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# Lianas have more acquisitive traits than trees in a dry but not in a wet forest

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## Abstract

1. Lianas are increasing in relative abundance and biomass in many tropical forests. We tested the hypothesis that lianas conform to the fast and acquisitive end of the continuum of plant strategies, allowing lianas to acquire resources faster than trees.
2. We assessed functional traits representative of the leaf (LES) and wood economics spectrum (WES), including plant hydraulics, in 16 liana and 16 tree species in the canopy of two tropical forests at the extremes of the climatic and geological gradient across the Isthmus of Panama.
3. For both forests, we observed a trade-off between the construction of more productive leaves with rapid turnover and expensive leaves with slower turnover. We also found trait variation associated with wood and hydraulic traits. These two axes were orthogonal, suggesting that trade-offs at the leaf and stem, including plant hydraulics, operate independently.
4. For the dry forest, lianas had cheaper and more efficient leaves than trees. For the wet forest, lianas and trees overlapped in leaf and stem characteristics. Moreover, the duration of green foliage highly explained the variation between dry forest species, reflecting different adaptations to drought. In the wet forest, fast-growing species benefited from a higher return on investments of leaf vascular tissues than slow-growing species and they had a higher capacity to transport water through the leaf.
5. A higher capacity to construct more productive leaves and display leaves with lower costs may favour lianas over trees in light interception, photosynthetic rates, and growth under high light and nutrient availability in dry forests.
6. *Synthesis.* Lianas in a dry tropical forest had a more acquisitive strategy than trees, characterized by more productive leaves and more efficient display for light interception. In dry environments, lianas appear to benefit from high-light and nutrient-rich soils and thus take advantage of higher resource conditions compared to trees. By contrast, in a wet tropical forest, lianas and trees overlapped in leaf and stem characteristics and lianas were not more acquisitive than trees. In

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wet environments, low light availability and nutrient-poor soils in a context of low water limitation may constrain variation in resource acquisition strategies between lianas and trees.

#### KEYWORDS

canopy, functional diversity, functional traits, lianas, plant functional types, plant strategies, trees, tropical forests

## 1 | INTRODUCTION

Lianas (woody vines) are an abundant and diverse plant group in forests worldwide, particularly in lowland tropical forests (Gentry, 1992), where they account for c. 19%–35% of species diversity (Appanah et al., 1993; Jongkind & Hawthorne, 2005; Schnitzer et al., 2012) and constitute up to 40% of the woody stems (Schnitzer & Bongers, 2011) and leaf productivity (Hegarty & Caballé, 1992; Phillips et al., 2002). Several reports suggest that lianas are increasing in density and biomass relative to trees in some tropical forest areas (Schnitzer & Bongers, 2011; Wright, Calderón, et al., 2004). An increase in lianas relative to trees may pose negative effects on the dynamics of trees and tropical forests. Lianas suppress tree regeneration (Schnitzer & Carson, 2010), growth (van der Heijden et al., 2015, 2019), reproduction (García León et al., 2018; Wright et al., 2015) and survival (Ingwell et al., 2010; Wright et al., 2015).

Lianas may have distinct functional strategies in relation to resource acquisition leaf and stem traits than do trees and lianas may conform more to the fast and acquisitive end of a continuum of plant strategies (Wright, Reich, et al., 2004), but evidence for differences in hydraulic traits is lacking. Trait differences could allow lianas to acquire resources faster than trees (Smith-Martin et al., 2019; Werden et al., 2018; Zhu & Cao, 2009). However, not all studies have found clear trait differences in leaf and stem properties between lianas and trees (e.g. Collins et al., 2016; Smith-Martin et al., 2019; Zhang et al., 2019). Moreover, multi-species comparisons of large individuals that reside in the upper canopy of tropical forests are scarce, as well as comparisons between individuals from multiple forest sites. The study of canopy lianas and trees is important given that large lianas and trees can intercept more light but also lose more water under full exposure in the upper forest canopy, affecting overall plant carbon exchange.

Plant functional traits are any morphological, physiological or phenological feature that affects plant growth, survival and reproduction (Violle et al., 2007). Traits are thought to reflect the ecological strategy of individuals and species (McGill et al., 2006; Reich & Cornelissen, 2014). At the leaf level, species traits tend to covary along a continuum that runs from fast to slow returns on investments of nutrients and dry mass of leaves (Wright, Reich, et al., 2004), which is also known as the leaf economics spectrum (LES). 'Fast' acquisitive trait values increase plant growth, whereas 'slow' conservative traits increase leaf and plant survival (Sterck et al., 2006). At the stem level, a similar trait continuum exists, which is known as the

wood economics spectrum (WES), where wood density is thought to determine the mechanical and hydraulic properties of the stem, leading to a trade-off between growth and survival potential (Chave et al., 2009). These leaf and stem traits, combined with reproductive and whole-plant traits, form the main dimensions of ecological variation among plants (Díaz et al., 2016; Westoby et al., 2002).

Plant hydraulics are inherently coupled to stem and leaf traits (Brodribb & Feild, 2000; Sperry, 2000), and thus potentially to the LES and WES (Sterck et al., 2011, 2014). Acquisitive plants tend to have high leaf stomatal conductance, which is required for the maintenance of high photosynthetic rates and rapid growth. Since high leaf conductance comes with high water losses via transpiration, acquisitive plants require efficient water transport through the stem and leaves (Brodribb et al., 2002; Sack & Holbrook, 2006; Sperry, 2000), which is linked to trait adaptations such as large xylem conduit diameters (Sack & Frole, 2006; Sack & Scoffoni, 2013; Tyree & Ewers, 1991). However, such trait adaptations may come with reduced safety against cavitation during droughts (Markesteijn et al., 2011; Sack & Scoffoni, 2013) and may, in turn, lead to lower water transport, lower photosynthesis and ultimately even plant death (Engelbrecht et al., 2005; Rowland et al., 2015). There is some support for hydraulic trait adaptations in leaves and stem for lianas versus trees (De Guzman et al., 2017; Marechaux et al., 2017), but support for a hydraulic efficiency versus safety trade-off between lianas and trees remains ambiguous (e.g. Zhang et al., 2019).

Lianas tend to be more abundant and diverse in highly seasonal forests compared to wet aseasonal forests (DeWalt et al., 2010; Parolari et al., 2020; Swaine & Grace, 2007). This unique distribution of lianas is suggested to be driven by their ability to grow more than co-occurring trees during seasonal drought (Schnitzer, 2005). Lianas are thought to have a greater physiological capacity to take up water than co-occurring trees, and coupled with more acquisitive trait syndromes, lianas may benefit and take advantage from the high dry-season light conditions while trees cannot (Schnitzer, 2005; Schnitzer & Bongers, 2011). Several studies indicate that at the stem level, lianas have wider and longer vessels than other land plants, which facilitate faster water transport, and therefore higher stomatal conductance and gas exchange (Gartner et al., 1990; Jacobsen et al., 2012; Zhu & Cao, 2009). At the leaf level, lianas tend to have lower LMA (leaf mass per area; i.e. the amount of biomass invested in constructing a unit area) and shorter leaf longevity than trees (Asner & Martin, 2012; Wyka et al., 2013; Zhu & Cao, 2010), but higher mass-based foliar nutrient concentrations (Asner & Martin, 2012; Wyka et al., 2013).

Given that organisms function as an integrated whole unit, linked traits via common functional activities are expected to covary (Cheverud, 1996). Consequently, traits at the leaf, stem and root levels that are involved in the carbon, nutrients and water economy of the plant are expected to be coordinated into a single plant economics spectrum running from fast to slow species, with fast species being fast in all organs and the opposite for slow species (Reich & Cornelissen, 2014). A combination of fast traits allows species to attain high growth rates and increase their competitive ability at high resource sites but leads to slow growth rates and poor survival in low resource environments (Díaz et al., 2004; Sterck et al., 2006; Wright, Reich, et al., 2004). This fast and acquisitive strategy could explain why lianas do particularly well in high light environments (Arroyo-Rodríguez & Toledo-Aceves, 2009; Laurance et al., 2001; Medina-Vega, Bongers, Schnitzer, et al., 2021), and why lianas are abundant early in forest succession (Barry et al., 2015; Dewalt et al., 2000; Letcher & Chazdon, 2009; Madeira et al., 2009). However, not all liana species have a more acquisitive strategy than trees (see Gerwing, 2004; Gilbert et al., 2006). Some studies indicate that lianas and trees do not differ in wood density and stem hydraulic conductivity (Zhang et al., 2019), that lianas do not have higher mass-based (Collins et al., 2016; Smith-Martin et al., 2019) and area-based (Asner & Martin, 2012) nutrient concentrations of the leaf (Nitrogen and Phosphorus) than trees and that lianas and trees do not differ in water-use strategies (Werden et al., 2018) and efficiencies (Smith-Martin et al., 2019).

Moreover, in a large study including 48 humid tropical forests, Asner and Martin (2012) observed that trait values associated with light capture and growth are less likely to be higher in lianas than in trees in forests with precipitations above c. 2,500 mm/year. Leaf level attributes in woody plants are mediated by climate conditions and soil fertility (Martin & Asner, 2009; Umaña et al., 2021). Dry forests tend to be rich in nutrient supply (Austin & Vitousek, 1998; Santiago et al., 2004, 2005). It is thus reasonable to find more acquisitive woody plants in those dry forests than in the relatively nutrient-poor wet forests (Ordoñez et al., 2009; Umaña et al., 2021). With increasing precipitation, there is a shift from deciduous to more evergreen tree species (Guan et al., 2015; Santiago & Mulkey, 2004) characterized by lower leaf-level nitrogen concentration and net photosynthesis as well as higher leaf lamina thickness and leaf toughness for green leaves (Santiago et al., 2004; Santiago & Mulkey, 2004; Umaña et al., 2021). Consequently, woody plants in high precipitation sites tend to conserve nutrients in long-lived tissues (see Osnas et al., 2018) and produce litter with high lignin content (Santiago & Mulkey, 2004), which is associated with lower rates of N mineralization and low extractable soil P (Santiago et al., 2005). Such negative plant–soil feedback loop further reduces soil fertility (Aerts & Chapin, 2000; Berendse, 1994; Crews et al., 1995; Santiago & Mulkey, 2004; Townsend et al., 2008) which, in turn, favours plants with a more conservative resource-use strategy.

Overall, available literature suggests that liana species may not always conform to the fast, and more acquisitive end of a continuum of plant strategies and that trait and functional differences between lianas and trees may be site-dependent. Here we evaluate functional

traits for 16 liana and 16 tree species from two lowland tropical forests located at the extreme of the climatic and geological gradient across the Isthmus of Panama. We explored the level of association among 17 leaf and stem traits that are representative of the leaf economics spectrum (LES), wood economics spectrum (WES), which include multiple hydraulic traits, and that are important for overall plant economics and growth. We assessed potential differences between life-forms to gain insights into the strategies that may mediate different resource acquisition and growth under similar resource conditions. We tested three hypotheses:

1. Leaf traits covary with stem traits (of branches) and hydraulic traits across life-forms. We predict that changes in the mean trait values at the leaf and stem level, including hydraulic traits, vary in the same direction.
2. There is one major trait spectrum, characterized by species with acquisitive ('fast') trait values in one end versus conservative ('slow') trait values in the other end of the spectrum.
3. Lianas are representative of species with a higher resource acquisition strategy and trees of a more conservative resource acquisition strategy and this difference between lianas and trees is more evident in drier conditions due to higher resource (i.e. light and nutrients) availability.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites and species selection

We measured leaves and collected samples from two canopy cranes, operated by the Smithsonian Tropical Research Institute (STRI). Each canopy crane was located at one extreme of the climatic and geological gradient across the Isthmus of Panama. This gradient is characterized by high variability in precipitation and heterogeneous soil parent material (Condit et al., 2013; Santiago et al., 2005; Turner & Engelbrecht, 2010). In this gradient, forests are strongly spatially distributed at the landscape scale (Pyke et al., 2001) and tree species composition is primarily determined by dry season intensity and P (phosphorus) availability (Condit et al., 2013), with soil P being primarily determined by lithology and not by vegetation or climate (Turner & Engelbrecht, 2010).

One crane is located in Parque Natural Metropolitano (PNM, 8°59'41.55"N, 79°32'35.22"W), a seasonally dry forest near Panama City and the Pacific coast. This crane is 42 m tall with a 51 m jib giving access to 0.81 ha of forest. Annual rainfall averages 1,864.3 mm and a severe dry season lasts from January to April, with cumulative precipitation of 153.5 mm for this 4-month dry period (means from 1995 to 2017, data provided by the Physical Monitoring Program of STRI). Mean annual temperature is 26.1°C.

The second canopy crane is located in the Bosque Protector San Lorenzo (BPSL, 9°16'51.71"N, 79°58'28.27"W). This canopy crane is 52 m tall with a 54 m jib giving access to 0.91 ha of forest. BPSL is a wet evergreen forest near the Caribbean coast of Panama, with an

annual rainfall of 3,292.7 mm and a less intense dry season than the PNM. The cumulative precipitation from January to March in BPSL is 159.8 mm and the monthly precipitation for April is 145.4 mm (means from 1997 to 2017). Mean annual temperature is 25.4°C. Parque Natural Metropolitano (PNM) and Bosque Protector San Lorenzo (BPSL) will hereafter be referred to as the dry forest and the wet forest, respectively (Holdridge, 1967).

At each crane site, we selected eight liana and eight tree species from those species with (at least) two or more canopy individuals present (Table 1). These individuals and species were used to collect samples for the estimation of the leaf, stem (of branches) and hydraulic functional traits (Table 2). We included both evergreen and deciduous species representative of each site. There was no species overlap between sites, which is consistent with the strong effect of

seasonality and soil conditions on regional plant distributions (Condit et al., 2013). The 32 species belonged to 22 families.

## 2.2 | Leaf traits

We collected leaf samples from (at least) two full-sun-exposed canopy individuals and a third or fourth canopy individual per species if accessible from the cranes. Leaf samples were collected at different collection times but always during the wet season unless stated otherwise. All collected leaves were fully exposed and fully expanded. To measure leaf mass per area (LMA, g/cm<sup>2</sup>) and petiole length (PL, cm), we first collected a set of 15 leaves per each of the 32 species. LMA was calculated as the ratio between leaf mass and leaf

Site	Life-form	Family	Species
Dry forest— PNM	Liana	Bignoniaceae	<i>Amphilophium crucigerum</i> (L.) L.G. Lohmann
		Bignoniaceae	<i>Callichlamys latifolia</i> (Rich.) K. Schum.
		Bignoniaceae	<i>Stizophyllum riparium</i> (Kunth) Sandwith
		Convolvulaceae	<i>Bonamia trichantha</i> Hallier f.
		Malpighiaceae	<i>Stigmaphyllon hypargyreum</i> Triana & Planch.
		Petiveriaceae	<i>Trichostigma octandrum</i> (L.) H. Walter
		Sapindaceae	<i>Serjania mexicana</i> (L.) Willd.
		Vitaceae	<i>Vitis tiliifolia</i> Humb. & Bonpl. ex Schult.
	Tree	Anacardiaceae	<i>Anacardium excelsum</i> (Bertero & Balb. ex Kunth) Skeels
		Anacardiaceae	<i>Astronium graveolens</i> Jacq.
		Annonaceae	<i>Annona spraguei</i> Saff.
		Boraginaceae	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken
		Lauraceae	<i>Cinnamomum triplinerve</i> (Ruiz & Pav.) Kosterm.
		Malvaceae	<i>Guazuma ulmifolia</i> Lam.
		Malvaceae	<i>Luehea seemannii</i> Triana & Planch
		Rubiaceae	<i>Pittoniotis trichantha</i> Griseb.
Wet forest— BPSL	Liana	Bignoniaceae	<i>Pleotoma variabilis</i> (Jacq.) Miers
		Celastraceae	<i>Salacia multiflora</i> (Lam.) DC.
		Celastraceae	<i>Tontelea passiflora</i> (Vell.) Lombardi
		Convolvulaceae	<i>Maripa panamensis</i> Hemsl.
		Dilleniaceae	<i>Dolioscarpus multiflorus</i> Standl.
		Euphorbiaceae	<i>Omphalea diandra</i> L.
		Olacaceae	<i>Heisteria scandens</i> Ducke
		Polygonaceae	<i>Coccoloba excelsa</i> Benth.
	Tree	Annonaceae	<i>Guatteria dumetorum</i> R.E. Fr.
		Combretaceae	<i>Terminalia amazonia</i> (J.F. Gmel.) Exell
		Fabaceae	<i>Tachigali versicolor</i> Standl. & L.O. Williams
		Malvaceae	<i>Apeiba aspera</i> Aubl.
		Melastomataceae	<i>Miconia minutiflora</i> (Bonpl.) DC.
		Myristicaceae	<i>Virola multiflora</i> (Standl.) A.C. Sm.
		Rubiaceae	<i>Tocoyena pittieri</i> (Standl.) Standl.
		Vochysiaceae	<i>Vochysia ferruginea</i> Mart.

**TABLE 1** Study species classified by life-form (liana and tree) in a seasonally dry (PNM) and a wet evergreen tropical (BPSL) forest in Panama

**TABLE 2** Summary (mean  $\pm$  1 SE) for the functional traits used in the present study, the units and assignment to leaf, stem and twig

Trait (abbreviation)	Unit	Group	Mean ( $\pm$ 1 SE <sup>a</sup> )
Leaf mass per area (LMA)	g/cm <sup>2</sup>	Leaf	0.0087 $\pm$ 0.0006
Leaf longevity (LL)	days	Leaf	222 $\pm$ 18
Leaf density (LD)	g/cm <sup>3</sup>	Leaf	0.42 $\pm$ 0.02
Leaf lamina thickness (LamT)	mm	Leaf	0.21 $\pm$ 0.01
Leaf lamina fractal toughness (LamFT)	g per 2.27 mm <sup>2</sup>	Leaf	84.3 $\pm$ 6.2
Foliar nitrogen (N <sub>mass</sub> )	mmol/kg	Leaf	1588.6 $\pm$ 84.8
Foliar phosphorus (P <sub>mass</sub> )	mmol/kg	Leaf	41.3 $\pm$ 3.7
Minimum leaf water potential ( $\Psi_{min}$ )	$\Psi$ (MPa)	Leaf	-2.07 $\pm$ 0.08
The osmotic potential at turgor loss ( $\Psi_{turg}$ )	$\Psi$ (MPa)	Leaf	-1.90 $\pm$ 0.07
Leaf P50 (P50 <sub>leaf</sub> )	$\Psi$ (MPa)	Leaf	-0.21 $\pm$ 0.03
Leaf hydraulic conductance (K <sub>leaf</sub> )	mmol m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup>	Leaf	8.6 $\pm$ 1.1
Petiole length (PL)	cm	Leaf	2.91 $\pm$ 0.36
Stem P50 (P50 <sub>stem</sub> )	$\Psi$ (MPa)	Stem	-1.79 $\pm$ 0.16
Sapwood-specific hydraulic conductivity (K <sub>s</sub> )	kg m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup>	Stem	4.8 $\pm$ 0.7
Stem specific density (SSD)	g/cm <sup>3</sup>	Stem	0.52 $\pm$ 0.03
Huber value (HV)	cm <sup>2</sup> /cm <sup>2</sup>	Branch	0.00041 $\pm$ 0.00004
Duration of green foliage (E)	days	Branch	203 $\pm$ 12

<sup>a</sup>SE is the standard error of the mean and was estimated as the sample standard deviation divided by the square root of the sample size ( $n = 32$ ).

area, without including the petiole (and rachis for compound leaves). We used an LI-3100C leaf area meter to measure leaf area. For leaf dry mass, every leaf was oven-dried at 70°C for 48 hr and dry mass measured with a precision balance ( $\pm 0.0001$  g). We measured PL with a measuring tape.

We collected a second set of 15 leaves per species to estimate leaf density (LD, g/cm<sup>3</sup>), leaf lamina thickness (LamT, mm) and leaf lamina fracture toughness (LamFT, g per 2.27 mm<sup>2</sup> to perforate [5.34 mm of circumference]). Leaf density was estimated as follows:  $LD = LMA \times LamT^{-1}$  (Kitajima & Poorter, 2010). Lamina thickness (LamT) and lamina fracture toughness (LamFT) were estimated with an outside micrometre (Mitutoyo), and a penetrometer (Pesola Spring Scale 600 g and the pressure set 4.004), respectively, on three positions, the upper, mid and lower part of the leaf, avoiding contact with the veins. LamT and LamFT for each leaf were calculated by averaging all three measurements.

We collected a third set of 20 leaves per species to estimate leaf nitrogen (N<sub>mass</sub>) and phosphorus (P<sub>mass</sub>) concentration (mmol/kg). N<sub>mass</sub> and P<sub>mass</sub> were determined using the digestion technique (digestion in tubes with sulphuric acid, salicylic acid, hydrogen peroxide and selenium; Novozamsky et al., 2008) on a composite sample made by physically mixing all the individual leaves per species.

We collected a fourth set of five leaves per species to estimate the osmotic potential at turgor loss ( $\Psi_{turg}$ , MPa). We estimated this turgor loss point by constructing one pressure–volume curve per collected leaf using the ‘bench dry method’ as described in Sack

et al. (2010). We collected a fifth set of at least 25 leaves per species to estimate leaf hydraulic conductance (K<sub>leaf</sub>, mmol m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup>) and leaf vulnerability to cavitation (P50<sub>leaf</sub>, MPa) using the evaporative flux method as described in Sack and Scoffoni (2012).

We benefited from an 18-month census of canopy branches to estimate leaf longevity (LL, in days). We measured leaf longevity starting in November 2015 by selecting two individuals per species and four fully exposed branches per individual. Branches ranged from 30 to 70 cm in length. We numbered sequentially every leaf if present on each selected branch with a permanent marker. We returned 13 times through May 2017 to mark new leaves and record presence/absence of previously marked leaves. We marked only fully expanded leaves. If a branch was lost to natural death or disturbance, we selected a replacement branch, so every individual had at least four branches for the entire study. To avoid bias due to different exposures to direct sunlight, we initially selected branches in full sunlight and prevented other branches from overtopping the census branches. The median age in days of leaf death was estimated using the Kaplan–Meier method (Efron, 1988).

For minimum leaf water potential ( $\Psi_{min}$ , MPa), we monitored two individuals per species 15 times over 17 months. We randomly selected three fully exposed leaves per individual per census from 12:00 to 13:00 hr and measured them with a Scholander pressure chamber (PMS instruments model 1000). When deciduous species lost their leaves, we collected and measured the tip of a branch

following the same procedure. From our minimum leaf water potential measurements, April 2016 showed the lowest water potentials for all species, and these measurements were used as the  $\Psi_{\min}$  baseline.

## 2.3 | Stem traits

We collected two sets of fully sun-exposed branches per species to estimate sapwood-specific hydraulic conductivity ( $K_s$ ,  $\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ ) and stem vulnerability to cavitation ( $P50_{\text{stem}}$ , MPa). The first set included four branches per species and was used to estimate  $K_s$ . These branches were different from the census branches used to estimate LL (section leaf traits). For comparability, we selected branches with a length of at least 1 m, with leaves present and without long leafless terminals. These branches were harvested and transported to a laboratory in Gamboa, Panama, for further processing. Lateral branches and leaves were cut from the main stem and wounds were sealed with super glue. The stems were re-cut to a length of ~30 cm under distilled water and trimmed with a razor blade. Each segment contained a central internode and at least two nodes located between the cut ends (see Jacobsen & Pratt, 2012). Bark was removed around 1 cm of the shoots ends. While submerged, we wrapped the trimmed basal end with Parafilm (Pechiney Plastic Packaging) and connected it to a three-way stopcock attached to a pressurized reservoir (150 kPa) filled with a flow solution of 20 mM KCl in degassed and filtered (0.2  $\mu\text{m}$ ) distilled water. Stems were flushed for 30 min to remove any emboli and connected to a hydraulic apparatus (Sperry et al., 1988), supplying the same flow solution to the stems at 20 kPa for 10 min before measuring. We took six repeated measurements to assure that water flow had reached a steady state. We then estimated the sapwood area as the cross-sectional stem area without bark minus the area of the pith. Sapwood-specific hydraulic conductivity ( $K_s$ ) was calculated by dividing the measured conductance of the branch segment by the sapwood area.

The second set included five branches per species and was used to determine xylem vulnerability to cavitation ( $P50_{\text{stem}}$ , MPa) using the pneumatic method (Pereira et al., 2016). We selected these branches following the same procedure as described for the first set of branches. For each branch, we first measured the air discharge (AD) several times at different xylem water potentials. We then obtained the percentage of air discharged (PAD) by considering well-hydrated (as the minimum [0%] PAD) and dehydrated measurements (as the maximum [100%] PAD; see Pereira et al., 2016). Paired PAD and xylem pressure measurements of each branch were pooled and then plotted to determine the xylem pressure when PAD equals 50% ( $P50_{\text{stem}}$ ) for each of the 32 species by fitting the pooled data per species to an exponential sigmoidal function following Pammenter and Van der Willigen (1998).

We further determined stem specific density (SSD,  $\text{g/cm}^3$ ) for each species following (Cornelissen et al., 2003). We used five branch segments of five centimetres length per species collected from the branches used to measure  $P50_{\text{stem}}$ . We collected each segment at 1 m from the distal end of the branches. Branch segments differed

in diameter and the diameter was not larger than 2 cm. For each segment, we estimated the fresh volume without the bark and pith using the water displacement method (Illic et al., 2000). Samples were oven-dried for 72 hr at 70°C. We measured the dry mass of the sample with a precision balance ( $\pm 0.0001$  g) and estimated stem specific density (SSD) as the ratio between the dry mass and the fresh volume of the segment.

## 2.4 | Whole branch organ traits

From the same branches that were used to estimate LL (refer to leaf traits section), we estimated the Huber value (HV,  $\text{cm}^2/\text{cm}^2$ ) of each branch as the ratio between branch cross-sectional area and leaf area (Tyree & Ewers, 1991). Branch cross-sectional area was estimated using diameter measurements recorded at the same position on every census and included, therefore, the pith and the bark. Branch leaf area was calculated from leaf numbers and species-specific leaf area. The species-specific HV was estimated as the mean HV among branches and censuses. Branches without leaves were removed from the calculation.

We estimated the duration of green foliage (E) of each species from the census used to estimate LL. We defined E as the number of days when the net change in the number of leaves (new leaves—death leaves) was  $\geq 0$ . For each branch, we estimated the net change in the number of leaves for each census and then used cubic polynomial interpolation splines (Forsythe et al., 1977) to estimate the daily net change in the number of leaves. We averaged the daily net change in the number of leaves among the observed branches per species and the species-specific E was estimated as the cumulative number of days when the net change in the number of leaves was  $\geq 0$  in the year 2016.

## 2.5 | Data treatment and statistical analysis

We compiled a dataset with species mean trait values. All analyses were done in R version 3.6.3 (R Core Team, 2020) unless stated otherwise. We checked the distribution shapes of each functional trait across species and transformed the ones that departed from normality. We normalized LMA, LL, LD,  $N_{\text{mass}}$ ,  $P_{\text{mass}}$ ,  $K_{\text{leaf}}$ , PL,  $K_s$ , SSD, HV and E, using a log (base e) transformation and  $P50_{\text{leaf}}$  and  $P50_{\text{stem}}$  using a cube root transformation. We used a cube root transformation on the original data for  $P50_{\text{leaf}}$  and  $P50_{\text{stem}}$  because it allows us to maintain the ecological interpretation of the trait, higher values (less negative) interpreted as more vulnerable. LamT, LamFT,  $\Psi_{\min}$  and  $\Psi_{\text{tip}}$  values were normally distributed and therefore, not transformed.

We used a principal component analysis (PCA; Abdi & Williams, 2010) to test for overall associations between traits (hypothesis one), as well as for the existence of a major fast-slow trait spectrum (hypothesis two). We constructed both a global PCA, including all liana and tree species from both forest sites and a local



PCA for each forest site, using the base R function `prcomp`. We used a correlation PCA instead of a covariance PCA due to different dimensions of the variables (functional traits) and because we aimed to discover potential structures in the data by finding correlations among descriptor variables (Ramette, 2007). For the PCAs, we standardized each functional trait by transforming the normalized trait values into z-scores. We computed the differences between each trait value and the mean trait and then divided each difference by the standard deviation of the trait. Each functional trait thus contributed to the same extent to the ordination of species independent from the variance of the original trait. We selected the number of significant PCA axes for inference using a generalized cross-validation approximation (GCV) as proposed by Josse and Husson (2012) and implemented in the R package `FACTOMINER` version 2.3 (Lê et al., 2008).

We presented the results of the PCAs using biplots, where the axes correspond to the principal components, and both species and traits are represented. We identified the functional traits that accounted for the separation of species in the axes and planes by examining their contribution and loadings to the principal components. To test for different ecological strategies between lianas and trees (hypothesis three), we tested for differences between life-forms in the functional traits that had an important contribution to the main principal components and the principal components themselves using one-way analysis of variance (ANOVA) with the base R function `aov`. Hypothesis three was tested for each forest site separately.

Coupled with the use of PCAs, we also estimated the degree of association between functional traits using correlation  $r^2$  and  $p$  values based on standard Pearson correlation analyses. We estimated the  $r$  correlation coefficients via the R package `Hmisc` version 4.4.1 (Harrell & Dupont, 2020). The square of the correlation coefficient ( $r^2$ ) represents the proportion of variation in one variable that is accounted for by the variation in the other variable (Aggarwal & Ranganathan, 2016). We further tested the consistency of the bivariate trait associations across lineages by assessing whether (inferred) evolutionary divergences in each trait were correlated with those in the other traits using phylogenetically independent contrasts (PIC, see Appendix S1 in Supporting Information; Felsenstein, 1985; Westoby, 1999). Observable differences in the result from the two types of analyses, all-species and evolutionary divergences bivariate trait associations, may indicate that taxonomic biases contributed to the all-species results.

For hypothesis three, we further described the relationship of all the significant all-species bivariate trait associations via their standardized major axes (SMA) and assessed whether these associations were consistent among life-forms between and within forest sites. For all life-form contrasts in this study, the reference level is lianas (lianas = 0; trees = 1). SMA (or model II regression) analyses are appropriate when the purpose is to summarize the relationship between variables using line-fitting rather than predicting one variable from another (Warton et al., 2012). We first tested for differences in slopes between life-forms. If the difference between slopes was not significant, we tested for shifts in elevation (i.e. intercept) and

whether growth forms were separated with a common slope. We implemented SMA using the R package `SMATR` version 3.4.8 (Warton et al., 2012). To account for the multiplicity problem in multiple significance testing, we adjusted  $p$  values, when needed, by controlling for the false discovery rate (FDR) as described in Benjamini and Hochberg (1995).

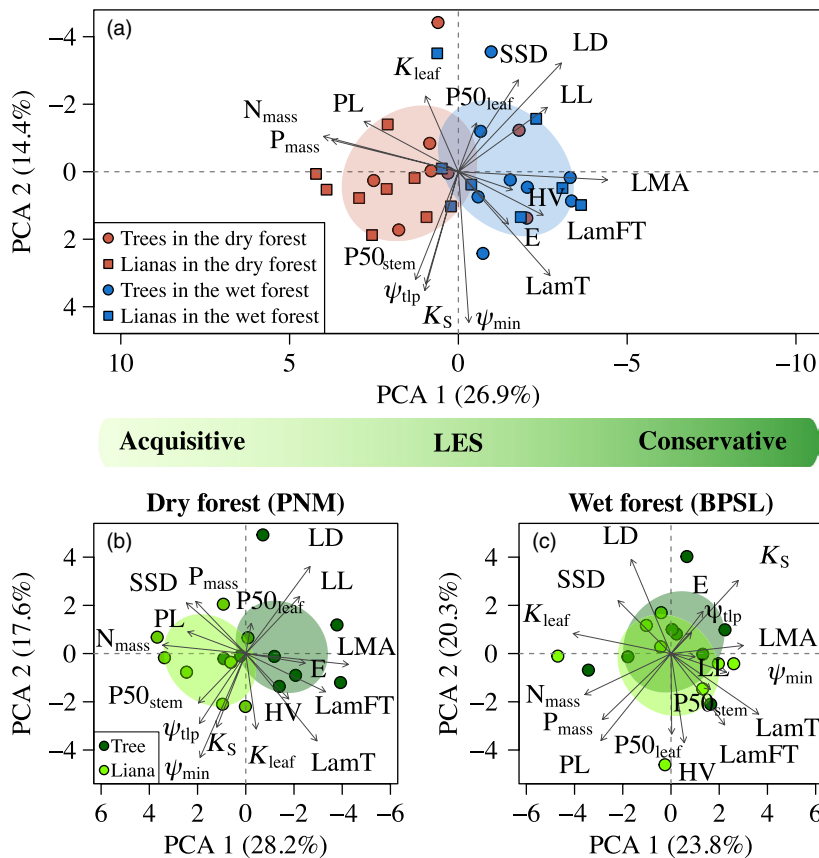
### 3 | RESULTS

#### 3.1 | Multivariate analyses and trait associations

We observed a systematic variation among leaf-level functional traits, largely independent from the variation in stem traits (of branches) and hydraulic traits. This observation was consistent in the global PCA including all species and the local PCA for each forest site, rejecting the hypothesis that leaf traits covary with stem traits (of branches) and hydraulic traits across life-forms. In the global PCA that includes lianas and trees from both forests (Figure 1a), the first two components explained 41% of the inertia (Table S1). The first component of this PCA was associated with the LES. We observed that all liana and tree species in the dry forest tended to have relatively higher foliar nutrient concentrations ( $N_{\text{mass}}$ ,  $P_{\text{mass}}$ ), longer petioles (PL) and lower biomass invested in constructing a unit of leaf area (LMA), coupled to shorter leaf longevity (LL) and lower lamina fractal toughness (LamFT) than liana and tree species in the wet forest. The second component, independent from the first component, mainly represented plant hydraulics coupled to stem specific density and leaf density.

For the dry forest, the PCA showed contrasting differences between lianas and trees. The first two components of the PCA for the dry forest accounted for 45.8% of inertia (Table S1; Figure 1b). The generalized cross-validation approximation (GCV) indicated that these two components were the optimal number of explanatory dimensions. That is, adding the third component of the PCA did not improve the predictive power of the model. The first dimension primarily represented the LES. LMA was the main contributor to the first component, followed by foliar nutrient concentrations ( $N_{\text{mass}}$ ,  $P_{\text{mass}}$ ), lamina fractal toughness (LamFT), duration of green foliage (E) and petiole length (PL). The first component runs from species with cheaply constructed acquisitive leaves (low LMA—high  $N_{\text{mass}}$  and  $P_{\text{mass}}$ ) with lower LamFT, longer petioles and crowns with shorter duration of green foliage to more conservative leaves (high LMA—low  $N_{\text{mass}}$  and  $P_{\text{mass}}$ ) with higher LamFT, shorter petioles and crowns with longer duration green foliage (Figure 1b). This main dimension, primarily consisting of leaf-level traits, supports hypothesis two for the dry forest; the existence of a major trait spectrum, characterized by species with acquisitive trait values in one end versus conservative trait values in the other end of the spectrum. There was a significant difference between lianas and trees in the first component scores ( $F_{1,14} = 13.79$ ,  $p = 0.002$ , Figure S1a), with lianas occupying the more acquisitive side of the gradient and trees occupying the most conservative side, supporting hypothesis three for the dry forest. Lianas





**FIGURE 1** Trait dimensions from principal component analysis (PCA) for all species (panel a), for lianas and trees in the dry (PNM) forest (panel b) and lianas and trees in the wet (BPSL) forest (panel c). For panel a, blue marks are for species in the wet forest and orange marks for species in the dry forest. Circles represent trees and squares lianas. For panels (b and c), dark green circles are trees and light green circles are lianas. Confidence ellipses in panel a are represented for each forest site, and in panels b and c are represented for each life-form (lianas and trees). Variables (plant functional traits) used for the PCA are displayed with their vector. Functional traits were normalized and standardized by transforming the observations into z-scores. For abbreviations, refer to Table 2

had significantly longer petioles ( $F_{1,14} = 23.24$ ,  $p < 0.001$ , Figure S2l) and lower LMA ( $F_{1,14} = 4.79$ ,  $p < 0.05$ , Figure S2a) than trees, but did not significantly differ in LamFT ( $F_{1,14} = 1.42$ ,  $p = 0.25$ , Figure S2e), duration of green foliage ( $F_{1,14} = 0.97$ ,  $p = 0.34$ , Figure S2q),  $N_{mass}$  ( $F_{1,14} = 2.78$ ,  $p = 0.12$ , Figure S2f) and  $P_{mass}$  ( $F_{1,14} = 0.63$ ,  $p = 0.44$ , Figure S2g).

The second component for the dry forest showed LD, LL and SSD opposed to LamT,  $\psi_{min}$ ,  $\psi_{tlp}$ ,  $K_{leaf}$  and  $K_s$  (Table S1; Figure 1b).  $\psi_{min}$  was the main contributor to the second component. This component runs from species characterized by longer leaf longevity (LL), higher LD and higher SSD with reduced hydraulic capacity at the leaf and stem level (low  $K_s$  and  $K_{leaf}$  [Figures S3–S6]) to species characterized by shorter leaf longevity (LL), lower LD and lower SSD with increased hydraulic capacity at the leaf and stem level (high  $K_s$  and  $K_{leaf}$ ) and higher (less negative)  $\psi_{min}$  and  $\psi_{tlp}$ , indicating that these species maintain high hydraulic efficiencies when water availability is high enough not to induce water stress. We did not observe differences between lianas and trees in the second component scores (Figure S1c). However, lianas showed a significantly higher  $\psi_{min}$  ( $F_{1,14} = 9.1$ ,  $p < 0.01$ , Figure S2h) and tended to have a lower LD ( $F_{1,14} = 4.47$ ,  $p = 0.09$ , Figure S2c) and LL than trees ( $F_{1,14} = 1.68$ ,  $p = 0.22$ , Figure S2b), although only marginally significant. For LL, we observed the influence of an outlier (*Serjania mexicana*, Dixon Q test for outliers,  $Q = 0.7$ ,  $p = 0.02$ ) and after removing it, the seven remaining liana species showed shorter LL than trees ( $F_{1,13} = 4.8$ ,  $p = 0.04$ ). For LamT,  $K_{leaf}$ ,  $K_s$  and  $\psi_{tlp}$ , lianas and trees were similar (Figures S2d,k,n,i).

For the wet forest, we observed that the first component of the PCA represented the LES (Figure 1c), supporting hypothesis two. Although in the wet forest the first and second components of the PCA accounted for 44.1% of inertia (Table S1), the GCV indicated a lack of optimal explanatory dimensions, most likely due to a non-systematic variability among species traits. This lack of optimal dimensionality was also reflected in a lack of differences between lianas and trees, rejecting hypothesis three for the wet forest (Figure 1c). Only one trait differed significantly between lianas and trees in the wet forest, the duration of green foliage (E). Lianas in the wet forest had shorter E than trees ( $F_{1,14} = 7.18$ ,  $p = 0.02$ , Figure S2q).

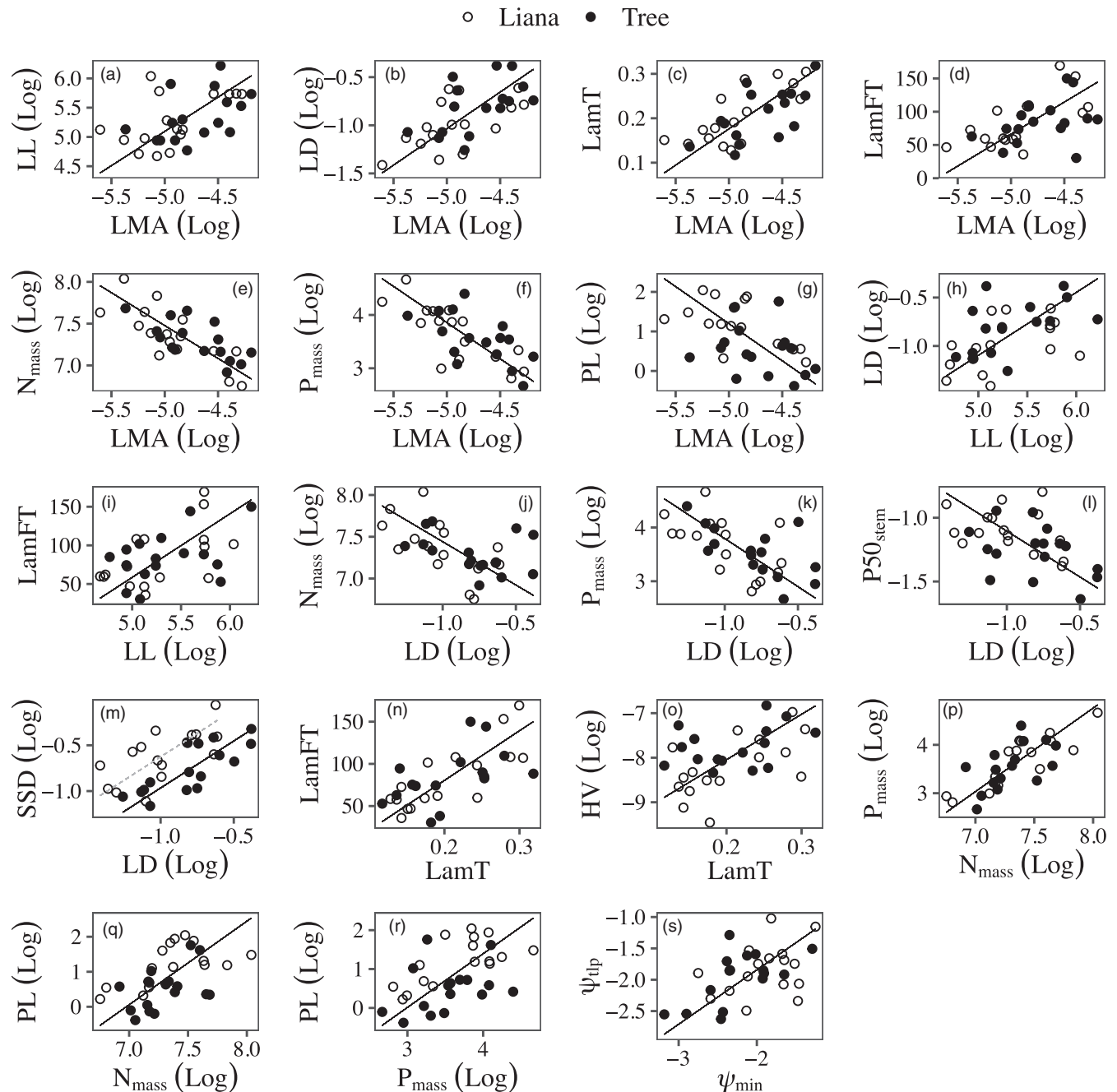
### 3.2 | Bivariate trait associations

We observed that among all species, LMA was positively associated with leaf toughness (LD, LamT and LamFT) and leaf longevity (LL) and negatively associated with leaf nutrient concentrations ( $N_{mass}$ ,  $P_{mass}$ ) and petiole length (Table 3; Figure 2a–g). LL was positively associated with LD and LamFT (Figure 2h–i). The density of leaves (LD) was positively associated with the stem specific density (SSD) but negatively associated with leaf nutrient concentrations ( $N_{mass}$ ,  $P_{mass}$ ) and  $P50_{stem}$  (Figure 2j–m). LamT increased with LamFT and HV (Figure 2n–o).  $N_{mass}$  and  $P_{mass}$  were positively associated between them and with PL (Figure 2p–r), and  $\psi_{tlp}$  increased with  $\psi_{min}$  (Figure 2s). From these associations, the relationships between

**TABLE 3** The squared correlation coefficient ( $r^2$ ) of the pairwise (below the diagonal) and PIC relationship (above the diagonal) among the 17 functional traits from all-species analysis ( $n = 32$ )

	LMA	LL	LD	LamT	LamFT	N <sub>mass</sub>	P <sub>mass</sub>	$\psi_{\min}$	$\psi_{\text{tip}}$	P50 <sub>leaf</sub>	K <sub>leaf</sub>	PL	P50 <sub>stem</sub>	K <sub>s</sub>	SSD	HV	E
LMA		0.14	0.01	0.48 +	0.48 +	0.29 –	0.18	0.05	0.06	0.06	0.01	0.32 –	0	0.02	0.18	0.01	0.05
LL	0.25 +		0.04	0.01	0.14	0.03	0.01	0	0.01	0.11	0.01	0.01	0.03	0.03	0.15	0.05	0.03
LD	0.37 +	0.24 +		0.05	0.05	0.17	0.36 –	0.07	0	0	0.12	0.01	0.21 –	0.1	0.18	0.01	0.01
LamT	0.46 +	0.04	0.03		0.59 +	0.29 –	0.14	0.07	0.05	0.01	0	0.29 –	0.03	0.05	0.01	0.02	0.03
LamFT	0.27 +	0.25 +	0	0.45 +		0.27 –	0.06	0.09	0.05	0.08	0.07	0.14	0.09	0.02	0.01	0.03	0.01
N <sub>mass</sub>	0.53 –	0.21 –	0.25 –	0.2 –	0.2 –		0.69 +	0.02	0.05	0.01	0.02	0.28 +	0	0.02	0.07	0	0.04
P <sub>mass</sub>	0.49 –	0.09	0.36 –	0.1	0.06	0.56 +		0.01	0.12	0.02	0.1	0.14	0.02	0.01	0.06	0.05	0
$\psi_{\min}$	0	0.04	0.03	0.04	0.01	0.05	0.14		0.29 +	0	0	0.02	0.41 +	0.27 +	0	0.02	0.07
$\psi_{\text{tip}}$	0.03	0.04	0.03	0	0.01	0.04	0.01	0.26 +		0	0.02	0.08	0.16	0.1	0	0.02	0.01
P50 <sub>leaf</sub>	0	0.08	0.01	0	0.08	0	0.02	0	0		0.03	0.04	0.05	0.06	0	0.05	0.03
K <sub>leaf</sub>	0.04	0	0	0.06	0	0.05	0.01	0.01	0	0.06		0	0.03	0.02	0	0.03	0
PL	0.25 –	0.01	0.1	0.1	0.01	0.27 +	0.25 +	0	0	0.04	0.05		0	0.1	0	0.01	0.18
P50 <sub>stem</sub>	0.11	0	0.22 –	0	0.02	0	0.01	0.14	0.13	0.04	0	0.01		0.12	0.04	0.03	0
K <sub>s</sub>	0.02	0.05	0.04	0	0.01	0	0	0.12	0.07	0.1	0	0.01	0.04		0.08	0.08	0
SSD	0.09	0.06	0.32 +	0.02	0	0.09	0.19 –	0	0	0	0.04	0.01	0.03	0.09		0.08	0
HV	0.15	0.01	0	0.23 +	0.03	0.01	0.04	0	0	0.03	0	0.07	0.05	0.14	0.02		0.04
E	0.06	0	0.01	0.03	0	0.08	0.04	0	0	0.04	0.1	0.2 –	0.03	0.01	0.03	0	

Note: Correlation data are given for all-species-based analysis below the diagonal and PIC analysis above the diagonal. The sign ( $\pm$ ) of the correlation  $r$ -value is indicated for relationships  $p < 0.1$ . Relationships with  $p < 0.05$  are in bold.  $p$  values were adjusted by controlling for the false discovery rate (FDR) as described in Benjamini and Hochberg (1995). Traits were normalized as described in Methods. For abbreviations, refer to Table 2.



**FIGURE 2** Bivariate trait relationships among 16 liana and 16 tree species from the dry (PNM) and the wet (BPSL) forest. Panels are labeled from 'a' to 's' and show the bivariate relationship for each of the 19 significant ( $p < 0.05$ ) correlations in Table 3. Each data point represents the mean species-specific trait value. Correlation statistics are given in Table 3. Standardized Major Axis (SMA) coefficients for differences in slope and shifts in elevation between life-forms are given in Table 4. Filled dots represent trees and empty dots lianas. Differences between lianas and trees (panel m) are indicated by a grey coloured dashed line and a black coloured solid line, respectively. The single solid line represents a significant association but no differences between lianas and trees

LMA and foliar nutrient concentrations ( $N_{\text{mass}}$ ,  $P_{\text{mass}}$ ), related to the LES, were the strongest (Table 3). In the LMA- $N_{\text{mass}}$  relationship, 53% of the variation in  $N_{\text{mass}}$  was accounted for by the variation in LMA. For the LMA- $P_{\text{mass}}$  relationship, 49% of the variation in  $P_{\text{mass}}$  was accounted for by LMA, and for the  $P_{\text{mass}}$ - $N_{\text{mass}}$  association, 56% of the variation in  $P_{\text{mass}}$  was accounted for by the variation in  $N_{\text{mass}}$ .

For the significant all-species bivariate trait associations, lianas ( $n = 16$ ) showed a lower LD than trees ( $n = 16$ ) at the same SSD

(Figure 2m), and this relationship was consistently maintained in the dry forest, but not in the wet forest (Table 4). In the dry forest, we also observed that lianas had lower LMA and higher foliar nutrient concentrations ( $N_{\text{mass}}$ ,  $P_{\text{mass}}$ ) per unit petiole length (PL; Table 4). In contrast, for the wet forest, liana and tree species were very similar in their bivariate trait associations, as indicated by the lack of differences in slope, shifts in elevation, and shifts along the axis with a common slope (Table 4). These observations were consistent with

**TABLE 4** Differences in slope and shifts in elevation (intercept) between all sampled lianas ( $n = 16$ ) and trees ( $n = 16$ ) and between lianas and trees in the dry (PNM) forest and in the wet (BPSL) forest

x	y	All-species						Dry forest						Wet forest					
		Slope			Elevation			Slope			Elevation			Slope			Elevation		
		Lianas	Trees		Lianas	Trees		Lianas	Trees		Lianas	Trees		Lianas	Trees		Lianas	Trees	
LMA	LL	1.18	1.28		11.3	11.1		-1.82	1.63		13.86	13.65		1	1.25		10.73	10.42	
LMA	LD	0.69	0.82		2.7	2.72		0.67	0.83		2.63	2.6		0.76	0.69		2.55	2.63	
LMA	LamT	0.17	0.18		1.05	1.01		0.14	0.19		1.02	0.99		0.25	0.23		1.34	1.3	
LMA	LamFT	102.45	98.7		580.9	559.9		95.89	131.56		693.45	676.38		150.03	-81.8		657.59	624.38	
LMA	N <sub>mass</sub>	-0.9	-0.7		3.37	3.48		-1	-0.83		3.03	3.09		-0.73	-0.59		3.97	4.14	
LMA	P <sub>mass</sub>	-1.42	-1.4		-3.29	-3.11		-1.41	-0.95		-2.36	-2.11		-1.45	-1.08		-2.62	-2.58	
LMA	PL	-1.56	-1.85		-7.03	-7.36		1.41	1.31		<b>8.63<sup>a</sup></b>	<b>7.30<sup>b</sup></b>		-1.69	-2.77		-9.02	-9.24	
LL	LD	0.58	0.64		-4.22	-4.08		0.37	0.51		-3.51	-3.46		0.76	0.55		-4.4	-4.1	
LL	LamFT	86.91	77.42		-351.64	-356.27		52.78	80.65		-255.26	-255.23		149.91	65.55		-474.65	-474.45	
LD	N <sub>mass</sub>	-1.3	-0.86		6.28	6.42		-1.5	-1		6.18	6.22		-0.95	0.86		6.37	6.62	
LD	P <sub>mass</sub>	-2.06	-1.71		1.82	2.05		-2.11	-1.14		2.23	2.41		-1.91	-1.58		1.9	2.08	
LD	P50 <sub>stem</sub>	-0.65	-0.73		-1.78	-1.82		-0.59	-0.86		-1.87	-1.91		-0.94	-0.96		-1.91	-1.9	
LD	SSD	1.08	0.99		<b>0.40<sup>a</sup></b>	<b>0.06<sup>b</sup></b>		1.24	0.56		<b>0.03<sup>a</sup></b>	-0.29 <sup>b</sup>		1.14	1.19		0.5	0.18	
LamT	LamFT	612.78	559.67		-37.56	-39.7		676.16	704.51		-56.13	-54.26		598.08	359.9		-23.69	-33.42	
LamT	HV	10.67	7.87		-10.12	-9.72		20.34	8.27		-11.22	-10.98		7.31	7.32		-9.6	-9.23	
N <sub>mass</sub>	P <sub>mass</sub>	1.58	2		-8.75	-8.77		1.41	1.14		-5.77	-5.62		2	1.84		-10.57	-10.85	
N <sub>mass</sub>	PL	1.74	2.62		-14.21	-14.77		-1.41	1.58		<b>12.81<sup>a</sup></b>	<b>11.58<sup>b</sup></b>		2.33	4.69		-24.78	-25.56	
P <sub>mass</sub>	PL	1.1	1.32		-3.12	-3.67		-1	1.38		<b>6.26<sup>a</sup></b>	<b>5.20<sup>b</sup></b>		1.17	2.55		-4.05	-4.35	
ψ <sub>min</sub>	ψ <sub>tip</sub>	0.97	0.88		-0.1	0.09		1.11	1.46		0.83	1.18		0.65	0.46		-0.96	-0.74	

Note: Significant differences ( $p < 0.05$ ) between lianas and trees are indicated by the superscripts a and b and are marked in bold.  $p$  values were adjusted by controlling for the false discovery rate (FDR) as described in Benjamini and Hochberg (1995). Traits were normalized as described in Methods. For abbreviations, refer to Table 2. There were no significant shifts along the standardized major axis with a common slope. Consequently, only differences in slope and elevation are indicated.

the data structure observed in the PCAs, with lianas being more acquisitive than tree species in the dry forest (Figure 1b) and no differences between lianas and trees in the wet forest (Figure 1c). We did not observe any significant shifts along the standardized major axis with a common slope between life-forms.

For most of the bivariate trait associations, species in the dry forest occupied a different region than species in the wet forest (Figure S7). The two forest sites occupied significantly different positions along a common slope indicating that the average functional trait values differ between sites, but that the bivariate relationships remain relatively the same (Table S3). Compared to the wet forest species, dry forest species had a relatively lower LMA, LL, LD, LamT, LamFT and SSD; and relatively higher  $N_{\text{mass}}$ ,  $P_{\text{mass}}$ , PL and  $P50_{\text{stem}}$  (Table S3, Figure S7).

### 3.3 | Phylogenetic correlations

Of the tested relationships, most cross-species associations and phylogenetic analyses were congruent, with some exceptions. For LD- $P50_{\text{stem}}$ , LD-SSD, LamT-HV and  $P_{\text{mass}}$ -PL trait pairs, only the cross-species correlations were significant. For  $N_{\text{mass}}$ -LamT,  $N_{\text{mass}}$ -LamFT, PL-LamT,  $\Psi_{\text{min}}$ - $P50_{\text{stem}}$  and  $\Psi_{\text{min}}$ - $K_s$  trait pairs, only the phylogenetic correlations were significant (Table 3).

## 4 | DISCUSSION

### 4.1 | Coordination between leaf and stem traits

Our data did not support the hypothesis that leaf traits covary with stem traits (of branches) and hydraulic traits across life-forms, and we did not find strong coordination between leaf, stem and hydraulic traits. Species adapted to high resource conditions were expected to have fast growth rates facilitated by cheap stem volumetric costs, high water supply to leaves, cheaper leaves and faster gas exchange (Sterck et al., 2011, 2014). Species adapted to low resource conditions were expected to have the opposite suite of traits that would facilitate high survival (Grime et al., 1997; Reich & Cornelissen, 2014). We did not find support for hypothesis one across species and life-forms. First, the first axes of the multivariate PCAs were mostly associated with LES, whereas the second—orthogonal—axes of the PCAs were associated with the WES traits but also included hydraulic leaf and stem traits. Second, bivariate trait analysis showed that there were no associations between leaf and stem traits.

A decoupling between the first axis associated with LES and the second axis associated with WES and plant hydraulics (Figure 1) suggests that leaf economics vary independently from stem economics and plant hydraulics, allowing for multiple trait combinations and strategies. Similar results have been observed for a set of 668 Neotropical forest tree species from nine forest plots across a precipitation and geological substrate gradient in French Guiana. In that study, Baraloto et al. (2010) reported that trade-offs operate independently at the

leaf and stem level. Moreover, Li et al. (2015) observed that leaf economics and leaf hydraulics also operate independently for a set of 85 woody angiosperms, including trees and shrubs, from five tropical–subtropical forests in China. In our analysis, we extended these observations and found that trade-offs at the leaf level and trade-offs associated with plant hydraulics and stem specific density, including drought tolerance related traits (minimum leaf water potential [ $\Psi_{\text{min}}$ ] and the osmotic potential at turgor loss [ $\Psi_{\text{tlp}}$ ]), operate largely independently, with more clear differentiation in the dry forest (Table S1; Figure 1b–c). From the correlation table, we observed that LMA is more driven by leaf lamina thickness (LamT) than by leaf density (LD). Under high light conditions in the canopy, leaves become thicker because of stacking of more mesophyll layers (Kitajima et al., 2016; Niinemets & Sack, 2006; Terashima et al., 2011), which partially uncouples the cost of leaf construction (LMA) from investments in the stem (SSD), explaining part of the observed differentiation between the first and second axes. The uncoupling between the axis representing the leaf economics spectrum (LES) and the axis representing plant hydraulics, wood and leaf density suggests the existence of a wide space with multiple combinations of possible strategies depending on the species and resource availability.

### 4.2 | The major trait-strategy spectrum

Our data supported hypothesis two, that one major trait-strategy spectrum is characterized by species with acquisitive (fast) versus conservative (slow) trait values. We observed that the main axis of variation in the global PCA and within forest sites follows the leaf economics spectrum (LES; Wright, Reich, et al., 2004). The second axis showed overlap between the functional groups and species separated along this axis. In both forest sites, the spectrum of strategies runs from a most acquisitive end, characterized by species with low LMA, short leaf longevity and increased foliar nutrient concentration ( $N_{\text{mass}}$  and  $P_{\text{mass}}$ ) to a more conservative end characterized by the opposite patterns. Our analysis expands the traits considered in LES, by including other leaf functional traits. For instance, lamina fractal toughness (LamFT) had an important contribution in explaining the variation of the study species in both forest sites (Table S1). LamFT has important implications for defence against herbivores and to prolong leaf longevity (Kitajima & Poorter, 2010), explaining the positive association between LamFT and leaf longevity (LL) observed in this study (Table 3). Coupled to LamFT, leaf density (LD) and lamina thickness (LamT) also had an important contribution to the main axes of variation, particularly in the dry forest, which is expected since LMA, one of the highest contributors in explaining the variation among species (Table S1), is a product of both traits (Kitajima & Poorter, 2010). We also observed an important contribution of petiole length (PL) to the first axis, which was associated with high foliar nutrient concentrations ( $N_{\text{mass}}$  and  $P_{\text{mass}}$ ) and low LMA. Longer petioles may contribute to more extensive light capture per unit leaf area due to a reduced aggregation of leaf area and thus less self-shading (Takenaka, 1994). Plant species in both forest sites

run from a more acquisitive strategy, characterized by species with lower leaf construction costs (LMA, LD, LamT and LamFT), shorter leaf longevity (LL), high foliar nutrient concentrations ( $N_{\text{mass}}$  and  $P_{\text{mass}}$ ) and better leaf positioning for light capture (i.e. longer petioles, PL) to a more conservative strategy characterized by expensive leaves with longer returns on investments and lower foliar nutrient concentrations.

An important difference between forest sites is the high contribution of the duration of green foliage (E) and leaf hydraulic conductance ( $K_{\text{leaf}}$ ) to the main axis of variation for the dry (Figure 1b) and wet (Figure 1c) forest, respectively. In the dry forest, with a precipitation <2,000 mm/year, there was a larger proportion of deciduous species than in the wet forest (see Santiago et al., 2004), which is consistent with observations for tropical forests worldwide (Guan et al., 2015). A large proportion of drought avoiding deciduous species contributes to the high variability of the duration of green foliage (E) observed for species in the dry forest. Species that maintained leaves in their crowns for longer times (larger E) were able to do so because they produced physically well-protected leaves (LamFT in Table S1 and Figure 1b). Surprisingly, these species that maintained their green crowns for longer times (large E) were not physiologically more drought tolerant. E was largely orthogonal to the minimum leaf water potential ( $\Psi_{\text{min}}$ ) and the osmotic potential at turgor loss ( $\Psi_{\text{tlp}}$ ; Figure 1b), which suggests that dry forest species maintained their green crowns by either rapidly replacing (more hydraulically vulnerable) short-lived leaves or by maintaining (less hydraulically vulnerable) long-lived leaves (Figure 1b). In the wet forest, plant species with a more acquisitive strategy at the leaf level were also more efficient in transporting water through the leaf ( $K_{\text{leaf}}$ ; Figure 1c). Perhaps, in an environment that is wet throughout the year, it is more beneficial to make structural investments in water transport capacity and differ largely in leaf hydraulic conductance ( $K_{\text{leaf}}$ ). High  $K_{\text{leaf}}$  requires high investments in vascular tissues (e.g. wide xylem conduits in the midrib and higher venation densities; Aasamaa et al., 2001; Sack & Scoffoni, 2013). Fast-growing species may receive a high return on this investment (Sack et al., 2005), and thus be associated with high  $K_{\text{leaf}}$  while slow-growing species may not.

### 4.3 | Resource acquisition strategies in lianas and trees

Our data supported the hypothesis that lianas are adapted to high resource conditions (i.e. light and nutrients) and have trait values that would allow them to acquire resources more rapidly and grow faster than trees (hypothesis three) in the dry forest but not in the wet forest. For the dry forest, lianas and trees mainly differed in the main axis of the PCA, with higher acquisitive trait values than trees at the leaf level. For the wet forest, trait strategies of lianas and trees overlapped in the multivariate space due to a high interspecific variation not accounted for by the functional group (i.e. a high degree of species-specific niche differentiation), possibly due to a high micro-site variation (see Kraft et al., 2008).

Our finding that lianas are adapted differently than trees to high resource conditions in dry but not wet forests is supported by other published data. For the same study sites, Sánchez-Azofeifa et al. (2009) showed a higher differentiation in leaf traits, leaf internal structure and spectral reflectance between lianas and trees in the dry forest than in the wet forest. At a global scale, Asner and Martin (2012) studied 563 lianas species and 3,322 tree species (mostly one replicate per species) from 48 humid tropical forests from Madagascar, Australia, Malaysia and from several countries from the Americas and observed that above 2,500 mm of annual precipitation, light capture and growth chemical traits in lianas did not differ from trees. In the dry forest, with a precipitation c. 1,864 mm/year, lianas and trees differ in LMA and (marginally) in  $N_{\text{mass}}$ . We also observed that lianas in the dry forest have longer petioles than trees, which is associated with increases in light absorption and lower self-shading (Percy & Yang, 1998). By contrast, lianas and trees in the wet forest showed high variability in trait values not accounted for by functional group, not only at the leaf level but also at the stem/twig level and plant hydraulics. The exception was the duration of the green foliage (E), with lianas having shorter evergreen status than trees in the wet forest. However, this difference between lianas and trees in the wet forest did not drive any different pattern in their resource acquisition strategy, as observed by the high variability of species in the constructed PCA.

Other similar studies at the same forest sites did not detect differences between lianas and trees. For example, Slot and Winter (2017) showed that the temperature optimum of photosynthesis was similar for lianas and trees in both the dry and wet forests, and suggested that photosynthetic performance is optimized under current temperatures. In another study, Norby et al. (2017) found no differences in photosynthetic parameters (i.e. maximal Rubisco carboxylation rate [ $V_{\text{cmax}}$ ]) and nutrients (i.e. N:P ratios) between lianas and trees in the dry forest site, and concluded that such photosynthetic properties may depend more on edaphic conditions rather than on species per se. It could be argued that—withstanding leaf structural trait differences (related to leaf life span) between lianas and trees in the dry forest—trees and lianas acclimate and converge in physiological photosynthetic responses or that lianas and trees may differ in the seasonality of such physiological responses. We lack the data to confirm these potential explanations.

Why are there large differences between lianas and trees in the dry forest and not in the wet forest? The answer may be due to light and nutrient availability in the context of low water limitation. In wet forests, more persistent clouds lead to low light availability at the forest canopy, and the more evergreen and shade-tolerant species dominated canopy (Guan et al., 2015; Santiago et al., 2004; Vazquez & Givnish, 1998) likely results in deep shade in the forest understory throughout the year (Brenes-Arguedas et al., 2011; Chazdon & Fetcher, 1984). Simultaneously, high precipitation in wet forests could lead to high rates of soil weathering and nutrient leaching (Austin & Vitousek, 1998; Radulovich & Sollins, 1991; Schuur & Matson, 2001). The wet and dry forests in our study also differed in soil parent material (Turner & Engelbrecht, 2010), with the wet forest having lower soil extractable and resin extractable P than



the dry forest (Santiago et al., 2005). Plant species in wet forests, regardless of life-form, tolerate such low-light and low-nutrient conditions, possibly because of their more conservative trait values and long-lived leaf and stem tissues (Aerts & Chapin, 2000; Osnas et al., 2018; Umaña et al., 2021). By contrast, seasonal droughts and greater nutrient availability in dry forests may result in a wider range of plant strategies. In dry forests, high-nutrient conditions allow plants to be acquisitive (Umaña et al., 2021), and the high-light conditions due to low cloud cover (Graham et al., 2003), coupled with the high proportion of deciduous species (Santiago & Mulkey, 2004), may lead to a wider range of light conditions in space and time than wet forests (Brenes-Arguedas et al., 2011). Our study suggests that lianas were better adapted than trees to the high light and nutrient availability in dry forests (see also Medina-Vega, Bongers, Schnitzer, et al., 2021), although they were faced with strong seasonal water shortages during the dry season (Schnitzer, 2018; Schnitzer & van der Heijden, 2019).

## 5 | CONCLUSIONS

We observed two axes of variation in the ecological strategies of lianas and trees. The first axis was associated with the leaf economic spectrum and the second axis, orthogonal to the first, was related to plant hydraulics and stem (wood) and leaf density, suggesting that trade-offs at the leaf and stem, including plant hydraulics, operate independently. We observed a strong differentiation between lianas and trees in the dry forest, mostly driven by differences in leaf traits. In the wet forest, lianas and trees overlapped in their leaf and stem trait functionality. Differences between lianas and trees in the dry forest and the high overlap between life-forms in the wet forest may be driven by resource availability. In wet environments, relatively low light levels due to more cloudiness, and nutrient-poor soils (or lower soil nutrient cycling) may constrain a differentiation in resource acquisition strategies between lianas and trees. By contrast, in dry environments, lianas may benefit from high-light and nutrient-rich soils and thus take advantage of higher resource conditions. Given that the observed variation in light and soil nutrients is consistent with broader, generic, geographical gradients across the tropics, we hypothesize that our findings may apply to other dry and wet tropical forests, which can be tested with studies in multiple sites across large environmental gradients such as the one across the Isthmus of Panama.

We conclude that higher foliar nutrient concentration and a higher capacity to construct and display leaves with a lower cost may favour higher light interception, high photosynthetic rates and growth in lianas than in trees. These differences in leaf traits value favour lianas over trees in forests with lower precipitation and stronger seasonality, possibly explaining why lianas have higher performance than trees under high light and nutrient availability.

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## AUTHORS' CONTRIBUTIONS

F.J.S., F.B., S.A.S. and J.A.M.-V. conceived the ideas; F.J.S., F.B. and J.A.M.-V. designed the methodology; J.A.M.-V. collected and analysed the data; F.J.S., F.B., S.A.S., L.P. and J.A.M.-V. interpreted the data; J.A.M.-V. led the writing of the manuscript with comments from F.J.S., F.B., S.A.S. and L.P. All authors contributed critically to the drafts and gave final approval for publication.

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## DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.34tmpg4jr> (Medina-Vega, Bongers, Poorter, et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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