



# Liana functional assembly along the hydrological gradient in Central Amazonia

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## Abstract

Soil hydrology, nutrient availability, and forest disturbance determine the variation of tropical tree species composition locally. However, most habitat filtering is explained by tree species' hydraulic traits along the hydrological gradient. We asked whether these patterns apply to lianas. At the community level, we investigated whether hydrological gradient, soil fertility, and forest disturbance explain liana species composition and whether liana species-environment relationships are mediated by leaf and stem wood functional traits. We sampled liana species composition in 18 1-ha plots across a 64 km<sup>2</sup> landscape in Central Amazonia and measured eleven leaf and stem wood traits across 115 liana species in 2000 individuals. We correlated liana species composition, summarized using PCoA with the functional composition summarized using principal coordinate analysis (PCA), employing species mean values of traits at the plot level. We tested the relationship between ordination axes and environmental gradients. Liana species composition was highly correlated with functional composition. Taxonomic (PCoA) and functional (PCA) compositions were strongly associated with the hydrological gradient, with a slight influence from forest disturbance on functional composition. Species in valley areas had larger stomata size and higher proportions of self-supporting xylem than in plateaus. Liana species on plateaus invest more in fast-growing leaves (higher SLA), although they show a higher wood density. Our study reveals that lianas use different functional solutions in dealing with each end of the hydrological gradient and that the relationships among habitat preferences and traits explain lianas species distributions less directly than previously found in trees.

**Keywords** Functional traits · Species composition · Tropical forest · Water-use efficiency · Wood density

## Introduction

Tropical climates support high richness and morphological diversity in different groups of woody plants. In tropical forests, woody climbing plants (lianas) account for about 25% of the abundance and species diversity of woody

stems (Gentry 1991; Schnitzer and Bongers 2011), playing an essential role in forest dynamics (Schnitzer and Bongers 2002), carbon sequestration (Chen et al. 2015), and as food and canopy pathways for animals (Putz and Mooney 1991; Schnitzer and Bongers 2002). Despite this importance, biologists only recently began to unveil liana distribution patterns in tropical forests. On continental or

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global scales, high liana abundance and richness have been associated with low mean annual precipitation or high seasonality (Schnitzer 2005; DeWalt et al. 2015). At local and landscape scales, high liana abundance and richness were associated with greater availability of climbing supports (Nogueira et al. 2011), higher availability of soil nutrients, such as phosphorus (Malizia et al. 2010; Ledo et al. 2016), and with disturbances such as large-sized canopy gaps (Schnitzer and Carson 2010; Nogueira et al. 2011).

However, at the landscape scale, few studies have investigated the role of soil water on the spatial distribution of liana species (e.g., Schiatti et al. 2014; Manzané-Pinzón et al., 2018), especially pertaining how this distribution is related to the variation of leaf and wood traits across liana species. This knowledge gap is surprising given the large soil hydrological variation in tropical forests sites, especially in the Amazon rainforest (Costa et al. 2022). Perhaps the assumption that lianas have higher efficiency in obtaining and transporting water compared to trees (Yong et al. 2012; Chen et al. 2015) has influenced the lack of studies evaluating the filtering effects of local hydrological gradients. A higher capacity to access large volumes of soil water and more efficient stomatal aperture control have been proposed as strategies that reduce the risk of hydraulic failure in lianas (Campanello et al. 2016; Schnitzer 2018; van der Sande et al. 2019). If true, lianas would establish independently of local water availability. We still know very little about the variation of functional features of liana species along local hydrological gradients, and currently held beliefs about the impact of water availability (or seasonality) are largely based on broad-scale patterns of liana density (Schnitzer 2005; DeWalt et al. 2015).

Many liana species have large xylem vessels in a highly conductive vascular system (Ewers et al. 1991; Schnitzer 2005; Gerolamo and Angyalossy 2017), mostly thin stems with a high proportion of soft tissues (vascular parenchyma and secondary phloem), and a low percentage of fibers (Angyalossy et al. 2015). These features generate a stem with a low bending stiffness (Rowe et al. 2004; Gerolamo et al. 2020). This general description of liana structure gives the false impression that all liana species function similarly and form a homogeneous group, but this is far from true. For example, some liana species have the remarkable capacity to survive and re-sprout after falling from the canopy or suffering crown damage (Putz 1984), but this pattern varies greatly between species, and most have a limited ability to regenerate under such conditions (Rocha et al. 2020). In the same way, some liana species use more superficial water sources than trees during the dry season (De Deurwaerder et al. 2018), despite similar root depths (De Deurwaerder et al. 2018; Smith-Martin et al. 2019). The uncommon evaluation of lianas in contrast to trees may reinforce this

perception of homogeneity. A renewed focus on the ecology of liana assemblages on their own is needed.

The variation of resource availability across forest landscapes is expected to filter species according to the traits affecting establishment, survival, and reproduction, such that species composition along the resource gradients would reflect the distribution of functional traits following the plant economic spectrum (Wright et al. 2004; Chave et al. 2009; Diaz et al. 2016). Along the economic spectrum, plants with a fast-growing acquisitive strategy based on cheap tissue investments dominate in moist and fertile areas (Grime et al. 1997; Reich et al. 1999), while plants with a conservative strategy grow slowly with expensive tissue investments in low resource or high stress conditions (Wright et al. 2004; Reich 2014). These expectations rarely have been tested for lianas (but see Medina-Vega et al., 2021) and could explain variation in the strategies of lianas along ecological gradients, as observed for trees (Cosme et al. 2017; Toledo et al. 2017). We postulate that the considerable, yet underexplored, variation of functional traits within liana assemblages could explain the differential distribution of liana species in tropical forest landscapes (e.g., Vivek and Parthasarathy 2014; Medina-Vega et al. 2021).

In Central Amazonia, the vertical distance to the nearest drainage, a proxy for the water-table depth, is a robust hydrological predictor of plant species composition, explaining the variation of plant assemblages across the landscape (Schiatti et al. 2014). In this way, the hydrological gradient may provide a major habitat axis of plant species differing in water use requirements (Silvertown et al. 1999; Balvanera et al. 2011). If true, we expect this gradient to be strongly correlated with the variation in liana taxonomic and functional composition, followed by secondary ecological axes such as edaphic and forest disturbance gradients. This gradient would lead to differentiation of local species composition according to the hydrological niches of species (Jirka et al. 2007; Silvertown et al. 2015; Cosme et al. 2017; Oliveira et al. 2019), and the expected trade-off between cavitation resistance and water transport efficiency (van der Sande et al. 2019), which should be reflected in species morphological and anatomical traits.

This study investigated the distribution pattern of liana species and their functional traits by sampling lianas in permanent plots across a 64 km<sup>2</sup> landscape in a hyper-diverse Amazonian rainforest. We evaluated leaf and stem wood functional traits related to light capture, water transport, nutrient conservation, and mechanical support to address two main questions: (i) Are changes in the species composition of liana assemblages determined by hydrological, edaphic, and forest disturbance gradients? (ii) Do functional traits mediate liana species-environment relationships? We hypothesized that liana species composition is primarily explained by hydrological gradient and secondarily by

soil fertility and forest disturbance gradients in this moist tropical forest. Since species–environment relationships are presumed to be mediated by functional traits (Suding et al. 2008), we hypothesize that the combination of liana species in portions of the three distinct ecological gradients is mainly caused by leaf and stem wood functional traits varying across species.

## Materials and methods

### Study site

The study was conducted in the Reserva Florestal Ducke (hereafter Ducke Reserve) of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Central Amazonia, located 26 km north of Manaus (2°55' S, 59°59' W at reserve headquarters), Brazil. Ducke Reserve is a Brazilian Long-Term Ecological Research (LTER) site where ecological data on topography, soil properties, and species abundance have been systematically collected in permanent plots (<https://ppbio.inpa.gov.br>). The average annual temperature from 1966 to 2018 was *c.* 26 °C, and the annual rainfall was 2572 mm with a monthly maximum of 331.4 mm in April and a minimum of 98.8 mm in August (Ducke Reserve weather station data). The dry season occurs between July and September, but on average, only two months have rainfall less than 100 mm (Marques-Filho et al. 1981). Soils are derived from tertiary marine sediments of the Alter do Chão formation (Chauvel et al. 1987).

The predominant vegetation is terra firme forest. The well-dissected relief is formed by different topographic levels, slopes, soil types, and hydro-morphological conditions that range from plateau to valley (Chauvel et al. 1987). This well-dissected relief is typical of the old soils that originated on the Guiana Shield in the Central Amazon region (Sommer 2000). The plateaus are the highest areas (elevation above sea level between 90 and 120 m) with clayey, well-drained and generally more fertile soils (Hopkins 2005) with water table *c.* 20 m deep. In these portions of the forest, it is possible to find the largest and probably the oldest trees (30–40 m), including emergent trees such as *Dinizia excelsa* Ducke, reaching 60 m in height (Hopkins 2005). As the altitude decreases, there is a transition of environments and the clay content of the soil decreases while the sand gradually increases. Valleys are topographic portions of riparian areas with sandy and generally less fertile soils at lower altitudes, although phosphorus content may vary among valleys. Valleys are also mostly flat or gently sloping with the water table close to the surface (as shallow as 1 m depth) and seasonally waterlogged during the rainy season (Drucker et al. 2008; Tomasella et al. 2008). The height of the canopy in the valley is lower than in plateau regions and includes many

palm trees, such as *Oenocarpus bataua* Mart. and *Mauritia flexuosa* L.f. (Kahn and Castro 1985; Hopkins 2005).

### Sampling design and liana species composition

Lianas were sampled in 18 plots at least 1 km from one another, distributed over a 5 × 6 km grid (30 km<sup>2</sup>) and spanning a range of altitudes from 39 to 140 m (Ribeiro et al. 1999; Fig. S1). Each plot is 250 m long and 40-m wide following the RAPELD sampling system (<https://ppbio.inpa.gov.br/en/Methods/RAPELD>). The center line follows the terrain level isoline to minimize soil and water-table depth variations inside each plot (Magnusson et al. 2005; Costa and Magnusson 2010).

Lianas data in all plots were initially collected in 2004–2005 (Nogueira et al. 2011) and were resampled in 2014 (Gerolamo et al. 2018), following the liana census protocol developed by Gerwing et al. (2006). Lianas with multiple rooting points connected underground were not genetically distinguished, and each stem was considered an individual. All lianas (individual stems) with a diameter (*D*) ≥ 5 cm at 1.3 m above their rooting point were sampled throughout the 1 ha plot (250 m × 40 m). Thinner lianas (1 cm ≤ *D* ≤ 4.9 cm) were sampled in one subplot per hectare of 0.25 ha (250 × 10 m). In a previous study, 32 species of the tribe Bignoniaceae (Bignoniaceae) were investigated for species composition in the permanent plots of the Ducke Reserve (Schietti et al. 2014). In the present study, we expanded species identification to all individuals of lianas marked in the previous censuses. We collected vouchers of specimens for botanical identification between 2016 and 2019. Botanical specialists assisted plant identification mainly based on vegetative characters, such as phyllotaxy, stem form, wood anatomy, bark odor, color, texture, lenticel distribution, leaf type/parts, leaf form, venation, presence of exudate, and anchoring structures. Fertile specimens were also considered when available. Liana species composition data are available at [ppbio.inpa.gov.br/en/home](http://ppbio.inpa.gov.br/en/home) and [forest-plots.net](http://forest-plots.net).

### Functional plant traits

We selected eleven leaf and stem wood traits related to light capture, water transport, and nutrient conservation (see below) to describe the functional traits of each liana species (see plant traits studied in Table 1). In the field, we chose one individual per species per plot to collect plant samples, and in total, 3 to 10 individuals were sampled per species. We carefully selected stems growing approximately 1 m from the plant apex and multiple leaves from the liana's crown on the sunlit side for each individual. Leaves and stems were sampled, placed in sealed plastic bags, and kept moist until processed in the Ducke Reserve laboratory

**Table 1** Description of functional plant traits used to characterize each liana species assembly at the Ducke Reserve (Brazil)

Trait	abb.	Description	Related function*
Leaf dry matter content	LDMC	Oven-dry mass of a leaf divided by its water saturated fresh mass ( $\text{mg g}^{-1}$ )	Leaf tissue density, leaf physical resistance, stress tolerance
Leaf size	LS	Mean area-leaf ( $\text{cm}^2$ )	Photosynthetic capacity; leaf temperature
Leaf thickness	LT	Leaf blade thickness ( $\mu\text{m}$ )	Resistance and protection
Specific leaf area	SLA	One-sided area of a fresh leaf divided by its oven-dry mass ( $\text{cm}^2 \text{g}^{-1}$ )	Photosynthetic rate, leaf longevity, relative growth rate
Stomata density	SD	Stomata density ( $\text{no. mm}^{-2}$ )	Determine maximum leaf diffusive (stomatal) conductance of $\text{CO}_2$ ( $g_{\text{cmax}}$ ) to sites of assimilation
Stomata size	SS	Mean stomata length ( $\mu\text{m}$ )	–
Vein density	VLA	Vein length per unit area ( $\text{veins mm}^2$ )	Protection and water transport in plants
Lianescent xylem	Pxl	Fraction of the xylem area (or proportion) with the characteristics of the lianescent vascular syndrome (%)	Flexibility and greater water transport potential
Self-supporting xylem	Pxs	Fraction of the inner area (or proportion) of the xylem with a small diameter vessel and more fibers developed in the self-supporting phase (%)	Water transport and mechanic support
Vessel density	VD	Vessel density ( $\text{vessels mm}^2$ )	Xylem cells concerning long distance water transport in plants
Wood density	WD	Wood density ( $\text{g cm}^3$ )	Highly interactive trait of wood

\*Carlquist (1975); Grime et al. (1997); Cornelissen et al. (2003); Garnier and Navas (2012); Sack and Scoffoni (2013); Angyalosy et al. (2015)

## Leaf traits

We selected mostly intact leaves without injury for measuring leaf functional traits. Three mature leaves per stem were digitally scanned (HP Scanjet 200) and processed to calculate leaf area ( $\text{cm}^2$ ) using ImageJ software (National Institutes of Health, Bethesda, MD, USA; <http://rsb.info.nih.gov/ij/>). Leaf thickness (mm) was measured with a digital micrometer (accuracy 0.001 mm). We also measured the fresh leaf weight (g) and the dry leaf weight (g) on an electronic balance accurate to four decimal places. For dry weight, fresh leaves were dried at 60 °C in a dehydration oven for at least three days until a constant weight was recorded. We also calculated the leaf water content (LWC; %), leaf dry matter content (LDMC;  $\text{mg g}^{-1}$ ), and specific leaf area (SLA;  $\text{cm}^2 \text{g}^{-1}$ ) following Cornelissen et al. (2003).

Two additional mature leaves were fixed in FAA (formaldehyde, acetic acid, and 50% ethanol, Johansen 1940) in the field, and after 48 h, preserved in 70% alcohol. In the laboratory, we cut two one-centimeter squares from the leaves, avoiding the central vein, to evaluate stomatal density (SD; number  $\text{mm}^2$ ), stomatal size (SS;  $\mu\text{m}$ ), and vein length per unit area (VLA; also known as “vein density”). In one leaf square, the leaf epidermis was dissociated for stomata detection, with immersion in a solution of glacial acetic acid and hydrogen peroxide (1:1 v/v) at 60 °C for 48 h for most species. Some species (e.g., *Davilla rugosa*) required more time (Franklin 1945, modified by Kraus and Arduin 1997). Then, leaf samples were washed with distilled water, stained with 1% safranin, and mounted as semi-permanent slides with

glycerin (Bukatsch 1972, modified by Kraus and Arduin 1997). Photographs were taken using a light microscope (Leica DM500, Leica Microsystems, Wetzlar, Germany) under 200× magnification. Stomatal density (SD) and stomatal size (SS) were measured and counted in photos over an area of 0.45  $\text{mm}^2$  in each of the two leaves using ImageJ software. Stomatal size was defined as the length in micrometers between the junctions of the guard cells at each end of the stomata. To determine leaf vein density, we immersed a five  $\text{mm}^2$  leaf square of the second leaf cut in 20% sodium hydroxide solution until depigmentation occurred (Arnott, 1959). Then, we washed the samples in distilled water, photographed them with a stereomicroscope Leica (Leica M205 C, Leica Microsystems, Wetzlar, Germany), and estimated the vein density (VLA) using the leaf GUI software (<http://www.leafgui.org/>).

## Stem wood traits

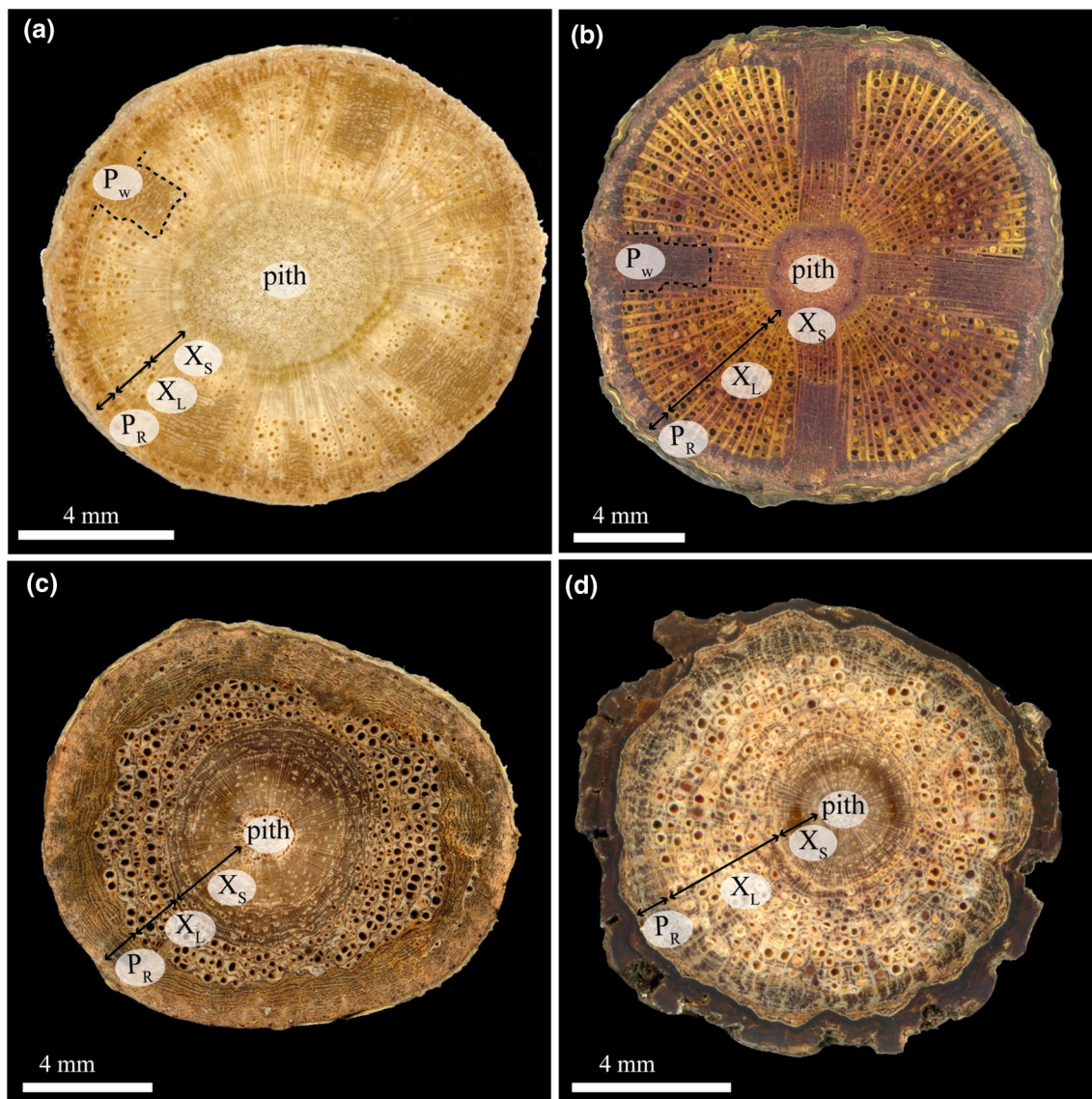
Using the same stems from which the leaves were obtained for each plant, we cut three stem samples of 0.5–2 cm in diameter and 2 cm in length from the basal-most part of the stem. The first sample was used to measure the cross-sectional area of stem tissues, the second for microscopic analyses of secondary xylem, and the third sample to estimate wood density.

To estimate the percentage of each stem tissues' cross-sectional area relative to the total area of the stem, we initially polished each stem sample with a decreasing series of sandpaper particle sizes (Barbosa et al. 2021). Then, we

scanned the cross-sectional area of stems on the high-resolution scanner indicated above and analyzed tissue distribution using ImageJ software. The cross-sectional stem area of each sample was categorized and measured as four distinct regions: pith, two parts of the secondary xylem (inner-formed dense xylem developed in juvenile and supposedly self-supporting phases, and lianescent xylem with wide vessels developed in climbing phases), and bark (all tissues outside of the vascular cambium). See Fig. 1 for details about

the four tissues categorized in the cross-sectional stem area. Recognition and classification of stem tissues and anatomical patterns of lianas were based on the descriptions of Angyalossy et al. (2015).

For microscopic xylem measurements, the stem sample was fixed in FAA (formaldehyde, acetic acid, and 50% ethanol, Johansen 1940) for at least 12 h and then preserved in 70% alcohol. In the laboratory, cross sections of each sample's secondary xylem (three to five individuals per species)



**Fig. 1** Stem cross sections of Bignoniaceae and Fabaceae species collected at Ducke Reserve along of the hydrologic gradient. **a** *Aneuropogon robustum* and **b** *Adenocalymma validum* species of Bignoniaceae; **c** *Machaerium multifoliolatum* and **d** *Machaerium macrophyllum* species of Fabaceae. Species in **a** and **c** are commonly found in lowland areas closer to the water table in riparian (valley) while species in **b** and **d** are commonly found in upland areas (plateaus). The self-supporting xylem ( $X_s$ ) is similar to the xylem of many trees

and shrubs. The self-supporting xylem is produced in most liana species during the initial phase of secondary xylem development and is recognized by having a predominance of fibers, fewer parenchyma and smaller vessels. The lianescent xylem ( $X_L$ ) is recognized by large vessels, abundant parenchyma, huge rays and fewer fiber. In the bark we can see the regular phloem region ( $P_R$ ) and in many lianas it is quite common to see cambial variants such as phloem wedges ( $P_w$ ) in species **a** and **b**)

were obtained with a sliding microtome, stained in 1% astra blue and 1% safranin (Bukatsch 1972, as modified by Kraus and Arduin 1997) to document cells with cellulose and those with cellulose and lignin. Permanent anatomical slides were prepared with a synthetic resin and then photographed with a light microscope (Leica DM500, Leica Microsystems, Wetzlar, Germany) at 200× magnification. To characterize the secondary xylem of each individual, we estimated the vessel lumen diameter ( $d$  in  $\mu\text{m}$ ), measuring at least 30 vessel elements and the number of vessels per square millimeter (VD) using at least two areas of  $1\text{ mm}^2$ . Both traits were measured using ImageJ software for each individual and then averaged by species.

We estimated each stem sample's wood density by removing the bark and determining the fresh xylem volume using the water displacement method. Then each sample was dried for at least 72 h at 105 °C and weighed until a constant weight was recorded. Wood density ( $\text{WD}$ — $\text{g cm}^3$ ) was determined as the ratio between the dry wood mass and the fresh wood volume (including pith).

### Ecological gradients: HAND, soil fertility, and tree turnover

Height above the nearest drainage (HAND) in the Ducke Reserve quantitatively describes the vertical distance of each plot to the nearest drainage. HAND is an indirect estimate of the hydrological gradient derived from the algorithm of Rennó et al. (2008) from the Shuttle Radar Topography Mission (SRTM) digital elevation model, with 90 m of spatial resolution (Schietti et al. 2014). High HAND values correspond to high elevation plots associated with ridges and plateaus vertically distant from the water table. In contrast, low HAND values represent plots in lowland areas closer to the water table in riparian (valley) areas. Soil texture and the sum of exchangeable cations (calcium, magnesium, potassium, and sodium) of each plot are highly correlated with HAND (Pearson  $r = 0.58$ ,  $P < 0.001$ ,  $n = 30$ ;  $r = 0.57$ ,  $P = 0.01$ ,  $n = 18$ , respectively) at the Ducke Reserve. Plots far from the water table (plateaus) have more clayey and cation-rich soils than plots closer to the water table. Therefore, the HAND gradient incorporates other correlated gradients, such as soil texture and fertility, given by the sum of cations and the vertical access to water (<https://ppbio.inpa.gov.br>). Soil concentration of available phosphorus ( $P$ ;  $\text{mg kg}^{-1}$ ) is not correlated to the HAND gradient ( $r = -0.21$ ,  $P = 0.39$ ,  $n = 18$ ). The phosphorus limitation in tropical soils can be an important axis in niche segregation (Condit et al. 2013). We used available phosphorus ( $P$ ) concentration to characterize the soil fertility independent of the HAND gradient and explain the compositional changes of liana species at the Ducke Reserve.

We also investigated the role of forest dynamics on the distribution of liana species. Our metric of forest dynamics was tree turnover, calculated as the average annual rate of tree mortality and recruitment (Phillips and Gentry 1994). Tree turnover estimation was based on numbers of dead and recruited trees with  $\text{DBH} > 10\text{ cm}$  over the five years of tree censuses between 2003 and 2009 (Castilho et al. 2010). Because we do not have tree turnover data that precisely match the liana census time interval, we assumed that our estimates of tree turnover rates reflect the forest's intrinsic properties and tendency to maintain similar levels for a relatively long period.

### Statistical analyses

We reduced the dimensionality of the species composition of lianas using Principal Coordinate Analysis (PCoA). Ordinations were based on species occurrence data (presence or absence of species) and relative species abundance data. In the first ordination, we applied the Sørensen dissimilarity index using species occurrence data. In the second ordination, we applied the Bray–Curtis dissimilarity index. We included both indexes to better understand the contribution of rare and abundant liana species in the distribution patterns. In both cases, only the first two axes of PCoA were used in subsequent analyses to test the relationship between the liana assemblage composition and the three environmental gradients (HAND, soil P, and tree turnover).

To explore the variation in the liana assemblage's functional traits relative to each plot, we also performed two Principal Component Analyses (PCA), one based on the species occurrence and the other on species relative abundances. In both multivariate analyses, we used the average of the eleven leaf and stem traits per species. The first PCA used the simple average of each trait across species found in each plot (qualitative functional PCA). The second PCA used average trait values per species weighted by each species' abundance in each plot (quantitative functional PCA). In both cases, only the first two axes of PCA were used in the subsequent analyses to test the relationship between the functional composition and the three environmental gradients (HAND, soil P and tree turnover).

The first two axes of the taxonomic-based PCoAs (PCoA-1 and 2) and functional-based PCAs (PCA-1 and 2) were used independently as response variables in our statistical modeling. We tested the relationship between the response variables (PCoA and PCA axes) and the three ecological gradients (HAND, soil  $P$ , and tree turnover). In all models, the HAND gradient was log-transformed to ensure linearity. We considered a set of models with multiple combinations of the main effects of the three ecological gradients. We used a model selection approach for each response

variable to evaluate the minimally adequate model from a set of models that included a null model (only the intercept without ecological gradients as fixed factors). The minimally adequate model had the lowest Akaike Information Criterion (AIC) value, and models with  $\Delta\text{AIC} < 2$  are similarly plausible. We also inspected the three ecological gradients' multicollinearity using the Variance Inflation Factor (VIF, Dormann et al. 2013), and the VIF values were always less than two in all cases.

Finally, we evaluated whether functional composition changes parallel floristic composition changes by performing a simple regression between the PCoA and PCA axes.

All statistical analyses were performed in R program version 3.4.0 (R Core Team 2017). PCoA and PCA were run with `vegdist` and `prcomp` functions of the `vegan` package, respectively (Oksanen et al. 2015). Model selection was performed with the `dredge` function of the `Mumin` package (Barton 2014).

## Results

### Are changes in the species composition of liana assemblages shaped by hydrological, edaphic, and forest disturbance gradients?

We sampled 2,000 individuals of 115 species of lianas distributed in 22 families, of which the richest families were (in order): *Bignoniaceae*, *Fabaceae*, *Celastraceae*, *Connaraceae*, and *Dilleniaceae*. The first two axes of the qualitative PCoA ordination captured 57% of the variance in species composition (Table 2; supporting information; Table S3), and the first two axes of the quantitative PCoA ordination captured 73% (supporting information; Table S4).

Liana species composition represented by the qualitative PCoA-1 axis was only related to the HAND gradient (model

1 of Table 2, Fig. 2). There was a gradual substitution of species from valleys to plateaus, described by the HAND gradient, as illustrated in Fig. 3 for the two most representative liana families in the Amazon Forest (*Fabaceae* and *Bignoniaceae*). High HAND plots (plateaus) had several exclusive species, such as the legumes *Mimosa guilandinae*, *Senegalia altiscandens*, and *Clitoria leptostachya* (Fig. 3A), the *Bignoniaceae* *Pleonotoma longiflora*, plus several *Adenocalymma* species (Fig. 3B). Exclusive species in the low HAND plots (valleys) were *Fridericia japurensis* and *Anemopaegma robustum* (Fig. 3B). The second compositional axis was not associated with any of the ecological gradients, and the null model was the minimum adequate model selected for the qualitative PCoA-2 axis (Table S3). The results based on the quantitative PCoA axes were similar to those presented here for qualitative data (supporting information; Table S4).

### Do functional traits mediate liana species-environment relationships?

The first two axes of the qualitative functional PCA captured 49% of the functional species composition variation, while the first two axes of quantitative functional PCA captured 59%. Along the qualitative PCA-1 axis, the average community values of stomatal size and self-supporting xylem increased, while leaf size, specific leaf area, and wood density decreased. Along the qualitative PCA-2 axis, stomatal density, vessel density, and leaf dry matter content increased while leaf thickness decreased (Fig. S2 and Table S1). The quantitative PCA axes were correlated with leaf and stem functional traits, similar to the qualitative PCA axes.

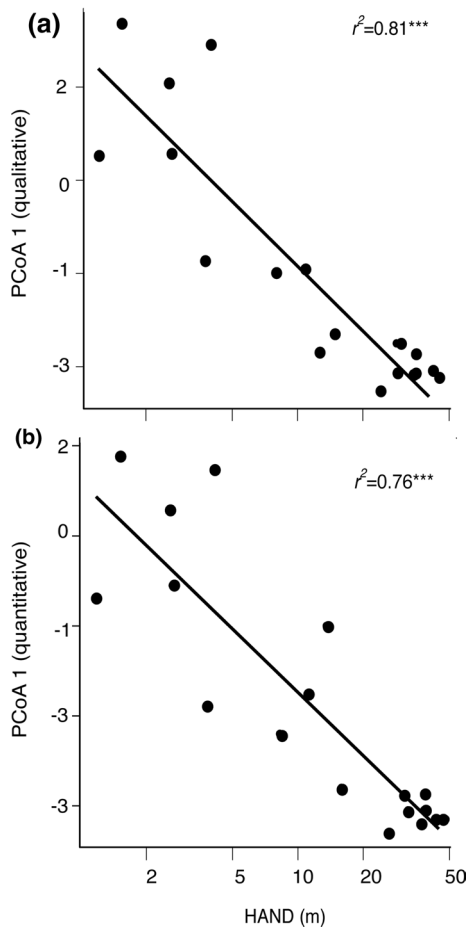
The qualitative functional PCA-1 axis was negatively related to the HAND gradient but not the other environmental predictors (model 1 of Table 3 and Fig. 4A). In contrast, the qualitative functional PCA-2 axis was not related to any predictor. Thus, in low HAND plots (valleys), liana species

**Table 2** Model selection results for liana species composition across 18 plots covering three distinct ecological gradients at Ducke Reserve, Central Amazonia

Models	Response variable	Fixed factors	K	AIC	$\Delta$ AIC
1	Qualitative	HAND	3	-21.2	0.00
2	PCoA1	HAND + Tree turnover	4	-19.4	1.75
3	(47%)*	HAND + Phosphorus	4	-19.2	1.94
4		HAND + Phosphorus + Tree turnover	5	-17.5	3.65
5		1	2	6.9	28.08
6		Phosphorus	3	7.8	28.94
7		Tree turnover	3	8.5	29.67
8		Phosphorus + Tree turnover	4	9.2	30.36

The response variable used here was the first axis of qualitative PCoA (PCoA-1), describing the liana species composition. The analysis of the second PCoA axis is available in S3 (supporting information). Gaussian error distribution was used in all models, including none or even the three fixed factors: log the hydrologic gradient (estimated as height above the nearest drainage, HAND), phosphorus soil content, and tree turnover (average annual rate of tree mortality and recruitment) gradients

\*Proportion of variance



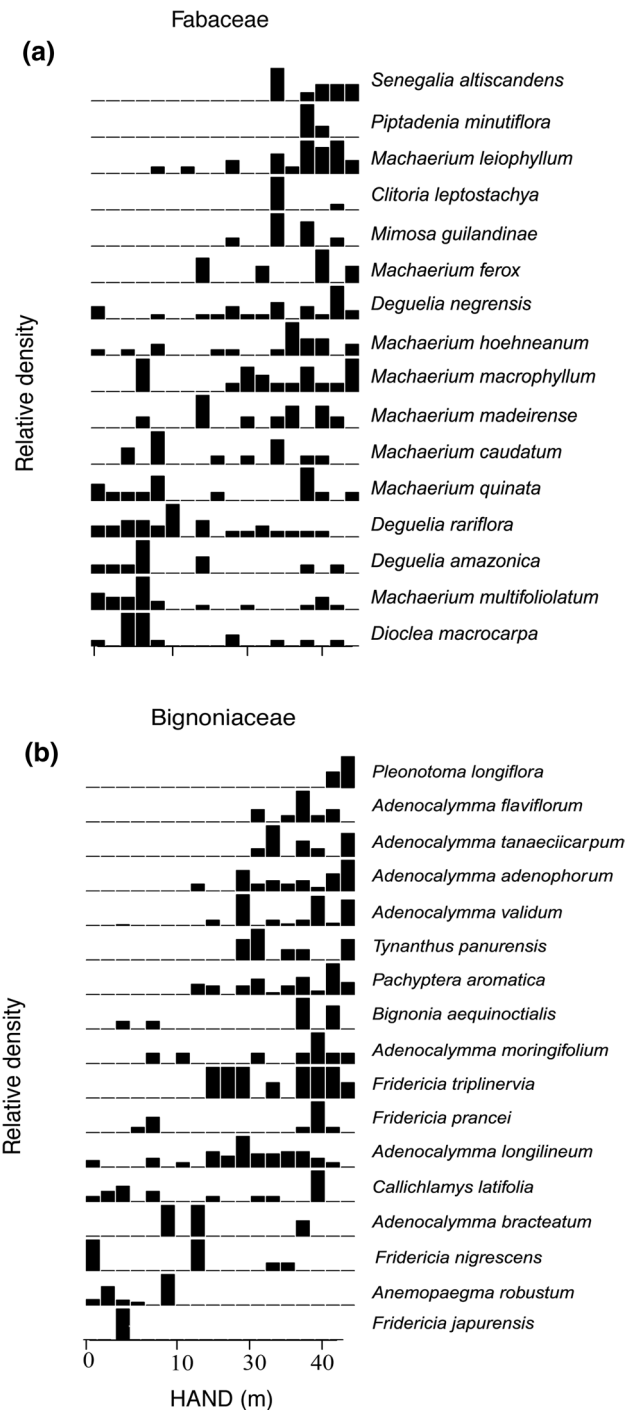
**Fig. 2** Relationship between lianas species composition (first PCoA axes) and the hydrologic gradient (estimated as height above the nearest drainage, HAND) in 18 permanent plots at Ducke Reserve. **a** Liana species composition represented by the qualitative PCoA-1. **b** Liana species composition represented by the quantitative PCoA-1.  $r^2$  adj and significance level (\*\*\*)  $P < 0.001$  are shown

had higher mean values of the area of self-supporting xylem (Pxs, Fig. 4B) and stomata size (SS), and lower mean values of leaf size (LS, Fig. 4C), specific leaf area (SLA, Fig. 4D), and wood density (WD). The quantitative PCA axes had a similar relationship to the environmental predictors as the qualitative PCA axes.

These functional changes of the qualitative PCA-1 axis were strongly correlated with taxonomic species composition changes captured in the qualitative PCOA-1 axis ( $r^2 = 0.53$ , Fig. 5).

### Discussion

We asked whether changes in the species composition of liana assemblages are shaped by hydrological, soil fertility, and forest disturbance gradients and if functional trait



**Fig. 3** Distribution of the liana species along the hydrologic gradient (estimated as height above the nearest drainage, HAND). **a** Liana species of the family Fabaceae. **b** Liana species of the family Bignoniaceae. Vertical bars are the relative abundance of each species (ranging from 0 to 1) along the HAND gradient in 18 permanent plots at Ducke Reserve. The bottom panel refers to the HAND values of each plot



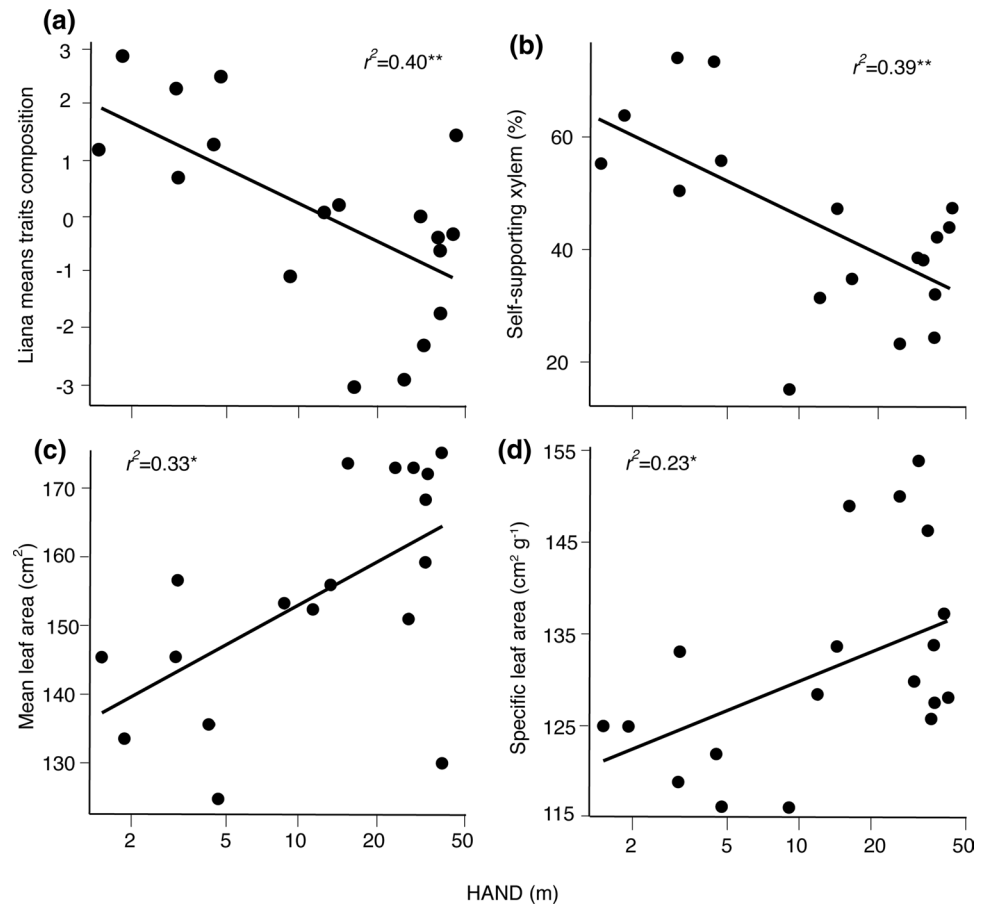
**Table 3** Model selection results for liana species composition across 18 plots covering three distinct ecological gradients at Ducke Reserve, Central Amazonia

Models	Response variable	Fixed factors	K	AIC	Δ AIC
9	First Axis	HAND	3	63.2	0.00
10	PC1	HAND + Tree turnover	4	64.9	1.77
11	(27.5%)*	HAND + Phosphorus	4	65.2	2.00
12		HAND + Phosphorus + Tree turnover	5	66.9	3.76
13		1	2	73.3	10.12
14		Phosphorus	3	74.7	11.54
15		Tree turnover	3	75.3	12.12
16		Phosphorus + Tree turnover	4	76.7	13.54

The response variable used here was the first axis of qualitative PCA (PCA-1), describing the liana species composition. The analysis of the second PCA axis is available in S6 (Supporting information). Gaussian error distribution was used in all models, including none or even the three fixed factors: log the hydrologic gradient (estimated as height above the nearest drainage, HAND), phosphorus soil content, and tree turnover (average annual rate of tree mortality and recruitment) gradients

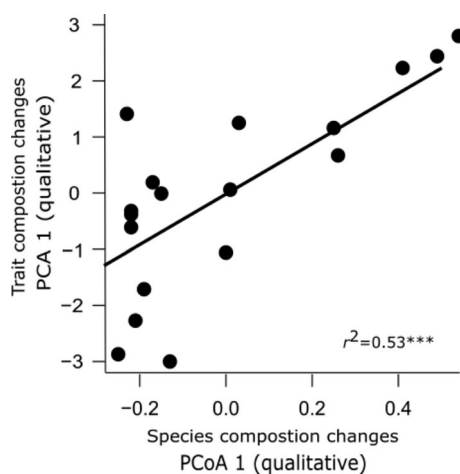
\*Proportion of variance

**Fig. 4** Relationship between the liana mean traits composition and some functional traits and the hydrologic gradient (estimated as height above the nearest drainage, HAND) in 18 permanent plots at Ducke Reserve. **a** Liana mean traits composition represented by the qualitative PCA 1 axis along the hydrological gradient (HAND). Along PCA-1, axis values of stomatal size and self-supporting xylem increased, while leaf size, specific leaf area and wood density decreased. **b–d**) Functional traits correlated with three other traits directly related to the hydrological gradient (HAND): self-supporting xylem **b**), leaf size **c**) and specific leaf area **d**).  $r^2$  adj and significance level (\* $P < 0.005$ ; \*\* $P < 0.01$ ) are shown



composition changes parallel the gradients. In accord with our predictions, we found that: (i) liana species composition was strongly correlated with the hydrological gradient represented by the terrain height above the nearest drainage (HAND), a proxy for the water-table depth; (ii) the turnover of liana species along the hydrological gradient is strongly correlated with differences in leaf and stem wood

functional traits across species, i.e., the taxonomic compositional turnover of lianas in space was strongly linked to the functional change. Thus, variation in leaf and stem wood traits explained the strong association between liana species composition and the hydrological gradient on the old dissected terrains distributed in the Central Amazonia rainforest.



**Fig. 5** - Relationship between liana mean traits composition represented by the qualitative PCA-1 and species composition represented by the qualitative PCoA 1 axis in 18 permanent plots at Ducke Reserve.  $r^2$  adj and significance level (\*\*\*)  $P < 0.001$  are shown

### The hydrological gradient explains landscape changes in liana species composition

Our results support the hypothesis that soil hydrology shapes local liana floristic patterns within Amazonian terra firme forests. We explained 81% of the species composition variation with only one predictor, the hydrological gradient (HAND). Simultaneously, soil fertility (P content) and forest dynamics (tree turnover) had only marginal effects in secondary models. Our results expand previous findings for the tribe Bignoniaceae in this same forest (Schietti et al. 2014; Gerolamo et al. in review), increasing the generality of the distribution pattern along the hydrological gradient to the full range of taxonomic entities in the liana assembly. Previous studies have detected a filtering effect of the water table depth on Amazonian tree species composition (Jirka et al. 2007; Schietti et al. 2014) and linked that to the selection of species-level functional traits (Cosme et al. 2017; Oliveira et al. 2019; Schmitt et al. 2020). To our knowledge, few studies show that liana species are also filtered along a hydrological gradient (Schietti et al. 2014; Manzané-Pinzón et al. 2018).

The turnover of liana species composition from valleys to plateaus indicates that variation in the soil water conditions plays an essential role for liana species distribution, similar to the patterns observed for herbs, trees, and palms (Costa et al. 2005, 2009; Schietti et al. 2014; Manzané-Pinzón et al. 2018). This pattern is surprising because lianas have been generically described as very efficient at obtaining and transporting water, which has created the expectation that lianas would establish independently from local water availability, the opposite of what we found here. However, in the Ducke Reserve, valleys have sandy soils close to stream courses

and are strongly influenced by waterlogging during the rainy season (Castilho et al. 2006; Toledo et al. 2017). Despite the expected rapid drainage of sandy soils, the constant inflow of groundwater from higher topographic positions generates a high water table in the valleys (Hodnett et al. 1997). Consequently, roots remain superficial and in contact with waterlogged soils during the wet season or year-round, depending on the micro-relief. Waterlogged soils have hypoxic to anoxic conditions that should restrict the colonization of plants without appropriate functional traits (Larcher 2000; Parolin et al. 2003). Thus, species composition in these environments is expected to be composed of hydro-edaphic specialist species (Kalliola and Puhakka 1988; Muscarella et al. 2019), capable of coping with these extreme soil conditions (e.g., Cosme et al. 2017; Oliveira et al. 2019). This pattern is also observed in herbs and woody plants with non-liana life-forms (Schietti et al. 2014; Muscarella et al. 2019). Therefore, our results confirm that soil hydrology is an essential factor determining local variation in plant assembly, independent of plant habit, in Amazonian terra firme forests.

### Patterns of functional composition change: are species-environment relationships mediated by functional traits?

Our results revealed that changes in the floristic composition of lianas along the hydrological gradient paralleled changes in functional trait composition, highlighting that liana assemblies are composed of species with different ecological strategies.

The plant economic spectrum proposes an organization of global trade-offs between resource acquisitive and conservative plant strategies (Wright et al. 2004; Chave et al. 2009), which are mainly influenced by resource availability as soil water, light, and nutrients (Aerts and Chapin 2000; Sandel et al. 2010). Along the economic spectrum, plants with a fast-growing acquisitive strategy based on cheap tissue investments can dominate in moist and fertile areas (Grime et al. 1997; Reich et al. 1999). At the other end of the spectrum, plants with a conservative strategy grow slowly with expensive tissue investments (Wright et al. 2004; Reich 2014), minimizing nutrient loss and increasing competitive abilities in drier and/or nutrient-poor environments (Hobbie 1992; Aerts 1995). In Central Amazonia, previous research revealed that tree species in valley areas had more acquisitive strategies (e.g., lower WD and higher SLA), while those on plateaus had a more conservative strategy (Cosme et al. 2017; Toledo et al. 2017). Similar results were found for tree species in French Guiana (Schmitt et al. 2020). We detected similar trends for liana stem traits, which were more acquisitive (lower WD) in valleys than plateaus.

We emphasize the importance of stem wood traits, still poorly investigated, to explain the liana species turnover patterns along the hydrological gradient. The lower investment in WD and higher proportions of self-supporting xylem in shallow water-table valleys may guarantee the needed fast growth in height during the self-supporting phase of lianas in this more dynamic portion of the forest. Indeed, liana recruitment rates are higher in this portion of the hydrological gradient (valleys) in the Ducke Reserve (Gerolamo et al. 2018). The sandy and waterlogged soils of valleys provide poor root anchorage, which, together with the shallow root systems (Fan et al. 2017), leads to higher tree uprooting and mortality than in the clayey slopes and plateaus (Toledo et al. 2011). Although a more dynamic environment is beneficial for liana development (Schnitzer et al. 2021), valleys have a higher density of palms (Kahn and Castro 1985), which are poor supports for lianas (Putz 1980; Vleut and Pérez-Salicrup 2005), making this environment less suitable for liana establishment. Under such conditions, stem traits allowing a fast-growth strategy and a higher investment in self-supporting xylem are essential for liana's success. Self-supporting xylem appears at early stages in liana wood development in the understory and in searcher branches produced while stems are elongating before finding climbing support (Ewers et al. 1991). After attaching to a support tree, the cambium produces a unique secondary tissue known as the lianescent xylem that strongly decreases stem stiffness, allowing the unique bending and twisting properties of lianas to climb toward the canopy (Rowe et al. 2004; Angyalossy et al. 2012, 2015). In sum, we argue that the correlation between higher proportions of self-supporting xylem and lower WD in shallow water tables supports the hypothesis that some liana species have biomechanical stem properties conferring success in a dynamic habitat where seasonal soil waterlogging and a scarcity of adequate host trees for liana's climbing may exist (Gerolamo et al. 2020).

Our results highlight that both stem wood traits and leaf anatomy in lianas are modified based on the hydrological gradient. In valley areas, we found mean stomata size to be larger at the assemblage level than in plateaus, which would favor higher water conductivity (large stomata and lower WD) under these moister conditions. A high specific hydraulic conductivity in lianas allows rapid diffusive conductance, and thus higher photosynthetic rates and water use efficiency (Chen et al. 2015). On the other hand, the opposite is expected in habitats with low water availability, such as plateaus, where we anticipate higher stomata density and smaller stomata size (Spence et al. 1986; Xu and Zhou 2008). Small stomata may limit water loss, keeping xylem tension within a safe range and reducing the risks of xylem dysfunction (Brodribb and Holbrook 2006; Johnson et al. 2011; Zhang et al. 2014). This morpho-functional mechanism has been used to explain the greater abundance

of lianas in more seasonal forests (Schnitzer, 2018; but see the review Amorin et al. 2018), and liana and tree ecological strategies within a wide range of soil water availability in tropical rainforests.

We did not detect correlations between foliar traits such as SLA and LA and stem wood traits in the liana assemblage. In contrast, tree species coordinate more acquisitive foliar and stem traits in valleys (higher SLA and lower WD) and the opposite in plateaus from the same study site (Cosme et al. 2017) as expected from the plant economic spectrum. Instead, lianas had more acquisitive stem traits (lower WD) but more conservative leaf traits (lower SLA and LA) in valleys. This decoupled pattern agrees with a correlational study in Central Panama, showing that the SLA was poorly correlated with hydraulic stem traits across lianas species (Van der Sande et al. 2019). These authors found more acquisitive traits in lianas than trees, generally associated with higher light and nutrient resource niches. Medina-Vega et al. (2021) also found a similar result for lianas characterized by the decoupling between leaf and stem traits along a gradient characterized by high variability in precipitation.

The stem and leaf functional trait decoupling at each extreme of the hydrological gradient highlights that each habitat may select trait combinations that violate, at least partially, the optimization principles of resource acquisition and conservation (Reich et al. 2014). This violation disappears when the trait values observed in this study are compared with regional and global values (Ordoñez et al. 2009), indicating that lianas at Ducke Reserve have a typical acquisitive strategy found globally (Table S2). At the same time, this general acquisitive strategy is made of alternative sets of features (more or less acquisitive) depending on where along the hydrological gradient the species are found. Therefore, this decoupling may arise under ecological conditions acting differentially on plant organs and not at the whole-plant level, as observed here for our liana assemblage and for Neotropical trees (Baraloto et al. 2010). The specific constraints of each habitat likely determine the optimal local strategy: high forest dynamism and water availability, with low availability of climbing supports for lianas in valleys versus understory light limitation, higher nutrient availability, and seasonal drought in plateaus. In the valleys, support limitation may favor lianas with well-developed self-supporting xylem, contributing to upward growth of the stems until reaching adequate support. The absence of water limitation allows low wood density, permeable stems, and larger stomatal size to be common. At the other extreme, in the plateaus, light limitation in the dense understory may favor lianas with traits providing rapid ascension (such as higher SLA), and this is combined with higher soil nitrogen availability and exchangeable bases (Luizão et al. 2004; Costa et al. 2005), while the seasonal water deficit in plateaus may favor denser wood and smaller stomata.

In conclusion, we observed a change in the composition of liana species along the hydrological gradient accompanied by a change in the functional trait composition. We observed a decoupling of leaf and stem traits along the hydrological gradient, indicating different ecological strategies associated with each habitat. Contrary to global observations of plant strategies, the optimization of resource acquisition and conservation in liana species is not easily understood locally (see Liu et al. 2021) until variations in functional design, optimized against a complex set of environmental conditions, are revealed. Thus, the biophysical constraints leading to a universal trait coupling indicated by Reich et al. 1997, 2014) are more flexible once the large-scale environmental filters (e.g., climate) have optimized a particular set of traits, allowing plant survival at the local scale.

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**Author contribution statement** EXR, AN, JS, RJB and FRCC conceived the ideas and methodological design. EXR, SCG and CFH collected the data. AN, EXR and RJB identified the plant species. EXR and CSG analyzed the data. All authors contributed to the writing and gave final approval for publication.

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**Availability of data and material** The datasets generated for this study are available on request to the corresponding author.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** Not applicable for that section.

**Consent for publication** Not applicable for that section.

**Consent to participate** Not applicable for that section.

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