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Comparing trait syndromes between Taiwanese subtropical terrestrial and epiphytic ferns and lycophytes at the species and community level

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Summary

- While functional trait-trait and trait-environment relationships are well studied in angiosperms, it is less clear if similar relationships, such as the leaf economics spectrum (LES), hold for ferns and lycophytes. Similarly, studies exploring potential differences in trait-trait and trait-environment relationships between terrestrial and epiphytic fern communities in a given ecosystem are largely lacking.
- We measured nine leaf traits for 76 terrestrial and 43 epiphytic fern and lycophyte species across 59 vegetation plots along an elevation gradient in the subtropical forest of Northern Taiwan. We explored trait-trait and trait-environment relationships at both the species- and community level for both species groups.
- Epiphytes differed from terrestrial ferns and lycophytes in species- and community-level trait values, mainly reflecting responses to higher drought and nutrient stress. The angiosperm LES was reflected in the trait-trait correlations of terrestrial ferns, but not of epiphytes. This suggests that epiphytic trait patterns are mainly shaped by water, rather than nutrient availability. Trait-environment relationships were nonetheless more-or-less similar for several drought-related traits across both species' groups.
- This study illustrates that ferns and lycophyte trait patterns are not equivalent for epiphytic and terrestrial species or communities, and should not be extrapolated across species groups or between the species- and community-level.

Key words

drought adaptation, elevation gradient, functional traits, ground fog, monsoon forest, subtropical montane cloud forest, trait-environment relationship

Introduction

Functional traits, i.e. morphological, physiological or phenological features that indirectly impact an organism's fitness (Violle *et al.*, 2007), often dictate under what environmental conditions plants will be able to thrive. This environmental trait filtering has been extensively studied and has increased our mechanistic understanding of community-level species composition (Lavorel & Garnier, 2002; Kraft *et al.*, 2015; Bruelheide *et al.*, 2018). Several functional traits furthermore covary systematically across plant species. The leaf economics spectrum (LES), for example, links several leaf traits that govern a species' leaf investment strategy, ranging from highly resource acquisitive, productive species characterized by high

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specific leaf area (SLA) and leaf nitrogen and phosphorous content, to more resource conservative, slow-growing species with high leaf dry matter content (LDMC) and leaf lifespan (Wilson *et al.*, 1999; Wright *et al.*, 2004; Díaz *et al.*, 2016). The LES is even retained when scaling up species-level traits to the community level (Bruelheide *et al.*, 2018). The discovery of the LES, and the links between LES traits and plant responses to several environmental stressors, such as low nutrient availability (Ordoñez *et al.*, 2009; Hodgson *et al.*, 2011) and low temperatures (Wright *et al.*, 2005; Dong *et al.*, 2020), have greatly increased our understanding of plant functioning and plant-environment interactions.

Most of this trait work has been performed on seed plants (spermatophytes) though, and it is unclear if the same trait-trait and trait-environment relationships hold for older vascular plant lineages, such as ferns (Polypodiophyta) and lycophytes (Lycopodiophyta) (Karst & Lechowicz, 2007). Since both ferns and lycophytes form separate evolutionary lineages from seed plants (Smith *et al.*, 2006), morphological and physiological traits are not guaranteed to be functionally equivalent across these groups (Peppe *et al.*, 2014). For example, recent work has suggested that the evolution of photosynthesis-related trait co-regulations and trade-offs, such as the LES, have been more strongly constrained by leaf water transport capacity in ferns (Sessa & Givnish, 2014; Zhang *et al.*, 2014). This seemed to be caused by the more limited potential for controlling evaporation, low water-use efficiency and xylem hydraulic limitations in ferns (Brodribb & Holbrook, 2004; Zhang *et al.*, 2014). This makes them more prone to drought stress and might explain the overall lower photosynthetic capacity and nutrient concentrations of fern leaves compared to angiosperm leaves (Tosens *et al.*, 2016). A few studies have nevertheless found some support for LES trait relationships across a limited number (i.e. 11-35 species) of terrestrial fern and lycophyte species of temperate (Karst & Lechowicz, 2007; Sessa & Givnish, 2014; Tosens *et al.*, 2016) and (sub)tropical ecosystems (Campany *et al.*, 2019; Lin *et al.*, 2020). However, strong evidence for global LES trade-offs across fern species, similar to those known for seed plants, is currently still lacking. Our limited understanding of trait-trait relationships in ferns and lycophytes (cf. Kessler *et al.*, 2016) is nonetheless surprising, considering that they contain more than 10,000 species in the world, second only to flowering plants (angiosperms) in terms of plant species diversity (Smith *et al.*, 2006; Tosens *et al.*, 2016).

Almost one third (29%) of all fern species are epiphytic (Dubuisson *et al.*, 2009). Especially in (sub)tropical regions, ferns form the predominant vascular epiphytic group, together with orchids (Schellenberger Costa *et al.*, 2018; Campany *et al.*, 2021). The beforementioned constrain of photosynthesis-related traits by water relationships are

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expected to be even more severe for epiphytic species, since they are likely to experience more frequent and extended drought periods than terrestrial species (Dubuisson *et al.*, 2009; Zhang *et al.*, 2014; Aros-Mualin *et al.*, 2021). Epiphytes are additionally confronted with low nutrient availability, since they have no access to the soil (Watkins Jr *et al.*, 2007). On average, epiphytic ferns indeed have higher water-use efficiency ($\delta^{13}C$ isotope ratio) and lower SLA, stomatal density and leaf N than terrestrial species in tropical forests, strongly suggesting the importance of water and nutrient stress in shaping their traits (Watkins Jr *et al.*, 2007; Nitta *et al.*, 2020; Campany *et al.*, 2021). It is consequently unclear if similar LES-related trait relationships can be expected for epiphytic and terrestrial ferns. A recent study on epiphytic plant communities along elevation in Tanzania, for instance, found markedly different trait-environment correlations for epiphytic ferns and epiphytic flowering plants (Schellenberger Costa *et al.*, 2018).

In ecosystems where both terrestrial and epiphytic ferns co-occur, such as (sub)tropical rain- and cloud forests, the environmental filtering of their respective communities might be governed by very different drivers. The proneness to drought of epiphytes suggests that their community composition will be more strongly filtered by water availability through precipitation, relative air humidity and ground fog cover (Dubuisson *et al.*, 2009; Zhang *et al.*, 2014; Aros-Mualin *et al.*, 2021). Additionally, woody species composition directly affects epiphyte substrate quality and availability, thus further impacting epiphyte community composition. Terrestrial species, on the other hand, will also be filtered by soil variation, through differences in soil nutrient and water availability, while the impact of temperature might be important for both lifeforms. Some research has, for example, found that several morphological leaf traits vary in response to temperature (elevation) and humidity gradients for both tropical terrestrial and epiphytic fern communities (Kessler *et al.*, 2007; Kluge & Kessler, 2007; Salazar *et al.*, 2012; Petter *et al.*, 2016). Nevertheless, studies separately exploring the importance of different environmental drivers on community-level trait composition of terrestrial and epiphytic ferns simultaneously for a given ecosystem are largely lacking (however see Wegner *et al.*, 2003).

In this study, we measured nine functional leaf traits, including four LES-related traits, that are known to respond to nutrient, water and cold stress in seed plants, for 76 terrestrial and 43 epiphytic fern and lycophyte species across 59 10 m × 10 m plots. These plots were spread along an elevation gradient from 870 to 2130 m a.s.l. in the subtropical forests of Northern Taiwan. Next to the measured species-level traits, we also calculated community

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mean trait values for each plot. Using this dataset, we explored the following research questions:

- Are traits of terrestrial and epiphytic species and communities systematically different?
- Do similar trait-trait correlations occur for terrestrial and epiphytic species and communities, and do these relationships mirror known trait patterns of seed plants, such as the LES?
- Do we find similar trait-environment relationships for the nine measured traits and elevation, ground fog frequency and heat load, for terrestrial and epiphytic ferns?

Materials and Methods

Study design

The study was conducted in the Wulai district of New Taipei City, in northern Taiwan. In this area we established 59 10 m × 10 m vegetation plots in natural, undisturbed vegetation along an elevational gradient ranging from Mount Meilu (870 m a.s.l., 24.85°N 121.53°E) to Mount Taman (2130 m a.s.l., 24.71°N 121.45°E) (Supporting Information Fig. S1). Vegetation along this gradient ranged from lowland *Pyrenaria-Machilus* subtropical winter monsoon forest to lower cloud zone *Quercus* montane evergreen broad-leaved cloud forest and *Chamaecyparis* montane mixed cloud forest (Li *et al*., 2013). The vegetation plots were evenly spread across six elevation zones (with centres at 850, 1100, 1350, 1600, 1850 and 2100 m a.s.l. ±50 m), with ten plots per elevation zone spaced at least 50 m apart (except for the 1850 m zone, where only nine plots were located due to logistic constraints). At each elevation zone, plots were positioned along a topographic gradient across the ridge, ranging from the southwest facing (leeward) to northeast facing slope (windward).

The climate in the study region is classified as a humid subtropical climate, with monthly mean temperature in January and July ranging from 12.8□ and 25.6□ (near Mt. Meilu) to 8.7□ and 21.1□ (near Mt. Taman), respectively (obtained from on-site microclimatic measurements in a subset of plots; Zelený *et al*., unpublished). Mean annual precipitation ranges from 2033 to 3396 mm along the gradient, with no obvious dry season (Lalashan and Fushan weather stations, Taiwan Central Weather Bureau). Microclimatic loggers installed at three sites at each elevation zone furthermore indicated very high relative humidity for most plots (median between 97.5 and 100% RH; Zelený *et al*., unpublished). Parent materials of the study area mainly consists of Miocene and Oligocene sandstone and slate (Central Geological Survey, MOEA). The soils covering this material are strongly acidic and have very high organic matter content, especially in higher elevation and on the ridges. Soils located near ridges have higher degrees of podzolization than those located on steeper

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slopes, due to lower degrees of soil layer disturbance on the flat microtopography of the ridges (Lin *et al.*, 1988).

Species composition and functional traits

In each plot, both the understory (terrestrial) and epiphytic fern and lycophyte species composition was recorded (presence-absence data), in May to October 2017 or 2018. Epiphytic species within reach were collected directly, while those out of reach were identified using binoculars and sampled for trait measurements using a 11m long telescopic knife. We measured nine functional leaf traits for 48 understory and 34 epiphytic fern and lycophyte species (respectively 63% and 79% of all recorded understory and epiphytic fern and lycophyte species) (Supporting Information Table S2). For each of these species, we collected leaves from, on average, 5 (range 1-12) individuals, directly in our plots, or within a 50 m radius. Only mature individuals were selected, preferentially those bearing sporangia when present. For species occurring across different elevation zones, we attempted to collect individuals across this full range. From each collected individual, we selected 1-6 leaves (fronds) for trait measurements, using the following criteria: 1) for dimorphic species, we selected the sterile tropophyll, rather than the fertile sporophyll; 2) the frond should be fully expanded and matured without visible herbivore or parasite-induced damage. For non-dimorphic species, traits were measured on sori-containing fronds. Collected fronds were stored in wet, sealed plastic bags at low temperatures (< 10°C) for a minimum of 12h before trait measurement, to allow full rehydration (cf. Pérez-Harguindeguy *et al*., 2013).

The measured traits consisted of leaf dry matter content (LDMC, mg g^{-1}), specific leaf area (SLA, mm^2 mg^{-1}), leaf nitrogen content (leaf N, mg g^{-1}), area-based leaf chlorophyll content (SPAD units), leaf area (cm^2), leaf thickness (mm), equivalent water thickness (EWT, mg mm^{-2}), leaf $^{13}C/^{12}C$ stable isotope ratio ($\delta^{13}C$, ‰) and leaf $^{15}N/^{14}N$ stable isotope ratio ($\delta^{15}N$, ‰). EWT is sometimes referred to as 'succulence' (Mantovani, 1999; Féret *et al.*, 2019). The first four of these traits are part of the LES for vascular plants (cf. Wilson *et al*., 1999; Wright *et al*., 2004), and thus position species along a gradient from resource acquisitive (high SLA and leaf N) to resource conservative (high LDMC and area-based leaf chlorophyll). The next four traits are expected to relate to drought stress, with small leaf area and high leaf thickness, EWT and $\delta^{13}C$ indicative of drought tolerance, with the latter trait a proxy of long-term water use efficiency (Farquhar *et al.*, 1982; Medeiros *et al.*, 2019; Maréchaux *et al.*, 2020). $\delta^{15}N$ reflects the nitrogen source used by a plant, with values around 0 ‰ usually indicating nitrogen fixation, while values around -2 and -6 ‰ indicating plant

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nitrogen acquisition through arbuscular and ectomycorrhiza, respectively (Craine *et al.*, 2015). Trait measurements largely followed standard protocols (Pérez-Harguindeguy *et al.*, 2013), but were partly adapted for fern leaves (Supporting Information Appendix S3 for all details). For four epiphytic ferns, leaves were too small to measure leaf chlorophyll content (Supporting Information Table S2).

For all traits, except leaf area, values with a Z-score larger than 2.5 at the species level were considered outliers caused by measurement error and were removed from the final dataset (<1% of data points). Next, all leaf level traits were averaged to the species level, resulting in a 48 species × 9 traits matrix for the terrestrial species and a 34 species × 9 traits matrix for the epiphytic species. Trait values were also translated to the plot-level by calculating community mean (CM) trait values, i.e. the average trait value across all species in the plot. Since no abundance data was collected, CM values were not abundance-weighted. Leaf area was logarithmically transformed before CM calculation for both species groups.

Climate proxies

In each plot we recorded exact elevation using a topographic map combined with the GPS coordinates (GPSMAP 64st, Garmin, USA), aspect using a compass (SILVA, Sweden) and slope using a clinometer (SUUNTO PM-5/360 PC Clinometer, SUUNTO, Finland). We then calculated heat load from the aspect folded on the prevailing wind direction (45°) and slope with equation 2 of McCune & Dylan (2002). We also used the ground fog frequency raster map for Taiwan of Schulz *et al.* (2017) (250 m per pixel resolution) to extract average annual ground fog frequency for each plot. Variation inflation factors indicated that the three climate proxies, namely elevation, fog frequency and heat load, were largely independent of each other (VIF < 1.5) (Zuur *et al.*, 2010).

Species-level analysis

Species-level trait-trait relationships were visualized through three principal component analyses (PCA) on the standardized species × trait matrices (i.e. zero mean, unit standard deviation), one for all species combined and one for either the terrestrial and epiphytic species separately. For all three ordinations, the first two PC axes together contained around 61-64% of the total trait variation (Supporting Information Table S4). Using the first three axes of the PCA performed on the full dataset, we constructed separate trait hypervolumes for the epiphytic and terrestrial species with the 'hypervolume' R package (Blonder *et al.*, 2014; Blonder, 2018), using the protocol described in Helsen *et al*. (2020). These hypervolumes

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were used to quantify the trait space size and overlap for both species' groups. Since PCA does not allow missing trait values, the missing leaf chlorophyll content values of four epiphytic species were replaced by mean chlorophyll content across all epiphytic species. All other analyses were performed without replacement of missing trait values. Pairwise species-level trait-trait correlations were tested separately for terrestrial and epiphytic species using Spearman rank correlations. Differences in average trait values between epiphytic and terrestrial species were assessed with a Mann-Whitney U test for each trait.

Community-level analysis

Community-level trait-trait relationships were visualized through three PCA analyses on the standardized plot × CM trait matrices, one for all species combined and one each for the terrestrial and epiphytic species separately. For all three ordinations, the first two PC axes together contained around 72-84% of the total CM trait variation (Supporting Information Table S5). CM trait space size and overlap for both species' groups was again assessed through trait hypervolume construction, based on the first three axes of the PCA performed on the full plot × CM trait matrix. Pairwise community-level trait-trait correlations were tested separately for terrestrial and epiphytic species using Spearman rank correlations. Differences in average trait values between epiphytic and terrestrial species were additionally assessed with Wilcoxon signed-rank tests for each trait. For each trait, we additionally performed a Spearman rank correlation between the plot-level CM trait of the epiphytic species and that of the terrestrial species.

Lastly, to explore relationships between the measured traits and the three climate proxies (elevation, fog frequency and heat load), we used the fourth-corner approach, which calculates (weighted) Pearson correlations between a single trait from the standardized species × trait matrix and a single environmental variable from the plot × environmental data matrix, weighted by the plot × species matrix (Legendre *et al.*, 1997; Dray & Legendre, 2008; ter Braak *et al.*, 2018). We computed both the original fourth-corner correlation coefficient and the Chessel fourth-corner correlation coefficient, following the recommendations of Peres-Neto *et al*. (2017). The latter is the fourth-corner correlation coefficient divided by its maximum attainable value, and thus provides a relative measure of how well the trait-environment correlation explains the species distribution (Peres-Neto *et al.*, 2017). The fourth corner correlations were tested by the 'max test' proposed by ter Braak *et al*. (2012), which overcomes Type-I error inflation issues often observed during trait-environment correlations (ter Braak *et al.*, 2012, 2018). The fourth-corner approach was performed separately for the

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epiphytic and terrestrial species/traits datasets. Before analyses, heat load was squared and leaf area logarithmically transformed for both species groups.

Significance levels of all trait-trait correlations and average trait comparisons between epiphytic and terrestrial species at both the species- and community-level were adjusted for Type-I error inflation using the false discovery rate method with the 'p.adjust' function in the 'stats' R base package (Benjamini & Hochberg, 1995). Ordinations were performed with the 'vegan' R package (Oksanen *et al.*, 2017), and fourth-corner analyses with the 'weimea' R package (Zelený, 2018; https://github.com/zdealveindy/weimea) all using R version 4.0.5 (https://www.r-project.org/).

Results

Species-level

Comparing the traits of the 48 terrestrial and 34 epiphytic fern and lycophyte species in our study showed that, on average, epiphytic species have lower SLA, leaf area, $\delta^{15}N$ and leaf N and higher EWT and $\delta^{13}C$ than terrestrial species (Fig. 1, Supporting Information Table S6). This was reflected in the PCA trait space, where epiphytic and terrestrial species were largely segregated (Fig 2A, Supporting Information Fig. S7), and thus both had a relatively large proportions of unique trait space (69.8 and 58.1%, respectively), following the hypervolume construction. The epiphytic species trait hypervolume was furthermore 28.1% larger than the terrestrial species trait hypervolume, despite containing less species. This seemed to be mainly caused by a larger variation in LDMC, EWT, leaf thickness and leaf chlorophyll values among epiphytic species, compared to terrestrial species (Fig. 1).

When comparing trait patterns separately for epiphytic and terrestrial species, different patterns emerge. For epiphytic species, LDMC seems fully disconnected from the LES, showing no relationship to leaf chlorophyll or leaf N, and even a slightly positive correlation with SLA (Fig 1B, Supporting Information Fig. S8). SLA is also more strongly related to EWT and leaf thickness for epiphytic species, than to the other leaf economics traits (Supporting Information Fig. S8). Epiphytes seem to cluster in three more-or-less distinct groups, one group with high-LDMC species, one group with high values for EWT and leaf thickness and one group with less extreme trait values, that largely overlaps the terrestrial species trait space (Fig. 2A&B).

For terrestrial species, the four measured leaf economics traits show the theoretical expected links (Fig. 2C), although these pairwise correlations are rather weak (Supporting Information Fig. S8). Overall, terrestrial species seem to be loosely spread along a LES axis,

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with high SLA species on one side and high LDMC species on the other side. An additional group of terrestrial species exhibits large EWT and leaf thickness, with intermediate SLA and LDMC values (Fig. 2C). This latter group is differentiated from the epiphyte species group with high EWT/ leaf thickness, by higher leaf area and leaf N levels (Fig. 2A).

Community-level

Community-level trait patterns largely mirror those observed at the species-level. Both the differentiation between the terrestrial and epiphytic species trait space (86.6% and 92.8% unique trait space for terrestrial and epiphytic species, respectively) and the difference in hypervolume size between the species groups (46.5% larger for epiphytes), are more pronounced at the community-level. Note that the constructed hypervolumes are larger than the convex hulls visualized in Fig. 2D, due to their probabilistic nature, explaining the slight overlap in hypervolumes but not convex hulls. Besides reflecting the species-level differences in SLA, leaf area, EWT, $\delta^{13}C$, $\delta^{15}N$ and leaf N between epiphytic and terrestrial species, community-level trait patterns also show higher CM LDMC and leaf thickness, and lower CM leaf chlorophyll for epiphytic species (Fig. 1, Supporting Information Table S6).

Not surprisingly, several pairwise trait correlations observed at the species-level were also present at the community-level for both species' groups. However, community-level patterns did not completely mirror those at the species-level. For example, while $\delta^{13}C$ and $\delta^{15}N$ showed almost no relationships to any other trait at the species-level for epiphytes (except for a link between $\delta^{15}N$ and leaf N), both traits were each related to four other traits at the community-level. LMDC was also more strongly linked to several other traits at the community-level than at the species-level, for both epiphytic and terrestrial species (Appendices S8 & S9). For instance, the positive correlation between species-level SLA and LDMC for epiphytes became even stronger at the community-level (Fig. 2, Appendices S8 & S9).

Community-level traits were furthermore only positively correlated between epiphytic and terrestrial species across the vegetation plots for LDMC, leaf thickness and EWT (Fig. 3, Supporting Information Table S10). For the other traits, CM values were not related, while CM $\delta^{13}C$ was even negatively correlated across lifeforms (Fig. 3, Supporting Information Table S10). Consequently, the results of the fourth-corner analysis showed that trait-environment relationships were not completely similar for both species groups. While elevation was negatively related to leaf thickness and EWT for both species groups, LDMC also showed a strong positive relationship with elevation only for terrestrial species, and $\delta^{13}C$

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was negatively related with elevation for epiphytic species (Table 1). Similarly, fog frequency was negatively related to EWT, and heat load was negatively related to LDMC, for both species' groups. Fog frequency was additionally positively related to LDMC for terrestrial species, and heat load showed relationships with three additional traits for epiphytic species (Table 1).

Discussion

Trait differences between epiphytic and terrestrial species

Epiphytic species were functionally differentiated from terrestrial species in our study, with six out of the nine measured leaf traits significantly different, at both the species and community level. These differences are in agreement with fern studies in other (sub)tropical regions in Asia, Central America and Polynesia. Higher leaf thickness, EWT and $\delta^{13}C$ of epiphytic species is usually attributed to the higher frequency and intensity of drought events experienced by these species, compared to terrestrial ferns (Watkins Jr *et al.*, 2007; Campany *et al.*, 2021). Lower leaf area for epiphytes has also been linked to water relations in a study in French Polynesia (Nitta *et al.*, 2020), although several other studies found no significant difference in leaf area between epiphytic and terrestrial ferns (Zhang *et al.*, 2014; Campany *et al.*, 2021). The importance of drought stress for epiphytic ferns is further supported by their lower stomatal density observed in previous studies (Zhang *et al.*, 2014; Campany *et al.*, 2021).

Other trait differences, such as low SLA and leaf N of epiphytes compared to terrestrial species are also in agreement with previous studies (Watkins Jr *et al.*, 2007; Zhang *et al.*, 2014; Nitta *et al.*, 2020; Campany *et al.*, 2021), and likely reflect a shift along the LES towards more resource conservative strategies for epiphytes (Wright & Cannon, 2001; Wright *et al.*, 2004), driven by the lower nutrient availability experiences by epiphytes compared to terrestrial species (Watkins Jr *et al.*, 2007). SLA differences could, however, also been indirectly caused by water stress avoidance (Campany *et al.*, 2021). The lower $\delta^{15}N$ signature of epiphytes has been hypothesized to reflect the uptake of depleted, atmospherically derived N sources, through precipitation and fog (Watkins Jr *et al.*, 2007; Craine *et al.*, 2015). Although not different at the species level, the community-level higher LDMC and lower leaf chlorophyll for epiphytes might also reflect more resource-conservative strategies, and suggest that epiphytes with high LDMC and low leaf chlorophyll are more common at the community-level (Wright *et al.*, 2004; Hodgson *et al.*, 2011).

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Trait variation was considerably larger among epiphytic species and communities than among terrestrial species and communities, reflecting patterns from previous studies (Watkins Jr *et al.*, 2007; Nitta *et al.*, 2020). This high variation seems to reflect the co-occurrence of three more-or-less distinct drought-coping trait syndromes for epiphytic ferns (Kessler *et al.*, 2007). The first group consists of species with very high LDMC and mainly contain filmy ferns (Hymenophyllaceae) (Supporting Information Fig. S7). These species, such as *Hymenophyllum badium* and *H. polyanthos*, can completely dry out when under water stress, and rehydrate after a drought period (Garcés Cea *et al.*, 2014). Kessler *et al*. (2007) classified this as a 'poikilohydric' drought strategy. The second group, termed 'xeromorphic' by Kessler *et al*. (2007), contains species that prevent desiccation through thick, fleshy leaves with high leaf thickness and EWT (e.g. *Lemmaphyllum microphyllum* and bird's nest ferns such as *Asplenium antiquum*). The third group has more intermediate trait values, with seemingly no pronounced drought-related traits and contains both mesomorphic species that avoid drought by growing in less drought-prone microclimates (e.g. *Lepidomicrosorium ningpoense* and *Vandenboschia auriculata*) and drought-deciduous species that avoid water stress by shedding their leaves during drought. The latter species usually have succulent rhizomes and mainly occur in the Davalliaceae and Polypodiaceae families in our study (e.g. *Arthromeris lehmannii*, *Davallia clarkei*, *Goniophlebium amoenum).* This higher trait variation among epiphytic species has been attributed to the strong vertical gradients in light intensity, temperature and humidity occurring in forests (Petter *et al.*, 2016). This allows epiphytes to sort vertically in different niches from the dark and humid understory to the sunny and dry outer canopy, thus presenting a more varied environment as experienced by terrestrial species, who can only sort horizontally along the forest floor (Hietz & Briones, 1998; Petter *et al.*, 2016; Nitta *et al.*, 2020).

Terrestrial species did not show similar distinct species groups as epiphytes, mainly due to the absence of species with very high LDMC (Poikilohydric group) and leaf thickness and EWT (xeromorphic group). Although only moderate compared to the xeromorphic epiphytes, some terrestrial species did nonetheless express higher leaf thickness and EWT values, thus likely presenting moderate xeromorphic adaptations (e.g. *Deparia formosana, Diplazium donianum* var. *donianum, Polystichum integripinnum*). Most terrestrial species, however, mainly spread along a LES-like axis, of which species on the conservative side (e.g. *Diplopterygium glaucum, Polystichum parvipinnulum*) fully overlap with the mesomorphic and drought-deciduous epiphytes in the trait space. The acquisitive side of this gradient contains several terrestrial (e.g. *Hymenasplenium adiantifrons*, *Monachosorum henryi*), but

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no epiphytic species. Overall, these trait patterns support the more severe drought (only poikilohydric and pronounced xeromorphic epiphytes) and nutrient limitation (only acquisitive terrestrial species) experienced by epiphytic compared to terrestrial species.

Trait-trait patterns

For terrestrial species, our data shows LES-related correlations between SLA, LDMC, leaf chlorophyll and leaf N. While these relationships were relatively weak at the species-level, they strengthened at the community-level. These results are in agreement with previous studies that observed similar LES relationships for terrestrial ferns as for angiosperms (Karst & Lechowicz, 2007; Sessa & Givnish, 2014; Tosens *et al.*, 2016; Campany *et al.*, 2019; Lin *et al.*, 2020).

For epiphytic species, LES patterns were visible at neither the species, nor the community level. This is in agreement with previous work that found no correlation between SLA and leaf N (Campany *et al.*, 2021) and SLA and maximum photosynthetic rate for epiphytic ferns (Zhang *et al.*, 2014). These patterns are likely due to a combination of factors. Firstly, epiphytic species seem to consist of only relatively resource-conservative species, thus lacking representatives at the acquisitive side of the spectrum. Secondly, the strong divergent trait adaptations to drought across the epiphytic groups also affected traits traditionally aligned with the LES. For example, LDMC is usually negatively related to SLA across species and communities, but unique trait composition of Poikilohydric fern species resulted in a positive correlation between both traits.

Trait-trait correlations did not only differ strongly between both species' groups, but also between the species and community level. This shows that trait patterns should not be extrapolated from the species to the community level, since species filtering at different sites can result in different trait – trait correlations at the community level. Similarly, trait patterns cannot be extrapolated from terrestrial to epiphytic fern species.

Trait-environment patterns

Despite the stark differences in mean traits between epiphytic and terrestrial species, several drought-related traits responded similarly to the climate proxies for both species' groups. These responses, such as increased leaf thickness and EWT at low elevation and fog frequency and high heat load seem to support the importance of water availability for fern community and trait composition (Kluge & Kessler, 2007; Petter *et al.*, 2016; Medeiros *et al.*, 2019). The positive correlation of CM of leaf thickness and EWT across species groups

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further illustrates their similar environmental response. The negative relationship between elevation and $\delta^{13}C$ for epiphytic species again suggests higher proneness to drought and associated higher water-use efficiency at low elevation (Farquhar *et al.*, 1982; Maréchaux *et al.*, 2020). This response was not found for terrestrial species, even resulting in an unexpected negative correlation for $\delta^{13}C$ across species groups.

The LES traits SLA, leaf N and leaf chlorophyll did not respond to any of the measured climate proxies for either of the two species groups. Several studies nevertheless found a significant decrease in SLA with elevation for both terrestrial and epiphytic ferns (Kessler *et al.*, 2007; Salazar *et al.*, 2012; Nitta *et al.*, 2020). The CMs of these traits were furthermore not correlated across species groups in our study, suggesting that their community-level variation is governed by different processes. Soil variation, for example, is expected to only directly impact leaf economics traits of terrestrial, but not epiphytic species (Watkins Jr *et al.*, 2007). We indeed previously observed significant effects of soil composition on leaf N of terrestrial ferns in our study area (Helsen *et al.*, 2021). LDMC, however, did show strong relationships with elevation and fog for terrestrial species and moderate relationship with heat load for both species' groups. The increase of LDMC with elevation might reflect a shift to more conservative leaf traits for terrestrial species due to lower temperatures, as often observed for angiosperms (cf. Helsen *et al.* 2018), or due to decreased nutrient availability at higher elevation. The LDMC patterns, however, more likely reflect water availability patterns. The consistently strong negative correlation between LDMC and EWT at both the species and community level for both species groups, further supports this.

Conclusion

Epiphytic ferns and lycophytes differ in mean species-level and community-level trait values from terrestrial fern and lycophyte species along an elevation gradient in Northern Taiwan. These trait differences seem to occur because epiphytes experience higher drought and nutrient stress than terrestrial species. Trait-trait correlations traditionally associated with the LES were present for terrestrial species. They did, however, not occur for epiphytes, likely because epiphytic trait patterns are driven by stronger gradients in water than in nutrient availability. Trait–environment relationships were more-or-less similar for several drought-related traits across both species' groups, while LES traits were not coordinated across species groups at the community level. Overall, these results illustrate that trait patterns are

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not equivalent for epiphytic and terrestrial species nor communities and should not be extrapolated across species groups or between the species- and community-level.

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Author Contribution

TYL and DZ conceived the original idea and collected data. KH elaborated the idea, analyzed data and lead the manuscript writing, with contributions from TYL and DZ. All coauthors commented on the final version of the manuscript. Data were collected as the part of Master thesis conducted by TYL at the National Taiwan University.

Data Availability

Upon acceptance, the raw data will be made available on the Dryad repository.

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Tables

Table 1. Fourth-corner results for individual trait – environment relationships for epiphytic and terrestrial species separately.

	elevation		fog		heat load^{sq}	
	epiphytic	terrestrial	epiphytic	terrestrial	epiphytic	terrestrial
SLA	0.08/ 0.11	>-0.01/ >-0.01	0.04/ 0.06	0.02/ 0.02	-0.05/ -0.07	0.04/ 0.05
LDMC	0.13/ 0.18	0.39/ 0.51***	0.06/ 0.08	0.30/ 0.39**	-0.11/ -0.15$^{(*)}$	-0.13/ -0.16*
leaf area^{log}	0.07/ 0.10	-0.05/ -0.06	0.11/ 0.15	-0.11/ -0.15	0.01/ 0.01	>-0.01/ >-0.01
leaf thickness	-0.22/ -0.29$^{(*)}$	-0.20/ -0.26$^{(*)}$	-0.13/ -0.17	-0.14/ -0.19	0.11/ 0.15*	0.05/0.06
leaf chlorophyll	0.11/ 0.14	0.03/ 0.04	0.12/ 0.16	-0.01/ -0.01	<0.01/ <0.01	-0.05/ -0.06
EWT	-0.21/ -0.29$^{(*)}$	-0.29/ -0.38*	-0.14/ -0.19$^{(*)}$	-0.24/ -0.32*	0.11/ 0.14$^{(*)}$	0.05/ 0.06
$\delta^{13}C$	-0.24/ -0.32$^{(*)}$	0.07/ 0.09	-0.09/ -0.13	0.05/ 0.07	0.04/ 0.06	-0.08/ -0.11
$\delta^{15}N$	-0.03/ -0.04	0.07/ 0.09	0.02/ 0.03	-0.03/ -0.04	0.12/ 0.16*	-0.05/ -0.06
leaf N	0.08/ 0.11	0.02/ 0.02	0.11/ 0.15	0.01/ 0.01	0.02/ 0.02	0.01/ 0.02

Fourth-corner correlation coefficient (*r*) and significance level before slash, Chessel-transformed *r* after slash. $^{(*)}$0.10≥ p-value> 0.05; *0.05≥ p-value> 0.01; **0.01≥ p-value> 0.001; ***0.001≥ p-value. $\delta^{13}C$ = the leaf $^{13}C/^{12}C$ stable isotope ratio, $\delta^{15}N$ = the leaf $^{15}N/^{14}N$ stable isotope ratio, EWT = equivalent water thickness, LDMC = leaf dry matter content, leaf N = leaf nitrogen content, SLA = specific leaf area. ^{sq} = squared transformation, ^{log} = logarithmic transformation.

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Figures

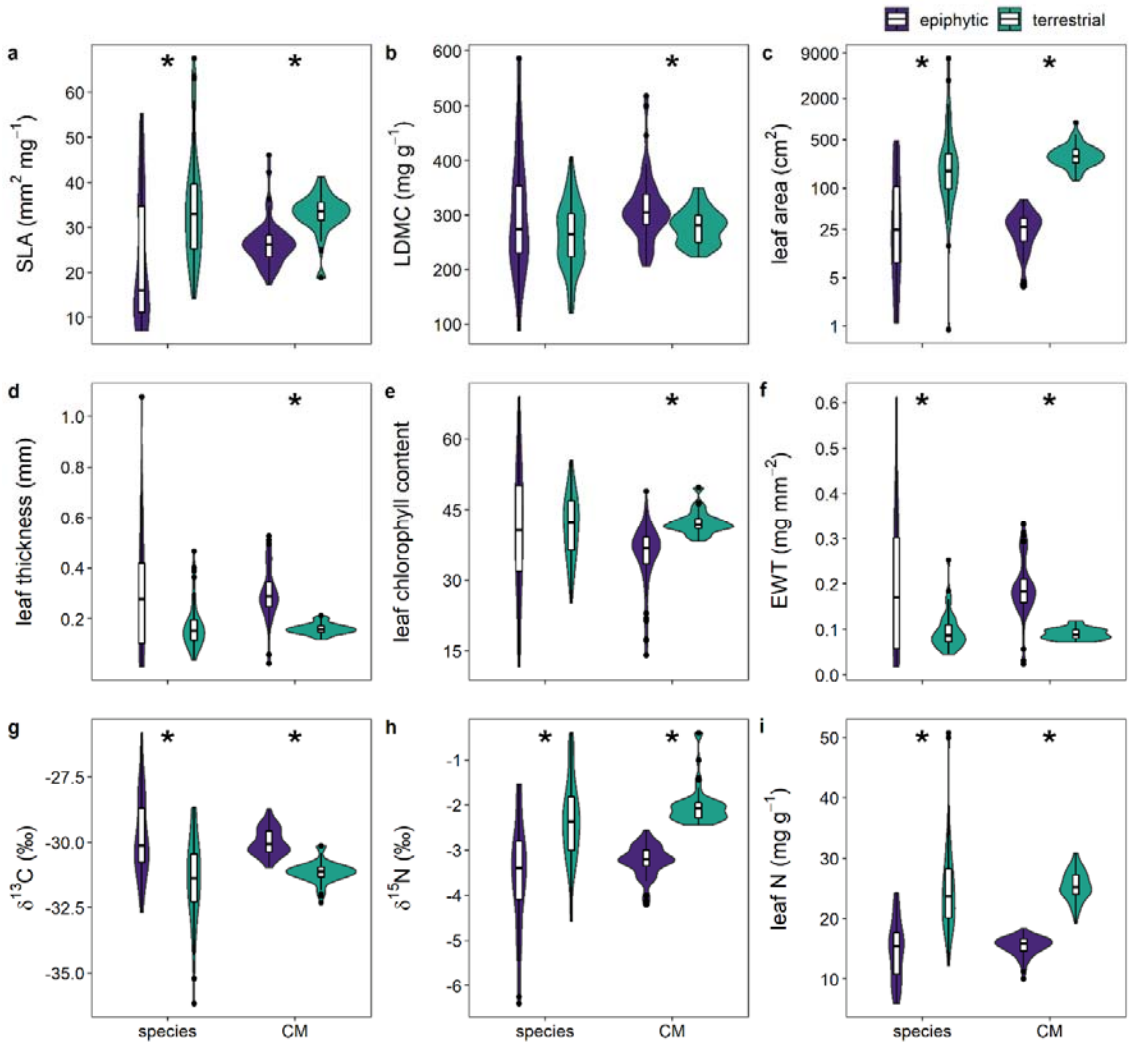

Figure 1. Violin plots for each trait separately, at both the species and community (CM) level. Separate plot for epiphytic (dark purple) and terrestrial species (light green). Asterix indicates significant difference between epiphytic and terrestrial species (Supporting Information Table S6).

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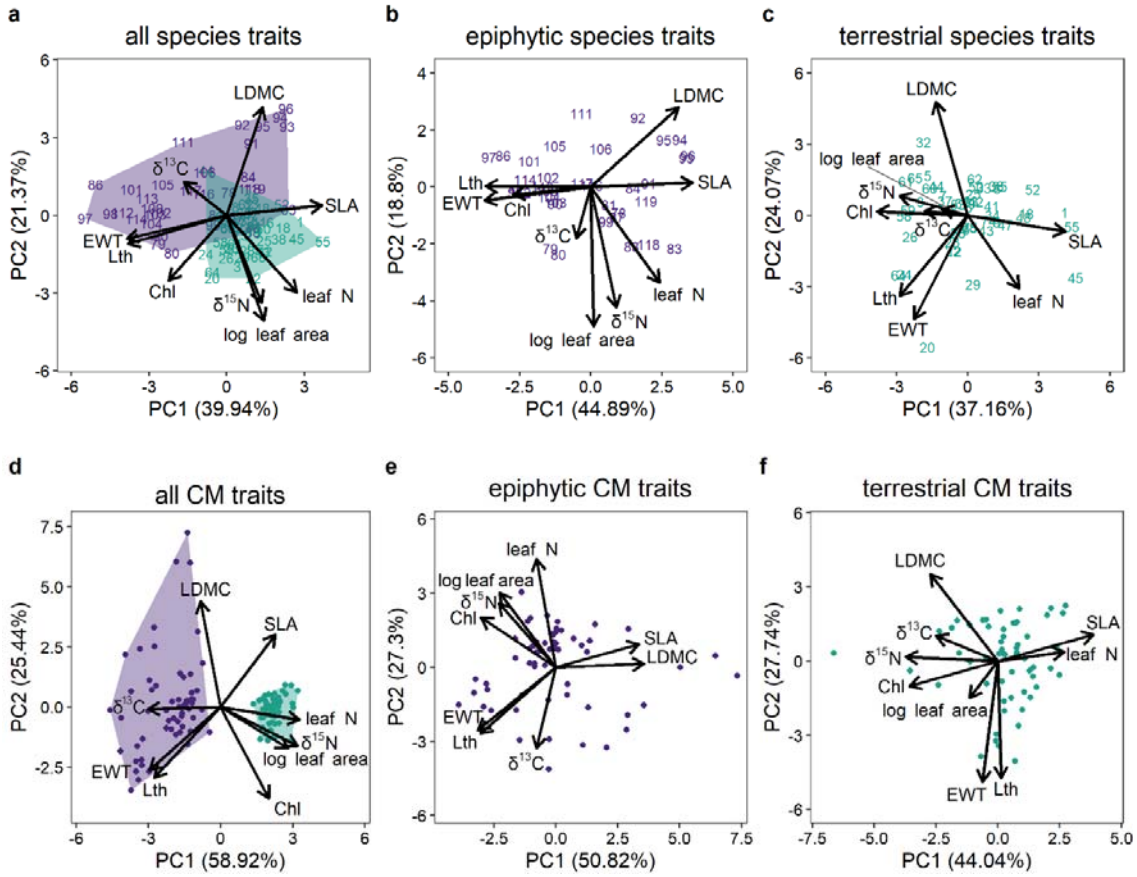

Figure 2. Biplots for the performed principal component analyses on A. the full species × trait matrix, B. the epiphytic species × trait matrix, C. the terrestrial species × trait matrix, D. the plot × community mean (CM) trait matrix using all species, E. the plot × epiphytic CM trait matrix and F. the plot × terrestrial CM trait matrix. Species visualized as codes (see Supporting Information Table S2), plots visualized as points, traits visualized as vectors. Light green = terrestrial species, dark purple = epiphytic species. Chl = leaf chlorophyll content, $\delta^{13}C$ = the leaf $^{13}C/^{12}C$ stable isotope ratio, $\delta^{15}N$ = the leaf $^{15}N/^{14}N$ stable isotope ratio, EWT = equivalent water thickness.

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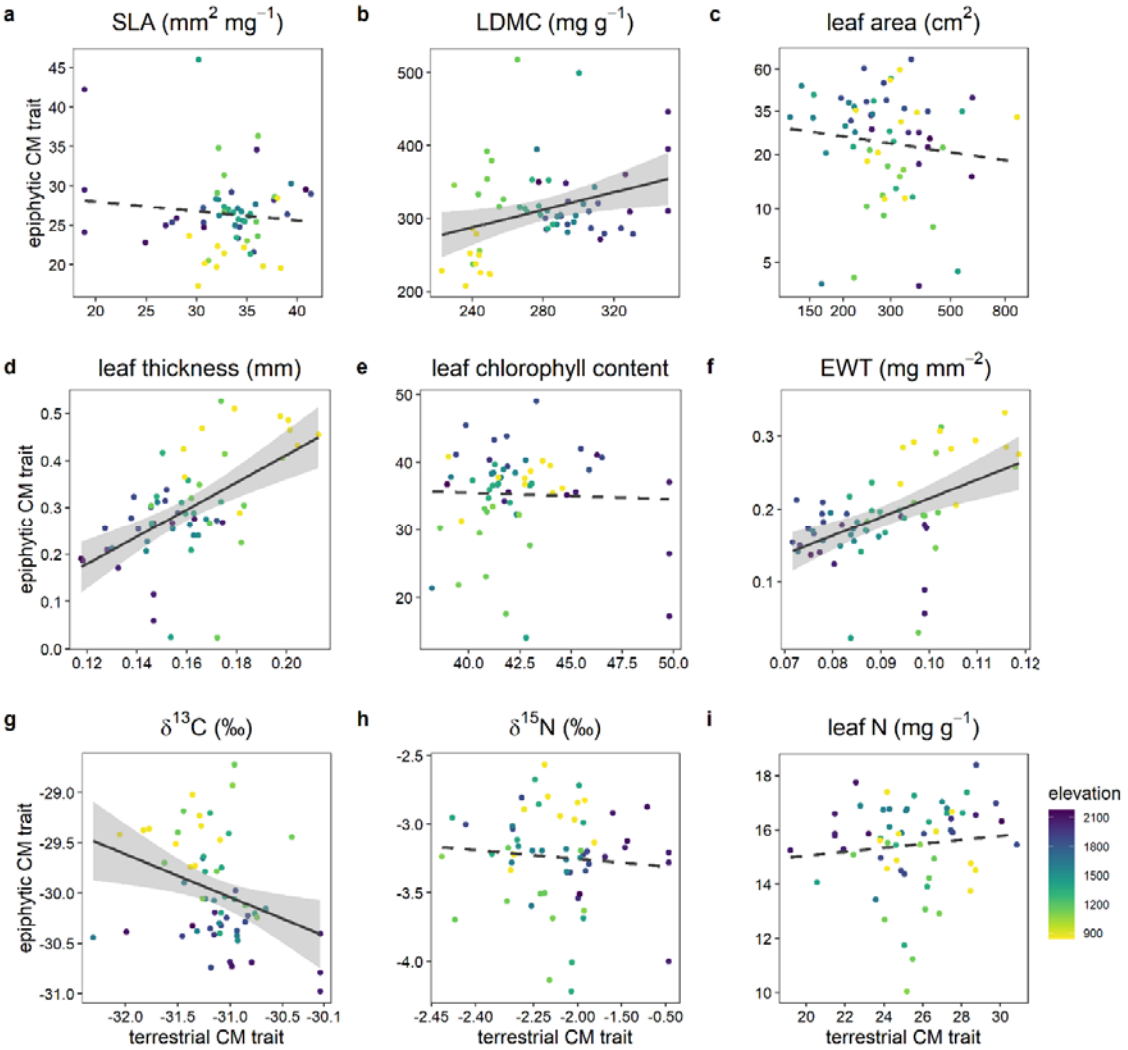

Figure 3. Scatterplots for pairwise correlations between plot-level terrestrial and epiphytic fern and lycophyte community mean (CM) trait values. Regression line + SE presented for significant correlations (see Supporting Information Table S10). Each datapoint corresponds to one vegetation plot, with colours indicating plot elevation. $\delta^{13}C$ = the leaf $^{13}C/^{12}C$ stable isotope ratio, $\delta^{15}N$ = the leaf $^{15}N/^{14}N$ stable isotope ratio, EWT = equivalent water thickness.