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RESEARCH ARTICLE

Putting vascular epiphytes on the traits map

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Abstract

1. Plant functional traits impact the fitness and environmental niche of plants. Major plant functional types have been characterized by their trait spectrum, and the environmental and phylogenetic imprints on traits have advanced several ecological fields. Yet, very few trait data on epiphytes, which represent almost 10% of vascular plants, are available.
2. We collated 76,561 trait observations for 2,882 species of vascular epiphytes and compared these to non-epiphytic herbs and trees to test hypotheses related to how the epiphytic habit affects traits, and if epiphytes occupy a distinct region in the global trait space. We also compared variation in traits among major groups of epiphytes, and investigated the coordination of traits in epiphytes, ground-rooted herbs and trees.
3. Epiphytes differ from ground-rooted plants mainly in traits related to water relations. Unexpectedly, we did not find lower leaf nutrient concentrations, except

for nitrogen. Mean photosynthetic rates are much lower than in ground-rooted plants and lower than expected from the nitrogen concentrations. Trait syndromes clearly distinguish epiphytes from trees and from most non-epiphytic herbs.
4. Among the three largest epiphytic taxa, orchids differ from bromeliads and ferns mainly by having smaller and more numerous stomata, while ferns differ from bromeliads by having thinner leaves, higher nutrient concentrations, and lower water content and water use efficiency.
5. Trait networks differ among epiphytes, herbs and trees. While all have central nodes represented by SLA and mass-based photosynthesis, in epiphytes, traits related to plant water relations have stronger connections, and nutrients other than potassium have weaker connections to the remainder of the trait network. Whereas stem-specific density reflects mechanical support related to plant size in herbs and trees, in epiphytes it mostly reflects water storage and scales with leaf water content.
6. *Synthesis*. Our findings advance our understanding of epiphyte ecology, but we note that currently mainly leaf traits are available. Important gaps are root, shoot and whole plant, demographic and gas exchange traits. We suggest how future research might use available data and fill data gaps.

KEYWORDS

epiphyte ecology, growth form, leaf traits, nutrient relations, plant functional traits, trait network, water relations

1 | INTRODUCTION

Plant functional traits (PFT) are defined as morphological, anatomical, biochemical, physiological or phenological characteristics that can be assessed at the level of an individual plant (Violle et al., 2007). The study of PFT allows broad comparisons across taxa as well as regions because PFT alleviate the idiosyncrasies caused by biogeographical and ecological history. They provide a link between species richness and functional diversity, and are associated with the performance of plants and their response to environmental factors (Grime, 1974; Wright et al., 2017). Individual PFT do not evolve in isolation but typically vary as trait syndromes (Grime, 1974). Just six major traits captured three-quarters of the variation in a two-dimensional global spectrum of plant form and function in a study involving 46,000 species of trees and herbs (Díaz et al., 2016). That study identified two major dimensions in the trait space, one reflecting the height, leaf and seed sizes as well as stem-specific density, and the other the slow–fast continuum of the leaf economic spectrum (LES, Wright et al., 2004). Woody and non-woody plants largely occupy different regions within the trait space, as do angiosperms, gymnosperms and pteridophytes, although the latter two were represented by only few species in that analysis.

Analysing the distribution of PFT in a plant group (woody and herbaceous plants: Díaz et al., 2016, aquatic plants: Pierce et al., 2012, or woody climbers: Santiago & Wright, 2007) identifies differences and general patterns associated with their growth habit and habitat. The Diaz et al.'s (2016) study, which is based on data from TRY (Kattge et al., 2020), covers a substantial proportion (*c*. 13%) of the known extant vascular plant diversity. However, vascular epiphytes, plants that live non-parasitically on other plants for their entire life and represent >31,000 species or *c*. 10% of global plant diversity (Zotz, Weigelt, et al., 2021) are strongly under-represented in that dataset with <50 species. Without soil root contact, and dependent on the stability of their host tree, epiphytes might differ substantially from ground-rooted plants and a PFT approach could show to which extent life in the tree canopy demands different adaptations, and how this structures the epiphytic trait space.

Ecophysiological studies have analysed selected traits for smaller and larger sets of epiphytic species (e.g. Griffiths & Smith, 1983; Hietz & Briones, 1998; Martin, 1994; Zotz & Ziegler, 1997), but so far epiphytes are neglected in macroecological functional analyses. Recent studies analysed sets of functional traits of entire epiphytic communities (Agudelo et al., 2019; Petter et al., 2016; Schellenberger Costa et al., 2018; Susan-Tepetlan et al., 2015; Wagner et al., 2021), but these were based on relatively small, local to regional datasets, and did not address the question of whether epiphytes *in general* occupy a distinct region within the global trait spectrum of vascular plants. This is the goal of the present paper, which we approach with

the analysis of a dataset that combines published data of ground-rooted plants with published as well as numerous unpublished data of epiphytes.

We expect the trait space of epiphytes to differ substantially from ground-rooted plants. Such an 'epiphyte syndrome' (Zotz, 2016) could result from the epiphytic habitat that poses a number of specific challenges. First, the epiphytic habitat is discontinuous, which should favour dispersal traits such as ornithochorous or anemochorous diaspores. Second, epiphytes, at least in the lowlands, have little or no suspended soil as rooting substrate, so epiphyte roots should hold plants to a surface they often cannot grow into, and absorb rainwater swiftly. Third, their substrate shows complex dynamics in three-dimensional space, being relatively unstable and short-lived. Even on a long-lived tree trunk, pieces of bark may detach and dislodge epiphytes (Cabral et al., 2015). Thus, we expect epiphytes to be relatively small and light, to reduce mechanical stress on the substrate and to reach sexual maturity before the substrate falls or they find themselves in unsuitable micro-sites (e.g. when parts of a tree are shaded by others). Fourth, the functional pressure for vertical growth fundamentally differs from ground-rooted plants because light competition among epiphytes is typically low and the light environment is primarily determined by the height of attachment on the tree and not by the size of the epiphyte. Epiphytes therefore need not be tall, and their leaves should be adapted to higher light conditions compared to herbaceous ground-rooted plants in similar vegetation. Fifth, the low water availability, even temporarily in wet forests, should be reflected in adaptations to drought, such as low SLA, high water use efficiency and the prevalence of Crassulacean acid metabolism (CAM). Finally, without direct contact to mineral soil, we expect leaf nutrient concentrations to be low and consequently for plants to have lower maximum photosynthetic rates (A_{max}), lower growth rates, lower SLA and higher leaf life span compared to ground-rooted plants. As a consequence, epiphytes as a group should be at the low end of the LES. Considering the effects of these environmental constraints, we outline expectations on how epiphyte PFT should differ from those of ground-rooted plants (Table 1). For some traits, different environmental constraints result in the same expectations (e.g. the need to reach maturity early and have low weight both suggest a small size), whereas for other traits expectations differ (e.g. higher photosynthetic rates for plants growing under higher light but low photosynthetic rates if water and nutrient limitations dominate).

Since the availability of data on epiphyte traits is much lower than for other plants (Kattge et al., 2020), our ability to answer the hypotheses outlined in Table 1 is limited. For example, there are hardly any root and dispersal trait data available, despite general observations of root types optimized for water and nutrient uptake, such as the orchid velamen, and the high incidence of anemochory already noted by Schimper (1888). We will nevertheless discuss these traits with qualitative information and can formally test expectations related to size- and leaf-related traits with sufficient data.

The present study relates plant size- and leaf-related traits of epiphytes to the global plant trait space to test the existence of an 'epiphyte syndrome' (Zotz, 2016) that reflects the functional

TABLE 1 Hypotheses how the epiphytic habitat should shape functional traits and summarized outcome where hypotheses have been confirmed (✓), rejected (✗), remained unanswered (?) or were only partially confirmed (✗/✓) in the present study

Constraints in epiphytic habitat	Expected traits	Confirmed
H1: discontinuous habitat (low probability for randomly dispersed diaspores)	Anemochorous or ornithochorous diaspores	(✓; 1)
H2: rooting substrate (bare bark to moderate depth of organic canopy soils)	(a) Mechanically strong roots as 'holdfasts'	?
	(b) Fast water absorption	?
	(c) Water storage	?
H3: low substrate stability	(a) Small size	✓
	(b) Fast growth	(✗; 1)
	(c) Early sexual maturity	(✗; 1)
H4: more light than for ground-rooted herbs	(a) Low height	✓
	(b) Higher A_{max}	✗
	(c) Higher stomatal density	✗
H5: water limitation, variable supply	(a) Low SLA and/or succulence	✓
	(b) High water use efficiency	✗/✓
	(c) Prevalence of CAM	✗/✓
	(d) Low water loss through stomata and cuticle	✓/? (✓; 2)
	(e) Low A_{max}	✓
H6: nutrient limitation (low availability in rainfall, no direct access to mineral soil)	(a) Low nutrient concentrations	✗/✓
	(b) Low SLA	✗/✓
	(c) Low A_{max}	✓
	(d) Long leaf life span	?

Note: Symbols in parentheses indicate good evidence from other sources but not tested here, numbers in parentheses refer to 1: Zotz (2016), 2: Helbsing et al. (2000).

distinctiveness of this growth form. We first characterize the data collected in terms of geographical, systematic and trait coverage. Second, we compare the epiphyte trait distribution against those of trees and non-epiphytic herbs, testing the expectations outlined above. Third, looking for variation in epiphytic strategies, we test for differences in both trait composition and syndrome among the most species-rich groups of epiphytes (i.e. orchids, bromeliads, ferns), which together account for *c*. 86% of all vascular epiphyte species. Finally, we explore how the epiphytic syndrome is structured in functional trait space by analysing pairwise correlations among traits and the network of trait correlations, again contrasting epiphytes with trees and ground-rooted herbs.

This is the first study analysing an extensive dataset of functional traits for epiphytes from different biomes and biogeographical regions. We expect to identify a combination of traits that sets epiphytes apart within the global plant functional trait space. This extensive functional analysis significantly extends our understanding of the functional ecology of all vascular plants, but also identifies specific knowledge and data gaps.

2 | MATERIALS AND METHODS

2.1 | Epiphyte dataset

We compiled a global dataset on plant traits of vascular epiphytes from various published and unpublished studies by the authors, complementing it with information retrieved from the literature. We rejected records known to be from juveniles, from plants growing in cultivation and from species classified as hemi-epiphytes or ambiguously classified as epiphytes (based on Zotz, Weigelt, et al., 2021). We excluded species that were not at least identified to genus level and limit the analysis in this paper to traits recorded from >40 epiphyte species. This left 76,561 trait observations on mature vascular epiphytes sampled in the field, belonging to 2,882 species and morphospecies in 40 families spanning five continents predominantly in tropical regions (Figure 1). Most data represent single measurements from one individual, although in some cases, particularly for data compiled from the literature, these can be averages from several individuals.

2.2 | Other growth forms

We compared epiphytes with ground-rooted herbs and trees to test whether epiphytes differ from ground-rooted plants. For the latter, we primarily used public datasets from TRY (Kattge et al., 2020; a list of data sources used in the study are provided in the Data sources section). Photosynthesis in the epiphyte dataset was measured as CO_2 uptake per leaf area under high light and ambient CO_2 concentrations, but photosynthesis data in the TRY dataset are not necessarily obtained under high light. For comparison with non-epiphytes, we thus used A_{max} values from Wright et al. (2004), which were measured under high light, ample soil moisture and ambient CO_2. TRY has relatively few data for stomatal size and density, which are available for many epiphytes and are of interest in terms of the regulation of gas exchange (Raven, 2014). We therefore included other published data on guard cell length and stomatal density (Brodribb et al., 2013; Li et al., 2015; Simonin & Roddy, 2018).

Growth forms are not unambiguously defined and there is no universal classification for all species. For epiphytes, we used an updated version of a comprehensive global species list (Zotz, Weigelt, et al., 2021), which has 31,311 records of vascular epiphytes. For trees, we used Global Tree Search (www.bgci.org/resources/bgci-databases/globaltree-portal/, Beech et al., 2017), which has *c*. 60,000 species classified as trees. We are not aware of a comparable list of herbs. A plant growth dataset for the New World (Engemann et al., 2016) classified species based on a majority (>2/3) of records in various databases. However, many species were classified based on single records and we found a number of errors in this dataset. Based on a species list of all records downloaded from TRY, we first matched all species with the epiphyte and the tree lists. For any species not found there, we searched for records of growth form in BIEN (bien.nceas.ucsb.edu/bien/), which appear to be more consistent than records in TRY, and selected species unambiguously classified as herbs. For the remaining species not covered in BIEN, we took TRY records for growth form and added species classified as herbs in TRY to our list of herb species. Species not classified as epiphyte, herb or tree were not included in our analysis. Thus, the analysis is based on 2,882 epiphyte, 8,771 non-epiphytic herb (hereafter simply called 'herbs') and 12,928 tree species. Only 2% of epiphyte species with traits belong to families in which woody forms dominate (Ericaceae, Gesneriaceae, Melastomataceae and Rubiaceae). We acknowledge that some assignments may be dubious because of questionable entries and because some species may fall into more than one growth form, but these individual species will hardly affect the outcome. Species names were checked with the Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/) and standardized with The Plant List (http://www.theplantlist.org/).

2.3 | Functional traits

Measurements of functional traits generally followed standard procedures (Pérez-Harguindeguy et al., 2013) but may vary somewhat, which is also true for traits in TRY or other compilations. For SLA, we used only data that excluded the petiole. Our epiphyte data as well as TRY data include leaf dry matter content (LDMC), which is dry mass/water saturated fresh mass. Saturation can be achieved in various ways (Vaieretti et al., 2007) but many, particularly older, data assumed saturation under field conditions or did not saturate at all. We thus used LDMC data to calculate water content per fresh mass (WC = 1 − LDMC) and pooled this with data that report fresh mass per dry mass [WC = 1 − 1/(fresh mass/dry mass)] or directly water content per fresh mass. We acknowledge that water content in fresh leaves can be substantially below saturated water content. Stems of

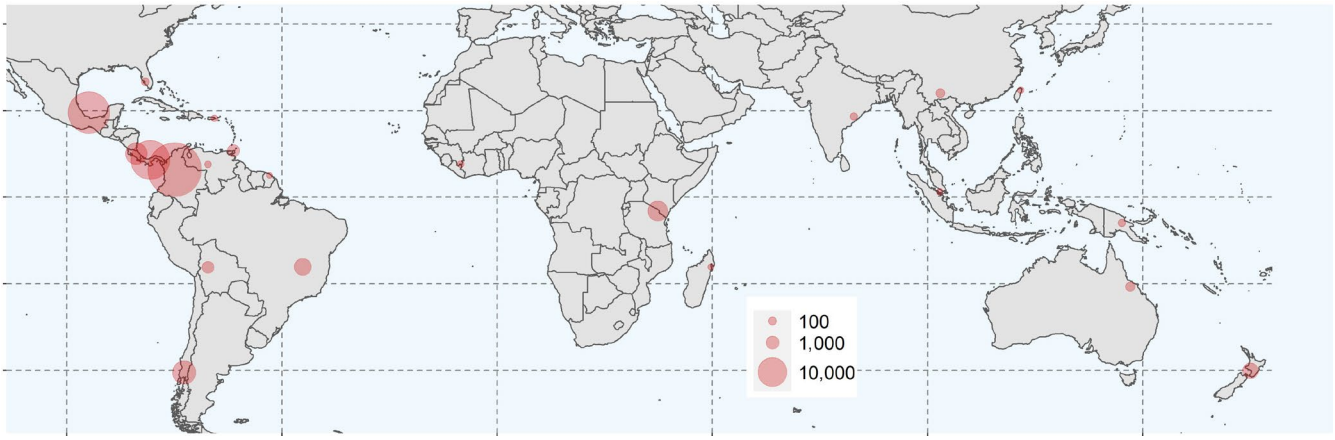

FIGURE 1 Geographical coverage of vascular epiphyte trait records. Symbol size represents number of species measured for traits

TABLE 2 List of functional traits for vascular epiphytic species with records for > 40 species

Trait	Abbreviation	Unit	Species	Records
Photosynthesis under high light	A_{max}	μmol m^{-2} s^{-1}	71	213
Leaf carbon content per leaf dry mass	C	% dry mass	698	3,152
Leaf calcium content per leaf dry mass	Ca	mg/g	125	523
Adult plant height	Height	m	240	1,834
Leaf potassium content per leaf dry mass	K	mg/g	126	527
Leaf area	LA	cm^2	415	10,453
Leaf thickness	LT	mm	432	10,611
Leaf magnesium content per leaf dry mass	Mg	mg/g	125	523
Leaf nitrogen content per leaf dry mass	N	mg/g	740	3,605
Leaf sodium content per leaf dry mass	Na	mg/g	115	510
Leaf phosphorus content per leaf dry mass	P	mg/g	303	1,539
Stomatal density abaxial	SD	mm^{-2}	443	4,297
Guard cell length	SL	μm	248	2,281
Specific leaf area	SLA	m^2/g	596	10,177
Stem-specific density	SSD	mg/mm^3	103	730
Leaf water content per fresh mass	WC	g/g	425	17,386
Leaf carbon isotope signature	$\delta^{13}C$	‰	2,112	5,160
Leaf nitrogen isotope signature	$\delta^{15}N$	‰	598	3,040

epiphytic cacti are treated as leaves as these are functionally equivalent. For species with A_{max} and SLA data, we calculated mass-based photosynthesis ($A_{mass} = A_{max} \times SLA$) and for species with N and P data, N:P ratios (Table 2).

We calculated means for each trait of each species, except for height, where we used the maximum per species. When comparing individual traits, we present non-transformed data and plot all species means to better visualize the distribution and variation of the data (Figures 3 and 6). For statistical tests, all trait data except for WC, SSD, C, $\delta^{13}C$ and $\delta^{15}N$ were log-transformed to improve normality based on results from quantile–quantile plots. Species-wise trait means were compared among groups by analysis of variance followed by HSD post-hoc test whether more than two groups were compared. For traits available for >8 species for both epiphytic and ground-rooted Araceae, Orchidaceae and ferns, we also tested for significant differences within groups.

To test whether and to what extent mean trait values of epiphytes, herbs and trees might be affected by a few large families, we plotted family-wise mean trait values against the number of species per family and growth form.

Since epiphytes are predominantly herbaceous plants from the humid tropics, we also compared them to tropical ground-rooted herbaceous plants and ground-rooted herbaceous plants from the humid tropics (see Supporting Information Methods).

Nutrient concentrations are often correlated to SLA and photosynthesis is related to SLA and leaf N (Wright et al., 2004). We therefore tested whether differences in N, P and A_{max} between growth forms are independent of SLA and N by analysis of co-variance followed by Tukey post-hoc tests.

Using species mean values, we ignore intraspecific variation. Our large dataset is poorly suited to explore such variation because data were collected in different places, by different people and on different plants. This is also true for TRY data that often lack sufficient information to understand the nature of intraspecific trait variation. However, when different traits are obtained from different individuals or even places, intraspecific variation may affect trait correlations and we would expect lower correlations compared to traits measured on the same individuals. If intraspecific variation is small relative to the among-species variation, this will not matter much in a comparison of numerous species. Except for the relatively few literature data included (<4%), the epiphyte dataset includes an ID for the individual plant so we could test whether correlations based on species means differ from correlations of traits measured on the same individuals. For some trait pairs, individual-wise correlations included fewer or no data points as some trait combinations were rarely or never assessed on the same plant. For other trait pairs, this included more data points if both were obtained from more than one individual per species. Overall, the patterns of species-wise and individual-wise trait correlations were very similar (Figure S3) and a dataset with all traits obtained from the same individuals would likely have produced a very similar overall pattern.

To test whether groups (growth forms or epiphyte clades) differ in their combination of traits, we scaled trait data to mean = 0 and $SD = 1$, and performed multivariate analysis of variance (MANOVA) and canonical discrimination analysis (CDA) using R library candisc with default settings. This requires a complete dataset, which substantially reduces the number of species than can be included. We therefore increased the number of species by imputing trait values in species for growth forms where only one trait value was missing and for epiphyte groups with one or two missing trait values (see Supporting Information Methods for details).

We used network analysis to analyse the coordination of traits in the traits space, which has been used in ecology (Delmas et al., 2019), including in the context of trait correlations (He et al., 2020; Kleyer et al., 2019). A network is a set of nodes (in our case traits) that are linked by edges where a high correlation between traits is represented by a stronger edge between nodes. Some traits with many significant connections are considered hub-traits while others have few connections or may be related to others indirectly. To analyse the trait network, we calculated pairwise Pearson correlations and weighted edges by the correlation coefficient (r^2). We here used A_{mass} because nutrient data are also mass-based and because mass-based, but not area-based photosynthesis, is strongly linked to SLA and leaf N (Wright et al., 2004). The trait network was visualized using the R library igraph (Csardi & Nepusz, 2006). Only significant ($p < 0.05$) correlations based on >17 trait pairs are shown. We decided for >17 to include correlations with A_{mass}, as this was found to be an important node for all growth forms but relatively few data were available for epiphytes. As a measure of centrality of each trait, we computed for each node the sum of all correlation coefficients (Σr^2) for all correlations with $p < 0.05$. We used the spin-glass algorithm of igraph with simulated annealing to identify clusters of traits. We calculated Pearson correlation matrices for the traits used in the network analysis and compared the trait correlations between epiphytes, herbs and trees with Mantel tests with 9999 permutations.

3 | RESULTS

3.1 | Data coverage

Epiphyte trait data were collected mainly from tropical regions with a few exceptions from subtropical to temperate regions. Records are well distributed across the tropical and subtropical biomes (Figure S1), but there is a strong geographical bias with >90% of records from the Neotropics (Figure 1).

Most traits were recorded for Orchidaceae, Bromeliaceae and Polypodiaceae, but many data were also available for Araceae and Dryopteridaceae (Table 3). Bromeliaceae had the highest proportion (51%) of species with trait records in our dataset, mostly due to one study that characterized carbon isotopes and photosynthetic pathways for the entire family (Crayn et al., 2004). Compared to these families, other important epiphyte families (Gesneriaceae, Piperaceae, Ericaceae) were rather underrepresented and we thus limited a comparison among different groups of epiphytes to orchids, bromeliads and ferns. Fern (pteridophytes excluding lycophytes) families were pooled as they belong to a clade and are in many respects distinct from angiosperms.

Compared to non-epiphytic species, a high number of data on $\delta^{13}C$, stomatal size and density were available for epiphytes, proportions for $\delta^{15}N$ and C were similar, but epiphytes were under-sampled for all other traits (Figure 2). Note that we do not list the many traits sampled for herbs or trees for which too few epiphyte data were available for meaningful comparisons.

3.2 | Are epiphytes different?

Epiphytes differed significantly from herbs in 17 out of 19 traits and from trees in all but SLA and Ca (Figure 3). On average, epiphytes had slightly lower SLA than ground-rooted herbs or trees, their leaves were thicker with a higher water content and their stems had a lower specific density. They had substantially lower stomatal density and A_{max}, but stomata size was similar to that of herbs. The bimodal carbon isotope signal reflects photosynthetic pathways. There are no known C4 plants among epiphytes and $\delta^{13}C$-values > −20‰ suggest CAM photosynthesis. Species with more negative $\delta^{13}C$ values may also fix some CO_2 via PEP-carboxylase, but here the contribution to total C-fixation is minor

Family	Epiphytic species	Records	Species w. records	% Species w. traits
Orchidaceae	21,116	38,234	1,192	5.6
Bromeliaceae	1,958	20,991	1,021	52.1
Polypodiaceae	1,437	17,847	202	14.1
Gesneriaceae	714	5,044	69	9.7
Piperaceae	618	2,265	25	4.0
Ericaceae	543	152	57	10.5
Araceae	512	4,372	40	7.8
Dryopteridaceae	423	7,187	123	29.1
Melastomataceae	413	2,918	97	23.5
Hymenophyllaceae	258	5,378	43	16.7
Apocynaceae	229	21	13	5.7
Rubiaceae	177	8	5	2.8
Aspleniaceae	126	1,384	19	15.1
Lycopodiaceae	120	489	9	7.5
Pteridaceae	114	445	11	9.6
Cactaceae	107	10	6	5.6

TABLE 3 Major families of vascular epiphytes (with >100 epiphytic species globally), the number of individual trait data per family, the number of species with some trait records and the proportion of species with at least one trait record. The species numbers follow Zotz, Almeda, et al. (2021)

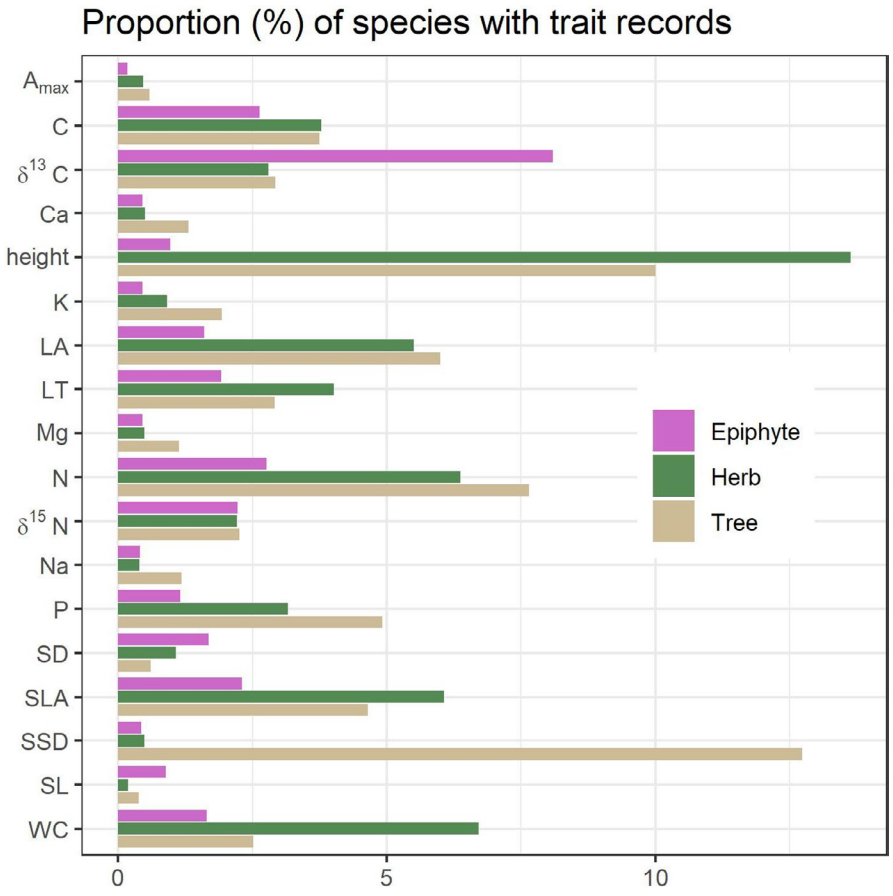

FIGURE 2 Proportion (%) of epiphytic and non-epiphytic species for which trait values are available. Trait abbreviations are explained in Table 2

(Winter & Holtum, 2014). Thus, $\delta^{13}C$ records indicate CAM in 27% of epiphyte species in our data. However, this is heavily biased by a large dataset on bromeliads (Crayn et al., 2004), where 43% of epiphytic species perform CAM. Excluding bromeliads, 9.9% of epiphytes were CAM plants. Most of the ground-rooted herbs with $\delta^{13}C$-values > −20‰ in the TRY dataset are Poaceae, where low $\delta^{13}C$ indicates C4 photosynthesis. In the $\delta^{13}C$ range for C3 photosynthesis, epiphyte values were similar to herbs ($p > 0.1$) but less negative than in trees ($p < 0.001$). A_{max} and SD in epiphytes were much lower than in herbs or trees.

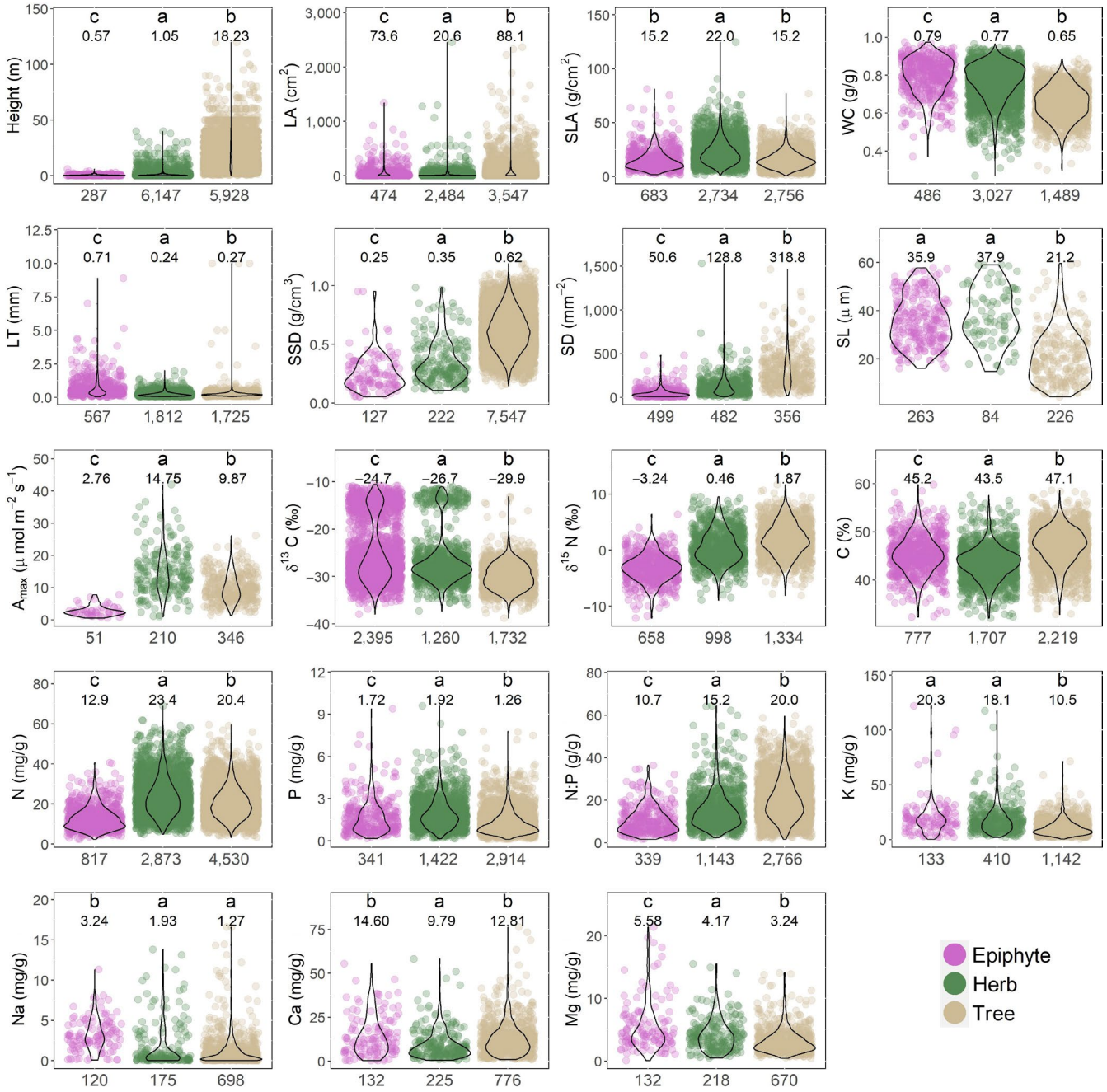

FIGURE 3 Functional traits of epiphytes compared to those of ground-rooted herbs and trees. Numbers below each panel show the number of species for which trait data are available, numbers below letters are group averages. Groups in a plot with different letters are significantly different (HSD post-hoc test, $p < 0.05$). Trait abbreviations follow Table 2

On average, epiphytes had 45% lower leaf N than ground-rooted plants, lower $\delta^{15}N$ values and higher Na and Mg concentrations. The concentrations of other nutrients in epiphytes were similar to herbs (K), trees (Ca) or in between herbs and trees (P). N:P ratios of epiphytes were substantially lower than in ground-rooted plants. The mean leaf C content of epiphytes was higher than in herbs and lower than in trees. Testing for differences between epiphytic and ground-rooted plants within Araceae, Orchidaceae or ferns confirmed the general pattern: SLA was lower in epiphytes, differences in WC are small, leaf N was about 40% lower in epiphytes but the concentration of other nutrients was as high or higher than in ground-rooted species from the same groups (Figure S6).

Except for leaf area, which was larger in wet tropical herbs than in the global herb dataset, but still lower than in epiphytes, trait values of tropical or wet tropical herbs were not more similar to epiphytes than for the global herb dataset (Figure S4). While epiphytes are dominated by a few families, differences between growth forms were in most cases remarkably homogeneous across small and large

families (Figure S5). However, for $\delta^{13}C$, the high mean value for epiphytes is biased by bromeliads and the low SL and high C content by orchids (Figure S5).

Nutrient concentrations are often related to SLA and the amount of N per dry matter was higher in leaves with greater SLA (Wright et al., 2004). Given the lower SLA of epiphytes, this might partially explain differences in N or A_{max}. However, compared to herbs and trees, epiphytes had significantly lower N, but similar P at a given SLA (Figure 4; Table S1). A_{max} at a given SLA was lower in epiphytes than in herbs or trees, and photosynthesis, expressed on an area or mass base per nitrogen was also lower, which indicates a lower photosynthetic nitrogen use efficiency (Figure 4; Table S1). While epiphytes had lower SD than trees, their stomata were substantially larger so that for a given guard cell size the SD was similar to that of trees but lower than in herbs (Figure 4; Table S1).

The CDA clearly separated trees from herbs and epiphytes by height along the first canonical dimension, and herbs from epiphytes with relatively little overlap by the latter, having thicker and larger leaves with higher WC and lower $\delta^{15}N$, [N] and SLA (Figure 5 top, MANOVA significance $p < 0.001$, Table S2a). Omitting plant height, where trees obviously differed from herbs and epiphytes, the main grouping remained (Figure S7) with highly significant group differences (MANOVA $p < 0.001$, Table S2b) although trees scaled less distinctly. Without height, epiphytes still separated from herbs mostly on the first canonical axis by higher LT, WC and lower N, N15 and SLA.

3.3 | Differences among epiphyte groups

SLA did not differ among ferns, orchids and bromeliads, but ferns had thinner leaves and somewhat lower water content per fresh mass (Figure 6). Stomatal density was highest in orchids and lowest in bromeliads, while guard cells were smallest in orchids and largest in ferns. SSD was somewhat higher in ferns (where stems are rhizomes) than in orchids, where stems are sometimes succulent pseudobulbs. In our dataset, 52% of bromeliads, 12% of orchids and 1% of ferns perform CAM ($\delta^{13}C > -20‰$). Omitting CAM species, $\delta^{13}C$ differed significantly ($p < 0.001$) between ferns (mean $\delta^{13}C = -30.9‰$), orchids (−28.6‰) and bromeliads (−26.5‰). Leaf $\delta^{15}N$ and nutrient concentrations were generally lowest in bromeliads, except for Na and K.

Orchids separated along the first canonical axis mainly by higher SD and lower SL, whereas ferns and bromeliads mainly separated

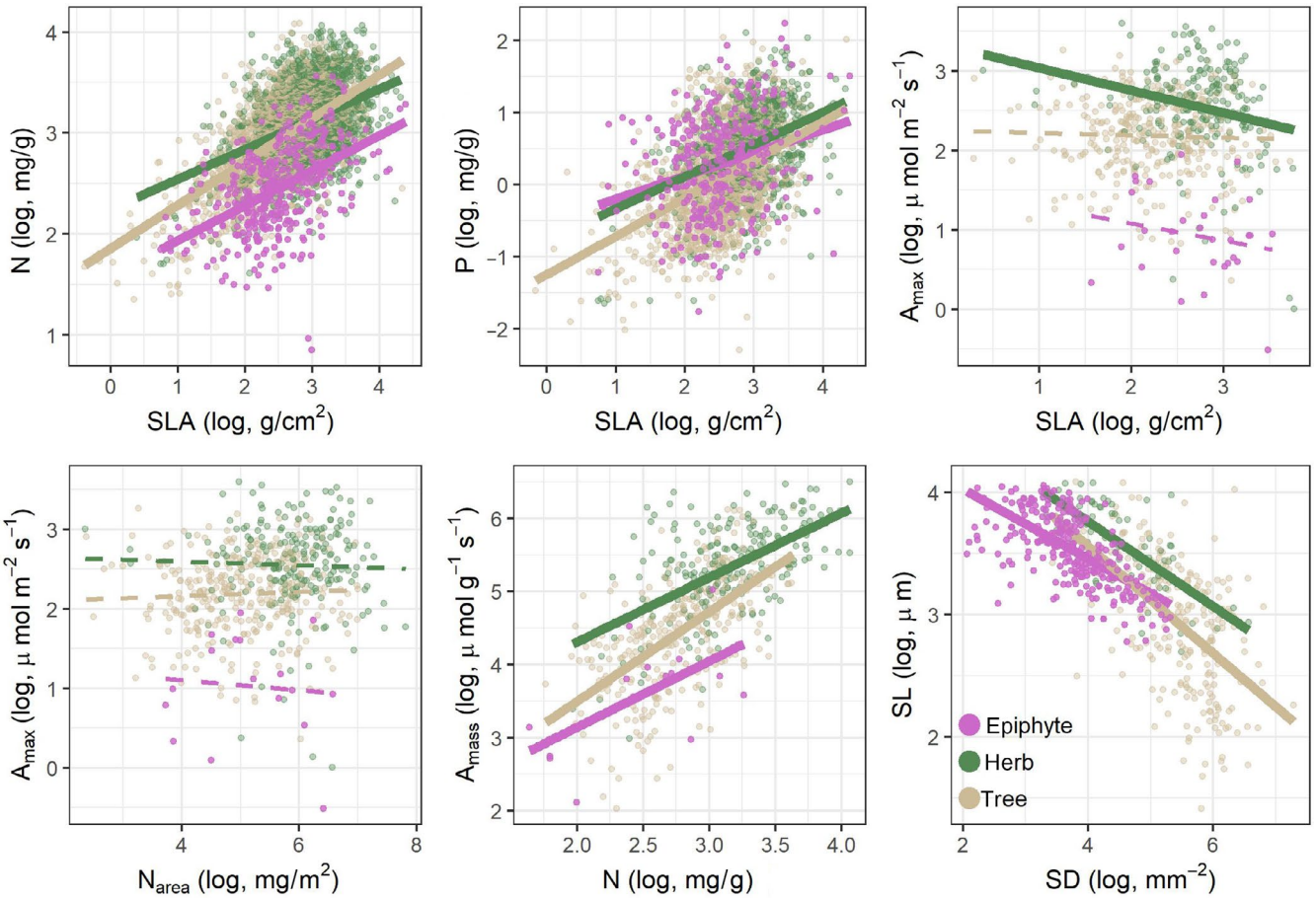

FIGURE 4 Selected bivariate relationships. Solid lines indicate significant ($p < 0.05$), broken lines non-significant correlations. N_{area} was calculated as N/SLA using species-means, and mass-based photosynthesis (A_{mass}) as $A_{max} \times SLA$

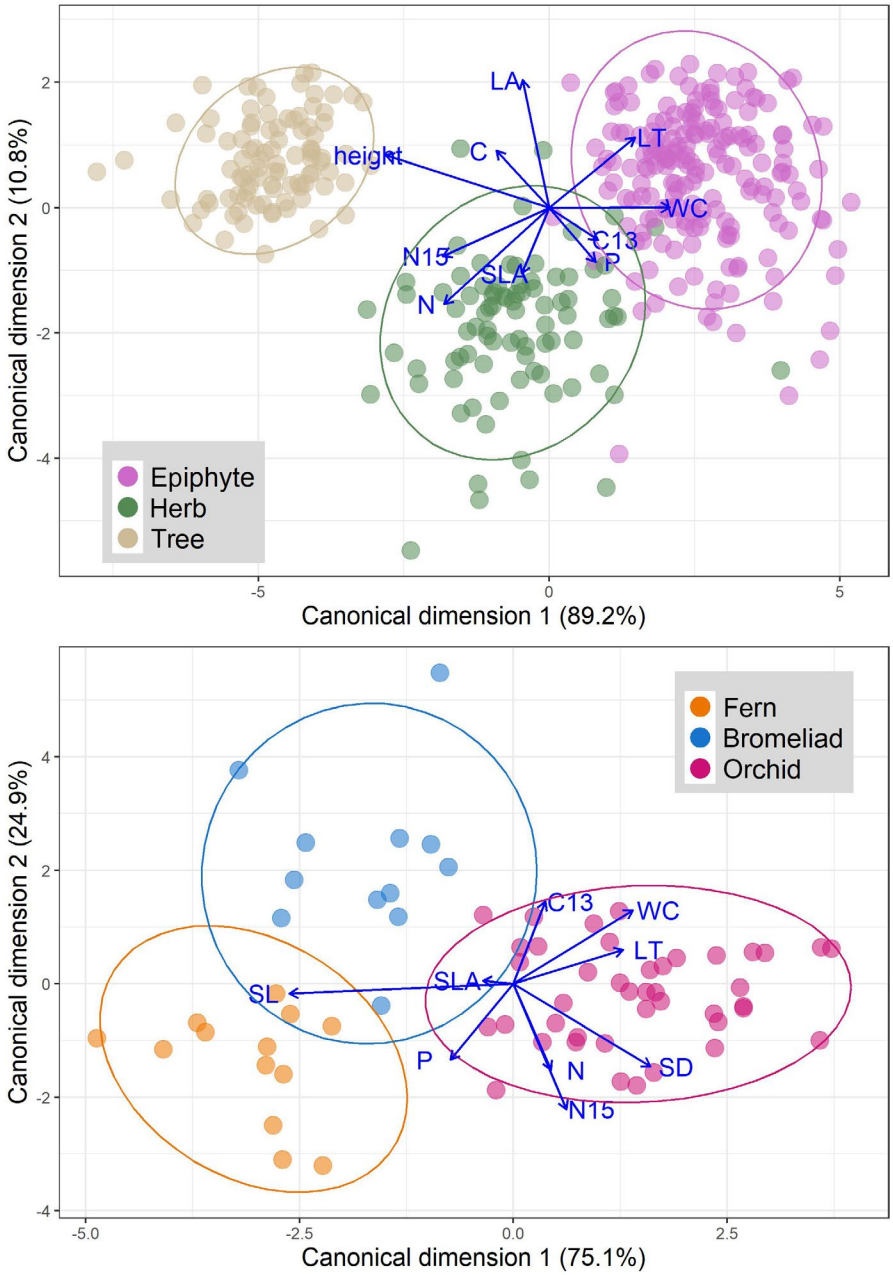

FIGURE 5 Canonical discrimination analysis of major functional traits to distinguish between epiphytes, ground-rooted herbs and trees (top panel) and between major groups of epiphytes (bottom panel). The ellipses enclose 95% of species within a group. For trait abbreviations, see Table 2

along the second axis with higher WC and $\delta^{13}C$ in bromeliads and higher N, P, and $\delta^{15}N$ ferns (Figure 5 bottom; Table S2d). Increasing the number of species almost threefold by imputing one or two trait values per species had little effect on the CDAs (Figure S2, note that mirroring along an axis is not relevant) and MANOVAs were highly significant (Table S2c and e).

3.4 | Trait networks

Trait networks of epiphytes, herbs and trees differed substantially (Figure 7; as with pairwise correlations, the trait network based on individual-wise correlations was similar to that using species means, Figures S8 and S9). In epiphytes, the node with the strongest links to other traits, measured as Σr^2 of significant correlations, was LT, followed by $\delta^{13}C$ K, SLA, SD and A_{mass} (Table S3). In herbs, dominant nodes were WC, followed by nutrients (N, P, K), SLA and A_{mass}. In trees, A_{mass} had the strongest links followed by SLA, nutrients (Ca, N, P) and LT. The expected negative correlation between SLA and leaf thickness was much stronger in trees than in herbs and epiphytes; in the latter, LT was most strongly linked to WC and $\delta^{13}C$. All nutrient concentrations were positively correlated in all groups except for negative correlations with Na in herbs and trees. In herbs, but not in trees or epiphytes, nutrients were also strongly linked to WC. In epiphytes, N was strongly linked to P and SLA but less to other nutrients, whereas in herbs all nutrients (except Na in herbs) formed a strongly linked cluster of nodes. Apart from the LES and nutrient correlations, the strongest links in epiphytes were found among traits related to succulence (LT, SLA, WC, SSD and $\delta^{13}C$). SSD was strongly linked to A_{mass} in herbs, but only weakly to

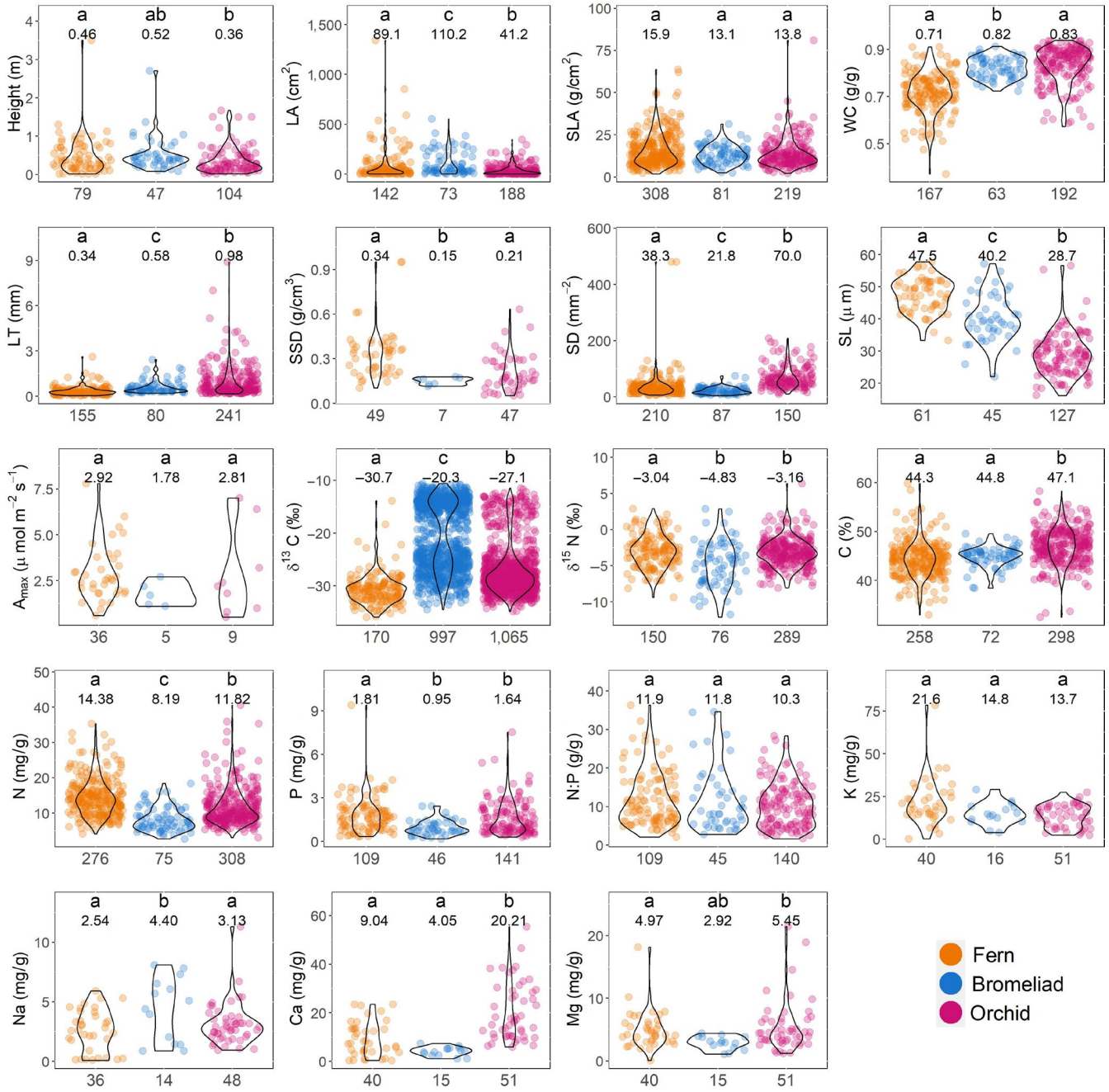

FIGURE 6 Functional traits of major epiphyte groups. Numbers below each panel show the number of species for which trait data are available. Groups with different letters are significantly different (HSD post-hoc test, $p < 0.05$), numbers below letters are group averages. Trait abbreviations follow Table 2

other traits in trees. SD and SL were strongly linked in all groups, but in epiphytes this pair was linked to C, $\delta^{13}C$ and A_{mass}, whereas in herbs and trees SD and SL were linked to WC. The graphic presentation in Figure 7 captures the modularity of the trait network, with modules being subsets of traits with more connections within the module than with surrounding traits. In epiphytes, dominant clusters in the trait network were formed by A_{mass}-δ^{13}C-LT-N-P-SLA, C-Ca-K-Mg-δ^{15}N-Na, SD-SL and Height-LA, in herbs by A_{mass}-C-δ^{13}C-LT-δ^{15}N-SLA-SSD, Ca-K-Mg-N-Na-P-WC, SD-SL and Height-LA and in trees by A_{mass}-LA-LT-N-SLA, C-Ca-Height-K-Mg-P, δ^{13}C-δ^{15}N-Na and SD-SSD-SLWC. By contrast, Figure S9 presents the same networks with traits equidistant along a circle, which makes it easier to compare edge densities and strengths between different networks. Trait correlations were more similar between herbs and trees (Mantel test, $r = 0.62$, $p = 0.0001$) than between epiphytes and herbs ($r = 0.12$, $p = 0.012$) or between epiphytes and trees ($r = 0.41$, $p = 0.0001$). Taking the sum of the Σr^2 for all traits in each group, general interdependence of the trait networks was higher in trees (22.8) than in epiphytes (17.5) or herbs (15.6, Table S3).

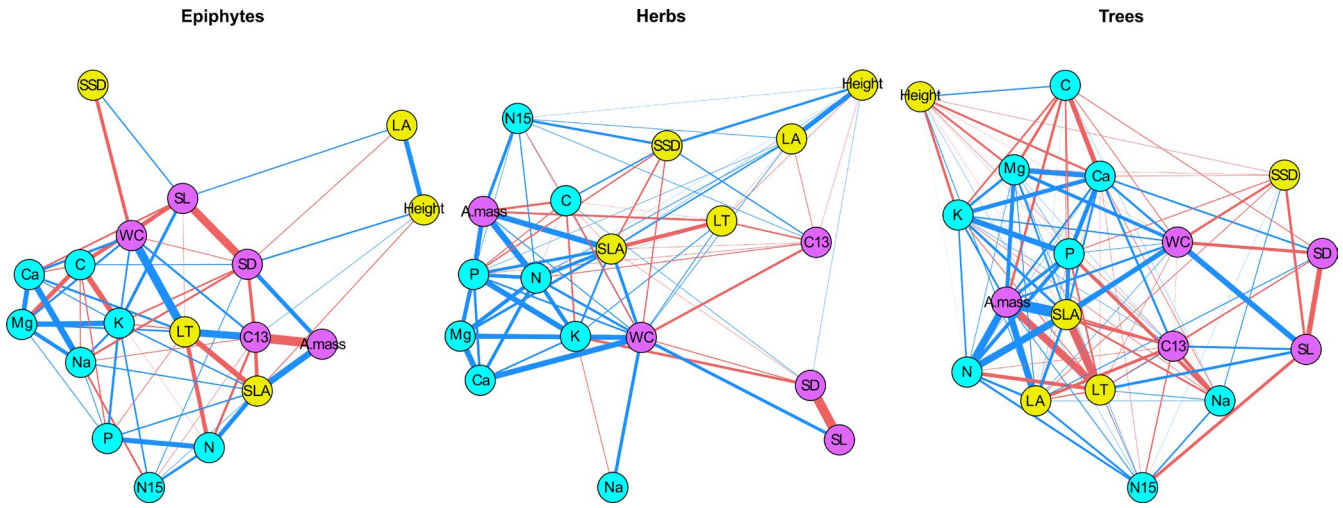

FIGURE 7 Trait networks for epiphytes, ground-rooted herbs and trees. Nodes (circles) present traits that are related to nutrients (cyan), water relations (purple) or allometrics (yellow). Lines connecting nodes represent significant ($p < 0.05$) trait correlations, with blue for positive and red for negative correlations. The thickness of the lines corresponds to the r^2 of the correlations (Table S4). For comparison, Figure S9 shows the correlations with traits equidistant along a circle

4 | DISCUSSION

4.1 | Data coverage

Moist to wet (sub)tropical biomes are well represented in our dataset (Figure S1), but the dataset is biased in terms of geographical distribution (Figure 1), phylogenetic representation (Table 3) and the traits covered (Figure 2). These biases reflect where functional ecologists are based or prefer to work, which epiphytic groups are considered of interest and which traits are thought to be particularly relevant for epiphytes and/or are easy to measure. Such biases are common in ecology (Daru et al., 2018; Meyer et al., 2016) and trait data are no exception (Sandel et al., 2015). Although epiphytes are particularly species rich in the Neotropics (Zotz, 2016), the overrepresentation in our data (with >90% of records) is probably due to a tradition of both European and US-American biologists to work there, and also reflects the growing number of local scientists working on epiphyte functional ecology. Apart from Bromeliaceae and Cactaceae, which are almost exclusively Neotropical, the biogeographical bias should not distort the epiphytic trait spectrum, as orchids and other families will adapt to similar environments in similar ways, irrespective of geographical location.

The fact that bromeliads are the best-represented family in our dataset is only partially explained by the interest in photosynthetic pathways in this family—carbon isotope records accounted for <10% of bromeliad trait data. Some very conspicuous features of epiphytic bromeliads, such as phytotelmata, atmospheric habit and water-absorbing trichomes, have long caught the interest of botanists (Mez, 1904; Tietze, 1906), and bromeliads have been studied as model epiphytes ever since. This does not necessarily make them 'typical' epiphytes (Figure 6). An average epiphyte would better be represented by an orchid, the family with by far the largest number of epiphyte species. While orchids are relatively under-represented, in our dataset they are still the group with the most trait records from the most species. By contrast, other families with a relatively large number of epiphytes including Gesneriaceae, Ericaceae, Melastomataceae and Rubiaceae are poorly represented and Apocynaceae is absent from our dataset (Table 3). These are mostly woody plants so they may thrive in the epiphytic habitat using other strategies, but insufficient data do not allow us to test whether their trait patterns differ from those of herbaceous epiphytes.

While our dataset is not systematically unbiased, this does not invalidate the comparison between epiphytes and other growth forms. Most traits that differ between epiphytes, herbs and trees, differ similarly across many families, large and small, and only in a few cases is the mean per growth form dominated by individual large families (Figure S5). Moreover, whenever epiphytes differ from herbs in the global dataset, they also differ from the subset of wet tropical herbs (Figure S4). Different trait values between epiphytes and herbs thus largely represent the effect of growth form, and not the effect of the specific climate epiphytes commonly thrive in.

Even with our dataset, epiphytes remain under-represented in traits data, and more so for some traits than for others (Figure 2). The proportion of epiphyte species for which stable isotope analyses have been performed, which commonly yield [C], [N], $\delta^{13}C$ and $\delta^{15}N$, is similar to that of trees and herbs. Most other available trait data for epiphytes are related to water relations (LT, SLA, stomata, WC) or nutrients. Epiphytes live under water and nutrient constraints different from most ground-rooted plants (Table 1) and researchers have been interested in the consequences of this. The most striking absence of data is for traits that are widely used to characterize the trait spectrum for other plants, particularly SSD, adult plant height, leaf area and diaspore mass.

4.2 | Are epiphytes different?

Using the available data, epiphytes differ in their trait spectrum from herbs and trees (Figure 5), but the lack of data for important traits means we currently cannot place epiphytes in the wider trait space used for other plants (Díaz et al., 2016). We outlined six characteristics of the epiphytic habitat that lead to specific hypotheses of how their traits would differ from those of ground-rooted plants (Table 1). We found few quantitative data on seed or diaspore mass and thus could not statistically test H1. Dispersal modes, however, are known for most epiphyte groups. Fern and orchid diaspores are almost all dust-like and wind dispersed. In bromeliads, all Tillandsioideae have wind-dispersed seeds and other subfamilies are animal dispersed (Benzing, 1990). Aroids and cacti have fleshy and zoochorous diaspores (Mayo et al., 1997). There is thus ample evidence supporting H1 that epiphytes reach suitable sites by either releasing many anemochorous diaspores or by attracting animal vectors for depositing them on trees. That said, comparable quantitative data diaspore size or terminal velocity might relate to different strategies in epiphyte families including their distribution within the canopy (Fischer & Araujo, 1995).

We hypothesized (H2) that roots of plants that need to hold on to surfaces should face particular mechanical demands and that roots with very intermittent contact with water face uptake demands different from roots in deeper and stable soil. Exploring this aspect for epiphytes was frustrated by the almost complete absence of data on root traits with the notable exception of a recent first study (Wagner et al., 2021). Roots of epiphytic bromeliads have been described as organs that typically serve only as holdfasts rather than for water and nutrient uptake (Benzing, 1990). Atmospheric bromeliads are characterized by a dense cover of absorbing trichomes on leaves. Whether their roots are less effective in absorption than those of tank bromeliads and if epiphyte roots in general have anatomical adaptations for greater mechanical strength and differ from ground roots is not known, but could easily be investigated (Liz Filartiga et al., 2020). Roots have been included rather late into the plant functional trait spectrum, but are important to understand plant strategies (Laliberté, 2017) and the lack of root data leaves a substantial gap in understanding epiphyte adaptations and their trait spectrum.

Small reproductive size is an advantage when the substrate is short-lived and plants complete their life cycle fast, but also when the weight of the epiphytes might break the branches or dislodge them from the branches or bark on which they grow (H3). Most epiphytic species are small- to medium-sized herbs, on average smaller than ground-rooted herbs. The fact that falling with or from their substrate is a considerable cause of mortality (Cabral et al., 2015; Hietz, 1997) should select fast growth and early maturity. We did not collect data on growth rates or age to maturity, but previous studies based on field observations found that epiphytes grow slowly and typically take many years to reach maturity (Zotz, 2016). H3 is therefore only partially supported. A notable exception are species that are specialized for living on thin twigs and can become reproductive within a year (Chase, 1987) and may have reduced vegetative and genome sizes (Chase et al., 2005). We do not have other data to compare the age to reproduction with substrate preference, but the special case of twig epiphytes underlines the advantage of maturing fast on unstable substrate. The available demographic data suggest that survival is much more important than growth or fecundity for vascular epiphytes (Zotz, 2016), although that particular analysis was based entirely on orchids and bromeliads. More data related to life history, including growth rates, reproductive age, longevity and a classification of epiphytic growth forms are needed to allow more general conclusions on the importance of particular life-history characteristics for epiphytes.

Although fast growth and early maturation represent a selective advantage on an unstable substrate, most epiphytes do not grow fast, do not mature fast and have substantially lower A_{max} than herbs or trees. At least the latter holds true for the three main groups for which sufficient data were available (Figures 3 and 6). This partially contradicts the expectation that epiphytes are taking advantage of the higher light in the canopy (H4). The lower than expected plant height (H4a) can also be explained under H3 and the lower SLA typical for leaves growing under high light can also be related to water or nutrient limitation (H5, H6).

Epiphytes frequently grow under limiting water supply and morphological, physiological and life-history traits to deal with this have been extensively documented (Zotz, 2016; Zotz & Hietz, 2001). By looking at a large number of species, we show that adaptations to water scarcity are characteristic features of the majority of epiphyte species and H5 was largely confirmed: on average, leaves of epiphytes are thicker, store more water, have lower photosynthetic rates and CAM is more common than in herbs or trees. However, data on CAM are biased by the prominence of bromeliads. Excluding bromeliads, the proportion of CAM in our epiphyte dataset (9.9%) is similar to a global estimate of 7% of all vascular plants (Winter & Smith, 1996), which questions the general importance of CAM for epiphytes (Zotz, Hietz, et al., 2021). Also, whereas average $\delta^{13}C$ values are highest in epiphytes, in the range of C3 plants $\delta^{13}C$ values do not differ between epiphytes and herbs, so we reject the hypothesis of generally higher water use efficiency, at least as estimated via carbon isotopes. Data on the control of water loss are scarce. Maximal stomatal conductance can be roughly estimated from SD and stomatal size (Willmer & Fricker, 1996). Epiphytes have much lower SD than ground-rooted plants, and for a given size have lower SD than herbs (but similar to trees), which should translate into lower maximum conductance. Epiphytes were also found to have exceptionally low cuticular water permeability, although only few species have been measured (Helbsing et al., 2000). The lipid components of cuticles are costly in terms of energy but cheap in terms of nutrients (Onoda et al., 2012), so investing in effective water barriers is an expected allocation of resources at least for epiphytes in the upper canopy or in more open forests with abundant light and high evaporative demand.

Apart from N, nutrient concentrations in epiphytes were not lower than in herbs and trees (Figure 2; Figure S6), which rejects

H6 for all nutrients other than N. Previous work suggested that P rather than N was limiting growth (Wanek & Zotz, 2011; Zotz & Asshoff, 2010), but the few bromeliad species used for these fertilization experiments may not be representative for epiphytes in general. N:P ratios are often taken as indicating whether growth is predominately N or P limited. At which N:P ratio nutrient limitation shifts from N to P is species specific, but controlled studies suggest that leaf N:P < 10 indicates mainly N and values >20 mainly P limitation (Güsewell, 2004). Average N:P was substantially higher in herbs or trees than in epiphytes, where 61% of species had N:P < 10 and only 7% >20, strongly supporting predominant N limitation in epiphytes.

Although data on photosynthesis were available for only 51 species, A_{max} in epiphytes is dramatically lower than in herbs or trees (Figure 3), which holds true, across all groups for which data are available (Figure 6; Figure S5). Photosynthesis on a leaf mass basis is strongly correlated with [N], which limits rubisco activity (Wright et al., 2004). This only partially explains the low A_{max} in epiphytes, as photosynthesis per leaf N is also lower in epiphytes than in herbs or trees (Figure 4). Thus, epiphytes have low photosynthetic nitrogen use efficiency (PNUE). PNUE is low if a large fraction of N is allocated to functions other than photosynthesis (Evans, 1989). Alternatively, under strong CO_2 limitation at rubisco CO_2 fixation and thus PNUE are also low. This is likely the case as epiphytes have thicker leaves, which may increase mesophyll resistance, and lower SD, which increases stomatal resistance. At a given diffusion resistance to CO_2 and water vapour, low [N] reduces water use efficiency (Livingston et al., 1999), which may explain why $\delta^{13}C$ values in C3 epiphytes are similar to herbs in spite of thicker leaves and lower SD. This also explains the apparent contradiction between the low A_{max} we found and the high photosynthetic capacity reported for 27 species (Stuntz & Zotz, 2001). Photosynthetic capacity was measured with an oxygen electrode under non-limiting CO_2 concentrations, whereas for leaves under natural conditions air CO_2 concentrations and diffusive resistance in the leaves are major constraints.

The combination of traits distinguishes epiphytes from non-epiphytic herbs and trees, and discriminant analysis correctly assigned most species to either group. Epiphytes differ from trees by having greater LT, $\delta^{13}C$ and WC and lower height, [N] and $\delta^{15}N$ values. There is more overlap with herbs, which differ from most trees and epiphytes by higher [N], [P] and SLA. The global trait spectrum of woody plants differs from non-woody ground-rooted herbs by larger leaves, heavier seeds, greater height, greater SSD and lower SLA and [N] (Díaz et al., 2016). We cannot yet place epiphytes on this trait map as sufficient data on SSD, leaf area and seed mass are lacking. Based on height, SLA and [N], epiphytes would be placed closer to trees, while based on SSD and seed mass epiphytes are closer to herbs in this PCA based on six traits. However, the spectrum presented by Díaz et al. (2016) does not include traits with a strong linkage to water relations. It is here that epiphytes differ most from ground-rooted plants and including traits such as LT, WC, $\delta^{13}C$, stomatal or cuticular conductance would likely produce a more complex spectrum of plant form and function and distinguish epiphytes and possibly other growth forms.

4.3 | Differences among epiphytes

The strong difference between epiphytes and most ground-rooted plants is remarkable considering how variable the epiphytic habitat is. Abiotic conditions range from the dark and moist stem base to the sun- and wind-exposed outer tree crown, and from arid and warm dry forests to cool montane forests mostly covered in clouds. For the present analysis, we did not attempt to relate variation in trait values to variation in the environment. Information on regional climate could be obtained from local weather stations or global gridded climate data, but microclimatic variation within the canopy of tropical forests is also substantial. This affects the distribution of species, whose trait values are related to their distribution within the canopy (Hietz & Briones, 1998), but also intraspecific trait variation (Petter et al., 2016). Such small-scale variation is highly important to understand the trait variation, adaptations of epiphytes to specific niches, and the functional and floristic diversity, but the majority of the trait data do not include information on the epiphytes' height on the tree or other environmental variables. This lack of metadata leaves part of the variation unexplained, as is the case with all similar analyses of species-wise trait data. We can, however, compare the trait variation among taxonomic groups of epiphytes, which is substantial for some and moderate for other traits.

Overall, differences among epiphytic clades are lower than differences between epiphytes and ground-rooted plants (Figures 3 and 6; Figure S5), which justifies describing an epiphyte traits syndrome. Ferns have the most variable and, on average, lowest WC, the thinnest leaves, the largest stomata and CAM is very rare. Succulent leaves are uncommon in ferns and most do not follow a strategy of drought avoidance by water storage. Consequently, WC per dry mass is lower than in bromeliads and orchids, whereas SLA values are similar. Hymenophyllaceae are poikilohydric, that is, they do not control water loss, and a number of epiphytic ferns in other families are desiccation tolerant, meaning that they survive almost complete water loss (Hietz, 2010). At least some ferns thus tend to tolerate substantial water loss by either closing stomata late or having high cuticular conductance. They operate at and recover from greater water deficits than epiphytic angiosperms, though some bromeliads have also been reported to recover from a 90% water loss (Zotz & Andrade, 1998). Fern stomata tend to be larger due to larger genome sizes, which makes them slower to respond (Simonin & Roddy, 2018), and ferns are mostly lacking vessels, which makes water transport less efficient (but see Pittermann et al., 2015). Their less controlled water loss results in lower water use efficiency, as seen in the lower $\delta^{13}C$ values (Figure 6, also omitting values > −20‰ indicative of CAM species) compared to bromeliads or orchids.

In the dataset analysed, the most conspicuous difference between bromeliads and orchids is the larger size and lower density of bromeliad stomata. Genome size in Epidendroideae, which

comprises most orchid epiphytes, are smaller than for other orchids (*c*. 5 pg, Leitch et al., 2009). However, genome size in bromeliads is substantially smaller (mostly < 2 pg, Müller et al., 2019) than in orchids, yet their stomata are larger, so this is unlikely to limit stomatal size in bromeliads. Alternatively, bromeliad SD might be low because a large part of the lamina is covered by trichomes and they compensate for lower densities by larger sizes. Across bromeliad growth forms, stomata and trichome densities display a weak inverse correlation (Males, 2016). CAM is often associated with succulence, but is more common in bromeliads than in orchids, although thick leaves are more common in the latter. Bromeliads also have lower N and A_{max} than orchids (Figure 6), and are generally found in the most conservative part of the leaf trait spectrum.

Different lineages of epiphytes thus follow different strategies. In the case of ferns, these appear to be related to their system of water transport and control of water loss that is not as highly evolved as in angiosperms (Brodribb et al., 2005; Gago et al., 2019) and is associated with greater desiccation tolerance (Hietz, 2010). For bromeliads, water absorbing trichomes, phytotelmata and CAM present clear advantages for plants with intermittent water supply. For orchids, a specialized mycorrhiza is hypothesized to be an advantage under nutrient-limited conditions. However, epiphyte nutrient concentrations, especially of P, are not particularly low, so a main reason for the exceptional number of epiphytic orchid species might be their minute and numerous seeds in a habitat with relatively low competition.

4.4 | Trait networks

Traits are correlated because of biophysical constraints (Messier et al., 2017; e.g. leaf N is related to A_{mass} through the importance of N in enzymes for photosynthesis) and selection (e.g. small seeds and high growth rates are both an advantage in early succession with high light availability; Westoby et al., 2002). Similar trait networks in different groups suggest that biophysical constraints dominate and individual traits cannot be modulated easily. On the other hand, if trait networks differ among groups this shows that individual traits are more flexible and can be modulated independently by selective pressure.

While trait networks are not directly comparable between studies that use different sets of traits, the malleability of trait networks has previously been shown for different growth forms (Flores-Moreno et al., 2019) and climates (Flores-Moreno et al., 2019; He et al., 2020). We found that trait networks differed significantly among growth forms (significant Mantel tests), highlighting that trait coordination can be adjusted. In all groups, SLA, which is strongly connected to A_{mass} and [N], was among the five traits with the strongest links, which supports the centrality of the LES for all growth forms. The strong links between SD and SL, and among nutrients were also seen in all three trait networks. Yet, trait networks also differed among growth forms. A_{mass} was stronger linked to other traits in trees than in herb or epiphytes. In epiphytes, the strength of the A_{mass} node in our dataset is likely somewhat reduced as there are few data of A_{mass} for epiphytes and consequently fewer significant links to other traits compared to herbs and trees. In epiphytes, three of the five traits with the strongest links were related to water relations (LT, $\delta^{13}C$, SD), which underlines the dominant effect of water supply to the trait spectrum. In herbs and trees, three were nutrients (N-P-K and Ca-N-P, respectively). While central to the LES, the importance of A_{mass} has not been observed in other network analyses of large plant trait datasets as these did not include photosynthesis (Flores-Moreno et al., 2019; Kleyer et al., 2019; Messier et al., 2017). Links to other traits are much stronger for A_{mass} than for A_{max}, and A_{mass} should thus be used in the analysis of the trait space and trait networks. Measuring A_{mass} in field-grown epiphytes is not difficult and more data would strengthen our understanding of its importance for epiphyte functional ecology. More laborious to obtain and completely lacking for epiphytes is information on leaf life span, which is an important component of the LES and informs on resource conservation and the return on investment (Wright et al., 2004).

Surprisingly, SSD was not strongly connected to any other node in any growth form including trees, although wood density is considered central to the wood economics spectrum (Chave et al., 2009). SSD was also found to be the least-connected trait in trait networks of woody and non-woody plants (Flores-Moreno et al., 2019). However, stem traits tend to be less correlated to leaf traits than to other stem traits (Baraloto et al., 2010), and in the study by Flores-Moreno and colleagues as well as in our study stem height and SSD were the only stem-related traits. Whether SSD turns out to be a central node in networks that include more stem traits remains to be tested.

Apart from looking at different trait combinations, comparing trait networks is also complicated by the fact that these may be studied across different environmental gradients. A network of the same traits based on trait correlations from different sources and settings differed strongly and had different central nodes from a network of traits from central European grasslands under similar climates (Kleyer et al., 2019). Traits across a large environmental gradient should result in stronger links: if two traits respond to the same environmental factor, the trait covariation across a longer gradient will produce a higher correlation coefficient. Since we compare the largest global datasets on all groups, these should reflect the largest gradients possible. Based on the traits studied, the connectedness of the trait network is stronger in trees than in epiphytes and herbs (Table S2).

The trait networks analysed do not present the complete picture as we by necessity focused on traits measured in epiphytes. This leaves the stem, root, reproductive, plant architecture and demographic dimensions of the trait network largely unexplored. Given the very different constraints for surviving without soil contact, we expect that these other aspects of the trait network will also differ between epiphytes and other growth forms.

4.5 | Future work and outlook

Our analysis is the first attempt to put epiphytes on a global plant traits map by presenting functional traits for a large and largely

representative number of epiphytic species and by comparing them with data of ground-rooted herbs and trees. Using this dataset to test hypotheses on the factors driving the epiphyte trait spectrum, we find strong evidence of limiting water supply to be a main driver, but weak evidence of nutrient limitation. Hypotheses on dispersal syndromes could not be directly tested with trait data but other evidence is available to address them. However, we also identified substantial gaps in epiphyte trait data. Completely missing are epiphyte root traits (root/shoot ratio, specific root length, root specific density, surface/volume ratios—first data were recently presented by Wagner et al., 2021), largely missing are diaspore traits (size, number, terminal velocity—although dispersal mode is generally known) and stem traits (SSD, height, hydraulic conductivity, water storage) as well as photosynthesis are strongly under-represented. Some of these (SSD, leaf life span, seed mass, demographic traits, A_{max}) are well sampled for other plants, but lacking these traits for epiphytes does not permit us locating epiphytes in the trait space that has been reported for trees and herbs (Díaz et al., 2016). Missing trait data also limits our understanding of epiphytes' adaptations to their environment and what might affect the coordination of their traits.

Some of these data could be obtained from alternative data sources. For instance, systematic descriptions of species commonly inform on plant height and leaf size. Also, the variation in epiphytic growth forms (rosettes, clonal, pendant, creeping, woody, etc.), which is likely related to other traits and would inform on ecological strategies, is known for most species. We are not aware of any annual epiphyte and only a few species of bromeliads are known to be monocarpic, but to what extent clonal growth or auto-pollination contribute to population maintenance is known only from a few species (CaraDonna & Ackerman, 2010; Cascante-Marín et al., 2006).

Some data are relatively easy to obtain (SSD, seed mass, leaf area, root/shoot ratio) and we encourage researchers to sample these for future comparative analyses. Given its dominant place of A_{mass} in the trait network and its importance for plant performance in general, a better understanding of the variation and limits of photosynthesis and growth in epiphytes is important. We found very few data on leaf conductance to water, either stomatal conductance or minimal conductance when stomata are closed. With the overarching importance of water limitation and the high variation in n epiphyte water relations, we expect epiphytes to have mostly low conductivities but to show substantial variation among lineages.

Whereas the three most species-rich groups of epiphytes are relatively well covered, other families have largely been neglected (Table 3). Groups such as cacti or woody epiphytes may differ from those presented here, although most traits were quite similar across epiphyte families (Figure S5) We excluded hemiepiphytes, which are epiphytic during the first part of their life (Zotz, Almeda, et al., 2021), to provide a clearer contrast between epiphytes and non-epiphytes and also because there are fewer data on these. Whether they occupy a space between epiphytes and non-epiphytes in their trait spectrum or their spectrum varies with life phase is also mostly unknown.

Traits reflect adaptations to the environment and thus define the theoretical niche of a species. The environment is defined by the local climate and by microclimatic and other small-scale variations within the canopy. These affect trait expressions, the fine-scale distribution of species and may be essential for niche separation and local diversity, but the information on fine-scale environmental variation is mostly unavailable for our data. Species-wise trait data can still be used to explain and explore the large- and fine-scale distribution of species, but at least for the latter with the caveat that intraspecific trait variation is ignored but may be important. Vascular epiphytes constitute a major component of plant diversity, particularly in humid tropical forests. Next to land-use change, tropical diversity is most threatened by climate change (Sala et al., 2000). Epiphytes, strongly dependent on the delicate water balance within the canopy, may be particularly sensitive to changes that affect water supply or demand (Gotsch et al., 2015). Understanding their trait coordination, the variations among epiphytes and the relationship with the environment will also be profitable for studies that explore the fate of epiphytes in a future environment.

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CONFLICT OF INTEREST

The authors declare no conflict of interest. Gerhard Zotz is an Associate Editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

AUTHORS' CONTRIBUTIONS

K.W. collated the epiphyte trait data; P.H. analysed the data and wrote the first draft of the manuscript; F.N.R., J.S.C. and G.Z. contributed to writing; J.K. contributed and helped interpret TRY data; P.H., K.W., J.S.C., G.Z., C.A., A.M.B., M.J.C.P., C.L.C., N.C.G., L.E.N.d.C., R.d.P.O., H.J.R.E., R.d.P.F., V.G.J., M.K., C.K., H.K., T.K., J.M., S.M.C., M.M.-C., G.P., C.R.-G., A.S., D.S.C., A.T., N.V.R., W.W. and C.L.W. contributed epiphyte data and all authors read and approved the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Epiphyte trait data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.7wm37pvtf (Hietz et al., 2021) and will also be available via TRY (www.try-db.org).

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