



Leaf habits and their relationship with leaf and wood traits in tropical dry forests

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Abstract

Key message For better categorization of species according to foliar habit, a set of leaf and wood traits must be observed.

Abstract Tropical forests are influenced by distinct regional rainfall regimes, microclimates, and dynamics of nutrient cycling, which are responsible for creating key biodiversity patterns and differences in leaf deciduousness to drought. Functional traits studies have improved understanding of the functioning and heterogeneity of complex ecosystems. We have reviewed the literature focusing mainly on tropical dry forests and relationships among leaf habits (evergreen and deciduous) and other leaf and wood traits. Thus, we have compiled 121 original papers, 2 reports, and 9 book chapters published since 2000. We also provide a meta-analysis of these traits from Neotropics. Tropical deciduous species often have high photosynthetic rates per mass and specific leaf area and traits that improve water flow throughout the plant, such as wide xylem diameters and high hydraulic conductivity, maximizing resource capture during a limited growing season because of an acquisition strategy. The opposite is observed in evergreen species, namely as conservative species. Regardless of the plant organ, more morphological than physiological traits are available to compare leaf habits. For better categorization of species according to foliar habit, a set of leaf and wood traits must be observed. However, while local comparisons based on one or few traits may group species according to leaf habit, multivariate analyses for large spatial scales can reveal a different pattern. We have identified some open questions that can be further addressed in this research field to contribute to the improvement of theoretical frameworks as well as the consequences of a changing climate for tropical dry forests.

Keywords Functional trade-off · Leaf shedding · Climatic control · Water restriction · Ecosystem functioning

Introduction

Tropical forests are home to more than half of the plant species described so far, including many endangered and endemic species (Myers et al. 2000; Dirzo and Raven 2003; Vitória et al. 2019). Tropical forests originally covered 12% of the world's land surface between the latitudes 33 °N and 35 °S, with the largest area of tropical forests being found in the Americas from northwest Mexico to northern Argentina

(Pennington et al. 2009; Linares-Palomino et al. 2011; Taubert et al. 2018). Despite the special attention given to rainforests, about 40% of tropical forests are in fact deciduous and semideciduous forests that are subject to some degree of water restriction (Malhi and Wright 2004; Allen et al. 2017; Hasnat et al. 2020). In addition, there is a consensus that the remaining tropical forest coverage (~60%) represents not only humid forests, but a gradient of forest types aligned with a moisture gradient (Malhi and Wright 2004).

The climate of tropical forests is characterized by a mean annual temperature of at least 20 °C, and high variation in the mean annual precipitation among regions, creating distinct forest types ranging from dry forests to moist forests to rainforests (FAO 2000; Meir et al. 2011; Hasnat et al. 2020). Dry forests include both deciduous and semideciduous forests, which are characterized by a high thermic variability, low to moderate mean annual precipitation (500–1500 mm),

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and a marked seasonality in which the drought season lasts from 5 to 8 months a year (FAO 2000). Humid forests have low thermic variability, a mean annual precipitation higher than 1.500 mm, and a lack of or very short rainfall season (FAO 2000). Some humid forests are in flooded areas associated with mean annual precipitation above 2.500 mm (Malhi and Wright 2004; Pantoja et al. 2019). In addition, edaphic and topographic heterogeneity act in combination with these climatic gradients, increasing both species and functional diversity within a given locality, between localities, and within a region (α , β , and γ diversities, respectively), as well as variation in vegetation physiognomy related to canopy height and tree density (Pennington et al. 2009; Linares-Palomino et al. 2011; Chaturvedi et al. 2011).

To adjust to environmental contexts, species adopt distinct morphological, phenological, and physiological traits (Violle et al. 2007; Kikuzawa and Lechowicz 2011; Missio et al. 2017; Vitória et al. 2018, 2019). This occurs in response to abiotic pressures (Violle et al. 2007) such as a decrease in specific leaf area along with an increase in irradiance (Vitória et al. 2016), and an increase in leaf fall, water-use efficiency, wood vessel density, leaf succulence and thickness associated with increased water restrictions (Kikuzawa and Lechowicz 2011; Marksteijn et al. 2011; Méndez-Alonzo et al. 2012; Pineda-García et al. 2015). Changes in functional traits are also observed among individuals within populations, mostly due to phenotypic plasticity (Valladares et al. 2007). In this sense, functional traits are key ecological indicators of how living organisms are affected by the environment and how they, in turn, affect the functioning and structure of communities and ecosystems, known as Response and Effect traits, respectively (Lavorel and Garnier 2002).

In tropical dry forests, vegetation physiognomy varies throughout the year, with leaf deciduousness playing a fundamental role in species' ability to cope with the dry season (Lal et al. 2011; Meir et al. 2011; Chaturvedi et al. 2011; Estrada-Medina et al. 2013; Reich 2014; Aguilar-Peralta et al. 2020). The establishment and survival of species in these forests also depend on the association between several other leaf, wood, and root traits, mostly in the form of functional trade-offs, as investments in one set of traits comes at the cost of others (Shipley et al. 2006; Wright et al. 2010; Li et al. 2015; Vitória et al. 2019). Strategies for dealing with water restrictions include investments in high leaf stomatal control, dense wood, root depth, water storage in wood and roots, and leaf deciduousness (Choat et al. 2006; Brodrribb et al. 2003; Hasselquist et al. 2010; Holanda et al. 2019; Marques et al. 2020; Yang et al. 2021), which is a key short-term response to drought. Despite a large number of studies on leaf deciduousness, there is no consensus on how drought deciduousness is directly and indirectly linked to leaf and wood traits relevant to water acquisition/conservation in

tropical dry forests (Choat et al. 2006; Kushwaha et al. 2010; Kikuzawa and Lechowicz 2011; Estrada-Medina et al. 2013; Méndez-Alonzo et al. 2013; Vitória et al. 2018; Tarelkin et al. 2019; Cuba et al. 2018; Marques et al. 2020; Chakrabarty et al. 2021).

This paper reviews the literature focusing mainly on tropical dry forests to assess current knowledge regarding the relationships between leaf habits, wood and other leaf traits, as well as to identify current knowledge gaps, open questions, and the implications of climate change in this research field. To this aim, we have compiled readily available published studies using the following keywords in the Google Scholar, Scielo, and Web of Science platforms: “evergreen species,” “deciduous species,” “tropical dry forest,” “leaf lifespan,” “functional traits,” and “wood density.” Keywords were also combined using: “tropical dry forest” AND all the other words; “leaf lifespan” AND “functional traits”; “leaf lifespan” AND “wood density”; and “leaf lifespan” AND “tropical dry forest” OR “evergreen species” OR “deciduous species”. These searches resulted in 121 original papers, 2 reports, and 9 book chapters published since 2000, which allowed us to describe patterns between leaf habits and functional traits at the local scale of the dry forests studied. To assess if local relationships reported worldwide correspond to broader scale patterns, we performed a meta-analysis for the Neotropical region with the focus on the tree and shrub species of tropical dry forests and rainforests, with the latter being included in order present the perspective of a distinct ecosystem (further details are described below).

Local context of leaf trait variation in tropical dry forests: acquisitive and conservative strategies

Since they reflect the main costs for leaf construction and maintenance and carbon gain (Prior et al. 2003; Brodrribb and Holbrook 2005; Kushwaha et al. 2010; Powers and Tiffin 2010; Kikuzawa and Lechowicz 2011; Álvarez-Yépez et al. 2017), leaf deciduousness and leaf longevity (or lifespan) have been widely associated with morphological leaf traits (e.g., specific leaf area). From the perspective of the leaf economics spectrum, these functional traits reflect a key trade-off between resource acquisition and conservation, with downstream impact on plant growth and survival (Wright et al. 2004; Donovan et al. 2011; Méndez-Alonzo et al. 2012; Collins et al. 2016; Sastry and Barua 2017; Werden et al. 2018). At one extreme of this spectrum, species display acquisitive strategies with high carbon fixation and a fast return on the costs involved in leaf construction and maintenance in spite of short leaf lifespan; the other extreme is dominated by conservative species with slow

carbon fixation and long leaf lifespan (Wright et al. 2004; Donovan et al. 2011).

In this regard, most, if not all, deciduous species of tropical dry forests are characterized by acquisitive strategies in comparison with co-occurring evergreen species making use of conservative strategies (Wright et al. 2004; Shipley et al. 2006; Curtis and Ackerly 2008; Donovan et al. 2011; Kikuzawa and Lechowicz 2011; Álvarez-Yépiz et al. 2017). Some leaf traits are very consistent in distinguishing deciduous and evergreen species (e.g., SLA or LMA, LDMC, and osmotic potential), while others lack a pattern (e.g., leaf thickness) or have been less analyzed to allow such as comparison (e.g., WUE) (see Table 1 and Fig. 1). The allocation of nitrogen and phosphorous in leaves and wood has been used as a means to distinguish acquisitive and conservative species (Hiremath 2000; Yan et al. 2016). In environments with low soil nutrient availability such as dry forests (Gei and Powers 2014; Powers et al. 2015; Carrasco-Carballido et al. 2019), deciduous species have developed greater efficiency in their use of nutrients, whereas evergreen species are better in terms of nutrient accumulation (Givnish 2002; Wright et al. 2004; Yan et al. 2016). For example, when nutrients are allocated to leaves, plants maximize photosynthetic activity and growth (i.e., acquisitive strategy), whereas when nutrients are allocated to branches and the trunk, plants improve the internal recycling of nutrients and the transport of photoassimilates in the phloem (i.e., conservative strategy) (Yan et al. 2016). In addition, long-lived leaves of evergreen species may have higher allocation of nutrients for non-photosynthetic functions such as anti-herbivory compounds or sclerophylly increases than the short-lived leaves of deciduous species (Givnish 2002; Wright et al. 2004; Zvereva and Koslov 2014; Yan et al. 2016; Álvarez-Yépiz et al. 2017).

Although many authors have long asserted that leaf longevity and leaf habits are closely related, pointing out, for example, that evergreen species always have long-lived leaves (Table 1), it is important to note that leaf habit describes the general status of the canopy and not of individual leaves, whereas leaf longevity is more closely linked with leaf maintenance and carbon gain (Hiremath 2000; Brodribb and Holbrook 2005; Kikuzawa and Lechowicz 2011; Russo and Kitajima 2016; Osnas et al. 2018). For example, in a tropical dry forest in Costa Rica, Brodribb and Holbrook (2005) showed that two evergreen species had a wide variation in leaf longevity; one species had a leaf duration of one year, and the other of 35–45 weeks, a longevity similar to that of deciduous species. This conceptual differentiation helps illustrate why, in a given environment, some deciduous and evergreen species can present remarkably similar leaf longevity. In part, this occurs because leaf longevity is strongly controlled by local environmental conditions. In deciduous species, leaves are discarded when leaf maintenance costs exceed gains, but prior to the leaf

shedding, water and nutrients are translocated from leaves to other plant organs (Kushwaha and Singh 2005; Poorter and Bongers 2006; Marchin et al. 2010). On the other hand, evergreen species have a greater control of water usage and flow through the stomates during the photosynthetic assimilation, particularly in the dry season (Givnish 2002; Lusk et al. 2003; Kikuzawa and Lechowicz 2011). This local difference emerges to balance the effects of drought along the soil–atmosphere continuum, with deciduous species being sensitive to both drought types, while evergreens are more sensitive to drought in soils (Souza et al. 2020).

To take advantage of a relatively short functional period, leaves of drought-deciduous species invest in high specific leaf area and photosynthetic rates per unit of leaf mass, as well as in thin leaves with low compaction of mesophyll cells to promote greater CO₂ diffusion (Fig. 1) (Eamus and Prior 2001; Prior et al. 2003; Wright et al. 2004; Poorter and Bongers 2006; Kushwaha et al. 2010). Deciduous species or species with short-lived leaves also display greater metabolic activity, as reflected in higher dark respiration rates when compared with evergreen species (Fig. 1) (Wright et al. 2004). Respiration occurs during the day and night, but because the CO₂ acquisition and loss occur simultaneously during the day, it is easier to detect respiration at night due to the lack of photosynthetic activity. Dark respiration is indeed one of the most important metabolic processes that transform organic molecules into simple products, such as the carbon skeletons necessary for the biosynthesis of other molecules, and the release of usable energy (Wright et al. 2005; Werden et al. 2018).

Stomatal regulation is another key mechanism for protecting plants as it helps avoiding the cavitation and embolism of wood xylem vessels (Westoby et al. 2002; Wright and Westoby 2002; Markesteijn et al. 2011; Fu et al. 2012; Chaturvedi et al. 2021). In addition, the investment in thick and scleromorphic leaves with high dry matter content and physical structures such as high lignin content and spines increases resistance to mechanical damage and herbivory (Hanley et al. 2007; Poorter and Bongers 2006; Carmona et al. 2011; Pérez-Harguindeguy et al. 2016). Other physical structures strongly associated with drought adaptation such as trichomes and cuticles also provide resistance to herbivory and contribute to leaf thickening (Haworth and McElwain 2008; Bickford 2016). The leaf dry matter content is related to leaf toughness and resistance to herbivory and drought, and high values of this trait reflect the presence of mesophyll cells with thick and rigid walls, particularly in the epidermis, which allows the maintenance of leaf turgor even under low water potential while minimizing possible damage to cells under severe drought (Kursar et al. 2009; Markesteijn et al. 2011). Evergreen species have higher leaf dry matter content than deciduous species (Fig. 1 and Table 1) as this also reduces leaf palatability, in part due to the low water

Table 1 Summary of differences in leaf and wood traits between drought-deciduous (D) and evergreen (E) species that have been reported in the literature of tropical dry forests (local scale studies)

Organ/type	Trait	Abbreviation	Unit	Leaf habits (qualitative)		Leaf habits (quantitative)		P value	References
				D	E	D	E		
Leaf morphology	Leaf area	LA	cm ²	+	-	\	\	<0.01	GermanVargas et al. (2021)
	Leaf area	LA	cm ²	+	-	85.0±16.6	33.4±13.0	<0.05	Souza et al. (2015, 2020)
	Leaf size	LS	cm ²	=	=	28.2±2.80	16.8±1.49	NS	Markesteyn et al. (2011)
	Leaf density	ρ_{leaf}	g cm ⁻³	-	+	0.36±0.02	0.50±0.04	<0.05	Fu et al. (2012)
	Leaf density	ρ_{leaf}	g cm ⁻³	-	+	0.23±0.03	0.53±0.09	<0.025	Souza et al. (2015, 2020)
	Leaf density	ρ_{leaf}	kg m ⁻³	=	=	\	\	NS	Prior et al. (2003)
	Leaf dry matter content	LDMC	g g ⁻¹	-	+	\	\	<0.0001	Chakrabarty et al. (2021)
	Leaf dry matter content	LDMC	g g ⁻¹	-	+	0.31±0.03	0.40±0.02	<0.05	Markesteyn et al. (2011)
	Leaf dry matter content	LDMC	mg g ⁻¹	-	+	315.2±19.7	463.3±28.9	<0.001	Souza et al. (2015, 2020)
	Specific leaf area	SLA	m ² Kg ⁻¹	+	-	14.97*	10.53*	<0.001	Choat et al. (2006)
	Specific leaf area	SLA	cm ² g ⁻¹	+	-	213±4.21	166±1.45	<0.05	Markesteyn et al. (2011)
	Specific leaf area	SLA	mm mg ⁻²	+	-	28.3±2.31	11.3±1.3	<0.001	Souza et al. (2015)
	Specific leaf area	SLA	cm ² g ⁻¹	+	-	\	\	<0.007	Pringle et al. (2011)
	Specific leaf area	SLA	cm ² g ⁻¹	+	-	\	\	<0.01	Silva et al. (2015)
	Specific leaf area	SLA	cm ² g ⁻¹	+	-	\	\	<0.01	GermanVargas et al. (2021)
	Leaf mass per area	LMA	g m ⁻²	-	+	93±12	137±7	<0.05	Bartlett et al. (2012)
	Leaf mass per area	LMA	g m ⁻²	-	+	95.36*	97.41*	\	Chen et al. (2009b)
	Leaf mass per area	LMA	g m ⁻²	-	+	53.4±6.5	94.3±17.6	<0.05	Fu et al. (2012)
	Leaf mass per area	LMA	mg mm ⁻²	-	+	0.03±0.0	0.09±0.0	<0.001	Souza et al. (2015, 2020)
	Leaf mass per area	LMA	g m ⁻²	-	+	\	\	<0.01	Chakrabarty et al. (2021)
	Leaf mass per area	LMA	g m ⁻²	-	+	\	\	<0.01	Prior et al. (2003)
	Leaf mass per area (dry season)	LMA	Kg m ⁻²	-	+	0.097*	0.125	<0.05	Ishida et al. (2006)
	Leaf thickness	T	mm	-	+	347.87*	391.17*	\	Chen et al. (2009b)
Leaf thickness	T	mm	-	+	\	\	<0.001	Silva et al. (2015)	
Leaf thickness	T	mm	-	+	\	\	<0.01	Prior et al. (2003)	
Leaf thickness	T	mm	=	=	152.6±22.2	184.4±25.9	NS	Fu et al. (2012)	
Leaf thickness	T	mm	=	=	0.21±0.02	0.21±0.05	NS	Souza et al. (2015, 2020)	
Leaf toughness	LT	g	-	+	\	\	<0.007	Pringle et al. (2011)	
Leaf water content	LWC	%	+	-	\	\	<0.007	Pringle et al. (2011)	

Table 1 (continued)

Organ/type	Trait	Abbreviation	Unit	Leaf habits (qualitative)		Leaf habits (quantitative)		P value	References
				D	E	D	E		
	Leaf water content	LWC	%	+	-	\	\	<0.001	Silva et al. (2015)
	Leaf succulence	LS	g m ⁻²	=	=	\	\	NS	Souza et al. (2015, 2020)
	Leaf saturated water content	SWC _{leaf}	g g ⁻¹	+	-	2.48±0.2	1.22±0.15	0.001	Souza et al. (2015, 2020)
	Leaf lifespan	LLS	Days	-	+	159.0±10.7	326.8±17.4	<0.001	Souza et al. (2015, 2020)
	Leaf lifespan	LLS	Months	-	+	7.8±1.0	23.3±5.3	<0.05	Fu et al. (2012)
	Leaf lifespan	LLS	Months	-	+	\	\	<0.05	Prior et al. (2003)
	Herbivory rate	HR	%	+	-	\	\	<0.007	Pringle et al. (2011)
	Herbivory rate	HR	%	+	-	\	\	<0.001	Silva et al. (2015)
Leaf physi- ology	Mass-based maximum photosynthetic capacity	A _{mass}	nmol g ⁻¹ s ⁻¹	+	-	232.2±25.6	80.8±10.9	<0.001	Souza et al. (2015, 2020)
	Mass-based maximum photosynthetic capacity	A _{mass}	μmol kg ⁻¹ s ⁻¹	+	-	117.44*	58.22*	<0.001	Choat et al. (2006)
	Mass-based maximum photosynthetic capacity	A _{mass}	nmol g ⁻¹ s ⁻¹	+	-	225±23	125±14	<0.05	Fu et al. (2012)
	Mass-based maximum photosynthetic capacity	A _{mass}	nmol g ⁻¹ s ⁻¹	=	=	\	\	NS	Prior et al. (2003)
	Mass-based maximum photosynthetic capacity (dry season)	A _{mass}	μmol Kg ⁻¹ s ⁻¹	+	-	92.7*	37	<0.05	Ishida et al. (2006)
	Area-based maximum photosynthetic capacity	A _{area}	μmol m ⁻¹ s ⁻¹	+	-	7.94*	5.68*	<0.05	Choat et al. (2006)
	Area-based photosynthetic capacity	A _{area}	μmol CO ₂ m ⁻² s ⁻¹	+	-	\	\	<0.05	Ávila-Lovera et al. (2019)
	Area-based maximum photosynthetic capacity (dry season)	A _{area}	μmol m ⁻² s ⁻¹	+	-	8.9*	4.6	<0.05	Ishida et al. (2006)
	Area-based maximum photosynthetic capacity	A _{area}	μmol m ⁻¹ s ⁻¹	-	+	\	\	<0.05	Prior et al. (2003)
	Area-based maximum photosynthetic capacity	A _{area}	μmol m ⁻¹ s ⁻¹	=	=	8.29±0.6	7.38±0.9	NS	Souza et al. (2015, 2020)
	Area-based maximum photosynthetic capacity	A _{area}	μmol m ⁻¹ s ⁻¹	=	=	11.64±1.4	10.4±0.6	NS	Fu et al. (2012)
	Nitrogen-based maximum photosynthetic capacity (dry season)	A _N	μmol mol N ⁻¹ s ⁻¹	+	-	60.5*	29.9	<0.05	Ishida et al. (2006)

Table 1 (continued)

Organ/type	Trait	Abbreviation	Unit	Leaf habits (qualitative)		Leaf habits (quantitative)		P value	References
				D	E	D	E		
	Carbon isotope composition	$\delta^{13}\text{C}$	‰	+	-	\	\	<0.05	Ávila-Lovera et al. (2019)
	Chlorophyll per area	Chl_{area}	$\mu\text{mol cm}^{-2}$	-	+	32.0 ± 1.5	43.3 ± 6.4	<0.05	Souza et al. (2015, 2020)
	Chlorophyll per area	Chl_{area}	mmol m^{-2}	-	+	\	\	<0.01	Prior et al. (2003)
	Chlorophyll per unit mass	Chl_{mass}	mgmol g^{-1}	-	+	2.24 ± 0.38	4.88 ± 0.73	<0.05	Souza et al. (2015, 2020)
	Chlorophyll per unit mass	Chl_{mass}	mmol Kg^{-1}	=	=	\	\	NS	Prior et al. (2003)
	Leaf specific conductivity	k_L	$\text{kg m}^{-1} \text{s}^{-1} \text{Mpa}^{-1}$	+	-	30.01*	5.92*	<0.05	Choat et al. (2005)
	Leaf specific conductivity	k_L	$\text{mmol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$	+	-	36.7 ± 1.93	20.2 ± 0.94	<0.05	Markestijn et al. (2011)
	Leaf specific conductivity	k_L	$\text{kg m}^{-1} \text{s}^{-1} \text{Mpa}^{-1}$	=	=	6.28 ± 1.37	3.70 ± 0.48	NS	Fu et al. (2012)
	Leaf saturate osmotic potential (dry season)	$\pi_{100 \text{ dry}}$	MPa	+	-	-1.47 ± 0.10	-2.39 ± 0.26	<0.05	Fu et al. (2012)
	Leaf saturate osmotic potential (wet season)	$\pi_{100 \text{ wet}}$	MPa	+	-	-1.37 ± 0.07	-1.91 ± 0.21	<0.05	Fu et al. (2012)
	Leaf turgor-loss point (dry season)	$\pi_{0 \text{ dry}}$	MPa	+	-	-1.65 ± 0.12	-2.82 ± 0.32	<0.05	Fu et al. (2012)
	Leaf turgor-loss point (wet season)	$\pi_{0 \text{ wet}}$	MPa	=	=	-1.64 ± 0.09	-2.22 ± 0.29	NS	Fu et al. (2012)
	Leaf water potential at turgor loss	π_{tip}	MPa	+	-	-2.11 ± 0.12	-2.50 ± 0.11	<0.05	Bartlett et al. (2012)
	Osmotic potential at full turgor	π_0	MPa	+	-	-1.68 ± 0.10	-2.06 ± 0.08	<0.05	Bartlett et al. (2012)
	Morning leaf water potential	Ψ_{leaf}	MPa	+	-	\	\	<0.05	Ávila-Lovera et al. (2019)
	Photosynthetic water-use efficiency	WUE	$\mu\text{mol mol}^{-1}$	-	+	49.7 ± 2.0	66.7 ± 4.9	<0.01	Fu et al. (2012)
	Photosynthetic water-use efficiency	WUE	$\mu\text{mol mol}^{-1}$	=	=	23.0 ± 1.7	24.8 ± 3.8	NS	Souza et al. (2015, 2020)
	Stomatal conductance	g_s	$\text{mol m}^{-2} \text{s}^{-1}$	+	-	0.25 ± 0.03	0.17 ± 0.02	<0.05	Fu et al. (2012)
	Stomatal conductance (dry season)	g_s	$\text{mol m}^{-2} \text{s}^{-1}$	+	-	0.184*	0.07	<0.05	Ishida et al. (2006)
	Stomatal conductance	g_s	$\text{mol m}^{-2} \text{s}^{-1}$	=	=	0.37 ± 0.02	0.31 ± 0.03	NS	Souza et al. (2015, 2020)
	leaf intercellular CO_2 concentration (dry season)	C_i	$\mu\text{mol mol}^{-1}$	+	-	247*	187	<0.05	Ishida et al. (2006)

Table 1 (continued)

Organ/type	Trait	Abbreviation	Unit	Leaf habits (qualitative)		Leaf habits (quantitative)		P value	References
				D	E	D	E		
Leaf bio-chemistry	Carbon to nitrogen ratio	C:N	%	-	+	\	\	<0.007	Pringle et al. (2011)
	Carbon to nitrogen ratio (dry season)	C:N	%	-	+	25.8*	32.4	<0.05	Ishida et al. (2006)
	Mass-based leaf carbon	C _{mass}	g g ⁻¹ (%)	=	=	\	\	NS	GermanVargas et al. (2021)
	Mass-based leaf nitrogen	N _{mass}	%	+	-	\	\	<0.01	Silva et al. (2015)
	Mass-based leaf nitrogen	N _{mass}	g g ⁻¹ (%)	+	-	\	\	<0.01	GermanVargas et al. (2021)
	Mass-based leaf nitrogen	N _{mass}	mg g ⁻¹	+	-	\	\	<0.05	Prior et al. 2003
	Mass-based leaf nitrogen (dry season)	N _{mass}	mol Kg ⁻¹	+	-	1.58*	1.32	<0.05	Ishida et al. (2006)
	Mass-based leaf nitrogen	N _{mass}	mg g ⁻¹ (%)	=	=	2.48±0.1	2.19±0.1	NS	Souza et al. (2015, 2020)
	Area-based leaf nitrogen (dry season)	N _{area}	mol m ⁻²	=	=	\	\	NS	Ishida et al. (2006)
	Mass-based phosphorus	P _{mass}	mg g ⁻¹	+	-	2.02±0.14	1.35±0.14	<0.05	Fu et al. (2012)
	Mass-based leaf phosphorus	P _{mass}	mg g ⁻¹	+	-	\	\	<0.05	Prior et al. (2003)
	Mass-based leaf phosphorus	P _{mass}	g g ⁻¹ (%)	=	=	\	\	NS	GermanVargas et al. (2021)
	Mass-based leaf phosphorus	P _{mass}	mg g ⁻¹ (%)	=	=	0.20±0.02	0.17±0.02	NS	Souza et al. (2015, 2020)
	Wood morphology	Protein precipitation capacity	PPC	mg/g	-	+	\	\	<0.05
Total phenolics		P _t	mg/g	-	+	\	\	<0.001	Silva et al. (2015)
Sapwood density		WD	g cm ⁻³	=	=	0.56±0.03	0.63±0.03	NS	Fu et al. (2012)
Wood density		WD	g cm ⁻³	-	+	0.28*	0.69*	<0.001	Choat et al. (2005)
Wood density		WD	g cm ⁻³	-	+	0.35±0.03	0.52±0.02	<0.05	Markestijn et al. (2011)
Wood density		WD	g cm ⁻³	+	-	\	\	<0.05	Méndez-Alonzo et al. (2013)
Wood density		WD	g cm ⁻³	=	=	\	\	NS	GermanVargas et al. (2021)
Wood anatomy	Xylem water content	WC	%	-	+	\	\	<0.05	Méndez-Alonzo et al. (2013)
	Bulk modulus of elasticity	ε	MPa	+	-	\	\	<0.05	Méndez-Alonzo et al. (2013)
	Bulk modulus of elasticity (dry season)	ε _{dry}	MPa	-	+	14.94±2.42	23.87±2.24	<0.05	Fu et al. (2012)
	Bulk modulus of elasticity (wet season)	ε _{wet}	MPa	-	+	16.19±1.76	26.64±2.22	<0.05	Fu et al. (2012)
	Maximum vessel length	MVL	cm	=	=	55.3±12.7	67.3±13.3	NS	Fu et al. (2012)

Table 1 (continued)

Organ/type	Trait	Abbreviation	Unit	Leaf habits (qualitative)		Leaf habits (quantitative)		P value	References
				D	E	D	E		
Wood physi- ology	Maximum vessel length	MVL	cm	=	=	80.3±1.01	75.7±0.85	NS	Markesteijn et al. (2011)
	Vessel density	V _{Dens}	Vessel mm ²	-	+	28.67*	98.67*	\	Chen et al. (2009a)
	Vessel density	V _{Dens}	Vessel mm ²	-	+	12*	150.5*	<0.001	Choat et al. (2005)
	Vessel density	V _{Dens}	Vessel mm ²	=	=	\	\	NS	Méndez-Alonzo et al. (2013)
	Vessel density	V _{Dens}	Vessel mm ²	=	=	30.5±15.9	82.0±30.5	NS	Fu et al. (2012)
	Vessel diameter	V _{diam}	µm	+	-	87.87*	40.27*	\	Chen et al. (2009b)
	Vessel diameter	V _{diam}	µm	+	-	97.15*	39.15*	<0.001	Choat et al. (2005)
	Vessel diameter	V _{diam}	µm	+	-	94.7±10.1	59.6±8.7	<0.05	Fu et al. (2012)
	Vessel diameter	V _{diam}	µm	=	=	\	\	NS	Méndez-Alonzo et al. (2013)
	Vessel resistance to implosion	(t/b) ²	(t/b) ²	+	-	\	\	<0.05	Méndez-Alonzo et al. (2013)
	Vulnerability index	VI	Unitless	=	=	8.49±3.70	2.55±1.55	NS	Fu et al. (2012)
	Huber value	HV	Unitless	=	=	1.06±0.15	1.41±0.21	NS	Fu et al. (2012)
	Huber value	HV	Unitless	=	=	151±4.45	181±2.76	NS	Markesteijn et al. (2011)
	Huber value	HV	Unitless	=	=	\	\	NS	GermanVargas et al. (2021)
	Moisture content	MC	%	+	-	73.5*	29*	<0.001	Choat et al. (2005)
	Hydraulic safety margin	HSM	MPa	=	=	\	\	NS	GermanVargas et al. (2021)
	Potential hydraulic conductivity	K _p	kg m ⁻¹ s ⁻¹ MPa ⁻¹	-	+	\	\	<0.05	Méndez-Alonzo et al. (2013)
	Maximum sapwood specific hydraulic conductivity	k _{S-max}	kg m ⁻¹ s ⁻¹ MPa ⁻¹	+	-	\	\	<0.05	Chen et al. (2009b)
	Sapwood specific hydraulic conductivity	k _S	Kg m ⁻² s ⁻¹ MPa ⁻¹	+	-	\	\	<0.001	GermanVargas et al. (2021)
	Sapwood specific hydraulic conductivity	k _S	kg m ⁻¹ s ⁻¹ MPa ⁻¹	+	-	7.23*	3.07*	<0.05	Choat et al. (2005)
Sapwood specific hydraulic conductivity	k _S	kg m ⁻¹ s ⁻¹ MPa ⁻¹	+	-	5.98±0.86	2.76±0.23	<0.05	Fu et al. (2012)	
Sapwood specific hydraulic conductivity	k _S	mol m ⁻¹ s ⁻¹ MPa ⁻¹	+	-	246±8.29	115±4.24	<0.05	Markesteijn et al. (2011)	
Sapwood specific hydraulic conductivity	k _S	kg m ⁻¹ s ⁻¹ MPa ⁻¹	+	-	\	\	<0.05	Méndez-Alonzo et al. (2013)	
Hydraulic conductivity	k _h	kg m ⁻¹ s ⁻¹ MPa ⁻¹	+	-	8.44*	0.94*	<0.05	Choat et al. (2005)	
Water potential at 50% loss of hydraulic conductivity	P ₅₀	MPa	+	-	-1.23*	-2.24*	\	Chen et al. (2009b)	

Table 1 (continued)

Organ/type	Trait	Abbreviation	Unit	Leaf habits (qualitative)		Leaf habits (quantitative)		P value	References
				D	E	D	E		
	Water potential at 50% loss of hydraulic conductivity	P ₅₀	MPa	+	-	-1.27 ± 0.26	-2.37 ± 0.40	< 0.05	Fu et al. (2012)
	Water potential at 50% loss of hydraulic conductivity	P ₅₀	MPa	+	-	\	\	< 0.05	Chen et al. (2009a)
	Water potential at 50% loss of hydraulic conductivity	P ₅₀	MPa	+	-	\	\	< 0.05	Vargas et al. (2021)
	Midday leaf water potential	Ψ _{MD}	MPa	=	=	1.16 ± 0.13	1.69 ± 0.12	NS	Markestijn et al. (2011)
	Water potential at turgor-loss point	Ψ _{TLP}	MPa	+	-	\	\	< 0.05	GermanVargas et al. (2021)

In the ‘Leaf habits (qualitative)’ column, positive and negative signs refer, respectively, to higher and lower trait values; and the equal sign refers to the lack of statistical difference. NS: refers to $P > 0.05$. \: refers to no value available. *: refers to mean values that we calculated from provided species data

content (Silva et al. 2015; Souza et al. 2015). Short-lived leaves of deciduous species also tend to be highly damaged by herbivores because of high nutrient concentrations (Westoby et al. 2002; Poorter et al. 2004; Wright et al. 2004; Poorter et al. 2005; Zvereva and Kozlov 2014).

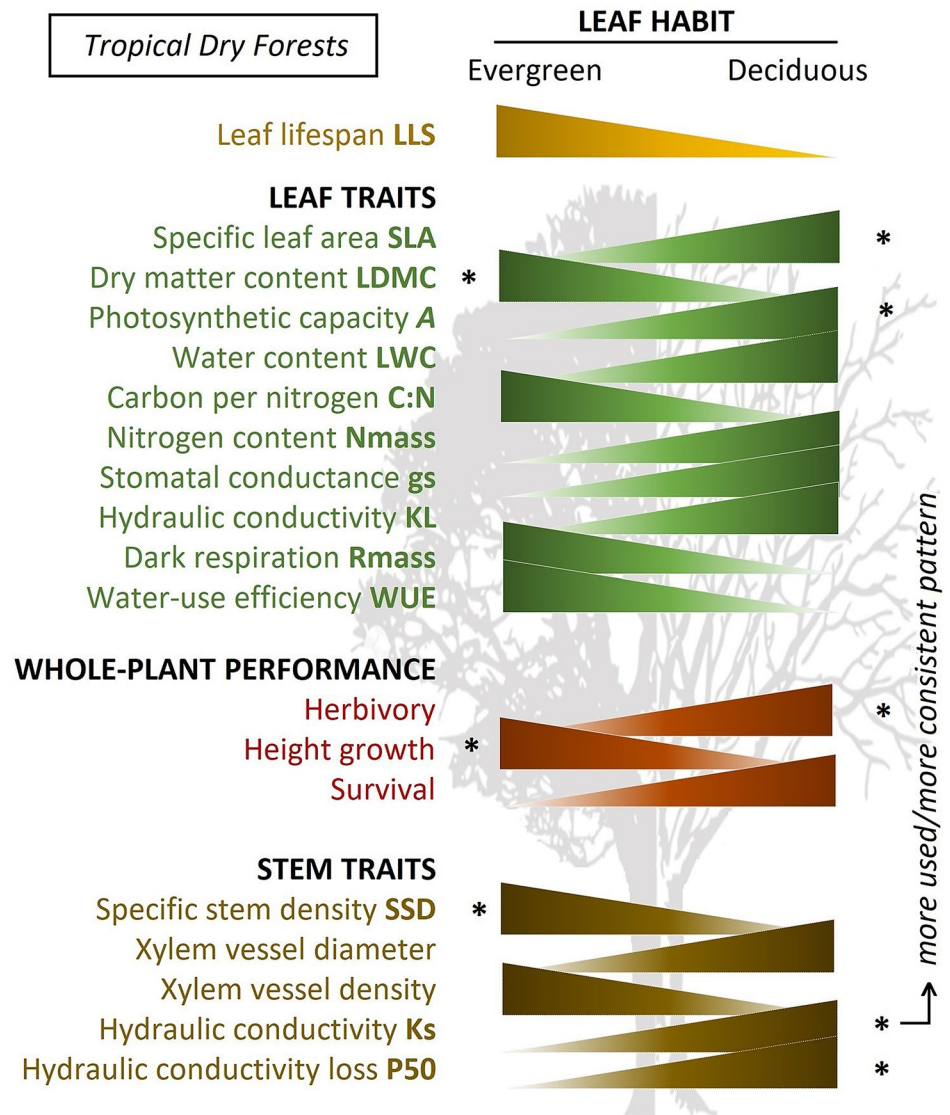
Local context of wood trait variation in tropical dry forests: resistance versus conductivity

In environments with low water availability such as tropical dry forests and savannas, natural selection favors species with resistance to xylem cavitation via wood traits that are closely coordinated with aboveground traits (Bucci et al. 2004, 2005; Worbes et al. 2013; Silva et al. 2019). This includes variation in xylem vessel diameter and pit length, wood porosity, resistance and durability of the pit membrane, and wood density (Chen et al. 2009a). As wood density is easy to measure and is available for a large number of species around the world, it has been widely used in eco-physiological and functional studies as a proxy for the quantity and availability of water in wood (Kushwaha and Singh 2005; Chave et al. 2009; Fan et al. 2018; Méndez-Alonzo et al. 2012; Chaturvedi et al. 2021). Besides being a predictor of wood stiffness, strength and safety, even in the seedling stage, wood density is closely related to plant survival

and has been used to estimate the mechanical support and resistance to physical damage (Falster 2006). In a seasonally dry tropical forest in India, deciduous species responded similarly to rainfall seasonality, but species with the lowest deciduousness also had the highest wood density and dry mass per leaf area (Kushwaha et al. 2010). By expanding this comparison, wood density decreases in inverse proportion with the duration of deciduousness of species (Fig. 1 and Table 1) (Kushwaha, et al. 2010; Chaturvedi et al. 2021). Despite the constraints dense wood presents for growth height (Swenson and Enquist 2007; Poorter et al. 2010; Hoeber et al. 2014; Poorter et al. 2019), individuals with such strategies are typically longer lived due to biomechanical support and larger hydraulic safety margins, which are made possible by thin vessels with thick cell walls at a high density per wood area (Baas et al. 2004; Chave et al. 2009). On the other hand, species with low wood density present rapid growth, because carbon will be invested elsewhere, for example, in the production of larger leaves (Pickup et al. 2005), increasing the risk of damage and mortality (Hacke et al. 2001; King et al. 2006; Sterck et al. 2006). In this sense, interspecific variation in wood density is a key indicator of water transport efficiency, water storage capacity, prevention of leaf turgor loss, and leaf water status regulation (Meinzer et al. 2003; Tarelkin et al. 2019).

Overall, species with greater hydraulic conductivity have wide vessel diameters, despite concurrent increases in the

Fig. 1 Scheme summarizing the main variations in leaf and wood traits, and whole-plant performance between drought-deciduous and evergreen species in the local scale context of tropical dry forests. See Table 1 for complementary information



susceptibility to xylem cavitation. In some cases, xylem cavitation is avoided by the partial or total displacement of leaves, but it can also be achieved by decreasing the efficiency in xylem conductance under negative pressure by investing in xylem vessels with thin diameters and thick and rigid cell walls (Hacke et al. 2001; Chen et al. 2009a; Méndez-Alonzo et al. 2012). Evergreen species are more vulnerable to the loss of efficiency in sapwood conductivity than deciduous species, as deciduous species are more efficient in this regard (Fig. 1) (Fu et al. 2012). While studying Euphorbiaceae deciduous and evergreen species in a seasonally tropical forest in southwestern China, by analyzing the correlation between xylem diameter and water potential at which 50% of hydraulic conductivity is lost (P50), Chen et al. (2009a) showed that the deciduous species were more vulnerable to xylem cavitation than the evergreen ones. In an Asian dry forest, evergreen species presented lower P50 and

leaf hydraulic conductance values and higher leaf water-use efficiency than deciduous species (Fu et al. 2012).

Growth rings are layers of cells visible as concentric circles of distinct width in a cross-section of the wood. They form due to an alteration between cambium activity and dormancy and provide information on tree age and the environmental conditions experienced during its lifetime. The causes of cambium activity dormancy can be triggered by seasonal environmental stress, such as water restriction, temperature restriction, or flooding (Callado et al. 2001, 2014; Brienen et al. 2016; Nath et al. 2016; Tarelkin et al. 2019). In general, drought-deciduous species show distinct growth rings due to a range of cambial activity according to the presence or absence of leaves, mainly as a function of the seasonal distribution of water availability (Callado et al. 2001; Tarelkin et al. 2019). On the other hand, evergreen species do not often form growth rings (O'Brien et al. 2008;

Nath et al. 2016), or if they do, growth rings vary widely, ranging from very distinct, scarcely distinct, or indistinct (Callado et al. 2001). Although Callado et al. (2001) carried out their work in an Atlantic tropical rainforest, these authors suggest that flooding influenced the growth ring formation in evergreen species, whereas leaf fall was related to growth ring formation in deciduous and semideciduous species (Callado et al. 2001).

Elevation is known to drive changes in forest species diversity and composition (Schiatti et al. 2014; Oliveira et al. 2018). Deciduous species at high elevations submitted to water restriction present high-density wood, thick xylem cell walls, low leaf water content, and conductivity (Méndez-Alonzo et al. 2013). In a seasonally dry forest in the Yucatán peninsula in Mexico, Hasselquist et al. (2010) observed lower values of isotopic oxygen ratio in the xylem sapwood of evergreen species compared to deciduous species, which suggests that evergreen species can access water in deeper soil layers. This is an example of how other environmental aspects influence wood traits beyond the climatic control, since elevation modifies water availability and soil fertility (Markesteijn et al. 2011; Méndez-Alonzo et al. 2013).

Larger spatial scales of leaf and wood trait variation across leaf habits

Traits relationships have been shown to be scale dependent, with some results pointing to a lack of support for the leaf economics spectrum at local scales (Messier et al. 2017). Our review shows a consistent pattern of variation in leaf and wood traits between deciduous and evergreen species at the local scale of tropical dry forests (Fig. 1 and Table 1). To apply this discussion to larger spatial contexts, we performed a meta-analysis focusing on Neotropical forests for both dry and rainforests to assess differences between distinct environmental contexts as well. For this aim, we used data from 82 published papers and doctoral and master's dissertations, which together allowed us to compare 9 functional traits of 90 deciduous and 64 evergreen species from tropical dry forests (Caatinga and the Seasonal Atlantic Forest), and 60 deciduous and 165 evergreen species from rainforests (Amazon and the Ombrophilous Atlantic Forest). Descriptions regarding data compilation and methodology are provided in the Supplementary Information 1.

Overall, our results suggest that local trait differences related to leaf habits may not be hold at larger spatial scales, with little or no difference among leaf habits in a multivariate trait ordination. It is worth noting that there was a great representation of the global whole-plant economic spectrum in our dataset (Fig. 2A, B). There was an

overlap in the functional spaces (i.e., convex hulls) of the leaf habits of species from tropical dry forests (Fig. 2C), which suggests selective filtering that converge species with some degree of traits similarity within this forest type. Nevertheless, there were clear functional gradients or continuums within each leaf habit, which also evidence divergences in the strategies species use to arrange a given leaf habit (Lohbeck et al. 2015; German Vargas et al. 2021), because some species vary in their degree of deciduousness according to drought intensity (Borchert et al. 2002). Other explanations are that the leaf habit could not necessarily predict leaf lifespan or other physiological processes (Brodribb and Holbrook, 2005) and that traits may vary in relation to other factors, such as local site conditions or phylogeny (Silva et al. 2021). This functional overlapping was lower in the rainforest (Fig. 2D) in comparison to dry forest (Fig. 2C), where evergreen species tended to diverge from deciduous species by showing more conservative leaf traits (e.g., high LMA and LDMC, and low Nmass and Pmass), although it was not seen for wood traits (mostly in the PC2). This may suggest that when deciduous species are present in rainforests, they benefit from high water availability and thus take greater advantage of this resource though their acquisitive strategy when compared with evergreen species, which partially corresponds to the local patterns reported in the literature.

We highlight that the trait–trait relationships from our study case corresponded to the ones in the global whole-plant economic spectrum (Díaz et al. 2016). In addition to the major traits explored in the global context (LMA, Nmass, SSD, and H), we were able to shed light into some traits not often measured and discussed, but that have gained increasing attention in the last decade, such as wood anatomy. The use of wood anatomy traits revealed patterns that are consistent with those reported in the literature, such as an increase in xylem vessel density related to wood density (Choat et al. 2005; Chave et al. 2009; Chen et al. 2009a). In summary, the results of our meta-analysis suggest that the differentiation of species based solely on leaf habits can obscure key information on the species functioning when taken from the context of local forests. In other words, trait patterns are more predictable at local scales for distinguishing leaf habits and assuming them as informative functional groups. This discussion could benefit from applying this analysis to larger scales than the Neotropics, in which high species diversity can create unclear/inconclusive patterns, such as those reported here. In addition, a relatively low number of studies used in the meta-analysis have been carried out in dry forests, reflecting the disproportionate historical sampling greatly centered on rainforests in the functional trait literature.

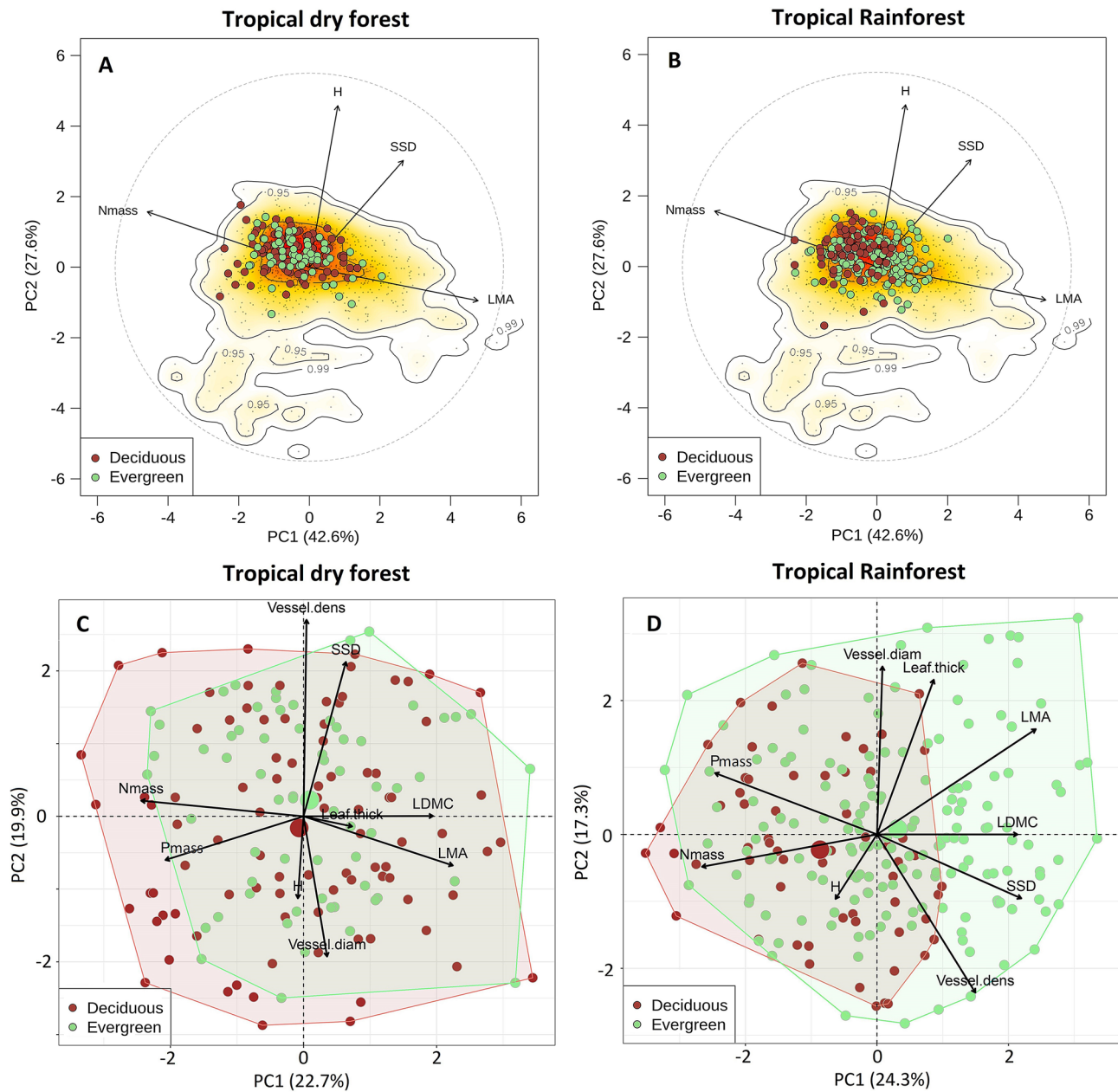


Fig. 2 Multivariate trait ordinations for tree and shrubs species from tropical dry forests and rainforests in the Neotropics. The global context of trait variations (yellow–red gradient in **A** and **B**) was explored relative to our dataset, which was produced in the PhenoSpace application (few key traits allowed) (Segrestin et al. 2021) based on Díaz et al. (2016)’s work. A higher number of traits were analyzed out of the global context to complement the functional evaluation (**C** and

D). Traits’ acronyms: *LMA* leaf mass per area, *Nmass* and *Pmass* leaf nitrogen and phosphorous contents per unit mass, *LDMC* leaf dry matter content, *Leaf.thick* leaf thickness, *SDD* specific stem density, *Vessel.diam* and *Vessel.dens* wood vessel diameter and density, *H* maximum plant height. Each point represents a species, and bigger points in **C** and **D** refer to average weights of convex hulls for each leaf habit

Tropical dry forest: knowledge gaps and climate change

Due to their usefulness for simplifying complex systems such as tropical forests (Vitória et al. 2019; Chave et al. 2009), trait-based approaches are appropriate for

categorizing species and vegetations. A strong knowledge base regarding the leaf and wood traits of tropical dry forests can enhance understanding of the functionality of this ecosystem. Despite scientific advances on traits in the last two decades, future studies should further investigate deciduousness in tropical dry forests and the conservation of this

biome. In addition, the role of intra-specific leaf phenology variation must be considered, as this could be responsible for some degree of overlap among distinct categories of leaf habits.

Leaf traits are the most extensively studied traits in tropical dry forests because of their accessibility (Singh and Verma 2000). However, these traits only provide partial evidence regarding ecosystem processes (Powers and Tiffin 2010). Therefore, wood, root, and seed traits and the economic spectrum should also be considered for a more robust overview. With respect to wood specifically, more information is needed mainly on physiological traits, despite important recent advances (German Vargas et al. 2021; Oliveira et al. 2021). For example, the use of specific wood hydraulics traits such as xylem-specific hydraulic conductivity (K_s , MPa) and hydraulic safety margin (HSM, MPa) in understanding the functional differences among leaf habit has only been tested just for a small number of species when compared to wood or vessel density. This highlights another gap for leaf and wood, as more information pertaining to morphological rather than physiological traits is available. It is essential that advances regarding the knowledge of physiological traits be made to effectively predict the extent to which leaf habits can be used to infer physiological functions of the ecosystem. Leaf habits can be monitored by remote sensing (Huechacona-Ruiz et al. 2020), helping to differentiate the plant functional types and ecosystem productivity. This is important in the context of climate change.

The forecast for this century is for an increase in the frequency of climatic extremes across the tropics (IPCC 2021), thus an impact on ecosystem dynamics and its productivity is expected, especially in environments not normally associated with water stress, such as tropical rainforests (Malhi et al. 2014; Aguirre-Gutierrez et al. 2019). There is evidence from models and observations to suggest that tropical dry forests will have undergone substantial changes in their rainfall regimes, mainly related to anthropogenic climate change (Greve et al. 2014; Allen et al. 2017; IPCC 2021). However, little is known about how individuals, species, and communities will deal with the increased frequency and intensity of droughts predicted by climate models. Several studies of species distribution modeling have been used to map the potential species richness (PSR) and assess how the spatial distribution of PSR will be affected by climate change scenarios. Modeling for Mesoamerican forests have shown that the length of the dry season was the main determinant of the PSR and that an increase in temperature and a decrease in rainfall can cause an overall reduction in the current PSR (Golicher et al. 2012). However, this response was spatially heterogeneous with rainforests suffering more losses than dry forests and the dry forest PSR was more stable under a moderate climate change scenario. Esser et al. (2018) modeling distinct climate change scenarios for the Atlantic

Forest also observed a spatially heterogeneous response, although with a distinct pattern where there was the occurrence of relatively stronger potential loss of suitable environment for semideciduous forest (Seasonally Dry Atlantic Forest), with semideciduous and rainforest species showing a lower degree of overlap in climate adequacy (6.7% in the current climate), which decreases with the climate change scenario (1.2% in Representative Concentration Pathway—RCP8.5/2070). Tropical dry forests are not necessarily more resilient than tropical rainforests, but they may be more resistant to specific disturbances such as fire and drought (Pulla et al. 2015).

In fact, it is possible that wetter tropical forests are either more sensitive or more resistant to climate change than tropical forests found in drier environments (Allen et al. 2017). Thus, studies that help to understand how changes in climate can modify the responses of the tropical forest are of great importance, mainly because the responses of tropical forests to an increasingly drier climate may change biodiversity composition in unexpected ways, with an increase or decrease in tree mortality (Bonal et al. 2016). The risk of tree mortality increases rapidly with the occurrence of extreme or repeated severe droughts (Meir et al. 2015). Tropical forests in West Africa respond differently to a drying climate, modifying their functional trait composition by changing the abundance of deciduous species, especially in drier forests in comparison with humid forests due to climatic water deficit between different forest types (Aguirre-Gutierrez et al. 2019). Since most deciduous species are physiologically and structurally distinct and better adapted to dry environments than evergreen species (Álvarez-Yépez et al. 2017), an increase in their abundance that would improve the ability to adapt ecologically to a drying environment is expected. However, little is known about the role of deciduous and evergreen species in this scenario in tropical forests elsewhere. Thus, expanding our knowledge of leaf habits and physiological traits is critical for overcoming the interlinked challenges of climate change, land use change, and the biodiversity crisis of tropical dry forests.

Conclusions

Deciduous species or species with short leaf lifespan often exhibit resource-acquisitive strategies, while evergreen species or species with long leaf longevity have resource-conservative strategies. Although leaf longevity is usually associated with leaf habits, they are not necessarily linked as the maintenance of the canopy, for example, may depend on the rapid replacement of short-lived leaves in some evergreen species. Regardless of the plant organ, more morphological than physiological/biochemical traits are available for comparing leaf habits. According to the literature that

differentiate leaf habits, a set of leaf and wood traits should be observed instead of using one or few traits. Lastly, leaf habit differentiation is clearer in terms of local contexts of tropical dry forests than in larger spatial contexts.

Author contribution statement All the authors have contributed sufficiently to this manuscript to be included as authors.

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Availability of data and material No applicable.

Declarations

Conflict of interest To the best of our knowledge, no conflict of interest, financial or other, exists.

References

- Aguilar-Peralta JS, González-Rodríguez A, Maldonado-López Y et al (2020) Contrasting patterns of morphology, fluctuating asymmetry and leaf herbivory in three plant species of different successional stages of a tropical dry forest. *Trees* 34:1075–1086. <https://doi.org/10.1007/s00468-020-01982-z>
- Aguirre-Gutiérrez J, Oliveras I, Rifai S, Fauset S, Adu-Bredu S, Affum-Baffoe K, Baker TR, Feldpausch TR, Gvozdevaite A, Hubau W, Kraft NJB, Lewis SL, Moore S, Niinemets Ü, Peprah T, Phillips OL, Ziemińska K, Enquist B, Malhi Y, Penuelas J (2019) Drier tropical forests are susceptible to functional changes in response to a long-term drought. *Ecol Lett* 22(5):855–865. <https://doi.org/10.1111/ele.13243>
- Allen K, Dupuy JM, Gei MG et al (2017) Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? *Environ Res Lett* 12:023001. <https://doi.org/10.1088/1748-9326/aa5968>
- Álvarez-Yépez JC, Búrquez A, Martínez-Yrizar A et al (2017) Resource partitioning by evergreen and deciduous species in a tropical dry forest. *Oecologia* 183:607–618. <https://doi.org/10.1007/s00442-016-3790-3>
- Ávila-Lovera E, Coronel RUI, Tezara W (2019) Seasonal gas exchange and resource-use efficiency in evergreen versus deciduous species from a tropical dry forest. *Tree Physiol* 39:1561–1571. <https://doi.org/10.1093/treephys/tpz060>
- Baas P, Ewers F, Davis SD et al (2004) The evolution of xylem physiology. In: Raven J, Edwards D (eds) *The evolution of plant physiology: from whole plants to ecosystems*. Academic Press, Cambridge, pp 273–295
- Bartlett MK, Scoffoni C, Sack L (2012) The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol Lett* 15:393–405. <https://doi.org/10.1111/j.1461-0248.2012.01751.x>
- Bickford CP (2016) Ecophysiology of leaf trichomes. *Funct Plant Biol* 43(9):807–814. <https://doi.org/10.1071/FP16095>
- Bonal D, Burban B, Stahl C et al (2016) The response of tropical rainforests to drought—lessons from recent research and future prospects. *Ann for Sci* 73(1):27–44. <https://doi.org/10.1007/s13595-015-0522-5>
- Borchert R, Rivera G, Hagnauer W (2002) Modification of vegetative phenology in a tropical semideciduous forest by abnormal drought and rain. *Biotropica* 34:27–39. <https://doi.org/10.1111/j.1744-7429.2002.tb00239.x>
- Brienen RJW, Schöngart J, Zuidema PA (2016) Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees. In: Goldstein G, Santiago L (eds) *Tropical tree physiology*. *Tree Physiol*, 6th edn. Springer, Cham, pp 439–461. https://doi.org/10.1007/978-3-319-27422-5_20
- Brodribb TJ, Holbrook NM (2005) Leaf physiology does not predict leaf habit; examples from tropical dry forest. *Trees* 19:290–295. <https://doi.org/10.1007/s00468-004-0390-3>
- Brodribb TJ, Holbrook NM, Edwards EJ et al (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant Cell Environ* 26:443–450. <https://doi.org/10.1046/j.1365-3040.2003.00975.x>
- Bucci SJ, Goldstein G, Meinzer FC et al (2004) Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiol* 24:891–899. <https://doi.org/10.1093/treephys/24.8.891>
- Bucci SJ, Goldstein G, Meinzer FC et al (2005) Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in neotropical savanna trees. *Trees* 19:296–304. <https://doi.org/10.1007/s00468-004-0391-2>
- Callado CH, Silva Neto SJ, Scarano FR et al (2001) Anatomical features of growth rings in flood-prone trees of the atlantic rain forest in Rio de Janeiro, Brazil. *IAWA Journal* 22(1):29–42
- Callado CH, Vasconcellos TJ, Costa MS et al (2014) Studies on cambial activity: advances and challenges in the knowledge of growth dynamics of Brazilian woody species. *An Acad Bras Ciênc* 86:277–284. <https://doi.org/10.1590/0001-3765201320130033>
- Carmona D, Lajeunesse MJ, Johnson MT (2011) Plant traits that predict resistance to herbivores. *Funct Ecol* 25(2):358–367. <https://doi.org/10.1111/j.1365-2435.2010.01794.x>
- Carrasco-Carballido V, Martínez-Garza C, Jiménez-Hernández H et al (2019) Effects of initial soil properties on three-year performance of six tree species in tropical dry forest restoration plantings. *Forests* 10(5):428. <https://doi.org/10.3390/f10050428>
- Chakrabarty S, Sharma S, Ganguly S et al (2021) Quantitative estimates of deciduousness in woody species from a seasonally dry tropical forest are related to leaf functional traits and the timing of leaf flush. *BioRxiv*. <https://doi.org/10.1101/2021.03.03.433407>
- Chaturvedi RK, Raghubanshi AS, Singh JS (2011) Plant functional traits with particular reference to tropical deciduous forests: a review. *J Biosci* 36:963–981. <https://doi.org/10.1007/s12038-011-9159-1>

- Chaturvedi RK, Tripathi A, Raghubanshi AS et al (2021) Functional traits indicate a continuum of tree drought strategies across a soil water availability gradient in a tropical dry forest. *For Ecol Manag* 482:118740. <https://doi.org/10.1016/j.foreco.2020.118740>
- Chave J, Coomes D, Jansen S et al (2009) Towards a worldwide wood economics spectrum. *Ecology Lett* 12:351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Chen JW, Zhang Q, Li XS et al (2009a) Independence of stem and leaf hydraulic traits in six *Euphorbiaceae* tree species with contrasting leaf phenology. *Planta* 230:459–468. <https://doi.org/10.1007/s00425-009-0959-6>
- Chen JW, Zhang Q, Cao KF (2009b) Inter-species variation of photosynthetic and xylem hydraulic traits in the deciduous and evergreen *Euphorbiaceae* tree species from a seasonally tropical forest in south-western China. *Ecol Res* 24:65–73. <https://doi.org/10.1007/s11284-008-0482-4>
- Choat B, Ball MC, Lully JG et al (2005) Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. *Trees* 19:305–311. <https://doi.org/10.1007/s00468-004-0392-1>
- Choat B, Ball MC, Lully JG et al (2006) Seasonal patterns of leaf gas exchange and water relations in dry rain forest trees of contrasting leaf phenology. *Tree Physiol* 26:657–664. <https://doi.org/10.1093/treephys/26.5.657>
- Collins CG, Wright SJ, Wurzburger N (2016) Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees. *Oecologia* 180:1037–1047. <https://doi.org/10.1007/s00442-015-3410-7>
- Cuba N, Lawrence D, Rogan J et al (2018) Local variability in the timing and intensity of tropical dry forest deciduousness is explained by differences in forest stand age. *Gisci Remote Sens* 55:437–456. <https://doi.org/10.1080/15481603.2017.1403136>
- Curtis PS, Ackerly DD (2008) Introduction to a “virtual special issue” on plant ecological strategy axes in leaf and wood traits. *New Phytol* 179:901–903. <https://doi.org/10.1111/j.1469-8137.2008.02593.x>
- Díaz S, Kattge J, Cornelissen JHC et al (2016) The global spectrum of plant form and function. *Nature* 529:167–183. <https://doi.org/10.1038/nature16489>
- Dirzo R, Raven PH (2003) Global state of biodiversity and loss. *Annu Rev Environ Resources* 28:137–167. <https://doi.org/10.1146/annurev.energy.28.050302.105532>
- Donovan LA, Maherali H, Caruso CM et al (2011) The evolution of the worldwide leaf economics spectrum. *Trends Ecology Evol* 26:88–95. <https://doi.org/10.1016/j.tree.2010.11.011>
- Eamus D, Prior L (2001) Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. *Adv Ecol Res* 32:113–197. [https://doi.org/10.1016/S0065-2504\(01\)32012-3](https://doi.org/10.1016/S0065-2504(01)32012-3)
- Esser LF, Neves D, Jarenkow JA (2018) Habitat-specific impacts of climate change in the Mata Atlântica biodiversity hotspot. *Divers Distrib* 25:1846–1856. <https://doi.org/10.1111/ddi.12984>
- Estrada-Medina H, Santiago LS, Graham RC et al (2013) Source water, phenology and growth of two tropical dry forest tree species growing on shallow karst soils. *Trees* 27:1297–1307. <https://doi.org/10.1007/s00468-013-0878-9>
- Falster DS (2006) Sapling strength and safety: the importance of wood density in tropical forests. *New Phytol* 171:237–239. <https://doi.org/10.1111/j.1469-8137.2006.01809.x>
- Fan D, Zhang S, Yan H et al (2018) Do karst woody plants control xylem tension to avoid substantial xylem cavitation in the wet season? *For Ecosyst* 5:1–11. <https://doi.org/10.1186/s40663-018-0158-7>
- FAO (2000) Global ecological zoning for the global forest resources assessment 2000 final report. *Forest Resources Assessment—WP* 56. http://www.fao.org/3/ad652e/ad652e07.htm#P470_31994. Accessed in 25 Sep 2020
- Fu P-L, Jiang Y-J, Wang A-Y et al (2012) Stem hydraulic traits and leaf water-stress tolerance are coordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest. *Ann Bot* 110:189–199. <https://doi.org/10.1093/aob/mcs092>
- Gei MG, Powers JS (2014) Nutrient cycling in tropical dry forests. In: Sanchez-Azofeifa A, Powers JS, Fernandes GW et al (eds) *Tropical dry forests in the Americas: ecology, conservation, and management*. CRC Press, Boca Raton, pp 141–156
- GermanVargas G, Brodribb TJ, Dupuy JM et al (2021) Beyond leaf habit: generalities in plant function across 97 tropical dry forest tree species. *New Phytol* Accepted. <https://doi.org/10.1111/nph.17584>
- Givnish TJ (2002) Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fenn* 36(3):703–743. <https://doi.org/10.14214/sf.535>
- Golicher DJ, Cayuela L, Newton AC (2012) Effects of climate change on the potential species richness of Mesoamerican forests. *Biotropica* 44(3):284–293. <https://doi.org/10.1111/j.1744-7429.2011.00815.x>
- Greve P, Orłowsky B, Mueller B et al (2014) Global assessment of trends in wetting and drying over land. *Nat Geosc* 7(10):716–721. <https://doi.org/10.1038/ngeo2247>
- Hacke UG, Sperry JS, Pockman WT et al (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461. <https://doi.org/10.1007/s004420100628>
- Hanley ME, Lamont BB, Fairbanks MM et al (2007) Plant structural traits and their role in anti-herbivore defence. *Perspect Plant Ecol Evol Syst* 8(4):157–178. <https://doi.org/10.1016/j.ppees.2007.01.001>
- Hasnat GNT, Hossain MK (2020) Global overview of tropical dry forests. In: Bhadouria R, Tripathi S, Srivastava P et al (eds) *Handbook of research on the conservation and restoration of tropical dry forests*, Pennsylvania, pp 1–23
- Hasselquist NJ, Allen MF, Santiago LS (2010) Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia* 164:881–890. <https://doi.org/10.1007/s00442-010-1725-y>
- Haworth M, McElwain J (2008) Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf and cuticular micromorphology. *Palaeogeogr Palaeoclimatol Palaeoecol* 262(1–2):79–90. <https://doi.org/10.1016/j.palaeo.2008.02.009>
- Hiremath AJ (2000) Photosynthetic nutrient-use efficiency in three fast-growing tropical trees with differing leaf longevities. *Tree Physiol* 20:937–944. <https://doi.org/10.1093/treephys/20.14.937>
- Hoerber S, Leuschner C, Köhler L et al (2014) The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate. *For Ecol Manag* 330:126–136. <https://doi.org/10.1016/j.foreco.2014.06.039>
- Holanda AER, Souza BC, Carvalho ECD et al (2019) How do leaf wetting events affect gas exchange and leaf lifespan of plants from seasonally dry tropical vegetation? *Plant Biol* 21:1097–1109. <https://doi.org/10.1111/plb.13023>
- Huechaona-Ruiz AH, Dupuy JM, Schwartz NB et al (2020) Mapping tree species deciduousness of tropical dry forests combining reflectance, spectral unmixing, and texture data from high-resolution imagery. *Forests* 11(11):1234. <https://doi.org/10.3390/f11111234>
- IPCC (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K,

- Lonny E, Matthews JBR, Maycock TK, Waterfield T, Yeleği O, Yu R, Zhou B (eds.). Cambridge University Press. In Press
- Ishida A, Diloksumpun S, Ladpala P et al (2006) Contrasting seasonal leaf habits of canopy trees between tropical dry-deciduous and evergreen forests in Thailand. *Tree Physiol* 26:643–656. <https://doi.org/10.1093/treephys/26.5.643>
- Kikuzawa K, Lechowicz MJ (2011) *Ecology of leaf longevity*. Springer, Berlin
- King DA, Davies SJ, Tan S et al (2006) The role of wood density and stem support costs in the growth and mortality of tropical trees. *J Ecol* 94(3):670–680. <https://doi.org/10.1111/j.1365-2745.2006.01112.x>
- Kursar TA, Engelbrecht BMJ, Burke A et al (2009) Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Funct Ecol* 23:93–102. <https://doi.org/10.1111/j.1365-2435.2008.01483.x>
- Kushwaha CP, Singh KP (2005) Diversity of leaf phenology in a tropical deciduous forest in India. *J Trop Ecol* 21:47–56. <https://doi.org/10.1017/S0266467404002032>
- Kushwaha CP, Tripathi SK, Singh KP et al (2010) Diversity deciduousness and phenological traits of key Indian dry tropical forest trees. *Ann Sci* 67:1–8. <https://doi.org/10.1051/forest/2009116>
- Lal CB, Annapurna C, Raghubanshi AS et al (2011) Effect of leaf habit and soil type on nutrient resorption and conservation in woody species of a dry tropical environment. *Can J Bot* 79:1066–1075. <https://doi.org/10.1139/b01-077>
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* 16:545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Li L, Mc Cormack ML, Ma C et al (2015) Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. *Ecol Lett* 18:899–906. <https://doi.org/10.1111/ele.12466>
- Linares-Palomino R, Oliveira-Filho AT, Pennington RT (2011) Neotropical seasonally dry forests: diversity, endemism, and biogeography of woody plants. In: Dirzo R, Young HS, Mooney HA et al (eds) *Seasonally dry tropical forests: ecology and conservation*. Island Press, Washington, pp 1–23
- Lohbeck M, Lebrija-Trejos E, Martínez-Ramos M et al (2015) Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. *PLoS One* 10(4):e0123741. <https://doi.org/10.1371/journal.pone.0123741>
- Lusk CH, Wright I, Reich PB (2003) Photosynthetic differences contribute to competitive advantage of evergreen angiosperm trees over evergreen conifers in productive habitats. *New Phytol* 160:329–336. <https://doi.org/10.1046/j.1469-8137.2003.00879.x>
- Malhi Y, Wright J (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philos Trans R Soc Lond [bio]* 359:311–329. <https://doi.org/10.1098/rstb.2003.1433>
- Malhi Y, Gardner TA, Goldsmith GR et al (2014) Tropical forests in the anthropocene. *Annu Rev Environ Resour* 39:125–159. <https://doi.org/10.1146/annurev-environ-030713-155141>
- Marchin R, Zeng H, Hoffmann W (2010) Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. *Oecologia* 163:845–854. <https://doi.org/10.1007/s00442-010-1614-4>
- Markesteijn L, Poorter L, Paz H et al (2011) Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant Cell Environ* 34:137–148. <https://doi.org/10.1111/j.1365-3040.2010.02231.x>
- Marques TV, Mendes K, Mutti P et al (2020) Environmental and biophysical controls of evapotranspiration from Seasonally Dry Tropical Forests (Caatinga) in the Brazilian Semiarid. *Agric for Meteorol* 287:107957. <https://doi.org/10.1016/j.agrformet.2020.107957>
- Meinzer FC, James SA, Goldstein G, Woodruff D (2003) Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant Cell Environ* 26:1147–1155. <https://doi.org/10.1046/j.1365-3040.2003.01039.x>
- Meir P, Pennington RT (2011) Climatic change and seasonally dry tropical forests. In: Dirzo R, Young HS, Mooney HA et al (eds) *Seasonally dry tropical forests*. Island Press, Washington, pp 279–299
- Meir P, Mencuccini M, Dewar RC (2015) Drought-related tree mortality: addressing the gaps in understanding and prediction. *New Phytol* 207(1):28–33. <https://doi.org/10.1111/nph.13382>
- Méndez-Alonzo R, Paz H, Zuluaga RC et al (2012) Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93:397–406. <https://doi.org/10.1890/1112-1213.1>
- Méndez-Alonzo R, Pineda-García F, Paz H et al (2013) Leaf phenology is associated with soil water availability and xylem traits in a tropical dry forest. *Trees* 27:745–754. <https://doi.org/10.1007/s00468-012-0829-x>
- Messier J, McGill BJ, Enquist BJ et al (2017) Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography* 40(6):685–697. <https://doi.org/10.1111/ecog.02006>
- Missio FDF, da Silva AC, Higuchi P et al (2017) Functional traits of tree species in a fragment of araucaria forest in Lages, Santa Catarina state. *Ciência Florestal* 27:215–224. <https://doi.org/10.5902/1980509826460>
- Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <https://doi.org/10.1038/35002501>
- Nath CD, Munoz F, Pélissier R et al (2016) Growth rings in tropical trees: role of functional traits, environment, and phylogeny. *Trees* 30:2153–2175. <https://doi.org/10.1007/s00468-016-1442-1>
- O'Brien JJ, Oberbauer SF, Clark DB et al (2008) Phenology and stem diameter increment seasonality in a Costa Rican wet tropical forest. *Biotropica* 40:151–159. <https://doi.org/10.1111/j.1744-7429.2007.00354.x>
- Oliveira RS, Costa FRC, Baalen E et al (2018) Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. *New Phytol* 221:1457–1465. <https://doi.org/10.1111/nph.15463>
- Oliveira RS, Eller CB, Barros FDV et al (2021) Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytol* 230(3):904–923. <https://doi.org/10.1111/nph.17266>
- Osnas JLD, Katabuchi M, Kitajima K et al (2018) Divergent drivers of leaf trait variation within species, among species, and among functional groups. *PNAS* 155:5480–5485. <https://doi.org/10.1073/pnas.1803989115>
- Pacifici M, Visconti P, Butchart SH et al (2017) Species' traits influenced their response to recent climate change. *Nat Clim Chang* 7(3):205–208. <https://doi.org/10.1038/nclimate3223>
- Pantoja MV, Mota MA, Jardim MAG (2019) Influence of rainfall in natural regeneration in a dense ombrophylous forest alluvial in eastern amazon, Pará, Brasil. *Rev Bras Geogr Fis* 12:1302–1309. <https://doi.org/10.26848/rbgf.v12.4.p1302-1309>
- Pennington RT, Lavin M, Oliveira-Filho A (2009) Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. *Annu Rev Ecol Evol Syst* 40:437–457. <https://doi.org/10.1146/annurev.ecolsys.110308.120327>
- Pérez-Harguindeguy N, Diaz S, Garnier E et al (2016) *New Handbook for standardized measurement of plant functional traits worldwide*. *Aust J Bot* 61:167–234. https://doi.org/10.1071/BT1225_CO
- Phillips OL, Aragão LE, Lewis SL et al (2009) Drought sensitivity of the Amazon rainforest. *Science* 323(5919):1344–1347. <https://doi.org/10.1126/science.1164033>

- Pickup M, Westoby M, Basden A (2005) Dry mass costs of deploying leaf area in relation to leaf size. *Funct Ecol* 19(1):88–97. <https://doi.org/10.1111/j.0269-8463.2005.00927.x>
- Pineda-García F, Paz H, Meinzer FC et al (2015) Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiol* 36:208–217. <https://doi.org/10.1093/treephys/tpv124>
- Poorter L, Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87:1733–1743. [https://doi.org/10.1890/0012-9658\(2006\)87\[1733:LTAGPJ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1733:LTAGPJ]2.0.CO;2)
- Poorter L, Van de Plassche M, Willems S, Boot RGA (2004) Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biol* 6:746–754. <https://doi.org/10.1055/s-2004-821269>
- Poorter L, Bongers F, Sterck FJ, Wöll H (2005) Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. *J Ecol* 93:256–267. <https://doi.org/10.1111/j.1365-2745.2004.00956.x>
- Poorter L, McDonald I, Alarcón A et al (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol* 185(2):481–492. <https://doi.org/10.1111/j.1469-8137.2009.03092.x>
- Poorter L, Rozendaal DM, Bongers F et al (2019) Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nat Ecol Evol* 3(6):928–934. <https://doi.org/10.1038/s41559-019-0882-6>
- Powers JS, Tiffin P (2010) Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. *Funct Ecol* 24:927–936. <https://doi.org/10.1111/j.1365-2435.2010.01701.x>
- Powers JS, Backlund KK, Gei MG et al (2015) Nutrient addition effects on tropical dry forests: a mini-review from microbial to ecosystem scales. *Front Earth Sci* 3:34. <https://doi.org/10.3389/feart.2015.00034>
- Pringle EG, Adams R, Broadbent E et al (2011) Distinct leaf-trait syndromes of evergreen and deciduous trees in a seasonally dry tropical forest. *Biotropica* 43:299–308. <https://doi.org/10.1111/j.1744-7429.2010.00697.x>
- Prior LD, Eamus D, Bowman DMJS (2003) Leaf attributes in the seasonally dry tropics: a comparison of four habitats in northern Australia. *Funct Ecol* 17:504–515. <https://doi.org/10.1046/j.1365-2435.2003.00761.x>
- Pulla S, Ramaswami G, Mondal N et al (2015) Assessing the resilience of global seasonally dry tropical forests. *Int for Rev* 17(3):91–113. <https://doi.org/10.1505/146554815815834796>
- Reich PB (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *J Ecology* 102:275–301. <https://doi.org/10.1111/1365-2745.12211>
- Russo SE, Kitajima K (2016) The ecophysiology of leaf lifespan in tropical forests: adaptive and plastic responses to environmental heterogeneity. In: Goldstein G, Santiago L (eds) *Tropical tree physiology*, 1st edn. Springer, Berlin, pp 357–383
- Sastry A, Barua D (2017) Leaf thermotolerance in tropical trees from a seasonally dry climate varies along the slow-fast resource acquisition spectrum. *Sci Rep* 7:11246. <https://doi.org/10.1038/s41598-017-11343-5>
- Schiatti J, Emilio T, Rennó CD et al (2014) Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecol Divers* 7:241–253. <https://doi.org/10.1080/17550874.2013.783642>
- Segrestin J, Sartori K, Navas ML et al (2021) PhenoSpace: a Shiny application to visualize trait data in the phenotypic space of the global spectrum of plant form and function. *Ecol Evol* 11:1526–1534. <https://doi.org/10.1002/ece3.6928>
- Shipley B, Lechowicz MJ, Wright I et al (2006) Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology* 87:535–541. <https://doi.org/10.1890/05-1051>
- Silva JO, Espírito-Santo MM, Moraes HC (2015) Leaf traits and herbivory on deciduous and evergreen trees in a tropical dry forest. *Basic Appl Ecol* 16:210–219. <https://doi.org/10.1016/j.baee.2015.02.005>
- Silva MS, Funch LS, Silva LB (2019) The growth ring concept: seeking a broader and unambiguous approach covering tropical species. *Biol Rev* 94:1161–1178. <https://doi.org/10.1111/brv.12495>
- Silva JLA, Souza AF, Vitória AP (2021) Historical and current environmental selection on functional traits of trees in the Atlantic Forest biodiversity hotspot. *J Veg Sci* 32:e13049. <https://doi.org/10.1111/jvs.13049>
- Singh S, Verma AK (2000) Plant functional traits in tropical dry forests: a review. In: Bhadouria R, Tripathi S, Srivastava P et al (eds) *Handbook of research on the conservation and restoration of tropical dry forests*, Pennsylvania, pp 66–88
- Souza BC, Oliveira RS, Araújo FS et al (2015) Functional divergences and strategies of resistance to drought between tropical deciduous and evergreen species. *Rodriguésia* 66(1):021–032. <https://doi.org/10.1590/2175-7860201566102>
- Souza BC, Carvalho ECD, Oliveira RS et al (2020) Drought response strategies of deciduous and evergreen woody species in a seasonally dry neotropical forest. *Oecologia* 194:221–236. <https://doi.org/10.1007/s00442-020-04760-3>
- Sterck FJ, van Gelder HA, Poorter L (2006) Mechanical branch constraints contribute to life-history variation across tree species in a Bolivian forest. *J Ecol* 94:1192–1200. <https://doi.org/10.1111/j.1365-2745.2006.01162.x>
- Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *Am J Bot* 94(3):451–459. <https://doi.org/10.3732/ajb.94.3.451>
- Tarelkin Y, Hufkens K, Hahn S et al (2019) Wood anatomy variability under contrasted environmental conditions of common deciduous and evergreen species from central African forests. *Trees* 33:893–909. <https://doi.org/10.1007/s00468-019-01826-5>
- Taubert F, Fischer R, Groeneveld J et al (2018) Global patterns of tropical forest fragmentation. *Nature* 554:519–522. <https://doi.org/10.1038/nature25508>
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. *New Phytol* 176:749–763. <https://doi.org/10.1111/j.1469-8137.2007.02275.x>
- Violle C, Navas ML, Vile D et al (2007) Let the concept of trait be functional. *Oikos* 116:882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Vitória AP, Vieira TO, de Camargo PB et al (2016) Using leaf $\delta^{13}\text{C}$ and photosynthetic parameters to understand acclimation to irradiance and leaf age effects during tropical forest regeneration. *For Ecol Manag* 379:50–60. <https://doi.org/10.1016/j.foreco.2016.07.048>
- Vitória AP, Ávila-Lovera E, Vieira TO et al (2018) Isotopic composition of leaf carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of deciduous and evergreen understorey trees in two tropical Brazilian Atlantic forests. *J Trop Ecol* 34:145–156. <https://doi.org/10.1017/S0266467418000093>
- Vitória AP, Alves LF, Santiago LS (2019) Atlantic forest and leaf traits: an overview. *Trees* 33:1535–1547. <https://doi.org/10.1007/s00468-019-01864-z>
- Werden LK, Waring BG, Smith-Martin CM et al (2018) Tropical dry forest trees and lianas differ in leaf economic spectrum traits but have overlapping water-use strategies. *Tree Physiol* 38:517–530. <https://doi.org/10.1093/treephys/tpx135>

- Westoby M, Falster DS, Moles AT et al (2002) Plant ecological strategies: some leading dimensions of variation between species. *Ann Rev Ecol Syst* 33(1):125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>
- Worbes M, Blanchart S, Fichtler E (2013) Relations between water balance, wood traits and phenological behavior of tree species from a tropical dry forest in Costa Rica—a multifactorial study. *Tree Physiol* 33:527–536. <https://doi.org/10.1093/treephys/tpt028>
- Wright IJ, Westoby M (2002) Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytol* 155:403–416. <https://doi.org/10.1046/j.1469-8137.2002.00479.x>
- Wright IJ, Reich PB, Westoby M et al (2004) The world-wide leaf economics spectrum. *Nature* 428:821–827. <https://doi.org/10.1038/nature02403>
- Wright IJ, Reich PB, Cornelissen JHC et al (2005) Modulation of leaf economic traits and trait relationships by climate. *Glob Ecol Biogeogr* 14:411–421. <https://doi.org/10.1111/j.1466-822x.2005.00172.x>
- Wright SJ, Kitajima K, Kraft NJB et al (2010) Functional traits and the growth-mortality tradeoff in tropical trees. *Ecology* 91:3664–3674. <https://doi.org/10.1890/09-2335.1>
- Yan Z, Li P, Chen Y et al (2016) Nutrient allocation strategies of woody plants: an approach from the scaling of nitrogen and phosphorus between twig stems and leaves. *Sci Rep* 6:20099. <https://doi.org/10.1038/srep20099>
- Yang Y-J, Bi M-H, Nie Z-F et al (2021) Evolution of stomatal closure to optimise water use efficiency in response to dehydration in ferns and seed plants. *New Phytol*. <https://doi.org/10.1111/nph.17278>
- Zvereva E, Kozlov MV (2014) Effects of herbivory on leaf life span in woody plants: a meta-analysis. *J Ecol* 102:873–881. <https://doi.org/10.1111/1365-2745.12252>

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