $P < 0.01$) and HSM ($F = 8.64$; df = 14; $P < 0.01$) (Fig. S5). In all of these comparisons, evergreen species in CO had higher values, evergreens in CR had intermediate values and those in PR had the lowest values. The values of $G_{leaf}$, $K_s$ and $\Psi_{TLP}$, did not vary significantly among evergreen species from different sites (Fig. S5). Comparing deciduous species at CR, MX and PR, we found significantly different values of LA ($F = 4.44$; df = 51; $P < 0.05$), $G_{leaf}$ ($F = 10.67$; df = 51; $P < 0.001$), HV ($F = 16.48$; df = 26, $P < 0.001$) and $K_S$ ($F = 19.45$; df = 24; $P < 0.001$) (Fig. S6). Deciduous species at CR, MX and PR did not have different values of SLA, $N_{leaf}$, $P_{leaf}$, WD, $\Psi_{TLP}$, $\Psi_{P50\text{-}leaf}$, or HSM (Fig. S6).
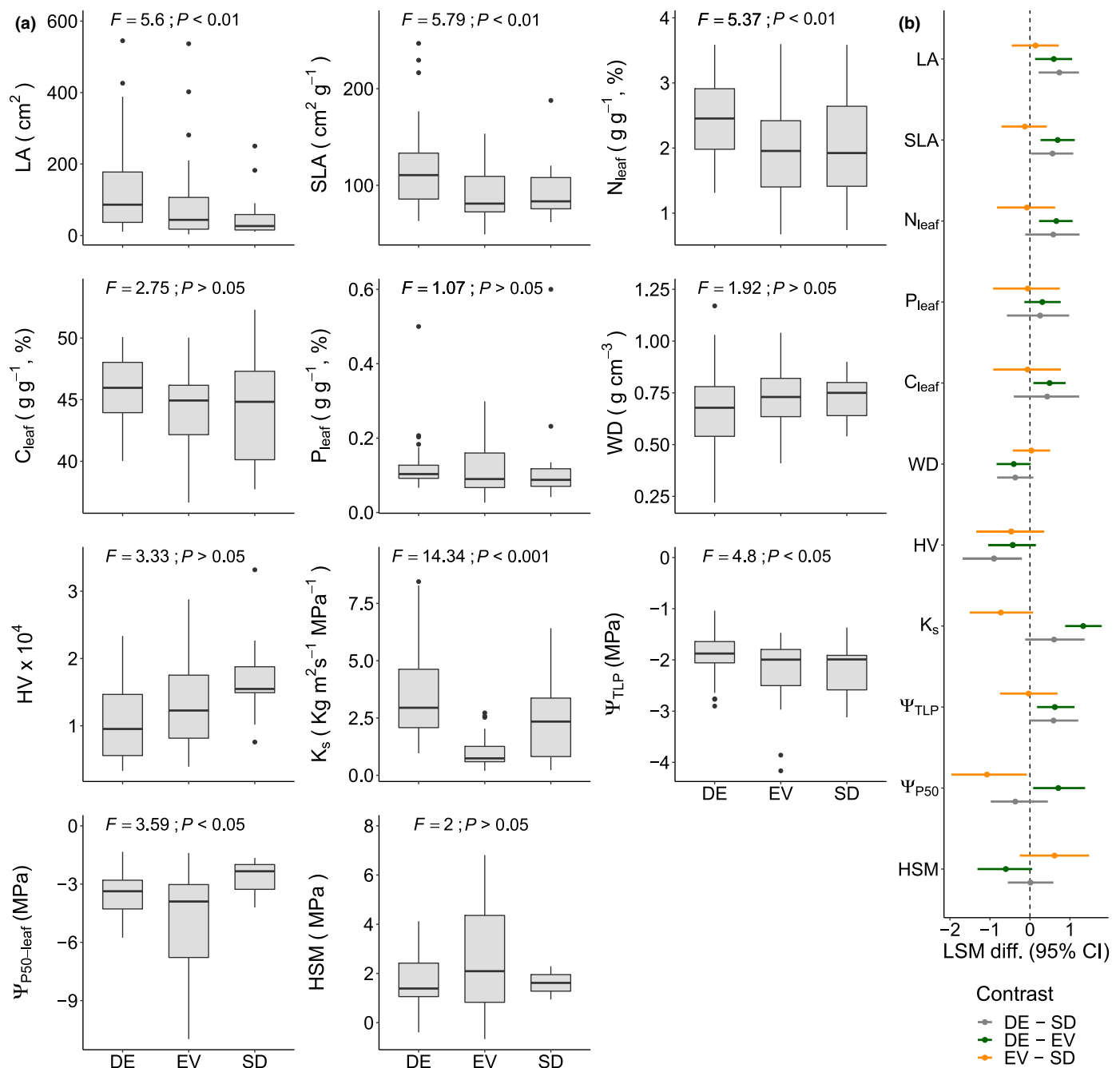
**Fig. 2** Comparison of functional trait values among leaf habits: deciduous (DE), evergreen (EV) and semi-deciduous (SD) at four tropical dry forest sites. (a) Box-plots and reported results from a one-way analysis of variance for each functional trait. (b) The standardized least square means differences (LSM diff.) with bootstrapped ($n = 5000$) 95% confidence intervals for Tukey's pairwise comparisons correction. Plant functional traits defined as: LA, leaf area; SLA, specific leaf area; $N_{leaf}$, foliar nitrogen concentration; $C_{leaf}$, foliar carbon concentration; $P_{leaf}$, foliar phosphorus concentration; WD, wood density; HV, Huber value; $K_S$, native xylem specific hydraulic conductivity; $\Psi_{TLP}$, water potential at turgor loss point; $\Psi_{P50\text{-leaf}}$, water potential at 50% accumulation of optical embolisms in leaf veins; HSM, hydraulic safety margin defined as $\Psi_{TLP} - \Psi_{P50\text{-leaf}}$.

## Community composition and deciduousness

Percent BA of deciduous trees varied among sites; MX and CR had c. 85% deciduous BA, PR was intermediate with c. 40% deciduous BA, and CO had c. 7%. Community weighted mean trait values varied systematically as a function of the proportion of species with deciduous leaf habit (Fig. 5). With the increase in

proportion of drought-deciduous trees in plots, there was an increase in LA, SLA, $N_{leaf}$, $C_{leaf}$, $K_S$ and $\Psi_{P50\text{-leaf}}$, and a decrease in $P_{leaf}$, HV and HSM (Fig. 5). In several, if not all, cases, relationships between the proportion of deciduous species and CWM traits were nonlinear (Fig. 5). Moreover, when we assigned community values according to either the site-defined or the biome-defined functional type classification the variability in trait values
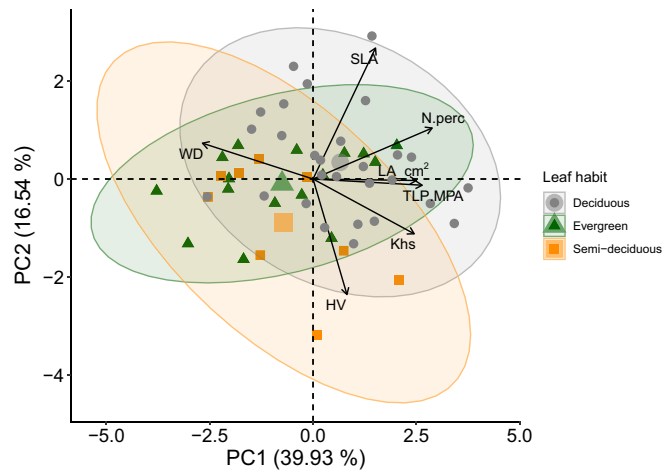
**Fig. 3** Bi-plot of the first two axes from a principal component analysis (PCA). Each dot represents a species, and colors correspond to their respective leaf habit: deciduous (gray, DE), evergreen (green, EV) and semi-deciduous (yellow, SD). Ellipses represent the 95% confidence interval of the bi-variate distribution between the first principal component (PC1) and the second principal component (PC2) of the PCA. Plant functional traits defined as: LA, leaf area; SLA, specific leaf area; $N_{leaf}$, foliar nitrogen concentration; WD, wood density; HV, Huber value; $K_S$, native xylem specific hydraulic conductivity; $\Psi_{TLP}$, water potential at turgor loss point; N.perc, foliar nitrogen content (%); Khs, xylem specific hydraulic conductivity (kg m$^{-1}$ s$^{-1}$ MPa$^{-1}$).

among plots decreased, yielding significant relations for all traits studied (Fig. 5). Similar results were observed when regressing the two first dimensions of the multivariate trait space (Fig. S7).

## Discussion

Our results show that common leaf habit classifications provide insight into physiological trait variation (Fig. 2), but the variance

in traits accounted for by leaf habit is relatively small when compared to site-specific or species-specific sources of variation (Fig. 4). Leaf habits occupied different regions of the 'fast-risky vs slow-safe' multivariate trait ordination, but trait variation was high (Fig. 3). Interestingly, many of the traits of both evergreen and deciduous species differed among sites, suggesting that trait-leaf habit relationships developed in one region should not be extrapolated to other regions. At the plant community level, trait variation was partially explained by the proportion of deciduous species (Fig. 5), which is linked to species-specific patterns of abundance and the physiological strategy successful at each site given environmental conditions.

### Leaf habits, hydraulics and plant economics

Our first question was whether trait values differed as a function of leaf habit. Drought-deciduous species had higher $K_S$, SLA, $N_{leaf}$, $\Psi_{TLP}$ and $\Psi_{P50-leaf}$ than both evergreen and semi-deciduous species (Fig. 2). The same pattern was observed in the multivariate trait ordination, as most deciduous species were associated with traits indicative of high productivity and drought avoidance (Fig. 3). This positions deciduous species as profligate resource users, which has been found in other seasonally dry environments (Sobrado, 1991; Eamus & Prior, 2001; Choat *et al.*, 2006; Méndez-Alonzo *et al.*, 2012; Lopez-Iglesias *et al.*, 2014; Pineda-García *et al.*, 2015). However, there was an overlap among trait values when species means were grouped by leaf habit, and indeed, the variance partitioning analysis revealed that leaf habit explained a modest amount of the variation in most traits (Fig. 4). Consequently, if we were to draw any random sample of deciduous species from the species pool, around 5.27% of the time it would have a $\Psi_{TLP}$ similar to an evergreen species and 10.90% of the time
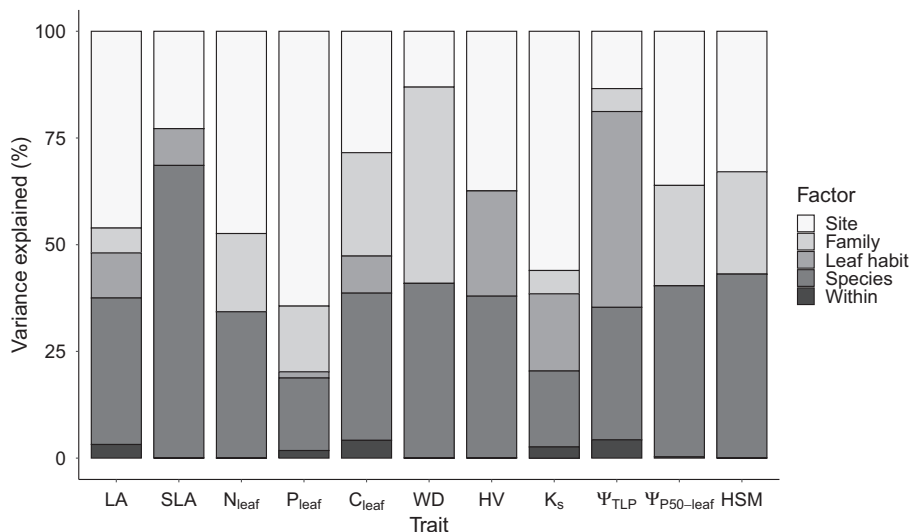


**Fig. 4** Stacked bar plot of variance partitioning for each trait across four nested sources of variation. To determine variance partitioning, we used a restricted maximum likelihood approach with a nested linear model for each trait (Messier *et al.*, 2010, 2016). For this approach we used the trait sampling scheme as our classification of variation sources: site, family, leaf habit, and species. Plant functional traits defined as: LA, leaf area; SLA, specific leaf area; $N_{leaf}$, foliar nitrogen concentration; $C_{leaf}$, foliar carbon concentration; $P_{leaf}$, foliar phosphorus concentration; WD, wood density; HV, Huber value; $K_S$, native xylem specific hydraulic conductivity; $\Psi_{TLP}$, water potential at turgor loss point; $\Psi_{P50-leaf}$, water potential at 50% accumulation of optical embolisms in leaf veins; HSM, hydraulic safety margin defined as $\Psi_{TLP} - \Psi_{P50-leaf}$.
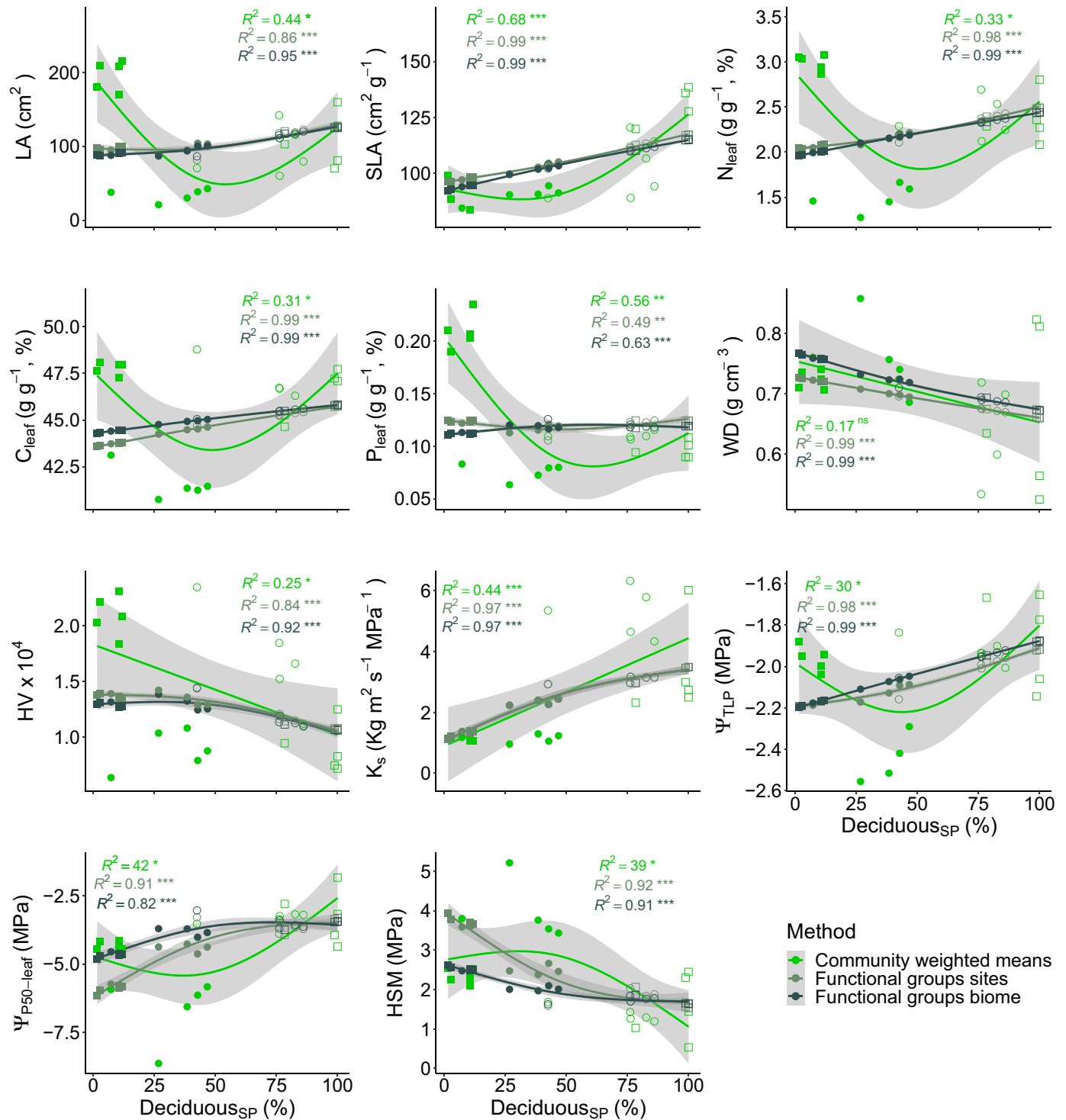
**Fig. 5** Community weighted mean functional trait values as function of community weighted proportion of deciduous trees (%) in four tropical dry forest sites: Tolima, Colombia (filled squares); Guanacaste, Costa Rica (open circles); Yucatán, Mexico (open squares); Guánica, Puerto Rico (filled circles). Each dot represents a plot, lines represent response mean and gray shading represents the 95% confidence interval of the mean response. Significant level at: ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Plant functional traits defined as: LA, leaf area; SLA, specific leaf area; $N_{leaf}$, foliar nitrogen concentration; $C_{leaf}$, foliar carbon concentration; $P_{leaf}$, foliar phosphorus concentration; WD, wood density; HV, Huber value, $K_S$, native xylem specific hydraulic conductivity; $\Psi_{TLP}$, water potential at turgor loss point; $\Psi_{P50-leaf}$, water potential at 50% accumulation of optical embolisms in leaf veins; HSM, hydraulic safety margin defined as $\Psi_{TLP} - \Psi_{P50-leaf}$.

similar to a semi-deciduous species (Fig. S8). These results were more obvious when considering the multivariate trait space, as we found greater degree of overlap among leaf habits in the multivariate ordination (Fig. 3). Therefore, rather than grouping species into distinct categories there is a continuum of trait values in which leaf habits can be arrayed.

There are many potential explanations for so much trait variability within leaf habits. First, some species vary in their degree of deciduousness depending on the intensity of their growing drought regime (Borchert, 1994; Borchert *et al.*, 2002). For example, the species *Astronium gravolens* Jacq., reported here as semi-deciduous in CO, displays an evergreen leaf habit in tropical dry forests of Panama and is deciduous in dry forests of CR (Frankie *et al.*, 1974; Reich & Borchert, 1984; Borchert *et al.*, 2002; Powers & Tiffin, 2010; Wolfe *et al.*, 2016). A second potential explanation is that leaf habit does not necessarily predict leaf life span or other physiological processes (Brodribb & Holbrook, 2005; Fu *et al.*, 2012). Certainly, deciduous species show leaf lifespans < 1 yr and remain leafless for periods longer than a week (Frankie *et al.*, 1974). However, evergreen species can also have short leaf lifespans (Borchert, 1994; Brodribb & Holbrook, 2005; Fu *et al.*, 2012). Beyond leaf habit, leaf lifespan links directly to construction costs, carbon assimilation and leaf drought tolerance (Reich *et al.*, 1991; Fu *et al.*, 2012; Gonzalez-Rebeles *et al.*, 2021). Last, traits may vary more in relation to other factors, such as site, family or species identity (Fig. 4). Indeed, some traits like WD appear to be highly conserved phylogenetically (Zanne *et al.*, 2010), while other traits vary significantly among sites likely in relation to edaphic or climatic factors (Ordoñez *et al.*, 2009; Liu *et al.*, 2020).

## Generalizations among plant functional types

Trait variability among evergreen or deciduous taxa provides insight into the extent to which trait syndromes can be generalized across species. For instance, deciduous species from MX, CR and PR showed similar values of SLA, $N_{leaf}$, $C_{leaf}$, $P_{leaf}$, $\Psi_{TLP}$, $\Psi_{P50-leaf}$ and HSM, but different values of HV, $K_S$ and LA (Fig. S6). The differences among deciduous species in $K_S$ could be explained by the differences in LA ($R^2 = 0.42$, $P < 0.0002$) (Fig. S9), as $K_S$ increases according to the demand in transpiration either by high $N_{leaf}$ or greater photosynthetic area (Becker *et al.*, 1999; Taylor & Eamus, 2008). By contrast, when comparing the trait values of evergreen species across sites we found many more traits that varied, including significant differences for LA, SLA, $N_{leaf}$, $C_{leaf}$, $P_{leaf}$, WD, $\Psi_{P50-leaf}$ and HSM (Fig. S5). Collectively, these results suggest that there are different ways a species can be an evergreen tree in the tropical dry forest. Contrary to deciduous species, the evergreen species studied here showed two clear axes of variation along resource use and drought tolerance. On the one hand, SLA, LA and foliar nutrient concentrations followed a clear pattern in which species in CO had the higher values, species in CR had intermediate values, and species in PR had the lowest values (Fig. S5). This suggests that edaphic conditions could be the cause of this variation as these traits are positively correlated to soil fertility (Ordoñez *et al.*, 2009), which is consistent with CO having more fertile soils (Waring *et al.*, 2021). Furthermore, $\Psi_{P50-leaf}$ and HSM also varied significantly among evergreen species (Fig. S5). We speculate that this variation follows site differences in drought regime and soil water retention capacity. For example, the species in PR had the greatest resistance to embolism and wider HSM. The PR site has the lowest MAR with *c.* 800 mm yr$^{-1}$, a *c.* 10 months dry season, a

very unpredictable wet season (Fig. 1), and species there grow on a karst formation with low water retention capacity (Govender *et al.*, 2013). This combination of factors may select for species adapted to resist drought stress. On the other hand, evergreen trees in CR had a lower HSM than both CO and PR. We believe this is related to differences in access to water during periods of drought stress. In the dry forests of CR, evergreen trees tend to be associated with areas of high soil moisture (Frankie *et al.*, 1974; Hartshorn, 1983; Borchert, 1994), either due to soils with high water retention capacity or proximity to water bodies (gallery forests).

The one trait that was the exception was $\Psi_{TLP}$: it showed little variation among sites within leaf habit groups, and the variance associated with $\Psi_{TLP}$ was mostly explained by leaf habit and species identity (Fig. 4). A clear distinction between evergreen and deciduous species in $\Psi_{TLP}$ indicates that they have different osmotic potentials (Tyree & Hammel, 1972; Bartlett *et al.*, 2012), with evergreen species having lower $\Psi_{TLP}$ allowing them to maintain turgor under drought stress (Fig. 2). This suggests that the osmotic limitations of carbon gain are different among deciduous and evergreen species (Deans *et al.*, 2020). While recent evidence shows that some tropical plant species can adjust their $\Psi_{TLP}$ during periods of drought (Inoue *et al.*, 2017; Maréchaux *et al.*, 2017), it remains unclear for most tropical trees whether there is seasonal variation of $\Psi_{TLP}$ and how this could be related to leaf habit. Addressing this question could provide mechanistic insight behind leaf habit classifications and their osmotic regulation capacity.

## Insights into forest function

Generally, trait values varied systematically as a function of the proportion of deciduous tree species when community means were calculated using species- or leaf habit-specific values. Forest plots dominated by deciduous trees had higher SLA, $\Psi_{TLP}$, $\Psi_{P50-leaf}$, $K_S$ and HSM than plots dominated by evergreen trees. However, the variation among plots decreased when we calculated community weighted values by assigning species trait values depending on their leaf habit (Fig. 5). We believe the reason for this loss of information links back to the fact that, within these functional types, traits vary greatly among species and within species. This highlights the fact that filtering processes occur independently at different scales, and species niches respond to local environmental conditions that act at the stand level (Messier *et al.*, 2018; Rosas *et al.*, 2019). For example, in MX plots are dominated by *Bursera simaruba* (L.) Sarg., *Caesalpinia gaumeri* Greenm., *Enterolobium cyclocarpum* (Jacq.) Griseb. and *Mimosa bahamensis* Benth., which are all deciduous species with $\Psi_{TLP}$ values of −1.56, −2.22, −1.75 and −2.90 MPa respectively. By contrast, the functional type mean for deciduous species is −2.03 MPa when looking at species only found in MX and −1.87 MPa when considering all the deciduous species sampled. Another example confirming these patterns are the trait values of a single species sampled in many sites: *B. simaruba* showed $\Psi_{TLP}$ values of −1.12 in CR, −1.28 in PR and −1.56 in MX. Such intra-specific variation in hydraulic traits has been found to be related to population genetics in species from temperate ecosystems (Martínez-Vilalta *et al.*, 2009; Rosas *et al.*, 2019;

Skelton *et al.*, 2019) and a tropical dry forest oak (Ramírez-Valiente & Cavender-Bares, 2017). Certainly, intra-specific trait variation provides insight into local adaptation in tropical plants (Hulshof & Swenson, 2010; Schmitt *et al.*, 2020), and species leaf phenology is no exception to this (Borchert *et al.*, 2002). Future research should quantify the role of intra-specific leaf phenology variation and its linkage to drought tolerance-avoidance strategies.

In conclusion, our data provide an important example of how of trait variation can limit generalizations drawn from plant functional types. Even though traits varied in relation to leaf habit, these patterns should be taken cautiously when informing models as there are many sources of variation that could affect trait values. Some of the sources include, but are not limited to, climate, topography, soil properties, and land-use history. Moreover, the fact that family and species informed so much trait variance suggests phylogenetic and intra-specific constraints on trait values. Therefore, understanding how these sources of variation affect plant hydraulics could provide crucial information to draw generalizations among plant functional types (i.e. modeling) and cross-scale trait patterns (i.e. remote sensing). Our results highlight the need to develop quantitative tools to account for trait variability in our current modeling approaches and to propagate the uncertainty when up-scaling from individual trees to stand level studies.

## Author contributions

GVG, JSP and DM developed the idea; GVG, JSP, DM, SJVB, CMH, CP, BS-N, BGW and JMD designed the study sampling scheme; TJB provided insight into hydraulic traits selection; GVG performed hydraulic traits sampling at all four sites (CO, CR, MX and PR); TAPA and SJVB provided climate and morphological traits for PR; CP, BS-N and RG-M provided climate and morphological traits for CO; JSP provided climate and morphological traits data for CR; NBS performed rainfall analyses; JMD provided climate and morphological traits data for MX; GVG performed data management and statistical analysis; JSP, CMH and JMD provided support on the interpretation of results; GVG wrote the manuscript with help from JSP and edits from all authors.

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## Data availability

The data that supports the findings of this study are available from https://doi.org/10.5061/dryad.ttdz08kzj. [Correction added after online publication 23 July 2021: a Data availability section has been added.]

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## Supporting Information

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

**Fig. S1** Visual quantification of leaf vein embolism of a deciduous and an evergreen species.

**Fig. S2** Optical vulnerability curves collected at four tropical dry forest sites during this study.

**Fig. S3** Difference between the branch segment length (cm) used for stem specific hydraulic conductivity ($K_S$) and maximum vessel length (cm).

**Fig. S4** Stem hydraulic conductivity ($K_S$) in relation to the difference with maximum vessel length.

**Fig. S5** Plant functional trait variation for evergreen species at three tropical dry forest sites.

**Fig. S6** Plant functional trait variation for deciduous species at three tropical dry forest sites.

**Fig. S7** Variation in the multivariate trait ordination axes from principal component analysis in response to the percentage of deciduous species at each plot.

**Fig. S8** Sampling distributions of plant functional traits.

**Fig. S9** Sapwood specific hydraulic conductivity ($K_S$) as a function of leaf area (LA) and the Huber value (HV).

**Notes S1** Details on rainfall regime characterization at each tropical dry forest site.

**Table S1** Rainfall records sources and date intervals for each tropical dry forest site.

**Table S2** Plot characteristics at each tropical dry forest site.

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