Functional leaf traits of vascular epiphytes: vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals

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Summary

1. Analysing functional traits along environmental gradients can improve our understanding of the mechanisms structuring plant communities. Within forests, vertical gradients in light intensity, temperature and humidity are often pronounced. Vascular epiphytes are particularly suitable for studying the influence of these vertical gradients on functional traits because they lack contact with the soil and thus individual plants are entirely exposed to different environmental conditions, from the dark and humid understorey to the sunny and dry outer canopy.

2. In this study, we analysed multiple aspects of the trait-based ecology of vascular epiphytes: shifts in trait values with height above ground (as a proxy for vertical environmental gradients) at community and species level, the importance of intra- vs. interspecific trait variability, and trait differences among taxonomic groups. We assessed ten leaf traits for 1151 individuals belonging to 83 epiphyte species of all major taxonomic groups co-occurring in a Panamanian lowland forest.

3. Community mean trait values of many leaf traits were strongly correlated with height and particularly specific leaf area and chlorophyll concentration showed nonlinear, negative trends.

4. Intraspecific trait variability was pronounced and accounted for one-third of total observed trait variance. Intraspecific trait adjustments along the vertical gradient were common and seventy per cent of all species showed significant trait–height relationships. In addition, intraspecific trait variability was positively correlated with the vertical range occupied by species.

5. We observed significant trait differences between major taxonomic groups (orchids, ferns, aroids, bromeliads). In ferns, for instance, leaf dry matter content was almost twofold higher than in the other taxonomic groups. This indicates that some leaf traits are taxonomically conserved.

6. Our study demonstrates that vertical environmental gradients strongly influence functional traits of vascular epiphytes. In order to understand community composition along such gradients, it is central to study several aspects of trait-based ecology, including both community *and* intraspecific trends of multiple traits.

Key-words: carbon isotope ratio δ^{13}C, LDMC, leaf chlorophyll concentration, leaf thickness, leaf nitrogen concentration, leaf water content, nitrogen isotope ratio δ^{15}N, specific leaf area (SLA), variance partitioning, vertical zonation

Introduction

Functional traits are measurable characteristics of individual plants impacting their growth, reproduction and survival (Violle *et al.* 2007). The analysis of functional traits along environmental gradients can help to unravel the mechanisms structuring plant communities (Wright *et al.* 2005; Ackerly & Cornwell 2007). Significant shifts in community mean trait values, for instance, indicate trait-based environmental filtering (Díaz, Cabido & Casanoves 1998;

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Cornwell & Ackerly 2009). Interestingly, studies based on global trait data sets show that large-scale changes in climatic conditions only explained a small proportion of observed variation in leaf traits, while trait variation among coexisting species within study plots was relatively high (Wright *et al.* 2004, 2005). In fact, the environment at small scales can be very heterogeneous, promoting the occurrence of species with different traits and ecological strategies. Moreover, particularly in forests, environmental factors such as light intensity, temperature and humidity normally show marked vertical gradients. Such vertical gradients, in turn, have the potential to explain a substantial part of trait variations at plot scale, and it has been demonstrated that several leaf traits of trees change significantly along vertical light gradients (Rozendaal, Hurtado & Poorter 2006; Markesteijn, Poorter & Bongers 2007).

Vascular epiphytes, plants growing non-parasitically on other plants without contact to the soil (Zotz 2013), are particularly suitable for studying the influence of vertical environmental gradients on functional traits, because individuals are entirely exposed to different environmental conditions from the dark and humid understorey to the sunny and dry outer canopy. As the leaf weight ratio (leaf mass/total plant mass) is generally high in epiphytes (Zotz & Asshoff 2010), leaf traits should be pivotal to their performance. The frequently pronounced vertical stratification of epiphyte species has long been recognized (Schimper 1888; Krömer, Kessler & Gradstein 2007), but few studies have attempted to relate their vertical distribution to functional leaf traits. Most of these studies assessed differences between sun and shade plants (e.g. Mantovani 1999) or used pre-defined zones within forests or trees (e.g. Johansson zones; Johansson 1974) as surrogates for different environmental conditions (Andrade & Nobel 1997; Hietz & Briones 1998; Stuntz & Zotz 2001). Zotz (2007) pointed out that height above ground might be more suitable to approximate the environmental gradients within forests than pre-defined zones. To our knowledge, only a single study related height above ground to leaf traits of vascular epiphytes (Cavaleri *et al.* 2010). However, as this study focused on leaf mass per area (LMA) and did not include epiphytes from important taxonomic groups such as orchids or bromeliads, many aspects of the vertical leaf trait distribution of epiphytes are still largely unexplored.

Along vertical environmental gradients, shifts in community mean trait values of functionally important leaf traits can be expected. An increase in specific leaf area (SLA = LMA^{-1}), for instance, increases the light-capture efficiency, which is advantageous under low-light conditions in the understorey (Wright *et al.* 2004). In contrast, an increase in leaf thickness can prevent overheating and minimize transpiration losses, which is favourable under drier and sunnier conditions in the canopy (Cornelissen *et al.* 2003; Rozendaal, Hurtado & Poorter 2006). Such shifts in community trait means might be caused by replacement of species with unsuitable traits. However, recent studies have also highlighted that intraspecific trait variability can be quite substantial and that individuals within species can adjust their traits in response to the environment (Bolnick *et al.* 2011; De Bello *et al.* 2011; Kichenin *et al.* 2013). Additionally, high intraspecific trait variability might be associated with a large ecological breadth or ecological generalism, possibly increasing the potential vertical range of epiphytes within forests (Van Valen 1965; Sides *et al.* 2014).

Vascular epiphytes are a taxonomically diverse group. Orchids account for 68% of all epiphyte species, but ferns and lycophytes, bromeliads and aroids are also prominent taxa (Zotz 2013). It is generally assumed that traits are taxonomically conserved and, consequently, trait differences between taxonomic groups can be expected. Moreover, epiphyte taxa independently evolved a variety of different morphological and physiological characteristics (e.g. velamen radicum, phytotelmata, specialized trichomes) to cope with nutrient and water limitation (Benzing 1990). Such differences between-taxa might affect the response of leaf traits to environmental conditions.

To analyse the multiple aspects of trait-based ecology along vertical environmental gradients, we studied ten leaf traits for 1151 individuals of 83 epiphyte species of all major taxonomic groups co-occurring in a Panamanian lowland forest. We tested the following hypotheses: (H1) trait means and trait syndromes change with height at the community level; (H2) variations in trait–height relationships among species influence community trait structure; (H3) vertical ranges of epiphyte species correlate with their intraspecific trait variability; and (H4) trait means, trait syndromes and trait–height relationships differ among taxonomic groups.

Materials and methods

STUDY SITE

This study was conducted at the San Lorenzo Canopy Crane Site at the Atlantic coast of Panama (9°17′ N, 79°58′ W, 130 m a.s.l.; Wright *et al.* 2003). Mean annual precipitation in this old-growth lowland tropical rain forest is around 3100 mm, with a pronounced dry season from January to March. Canopy height is variable and emergent trees reach maximum heights of *c.* 45 m. The use of a gondola attached to a construction crane allowed access to all strata of the forest within an area of *c.* 0·9 ha. A comprehensive census of the vascular epiphyte flora at the study site was conducted in 2010–2012 and yielded >22 000 individuals of >100 species (G. Mendieta-Leiva & G. Zotz, unpublished data; see Zotz & Schultz 2008 for methodology).

Among vertical environmental gradients, the light gradient is considered as most influential on leaf traits (e.g. Poorter 1999; Markesteijn, Poorter & Bongers 2007). Changes in light intensity with height above ground were measured *in situ* with light intensity loggers (HOBO UA-002–64; Onset Computer Corporation, Cape Cod, MA, USA; for more details, see Fig. S1 in Supporting Information).

LEAF TRAITS

As we focused on multiple aspects of trait-based ecology (e.g. community and intraspecific trends), we applied a two-tiered sampling strategy. First, we randomly sampled epiphytes along the vertical gradient within the entire area accessible by crane to represent the epiphyte community. Secondly, for species which were quite abundant in the study area (based on the census), but under-represented in our sample, we additionally increased the sample size to $n = 10$, which we regarded as minimum to analyse intraspecific trends. However, this applied to only few species and thus should not bias community trends.

We collected one leaf per epiphyte for 1151 individuals belonging to 83 species (51 species ≥10 samples) in 15 plant families (Table S1; the taxonomic nomenclature used in this paper follows *The Plant List* (2014): http://www.theplantlist.org). For each sampled individual, height above ground was recorded. We sampled adults and juveniles, but not seedlings. The juvenile phase can last several years in epiphytes, and by sampling these individuals, we were able to include more species in our analysis. However, we note that including juveniles can lead to increased intraspecific trait variability (~30% of all individuals were juveniles; ~60% of all species included juveniles). We aimed at sampling the youngest, fully expanded leaves without signs of herbivory or infections.

For each sample, we determined specific leaf area (SLA = leaf area/dry weight; $mm^2 mg^{-1}$), leaf dry matter content (LDMC = dry weight/fresh weight; $g g^{-1}$), leaf lamina thickness (Thickness; mm), leaf water content on an area basis (LWC_{area} = (fresh weight – dry weight)/leaf area; $g H_2O m^{-2}$), as well as leaf chlorophyll concentration on an area basis (Chl_{area}; $\mu g cm^{-2}$) and on a mass basis (Chl_{mass}; $mg g^{-1}$). Chlorophyll concentration was estimated by measuring red/infrared absorbance in the field with a SPAD-502 chlorophyll meter (Spectrum Technologies, Plainfield, IL, USA). SPAD measurements were converted into chlorophyll concentrations using the general relationship from Coste *et al.* (2010). Collected leaves were rewatered with de-ionized water for >6 h before taking additional measurements. Leaf thickness was measured with a calliper (precision: 0·05 mm). Each leaf was photographed and leaf area was determined in Adobe Photoshop 6·0 (Adobe Systems, San Jose, CA, USA). Leaves were weighed to obtain fresh weight (balance: A&D GR-202; A&D Company, Tokyo, Japan; precision: 0·1 mg), oven dried at 70 °C for 48 h and reweighed to obtain dry weight.

Additionally, for a subsample (224 individuals of 61 species), leaf nitrogen concentration on both mass (N_{mass}; $mg g^{-1}$) and area basis (N_{area}; $g m^{-2}$), as well as nitrogen isotope ($\delta^{15}N$; ‰) and carbon isotope ratios ($\delta^{13}C$; ‰) were determined after homogenization of the dried samples in a ball mill by elemental analyser-isotope ratio mass spectrometry (Delta PLUS; Thermo Electron, Bremen, Germany). As universal standards, atmospheric air was used for ^{15}N and the Vienna Pee Dee Belemnite for ^{13}C. In the following, we refer to the traits of this subsample as nitrogen–carbon (NC) traits.

DATA ANALYSES

Analyses were done in R 3.0.1 (R Development Core Team 2013). Analyses for each hypothesis are described separately in the following.

H1 – Trait means and trait syndromes change with height at the community level

We used linear models (LMs) to analyse the relationship between leaf traits and height. To test for nonlinearity, simple LMs (trait ~ height) and LMs including a quadratic term (trait ~ height + height²) were fitted and compared using the Akaike Information Criterion (AIC). Choosing a conservative approach, we selected the nonlinear model as minimal adequate model (MAM) if it received higher model support by $\Delta AIC > 10$ (Burnham & Anderson 2004). For each trait, LMs were applied to the entire data set consisting of all sampled individuals, as well as to community trait means calculated for all 1-m height intervals. CAM species, defined by $\delta^{13}C$ values >−20 ‰ (compare Zotz 2004), were excluded from analysis of vertical trends in $\delta^{13}C$. To check for potential sampling bias, we took advantage of a rare opportunity – the information about the vertical position and species identity of all >22 000 individuals in the epiphyte community (G. Mendieta-Leiva & G. Zotz, unpublished data). We used this information in combination with intraspecific trait–height relationships (see H2) to additionally predict community trends when considering the entire community (for details, see Fig. S2). Qualitative comparisons with the community trends based on sampled individuals were used to detect sampling bias in observed trends.

To assess how trait syndromes (i.e. combinations of multiple traits of individuals) are influenced by their vertical position, we first conducted a principal component analysis (PCA; R package 'vegan') based on the normalized and centred trait data of the extensively sampled traits. Some leaf traits covaried strongly (pairwise correlations between all traits were assessed by Pearson's correlation coefficient), and the PCA reduced correlated traits to independent components. Subsequently, LMs using the PCA scores of the first two PCA axes as dependent variables and height as independent variable were applied.

H2 – Variations in trait–height relationships among species influence community trait structure

We analysed the influence of variations in trait–height relationships among species on community trait structure by comparing LMs with different fixed effects (trait ~ fixed effects: height × species, height + species, height, species) based on AIC values. Simpler LMs with fewer fixed effects and no interactions were selected as MAM when $\Delta AIC \leq 10$ (Burnham & Anderson 2004). If the MAM included the interaction of height and species, the community trait structure was significantly influenced by differences in mean trait values *and* differences in trait responses to height among species. If the MAM included species as fixed effect but no interaction, only differences in mean trait values among species were significant.

Additionally, to assess the importance of intraspecific trait responses for each trait, we classified species based on the significance of their trait–height relationship (non-significant slopes, significant positive or negative slopes; $P < 0.05$). We only used species with ≥10 records per trait for these analyses ($n = 51$), which excluded the NC traits.

H3 – Vertical ranges of epiphyte species correlate with their intraspecific trait variability

To assess the general importance of intraspecific trait variability, we first carried out variance component analyses (R package 'varcomp'), which partition observed trait variability into within-species (intraspecific) and between-species (interspecific) components (Messier, McGill & Lechowicz 2010). Subsequently, we calculated two measures of trait variability for each species: the coefficient of variation (CV) and the trait range (TR: absolute difference between maximum and minimum trait value divided by the maximum, given in %). The relationship between these measures of intraspecific trait variability and species' vertical ranges was analysed with LMs (vertical range ~ trait

variability), whereby the vertical range for each species was estimated based on its maximum and minimum height observed in the census.

H4 – Trait means, trait syndromes and trait–height relationships differ among taxonomic groups

Differences in trait means among the major taxonomic groups (aroids, bromeliads, orchids, ferns; see Table 1 for number of species and individuals), based on trait means of associated species, were compared using max-*t* tests for multiple comparisons that account for unbalanced group sizes, non-normality and heteroscedasticity (R packages 'multcomp' and 'sandwich'; see Herberich, Sikorski & Hothorn 2010).

Differences in trait syndromes among the taxonomic groups were tested using a permutational multivariate analysis of variance (PERMANOVA, *adonis* from 'vegan' R package; Anderson 2001). Additionally, we used the PCA results to visualize differences among taxonomic groups.

Differences in trait–height relationships among the taxonomic groups were analysed using generalized linear mixed models (see Fig. S3 and Table S2 for details).

Results

H1 – TRAIT MEANS AND TRAIT SYNDROMES CHANGE WITH HEIGHT AT THE COMMUNITY LEVEL

All leaf traits were significantly correlated with height ($P < 0.05$, Fig. 1, Table S3). The strongest correlations between community trait means (for 1-m height intervals) and height were observed for SLA ($R^2 = 0.89$), Chl_{mass} ($R^2 = 0.76$), leaf thickness ($R^2 = 0.72$), $\delta^{13}C$ ($R^2 = 0.66$) and LWC_{area} ($R^2 = 0.64$). Trait–height correlations were generally much weaker when, instead of community means, traits of all sampled individuals were used as response variable: in this case only $\delta^{13}C$ ($R^2 = 0.35$), SLA ($R^2 = 0.30$) and Chl_{mass} ($R^2 = 0.16$) were moderately corre-

lated with height (Fig. 1). While SLA, Chl_{mass} and N_{mass} showed decreasing, nonlinear trends with height, leaf thickness, LWC_{area} and $\delta^{13}C$ showed positive linear trends with height (Fig. 1). LDMC and $\delta^{15}N$ showed slightly negative trends, but rather weak correlations. Observed community trends were largely consistent with those considering the entire censused community, indicating no substantial sampling bias (compare Figs 1 and S2, as well as Tables S3 and S4).

Many traits covaried significantly (Table S5; $P < 0.05$): for instance, leaf thickness and LWC_{area} ($r = 0.84$), Chl_{mass} and N_{mass} ($r = 0.67$), as well as SLA and Chl_{mass} ($r = 0.64$). The first two PCA axes explained 45% and 25%, respectively, of variation in leaf traits. Height explained 16% of variation along the first axis and 7% along the second axis ($P < 0.001$).

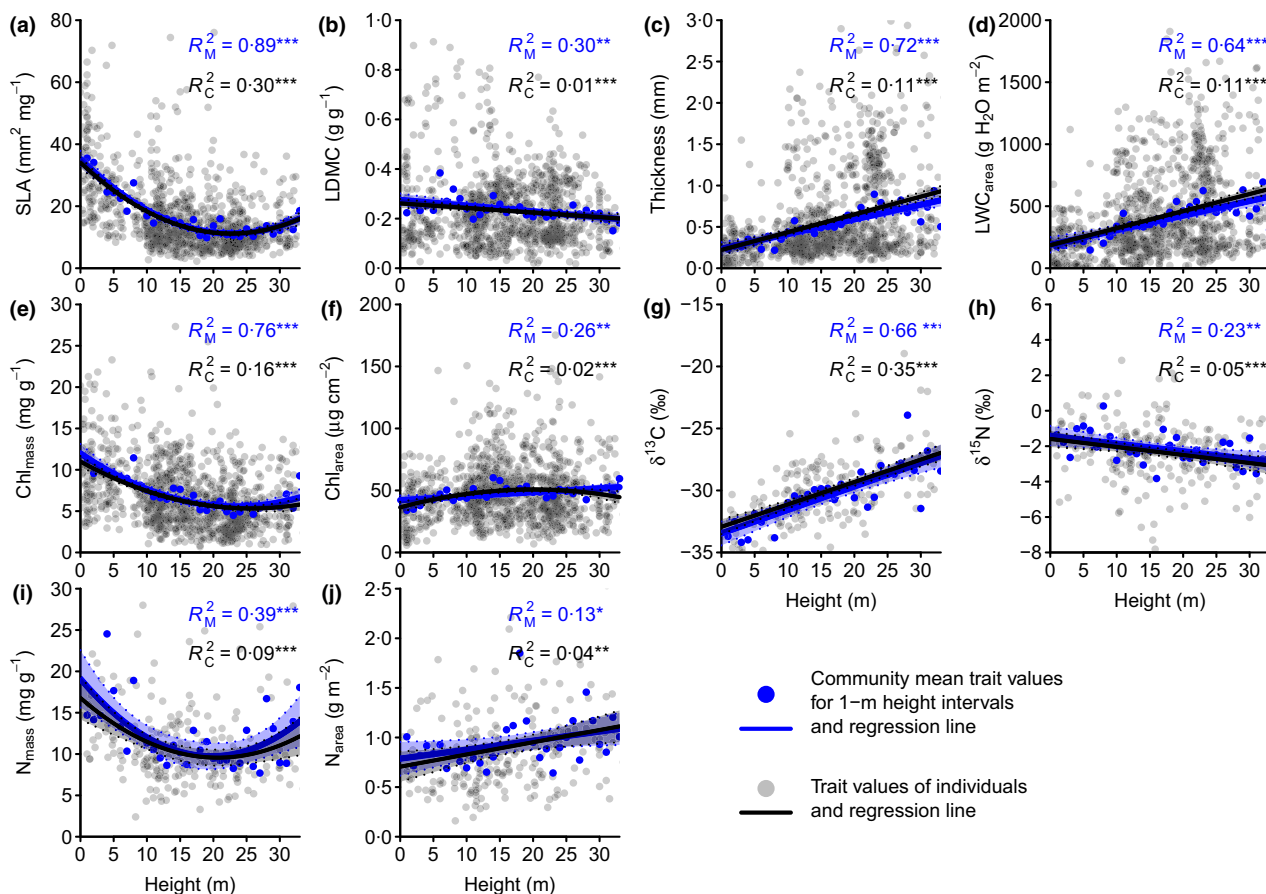### H2 – VARIATIONS IN TRAIT–HEIGHT RELATIONSHIPS AMONG SPECIES INFLUENCE COMMUNITY TRAIT STRUCTURE

The MAM for SLA, LDMC, leaf thickness and Chl_{mass} included the interaction between species and height, indicating that the community trait structure was best explained when considering that species differ in both their trait means *and* their trait responses to height (Table S6). In contrast, for Chl_{area} and LWC_{area} only between-species differences in trait means were significant (Table S6).

Seventy per cent of all species had at least one trait that was significantly correlated with height ($P < 0.05$). Significant intraspecific trait–height relationships were most common for SLA, for which 45% of all species revealed a significant relationship with height, followed by LDMC with 33% (Table S7; see Figs S4–S9 for intraspecific

Table 1. Mean leaf trait values $\pm$ SD of the major taxonomic groups of vascular epiphytes (aroids, bromeliads, orchids, ferns) in a Panamanian lowland forest. Species from all other taxa are summarized in 'Others'. CAM species were excluded from $\delta^{13}C$ analyses. Differences between taxonomic groups were analysed using max-*t* tests for multiple comparisons of means, and significant differences in trait means ($P < 0.05$) are indicated by different letters. Proportions of sampled individuals and species are given in parentheses.

	Aroids	Bromeliads	Orchids	Ferns	Others
Individuals	149 (12·9%)	62 (5·4%)	435 (37·8%)	379 (32·9%)	126 (10·9%)
Species	13 (15·7%)	5 (6%)	32 (38·6%)	24 (28·9%)	9 (10·8%)
Height (m)	12.2 ± 7.5^A	14.7 ± 7.4^{AB}	21.0 ± 6.4^B	11.1 ± 7.2^A	15.4 ± 3.0^A
SLA (mm^2 mg^{-1})	22.1 ± 10.9^{AB}	17.7 ± 7.5^{AB}	14.0 ± 5.7^A	24.2 ± 14.8^B	27.6 ± 11.2^B
LDMC (g g^{-1})	0.17 ± 0.05^A	0.18 ± 0.04^A	0.20 ± 0.10^A	0.34 ± 0.11^B	0.08 ± 0.05^C
Thickness (mm)	0.38 ± 0.13^A	0.59 ± 0.69^{AB}	0.70 ± 0.52^B	0.26 ± 0.12^A	0.96 ± 0.59^B
LWC_{area} (g H$_2$O m^{-2})	297 ± 102^A	378 ± 278^{ABC}	488 ± 344^B	168 ± 128^C	632 ± 325^B
Chl_{mass} (mg g^{-1})	10.1 ± 2.9^A	5.4 ± 3.2^{AB}	6.3 ± 2.6^B	7.5 ± 2.7^{AB}	8.3 ± 3.9^{AB}
Chl_{area} (µg cm^{-2})	55.3 ± 16.4^A	31.3 ± 9.1^B	47.6 ± 15.3^A	41.4 ± 19.1^{AB}	32.3 ± 9.6^B
$\delta^{13}C$ (‰)*	-29.7 ± 2.7^A	-29.9 ± 0.7^A	-29.7 ± 2.1^A	-31.2 ± 1.6^A	-30.4 ± 2.0^A
$\delta^{15}N$ (‰)*	-1.8 ± 1.9^{AB}	-2.8 ± 1.0^{AB}	-2.3 ± 1.0^{AB}	-1.7 ± 1.1^A	-3.8 ± 1.1^B
N_{mass} (mg g^{-1})*	14.5 ± 6.4^A	7.5 ± 2.1^B	11.6 ± 5.5^{AB}	12.0 ± 3.6^A	11.8 ± 4.0^{AB}
N_{area} (g m^{-2})*	1.07 ± 0.29^A	0.57 ± 0.36^A	0.92 ± 0.33^A	0.96 ± 0.38^A	0.69 ± 0.29^A

*For the NC traits, not all species were sampled. Species numbers assessed for NC traits were as follows: Aroids: $n = 10$, Bromeliads: $n = 5$, Orchids: $n = 19$-24, Ferns: $n = 17$, Others: $n = 5$, with on average 3–4 replicates per species (Table S1).

Fig. 1. Trait–height relationships of vascular epiphytes for ten leaf traits: (a) SLA: specific leaf area, (b) LDMC: leaf dry matter content, (c) Thickness: leaf thickness, (d) LWC_{area}: leaf water content per leaf area, (e) Chl_{mass}: mass-based chlorophyll concentration, (f) Chl_{area}: area-based chlorophyll concentration, (g) $\delta^{13}C$: carbon isotope ratio, (h) $\delta^{15}N$: nitrogen isotope ratio, (i) N_{mass}: mass-based nitrogen concentration, (j) N_{area}: area-based nitrogen concentration. Simple LMs (trait ~ height) and LMs including a quadratic term (trait ~ height + height^2) were fitted and compared by AIC. Nonlinear models were preferred when $\Delta AIC \leq 10$ (see Table S3 for summary statistics). R^2_M: amount of variance in community means explained by height. R^2_C: amount of variance in individuals' trait values explained by height. Asterisks indicate significance levels of trait–height relationships (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). Shaded areas indicate 95% CI.

trait–height relationships of all species). The directions of intraspecific trait–height relationships were largely consistent within traits. For instance, for SLA and Chl_{mass}, slopes were invariably negative (Table S7). However, for LDMC and thickness, there were a few species showing opposing trends (Table S7).

H3 – VERTICAL RANGES OF EPIPHYTE SPECIES CORRELATE WITH THEIR INTRASPECIFIC TRAIT VARIABILITY

Variance component analysis revealed that intraspecific variability, on average, accounted for 31% of observed variance (Fig. S10). The proportion of variance explained by intraspecific variability ranged from 16% (Thickness) to 51% (Chl_{area}).

We observed significant positive correlations between both measures of multivariate intraspecific trait variability (mean CV, mean TR) and vertical ranges of species (Fig. S11). The correlation was stronger for mean TR

($R^2 = 0.24$, $P < 0.001$) than for mean CV ($R^2 = 0.10$, $P = 0.009$).

H4 – TRAIT MEANS, TRAIT SYNDROMES AND TRAIT–HEIGHT RELATIONSHIPS DIFFER AMONG TAXONOMIC GROUPS

We found significant differences between trait means of taxonomic groups for all traits except N_{area}, $\delta^{13}C$ and $\delta^{15}N$ (Table 1). Trait differences were, however, often only significant between individual taxonomic groups; there was no trait for which all pairwise differences were significant. The only case in which a group's trait mean differed significantly from that of all other groups was LDMC, with almost twofold higher values in ferns (Table 1). Orchids had, on average, the thickest leaves, the highest LWC_{area} and the smallest SLA, but differences in these traits were consistently significant only compared to ferns (Table 1). Bromeliads tended towards low nitrogen and chlorophyll concentrations, although differences were not always

significant. In contrast, the highest nitrogen and chlorophyll concentrations were consistently found in aroids.

Taxonomic groups also differed significantly in height distributions. The mean height of orchid species (21.0 ± 6.4 m) was significantly higher ($P < 0.05$, max-t test) than that of aroids (12.2 ± 7.5 m) and ferns (11.1 ± 7.2 m), but did not differ significantly from that of bromeliads (14.7 ± 7.4 m; Table 1).

The PERMANOVA indicated significant differences in trait syndromes among all taxonomic groups ($P < 0.001$). The dispersion of species in PCA trait space showed that several species of different taxa shared similar trait syndromes, but also that there were unique tendencies within taxonomic groups (compare, e.g. orchids and ferns; Fig. 2).

The fixed-effect structure of the MAMs did not include the interaction between height and taxonomic group for any leaf trait, indicating that slopes of trait–height relationships did not differ significantly among taxonomic groups (Table S2). No significant differences in slopes or intercepts were observed for SLA and all NC traits (Fig. S3).

Discussion

H1 – TRAIT MEANS AND TRAIT SYNDROMES CHANGE WITH HEIGHT AT THE COMMUNITY LEVEL

Our results support the hypothesis that community trait means of vascular epiphytes are significantly correlated with height, but strength and direction of correlations varied considerably. The strongest correlations among the extensively sampled traits were found for SLA and Chl_{mass}, whose negative trends from the forest floor to the upper canopy are consistent with differences between sun and shade leaves of tropical trees (Rozendaal, Hurtado & Poorter 2006; Markesteijn, Poorter & Bongers 2007) and trends along tree height gradients (Rijkers, Pons & Bongers 2000). When considering that SLA and Chl_{mass} covaried considerably and that Chl_{area} did not show a strong vertical trend, it seems likely that changes in Chl_{mass} were mainly driven by changes in SLA ($Chl_{mass} = Chl_{area} \cdot SLA$). In soil-rooted plants, vertical gradients in SLA are commonly related to vertical light gradients (Poorter 1999; McMurtrie & Dewar 2011), but hydraulic constraints have also been discussed (Rijkers, Pons & Bongers 2000; Koch *et al.* 2004). A comparative study by Cavaleri *et al.* (2010) found that epiphytes were the only plant group for which light was most important in explaining vertical SLA profiles, which seems logical as epiphytes lack a hydraulic connection to the ground. Because SLA relates the light-capturing leaf area to investment in dry mass, an increase in SLA increases the potential carbon gain per biomass investment. However, increased light-capture efficiency via high SLA tends to be associated with higher respiration rates and shorter leaf life spans. Several such correlations between leaf traits capturing fundamental aspects of leaf economics
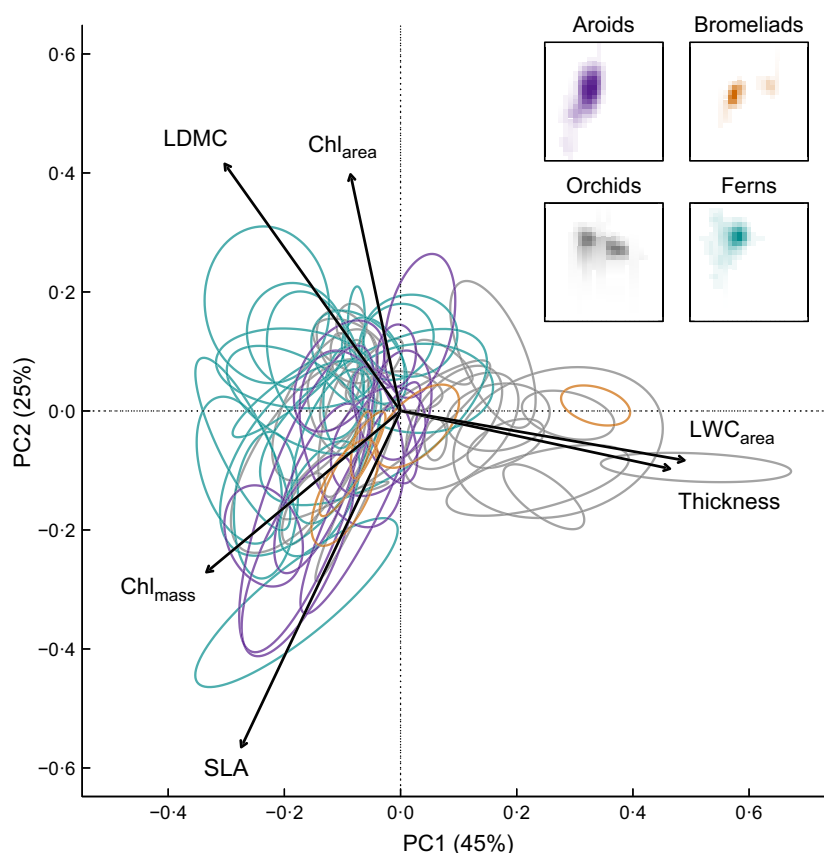
Fig. 2. Dispersion of trait syndromes of epiphyte species in the PCA trait space based on six leaf traits of 1151 individuals. Trait syndromes of all species belonging to four major taxonomic groups (aroids, bromeliads, orchids, ferns) are shown as ellipsoids of inertia, which encompass 95% of individuals of each species. The position and the spread of the ellipsoids thus illustrate mean trait syndromes and trait variability of each species. Insets in the upper right part show kernel densities for each taxonomic group. A PERMANOVA indicated significant differences in trait syndromes between all taxonomic groups ($P < 0.001$).

have been observed ('worldwide leaf economics spectrum'; Wright *et al.* 2004). Theoretical models have demonstrated that, when considering these between-trait correlations, the carbon gain over the leaf life span is maximized when SLA increases nonlinearly with decreasing light (Sims, Gebauer & Pearcy 1994; McMurtrie & Dewar 2011). The nonlinearly decreasing community means of SLA with height (Fig. 1a) agree with these expectations and corroborate the notion that light is the main driver of vertical SLA profiles in epiphytes.

The observed increase in leaf thickness with height is consistent with within-individual, intra- and interspecific vertical trends found in trees (Rozendaal, Hurtado & Poorter 2006; Markesteijn, Poorter & Bongers 2007). Apart from maximization of carbon gain, avoidance of damages and water loss minimization are also requirements of optimal leaf functioning: an increase in leaf thickness is regarded as adjustment to prevent overheating and to balance carbon gain and transpiration water loss under drier and sunnier conditions (Cornelissen *et al.* 2003; Rozendaal, Hurtado & Poorter 2006). Without anatomical adjustments that change the leaf tissue density, a decrease in SLA would induce an increase in leaf thickness, which partially explains their covariance ($r = -0.48$). Nevertheless, the linear increase in leaf thickness (Fig. 1c) in contrast to the nonlinear decrease in SLA (Fig. 1a) suggests that the trend in leaf thickness is not only related to SLA, but also to independent morphological adjustments which are probably more influenced by the vertical gradient in potential evapotranspiration than by the vertical light gradient.

In general, LDMC also tends to scale with SLA and is sometimes regarded as an alternative predictor of plant strategies (Wilson, Thompson & Hodgson 1999). Interestingly, the observed covariance between LDMC and SLA was rather low at community level ($r = -0.16$) and the LDMC-height correlation was rather weak (Fig. 1b). This suggests that plant functioning captured by SLA is more relevant along vertical gradients within forests.

It is well-established that the proportion of epiphytes with CAM increases with height (e.g. Zotz 2004). The positive trend in $\delta^{13}C$ of C_3 plants documented here (Fig. 1g) has arguably the same ecological background: more demanding water relations result in increasing stomatal limitations (Farquhar, Ehleringer & Hubick 1989). Tissue $\delta^{13}C$ correlates with water-use efficiency, and $\delta^{13}C$ is thus used as indicator of water stress. However, along vertical gradients in forests, interpretation may be confounded as the atmospheric $\delta^{13}C$ signature also shows a vertical trend (Quay, King & Wilbur 1989). Nevertheless, the strongest increase in atmospheric $\delta^{13}C$ signature occurs within a few metres above the forest floor due to soil respiration, and above this zone, the gradient in $\delta^{13}C$ is generally weak (Quay, King & Wilbur 1989). In contrast, our model predicted a linear trend with an average change of ~5.5 ‰ in $\delta^{13}C$ from the trunk base to the upper canopy (Fig. 1g), suggesting that a large part of the observed vari-

ance in tissue $\delta^{13}C$ can be attributed to differences in water-use efficiency. These results agree with observations for leaves of tropical trees (Medina & Minchin 1980). In contrast, the difference in $\delta^{13}C$ signals of epiphytes between the upper and lower tree zones of a lowland rain forest in Costa Rica was smaller (< 2 ‰; Wania, Hietz & Wanek 2002), possibly due to a less pronounced gradient of water stress than in our system (precipitation at that site is >6000 mm year^{-1}). Alternatively, the discrepancy may indicate that height above ground is a better predictor for water stress than the pre-defined Johansson zones used by Wania, Hietz & Wanek (2002), which subdivide host trees according to their principal structure without considering absolute height.

In line with Wania, Hietz & Wanek (2002), we observed a negative trend in tissue $\delta^{15}N$ with height (Fig. 1h). The $\delta^{15}N$ signatures of plants are mostly affected by their assimilatory pathway, but also by form (NO_4^+, NH_3^-, N_2) and $\delta^{15}N$ signature of the nitrogen source (Evans 2001). Epiphytes use a blend of different autochthonous (e.g. canopy soil, leachates) and allochthonous nitrogen sources (e.g. wet and dry deposition), which can vary substantially in $\delta^{15}N$ signatures (Wania, Hietz & Wanek 2002). The observed negative trend with height indicates an increasing contribution of atmospheric N to epiphyte N in the upper canopy. However, as we did not measure source $\delta^{15}N$ signatures, caution is needed when interpreting tissue $\delta^{15}N$ trends.

In summary, we found only moderate to weak correlations between leaf traits/leaf trait syndromes and height when considering all individuals, but often strong correlations between community means and height. This also reflects that height is a suitable proxy of general vertical trends in environmental conditions, although it does not capture all relevant factors and small-scale environmental variability (Fig. S1).

H2 – VARIATIONS IN TRAIT–HEIGHT RELATIONSHIPS AMONG SPECIES INFLUENCE COMMUNITY TRAIT STRUCTURE

For four out of six traits, the community trait structure could be best explained when including differences in intraspecific trait response to height, which supports our hypothesis for most traits. Intraspecific trait responses to height were particularly important for SLA, which was the trait with the highest frequency of significant trait–height relationships (45% of all species) and consistently showed only negative trends. SLA captures essentials of leaf economics (Wright *et al.* 2004) and is a suitable trait for intraspecific adjustments because it can be relatively easily adjusted by varying the size, number and cell wall thickness of different leaf cell types (Shipley *et al.* 2006; Kichenin *et al.* 2013). In general, although we cannot rule out genetic variation as source of intraspecific trait variability, we argue that, considering the spatial scale of our study, phenotypic trait plasticity in response to the environment

is probably more important (also see Grassein, Till-Bott-raud & Lavorel 2010).

Interestingly, the second most frequent significant intra-specific trait–height relationships were found for LDMC, which, in contrast, was rather weakly correlated with height at the community level. The high frequency might partly be explained by correlations between SLA and LDMC, which were often stronger at the species level than at the community level (compare Figs S4 and S5). How-ever, species-specific differences in strategies might also play a role (Wilson, Thompson & Hodgson 1999). For instance, in *Elaphoglossum doanense* only LDMC was strongly correlated with height ($R^2 = 0.81$), while there was no significant correlation for any of the other traits.

Although intraspecific trait response to height was com-mon in epiphytes, the absence of a significant intraspecific trait–height relationship was not always accompanied by limited trait variability. Most species that lacked a signifi-cant trait–height correlation had a pronounced intraspe-cific trait variability unrelated to height. Apart from the uncertainties associated with height as proxy for environ-mental gradients, plant size and age are additional sources of intraspecific trait variability (Zotz 2000; Wanek *et al.* 2002; Hietz & Wanek 2003), which might weaken trait–height relationships. It is therefore striking that height emerged as significant factor for intraspecific changes in leaf traits.

In summary, our results corroborate the growing evi-dence that not only differences in trait means, but also dif-ferences in intraspecific trait response to environmental gradients among species are non-negligible aspects of com-munity assembly (Bolnick *et al.* 2011; Kichenin *et al.* 2013).

H3 – VERTICAL RANGES OF EPIPHYTE SPECIES CORRELATE WITH THEIR INTRASPECIFIC TRAIT VARIABILITY

Intraspecific variability explained almost one-third of the observed variance in our trait data, which is in the same range as observed for terrestrial plants (Albert *et al.* 2010; Hulshof & Swenson 2010). This supports previous find-ings underlining the importance of considering trait vari-ability not only between but also within species (Albert *et al.* 2010). Such intraspecific variability seems to be important for species' spatial distribution, as our results supported the hypothesis that species occupying larger vertical ranges tended towards higher leaf trait variability (Fig. S11). The inherent ability of species to vary their leaf traits might increase their ability to tolerate a wider range of environmental conditions (Van Valen 1965). In this context, it is not surprising that TR explained a lar-ger amount of variation in species vertical ranges than CV (TR: $R^2 = 0.24$, CV: $R^2 = 0.10$). This is because TR is based on extreme trait values and is thus a better approximation of the theoretical maximal trait range of a species, whereas CV is affected by the trait frequency dis-tribution. Sides *et al.* (2014) conducted a comparable study of 21 herbaceous perennials along an elevational gradient of *c.* 700 m, using CV as measure of trait variability. They observed a stronger correlation between intraspecific trait variability in SLA and elevational range ($R^2 = 0.51$). The weaker correlation in our study might partly be explained by the uncertainties associated with the height gradient as approximation of environmental gradients. Furthermore, Sides *et al.* (2014) pointed out that intraspecific trait plasticity should be essential when strong trends in community mean trait values exist. Com-munity mean trends were less pronounced in our study, indicating that height was a weaker filter than elevation. In summary, epiphyte species that can adjust their leaf traits to the environment can potentially occupy larger vertical ranges. However, the substantial amount of unex-plained variance also emphasizes that unstudied charac-teristics (e.g. root traits, specific morphological and physiological characteristics) or other processes (e.g. ger-mination, seedling survival) might be likewise important in explaining why some species are restricted to smaller vertical ranges than others.

H4 – TRAIT MEANS, TRAIT SYNDROMES AND TRAIT–HEIGHT RELATIONSHIPS DIFFER AMONG TAXONOMIC GROUPS

For most traits, we found significant differences in trait means between taxonomic groups, which partly confirms our hypothesis. Trait differences were, however, often only significant between certain pairs of taxonomic groups. The frequent absence of pairwise differences was mainly due to the high trait variation between species within taxonomic groups, and, to a lesser extent, due to similarities in group trait means. The pronounced within-group trait variation and associated among-group trait overlap become appar-ent when comparing species' trait syndromes in the multi-variate trait space (Fig. 2). Nevertheless, the unique tendencies within taxonomic groups indicate that some leaf traits are taxonomically conserved (Fig. 2).

The marked differences in morphological leaf traits between orchids and ferns were consistent with previous studies reporting orchids having thicker leaves and lower SLA (Stuntz & Zotz 2001; Cardelús & Mack 2010). Com-munity means of leaf thickness and SLA were strongly correlated with height, which emphasizes their functional relevance along the vertical gradient. It is thus unsurpris-ing that differences in these traits were reflected in different height distributions of these taxa (Table 1; also see Fig. 3). This pattern might be partly explained by environmental filtering of species with unsuitable traits, but intraspecific leaf trait adjustments, particularly for SLA, might also be important. Interestingly, SLA was the only extensively sampled trait without significant differences in slopes or intercepts among the taxonomic groups (Fig. S3a). This suggests an optimal SLA value at a given height indepen-dent of taxonomic group and further indicates that
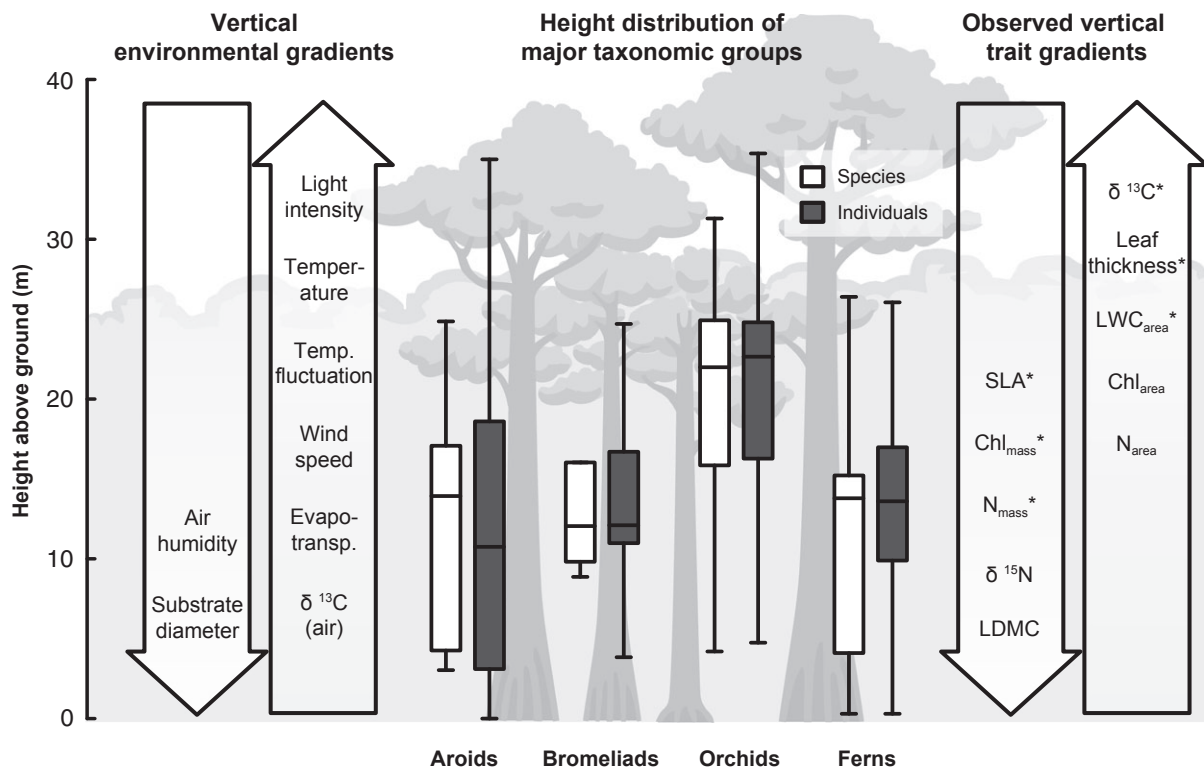
Fig. 3. Schematic diagram illustrating main findings. Arrows on left side: environmental factors commonly changing with height above ground within forests. In this study, only the vertical light gradient was measured (Fig. S1). Boxplots: height distribution of the major taxonomic groups of epiphytes at the study site in Panama. Height distributions are based on either the height of all individuals or the mean height of each species. Boxplots depict median heights (horizontal line), interquartile ranges (boxes) and approximate 95% confidence intervals (whiskers). Outliers are not shown. Arrows on right side: significant vertical leaf trait gradients at the study site (trait abbreviations as in Fig. 1). Leaf traits showing pronounced changes in community trait means with height are marked by *.

environmental changes along the height gradient act as a particularly strong filter on SLA.

The most striking among-group differences were observed for LDMC, with LDMC of ferns being twofold higher, on average, than in all other groups. LDMC values have not been reported for many epiphyte species, but Woods (2013) also found high LDMC values in two *Elaphoglossum* species and low values in one *Microgramma* species. This agrees with our results and shows that the LDMC of fern species can differ substantially (Table S1). However, the large number of fern species sampled in our study ($n = 24$) suggests that high LDMC values are more common in ferns.

Aroids had the highest leaf nitrogen and chlorophyll concentrations, whereas bromeliads consistently had the lowest. In fact, both traits were correlated ($r = 0.67$; Table S5). Chlorophyll concentrations have not yet been compared among major epiphyte taxa, but our results agree with reported leaf nitrogen values. For example, Stuntz & Zotz (2001) also found the highest nitrogen concentrations in aroids. The lowest nitrogen concentrations, in turn, were consistently observed in bromeliads (Hietz, Wanek & Popp 1999; Stuntz & Zotz 2001; Cardelús & Mack 2010). An increase in leaf nitrogen content is usually associated with an increase in photosynthetic capacity (Stuntz & Zotz 2001; Wright *et al.* 2004). Interestingly, differences in

photosynthetic nitrogen-use efficiency (PNUE) were observed among epiphyte taxa, with aroids having the lowest PNUE, and bromeliads having the highest (Stuntz & Zotz 2001). Thus, for a given nitrogen concentration, the photosynthetic capacity was higher in bromeliads. This suggests that the observed among-taxa differences in leaf nitrogen cannot be used to infer similar differences in photosynthetic capacity.

We did not observe significant among-group differences in $\delta^{13}C$ and $\delta^{15}N$ values. Our results largely agree with observations along an elevational gradient in Costa Rica (Cardelús & Mack 2010). In contrast, Hietz, Wanek & Popp (1999) observed significantly depleted $\delta^{15}N$ values in bromeliads, but these were mainly of atmospheric habit. All these studies found high variability in isotope ratios of species within taxonomic groups, suggesting that the environmental conditions and species-specific characteristics are more important in determining isotope ratios in leaf tissue of individual epiphytes than their taxonomic affiliation.

Compared to global trait means of non-epiphytic taxa (TRY; Kattge *et al.* 2011), both low nitrogen concentrations and thick leaves are particularly noticeable differences (see Table S1 for details). These trait differences can be regarded as an adaptation of epiphytes to an environment in which water and nutrients are only intermittently available.

Conclusions

Our findings indicate that analysing multiple aspects of trait-based ecology (e.g. community and intraspecific trends, inter- and intraspecific variability, correlations among traits) is key to advance the understanding of mechanisms structuring plant communities. Leaf trait syndromes and the intraspecific trait variability play important roles in explaining the vertical zonation of vascular epiphyte species and taxonomic groups (see Fig. 3 for a schematic representation of key findings). However, other adaptations of epiphytes, such as water- and nutrient-storing pseudobulbs in orchids or phytotelmata in bromeliads, are probably likewise important. As height above ground as proxy of vertical environmental gradients explained substantial amounts of total trait variations, we propose to use height in addition to the more frequently used zonation scheme by Johansson in trait-based studies of epiphytes.

Acknowledgements

Data accessibility

Trait data have been uploaded to the Plant Trait Database TRY: https://www.try-db.org/TryWeb/Data.php#11

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Vertical light gradient at the study site.

Fig. S2. Trait-height relationships at community level (census data).

Fig. S3. Trait-height relationships of taxonomic groups.

Figs S4-S9. Intraspecific trait-height relationships.

Fig. S10. Variance partitioning.

Fig. S11. Relationship between trait variability and vertical range.

Table S1. Detailed trait information on all sampled species.

Table S2. AIC-based comparisons of GLMMs testing H4.

Tables S3–S4. Summary statistics of LMs (community trends).

Table S5. Pairwise correlations between traits.

Table S6. AIC-based comparisons of LMs testing H2.

Table S7. Proportion of species with significant trait–height relationships.