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Life in the canopy: community trait assessments reveal substantial functional diversity among fern epiphytes

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Summary

- The expansion of angiosperm-dominated forests in the Cretaceous and early Cenozoic had a profound effect on terrestrial biota by creating novel ecological niches. The majority of modern fern lineages are hypothesized to have arisen in response to this expansion, particularly fern epiphytes that radiated into the canopy. Recent evidence, however, suggests that epiphytism does not correlate with increased diversification rates in ferns, calling into question the role of the canopy habitat in fern evolution.

- To understand the role of the canopy in structuring fern community diversity, we investigated functional traits of fern sporophytes and gametophytes across a broad phylogenetic sampling on the island of Moorea, French Polynesia, including > 120 species and representatives of multiple epiphytic radiations.

- While epiphytes showed convergence in small size and a higher frequency of non-cordate gametophytes, they showed greater functional diversity at the community level relative to terrestrial ferns.

• These results suggest previously overlooked functional diversity among fern epiphytes, and raise the hypothesis that while the angiosperm canopy acted as a complex filter that restricted plant size, it also facilitated diversification into finely partitioned niches. Characterizing these niche axes and adaptations of epiphytic ferns occupying them should be a priority for future pteridological research.

Key words: community ecology, epiphyte, fern, functional traits, gametophyte, Moorea, Society Islands, Tahiti.

Introduction

The appearance of angiosperm-dominated forests in the late Cretaceous and early Cenozoic fundamentally changed climates and had an immense effect on terrestrial ecosystems, including increased global precipitation and the creation of novel niches (Niklas *et al.*, 1983; Kenrick & Crane, 1997; Lloyd *et al.*, 2008; Boyce *et al.*, 2010). The heterogeneous niche space of the angiosperm canopy comprising stratified light and humidity levels and a range of substrates for growth became rapidly filled by a variety of epiphytic plants, including mosses (Fiz-Palacios *et al.*, 2011), leafy liverworts (Feldberg *et al.*, 2014), orchids (Givnish *et al.*, 2015), bromeliads (Givnish *et al.*, 2014), and ferns (Schneider *et al.*, 2004). The transition to epiphytic growth was particularly important for modern fern species diversity: *c.* 29% of all fern species are epiphytes vs. *c.* 10% across all vascular plants (Kress, 1986). Moreover, major transitions to epiphytism occurred at least five times within ferns, each followed by diversification during the late Cretaceous or early Cenozoic (Schuettpelz & Pryer, 2009; Watkins & Cardelús, 2012). This has led to the hypothesis that epiphytism was a key factor contributing to extant fern diversification (Schneider *et al.*, 2004; Schuettpelz & Pryer, 2009; Watkins & Cardelús, 2012). Recent studies exploring this idea (Sundue *et al.*, 2015; Testo & Sundue, 2016, 2018; Lehtonen *et al.*, 2017), however, have largely failed to identify evidence of rapid diversification associated with epiphytism in ferns, calling into question the role of the canopy habitat in fern evolution.

While shifts in diversification rate are relevant, they are only one way epiphytic growth may have influenced fern evolution. The impact of epiphytic growth could manifest in other ways, such as by shaping phylogenetic and functional diversity at the community level. For example, if the canopy is uniformly harsher than the terrestrial environment, we would expect functional convergence of epiphytes at the community level, which in turn may result in decreased phylogenetic diversity of epiphytic communities if traits are phylogenetically conserved (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009). Conversely, the stratification of the canopy may stimulate functional diversification by niche partitioning, leading to greater functional diversity within epiphytic communities. Furthermore, the role of the canopy as a promoter or inhibitor of community diversity may be modulated by overall abiotic conditions, including most notably relative humidity (RH) and temperature. For instance, elevation is a strong predictor of fern species richness, with maximal richness occurring at mid-elevations, especially in the tropics (Krömer *et al.*, 2005; Kessler *et al.*, 2011). Functional diversity is also correlated with species richness (Schleuter *et al.*, 2010). Thus, environmental variation along elevational gradients is expected to impact the functional, phylogenetic, and taxonomic diversity of epiphytic and terrestrial fern communities.

Fern epiphytes possess numerous adaptations that may contribute to their functional diversity. In contrast to most terrestrial plants, epiphytes must contend with greater stress in the form of nutrient limitation, increased evaporative demand, drought, and extreme oscillations in temperature (Zotz & Hietz, 2001; Watkins & Cardelús, 2009; Lowman & Schowalter, 2012). Epiphytic ferns tend to have morphological features that minimize water loss from their leaves, including shorter stipes (Watkins *et al.*, 2010), thicker leaves (Kluge & Kessler, 2007; Watkins *et al.*, 2007c), and protection with scales or hairs (Watkins *et al.*, 2006b). Additional specialized adaptations to epiphytic growth include humus collection (e.g., *Asplenium*; Benzing (1990), *Drynaria*; Janssen & Schneider (2005)), vegetative desiccation tolerance (e.g., Hymenophyllaceae; Shreve (1911), *Pleopeltis*; Pessin (1925)), CAM photosynthesis (e.g., *Pyrrosia*; Wong & Hew (1976)), and symbiotic relationships with ants (e.g., *Antrophyum*; Watkins *et al.* (2008), *Lecanopteris*; Gay (1993)).

While many similar adaptations are found in epiphytic seed plants and serve as key reference points (Benzing, 1990), the evolution of epiphytism in ferns is more complex owing to their unique life-cycle. Ferns produce a free-living gametophyte that is typically smaller than the sporophyte and relies on aquatic, motile sperm. Unlike the sporophyte, the fern gametophyte lacks vascular tissue, stomata, or a well developed cuticle, placing it in constant equilibrium with its external environment. In parallel with some of the adaptations of sporophytes, the gametophytes of some epiphytic ferns also exhibit morphological and physiological adaptations to minimize water loss and tolerate water scarcity. For example, extreme desiccation tolerance is prevalent in gametophytes of multiple lineages of epiphytic ferns, but is rare in sporophytes (Watkins *et al.*, 2007b; Pittermann *et al.*, 2013). In addition, epiphytic fern gametophytes tend to exhibit complex three-dimensional morphologies that may function to retain water and slow its loss (Watkins *et al.*, 2007b). Despite evidence for adaptations to epiphytism in multiple lineages in both sporophytes and gametophytes, no previous studies to our knowledge have analyzed the functional ecology of fern epiphytes in a broad phylogenetic context including both life stages.

Here, we seek to understand the role of the canopy in structuring fern community diversity by investigating putatively functional traits related to epiphytic growth in fern gametophytes and sporophytes on Moorea, French Polynesia. Moorea is an isolated tropical oceanic island with high phylogenetic diversity of ferns distributed across a steep elevational gradient, making it ideal for a community phylogenetic analysis of functional traits. Specifically, we test the following hypotheses related to epiphytic growth in ferns: 1) Epiphytic ferns have convergent morphologies in both sporophyte and gametophyte phases; 2) Epiphytic fern communities have lower functional and phylogenetic diversity relative to terrestrial communities.

Materials and Methods

Study site

Moorea, French Polynesia (17°32'S, 149°50'W) is a small (135 km^2) tropical oceanic island more than 5000 km from the nearest continental landmass. This distance acts as a strong barrier to dispersal

(Carson & Clague, 1995; Dassler & Farrar, 2001), which combined with the young age of the island (*c.* 1.5 MA; Duncan & McDougall, 1976) has led to a relatively small, yet phylogenetically diverse fern flora (*c.* 130 spp., 8/11 orders; Table S1; taxonomy follows Pteridophyte Phylogeny Group I, 2016). Ferns of Moorea include representatives of multiple Cretaceous epiphytic radiations (e.g., *Asplenium*, *Elaphoglossum*, Hymenophylloideae, Polypodiaceae, Vittarioideae; Schuettpelz & Pryer, 2009) and their terrestrial relatives, making them suitable for a comparative study of traits related to the evolution of epiphytic growth in ferns.

Community survey

A fern community survey was carried out on Moorea comprising 17, 10 m × 10 m plots spanning an elevational gradient from 20 m to 2000 m, with plots placed *c.* every 200 m (Nitta *et al.*, 2017). Most plots were located along trails leading to the three main peaks on the island, Mt. Rotui (899 m), Mt. Mouaputa (890 m), and Mt. Tohiea (1206 m). Each plot was divided into 25, 2 m × 2 m subplots. Presence/absence of all sporophytes in each subplot was scored and summed to produce an abundance ranking for each species per plot from zero (not observed) to 25 (observed in all subplots). Epiphytic ferns were sampled by hand to *c.* 2 m on tree trunks or confirmed visually from the ground. Species were categorized as epiphytic or terrestrial based on field observations (see 'Trait selection and measurements' below). The list of species in each plot was split into epiphytic and terrestrial groups and treated separately during data analysis, hereafter referred to as 'epiphytic' and 'terrestrial' communities. Vouchers were deposited at GH and UC (abbreviations follow Index Herbariorum; Thiers, 2020).

Environmental survey

Temperature and RH of epiphytic and terrestrial habitats were measured using Hobo Pro v2 dataloggers with the RS3 Solar Radiation Shield (Onset Corporation, USA). A pair of dataloggers was installed for each plot, one mounted at *c.* 2 m on a tree ('epiphytic datalogger'), and one at ground level ('terrestrial datalogger'), except for the Mt. Tohiea 1200 m plot, which only had an epiphytic datalogger. Temperature and RH were logged once every 15 min during two survey periods: a

preliminary survey from July 18, 2012 to July 6, 2013 at seven plots, and a final survey from July 7, 2013 to July 29, 2014 at 15 plots. Two plots were not included in the environmental survey. We used the 2013–2014 data for the analysis, with one exception: the terrestrial datalogger at the Mt. Tohiea 393 m plot malfunctioned and was missing data for a substantial part (March 12–July 5, 2014) of the final survey period, so we used data for the same dates from the preliminary survey period for this datalogger instead. Three others also failed early during the final survey period, but lacked data from the preliminary period, so were excluded from analysis. Other days missing data during the final survey period were excluded from the dataset. The final dataset included 244 days of data for 13 epiphytic dataloggers and 13 terrestrial dataloggers. We calculated vapor pressure deficit (VPD) from relative humidity and temperature using the 'plantecophys' R package (Duursma, 2015).

Trait selection and measurements

We selected several traits putatively relevant to epiphytic growth (Table 1 and Fig. 1). We preferred morphological traits over physiological traits because data for morphological traits are easier to gather at the scale of our study (*c.* 130 spp. distributed over an elevational gradient from 200 m to 1200 m). Plant morphology and physiology are closely linked, and physiological traits such as rates of photosynthesis and water use efficiency are known to be correlated with morphological traits such as stipe length in ferns (Watkins *et al.*, 2010).

Morphological traits of sporophytes were measured from herbarium specimens, or obtained from the literature when plant material was unavailable. Measurements were made directly on plants in the field for a few species with large fronds. A single leaf or rhizome per individual was measured on one to three separately collected individuals per species, and mean values were calculated for each species. Although trait values can vary within fern species with elevation (Kessler *et al.*, 2007), our study includes a broad phylogenetic sampling, so we assume intraspecific variation is outweighed by interspecies differences. To measure specific leaf area (SLA; $m^2 kg^{-1}$), *c.* 10–12, 2 mm or 4 mm diam. punches were taken of laminae between primary veins for a single leaf per individual using biopsy punches, dried at 60 °C for 24 h, and weighed. For species with < 2 mm between primary veins, leaf

fragments excluding primary veins were obtained by dissection, dried at 60 °C for 24 h, weighed, and scanned. ImageJ (Abràmoff *et al.*, 2004) software was used to measure area per fragment.

Morphological traits of gametophytes were all qualitative (either categorical or binary; Table 1). Traits were scored by observing gametophytes that were either collected in the field and identified using DNA barcoding (Nitta *et al.*, 2017), grown from spores of known species in the lab, taken from the literature, or inferred from taxonomic group (i.e., genus) if documented as a stable taxonomic character. For comparative analysis, gametophyte morphotypes were aggregated into two categories: either cordate (i.e., heart-shaped) or non-cordate (Ebihara *et al.*, 2013). Non-cordate morphotypes include elongate (strap or ribbon *sensu* Farrar *et al.* (2008)) and filamentous forms (Fig. 1). Gametophytes were cultivated on Bold's media (Bold, 1957) supplemented with Nitch's micronutrients (Nitsch, 1951).

Growth habit was coded as a binary trait (epiphytic or terrestrial) based on our field observations. Some species do not fall clearly into either category (e.g., hemi-epiphytes; Benzing, 1990; Dubuisson *et al.*, 2003; Zotz, 2013). We used connection to the soil as the criterion for defining binary growth habit; thus, epipetric plants were treated as epiphytic, and hemi-epiphytes and climbing plants were treated as terrestrial. For the purposes of this study, we treated growth habit as a fixed trait and used these categories to define epiphytic and terrestrial communities. Other studies have demonstrated that exceptional epiphytic growth of terrestrial fern species (and vice-versa) is rare (Cardelús *et al.*, 2006; Kluge & Kessler, 2006; Watkins & Cardelús, 2009), and we do not believe that such rare exceptions would affect our analysis.

Trait values and data sources are summarized in Table S2.

Statistical analysis

We calculated daily maximum, mean, minimum, and standard variation of temperature, RH, and VPD for each datalogger, then overall means from the daily values. We analyzed correlation between the mean values with Pearson's correlation coefficient, and retained a set with correlation coefficients less than 0.9 (a single variable was arbitrarily selected from each set of correlated variables; hereafter,

'climatic variables'). Variables relating to VPD, which have no meaning if less than zero, and some other variables that had skewed distributions, were square-root transformed prior to fitting models. We tested for differences between epiphytic and terrestrial dataloggers while accounting for elevation with ANCOVA, using growth habit as the categorical variable and elevation as the covariate. We identified the best-fitting linear model for each climatic variable in response to growth habit and elevation by constructing a set of models including the effect of each independent variable alone, in combination, and in combination with their interactions. We then calculated the corrected Akaike Information Criterion (AIC$_c$; Akaike, 1973) for each model and retained models within 2 AIC$_c$ of the lowest (i.e., 2 delta AIC$_c$). From these, we selected the model with the combination of the fewest non-significant parameters and lowest AIC$_c$ (for VPD, we the selected the model producing the smallest amount of negative predicted values). A single outlier plot with unusually high temperature and low humidity (Mt. Rotui, 830 m plot) was excluded from ANCOVA and linear models. Mt. Rotui is an isolated peak with greater exposure than the other two mountains where the rest of the plots were established (J. Nitta, pers. obs.).

For comparative analyses, we used the dated plastid phylogenetic tree of Nitta *et al.* (2017). *Microsorum maximum* (Brack.) Copel., a genetically verified hybrid between *M. grossum* (Langsd. & Fisch.) S. B. Andrews and *M. commutatum* Copel. (Nitta *et al.*, 2018) was excluded from analysis because it shares identical plastid sequences with *M. grossum*, so the plastid tree does not accurately represent its evolutionary distinctiveness.

We tested for phylogenetic signal in quantitative traits using Blomberg's K (Blomberg *et al.*, 2003) and Pagel's λ (Pagel, 1999), two metrics with slightly different interpretations and sensitivity to different evolutionary scenarios (Münkemüller *et al.*, 2012), with the 'phylosig' function in the 'phytools' R package (Revell, 2012). λ is a scaling parameter that ranges from 0 (traits evolving randomly) to 1 (traits evolving along branches according to Brownian motion (BM)). K describes the ratio between the amount of observed variance in traits vs. the amount of variance expected under BM: when $K > 1$, traits are more conserved than expected under BM; when $K < 1$, traits have less phylogenetic signal than expected under BM (Blomberg *et al.*, 2003). We tested for significance in K

by comparing observed values of K against a null distribution of trees with trait values randomized across the tips, and in λ by conducting a likelihood ratio test comparing the log likelihoods of observed values of λ vs. $\lambda = 0$ (no phylogenetic signal). We tested for phylogenetic signal in qualitative traits using Fritz and Purvis' D (Fritz & Purvis, 2010). Values of D range from 0 under a model of trait evolution by BM, to 1 under random distribution of traits. We analyzed D using the 'phylo.d' function in the 'caper' R package (Orme *et al.*, 2018), and conducted a significance test by comparing observed D to distributions of simulated values produced under two models: random shuffling of traits on the tree, or simulation of a binary trait under a BM model. To account for possible circularity in measuring the phylogenetic signal of traits that were scored based on taxonomy, we conducted the same analyses on a dataset excluding species that had been scored this way ('strict' dataset).

We detected significant phylogenetic signal in most traits, so we tested for differences between traits of epiphytic vs. terrestrial species using phylogenetic comparative methods. For quantitative traits, we used the 'brunch' function in the 'caper' package (Orme *et al.*, 2018), which calculates phylogenetically independent contrasts in a quantitative character between alternative states of a binary trait. For qualitative (binary) traits, we used Pagel's test of correlated evolution (Pagel, 1994) as implemented with the 'fitPagel' function in the 'phytools' package (Revell, 2012). This method compares likelihoods between alternative models for a pair of binary traits. In the first model, rates of evolution of the two traits are independent. In the second model, the rate of evolution of each trait depends on the other. A significantly better fit of the second model indicates that evolution of the two traits is correlated. The same analyses were also done on the 'strict' dataset.

We investigated differences in multivariate trait space between epiphytes and terrestrial species using principal components analysis (PCA). We used only quantitative traits, and included only species that had no missing data ($n = 103$ spp.). We first log-transformed traits as necessary to reduce skew, then scaled each trait by its standard deviation. We conducted standard and phylogenetically corrected PCA, using the 'PCA' and 'phyl.pca' functions in the 'FactoMineR' (Lê *et al.*, 2008) and 'phytools' (Revell, 2012) R packages, respectively.

We calculated community-weighted means (CWMs) and standard deviations of quantitative traits by using the overall mean trait value of each species weighted by their abundances in each community.

We used distance-based methods to analyze community phylogenetic and functional diversity. Mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) describe the mean distance between all species in a community (MPD) or the mean distance between the closest pairs of species in a community (MNTD; Webb, 2000; Webb *et al.*, 2002). Although these metrics were originally formulated for phylogenetic distances, they can be applied in the same way to trait-based distances, enabling a direct comparison between the two (Sessa *et al.*, 2018). For phylogenetic distances, we used the tree of Nitta *et al.* (2017). For functional distances, we log-transformed and scaled traits as in the PCA, excluded frond width and length (both frond size traits highly correlated with stipe length), then calculated the distance matrix using Gower's dissimilarity coefficient (Gower, 1971) with the 'gowdis' function in the R package 'FD' (Laliberté *et al.*, 2011), with equal weighting for sporophyte and gametophyte traits. To test for the effect of different trait selection schemes, we compared the results of running the same analyses for various sets of traits with and without log-transformation (Fig. S1).

Raw values of MPD and MNTD are statistically related to species richness (Swenson, 2014); to obtain metrics that are uncorrelated with species richness, we calculated their standard effect sizes (SES) by comparing observed values to a distribution of randomized communities. We constructed null communities using the 'independent swap' algorithm (Gotelli, 2000). We included all species of ferns from Moorea and the neighboring island of Tahiti with genetic data available (145 spp. total; Nitta *et al.*, 2017) for phylogenetic null communities, and all species with trait data available (128 spp.) for functional null communities. We used the 'ses.mpd' and 'ses.mntd' functions in the R package 'picante' (Kembel *et al.*, 2010) to calculate phylogenetic and functional diversity metrics. Hereafter, 'MPD$_{phy}$' and 'MNTD$_{phy}$', and 'MPD$_{func}$' and 'MNTD$_{func}$', refer to the standard effect sizes of MPD and MNTD as measured with phylogenetic and functional trait distances, respectively.

We tested the effects of climate and growth habit on diversity metrics using full-subsets multiple regression with general additive models (GAMs) as implemented in the 'FSSgamm' R package

(Fisher *et al.*, 2018). For each diversity metric, we built a set of models (Gaussian family, with plot as a random effect) taking into account all combinations of explanatory variables and their pairwise interactions, and ranked these by AIC_c to find the models that best explain the data. Our dataset included eight communities that lacked climate data and could not be included in full-subsets multiple regression analysis. Therefore, we also constructed linear models for each diversity metric in response to elevation and growth habit including all sites using the same model selection procedure as in the climate analysis. We checked for spatial autocorrelation in the model residuals with Moran's *I* (Moran, 1950) as implemented in the 'spdep' R package (Bivand *et al.*, 2013). If spatial autocorrelation was detected, a generalized linear mixed model was fit with a Mátern spatial correlation structure using the 'spAMM' R package (Rousset & Ferdy, 2014).

Data accessibility

Code to replicate all analyses, figures, and this manuscript is available at https://github.com/joelnitta/canopylife. Data are openly available from the Dryad repository at https://doi.org/10.5061/dryad.fqz612jps (Nitta *et al.*, 2020).

Results

Environmental survey

Mean, maximum, and standard deviation (SD) of temperature and mean, minimum, and SD of vapor pressure deficit (VPD) were retained after excluding variables with correlation coefficients > 0.9. Variables related to temperature changed with elevation but did not differ significantly between epiphytic and terrestrial dataloggers (Table S3; Fig. 2). Variables related to VPD differed by growth habit and elevation. Mean and maximum or minimum temperature and VPD all decreased with elevation, whereas SD of temperature increased, but SD of VPD decreased with elevation. Epiphytic dataloggers had higher values than terrestrial ones for variables related to VPD. Spatial autocorrelation was not detected in any of the climate models (Table S4).

Principal components analysis of trait data

Terrestrial and epiphytic species are partly differentiated in trait space, occupying mostly distinct areas but overlapping in the middle regardless of method used (Fig. 3**c**, **d**). The first two PC axes explained 70% and 62% of the variation in the trait data when analyzed using standard and phylogenetic PCA, respectively. In the standard PCA, size-related traits tended to load on PC1, with SLA, number of pinnae pairs, and degree of dissection on PC2. Loadings in the phylogenetic PCA are similar, but size-related traits are approximately reversed relative to the standard PCA.

Phylogenetic signal

Most measured traits showed some degree of phylogenetic signal, but the strength varied across traits (Tables 2, 3, Fig. 4), and for quantitative traits, different results were obtained for λ and K. When measured with λ, most sporophyte traits show phylogenetic signal (as expected under a BM model), with values of λ close to 1; only number of pinnae pairs had λ close to zero (Table 2). However, when measured with K, only frond width and rhizome diameter showed strong phylogenetic signal (more than expected under BM); other traits had values of $K < 1$ (Table 2). All binary gametophyte traits showed phylogenetic signal more conserved than expected under BM (Table 3). Growth habit showed phylogenetic signal similar to that expected under BM ($D = $ -0.11; Table 3). Similar results were obtained using the 'strict' dataset (Table S5).

Correlation of traits with growth habit

Most sporophyte traits, particularly those related to plant size, are significantly correlated with growth habit while taking phylogeny into account (Table 4). Epiphytic species tend to have smaller values for all traits (Table 4). Short stipe length in particular appears to be strongly correlated with epiphytic growth (phylogenetically independent contrasts, $P = 0.005$), as well as frond width ($P = 0.022$) and degree of laminae dissection ($P = 0.008$). For the gametophyte traits, only morphotype (non-cordate vs. cordate) was significantly correlated with growth habit (Pagel's test of correlated evolution, $P = 0.004$; Table 5). Similar results were obtained using the 'strict' dataset (Table S6).

Functional and phylogenetic diversity

In the full-subsets analysis including all climate variables and diversity metrics, growth habit and temperature emerged as the most important variables (Fig. 5). Most of the best-fitting models included growth habit or the interaction of growth habit and a temperature-related variable (Table S7). Spatial autocorrelation was not detected in any of the best-fitting general additive models (Table S7).

Community-weighted mean values (CWMs) were smaller for epiphytic than terrestrial ferns for size-related traits (frond length, frond width, stipe length, and rhizome diameter), frond dissection, and number of pinnae pairs (*t*-test, all $P < 0.05$; Fig. 6). Spatial autocorrelation was detected in the linear model for SLA, so a spatial generalized mixed model was used instead (see Methods). Specific leaf area decreased with elevation, and was slightly lower for epiphytic relative to terrestrial communities (spatial generalized linear mixed model, nu = 0.25, rho = 53.8, AIC = 195.3; Table S8). Degree of lamina dissection decreased with elevation in epiphytes, but increased in terrestrial communities (linear model, $R^2 = 0.48$, $P < 0.001$). Rhizome diameter decreased slightly with elevation for terrestrial communities, while increasing slightly for epiphytic communities (Fig. 6).

We observed a total of 103 spp. across all plots, including 45 epiphytic and 58 terrestrial spp. Mean species richness was 10.8 ± 4.8 spp. per plot for epiphytes and 12.7 ± 4.9 spp. per plot for terrestrial species (not significantly different; two-sided *t*-test, $P = 0.254$; Fig. 7). Species richness increased with elevation for both epiphytes and terrestrial communities (Fig. 7). Epiphytic communities were more diverse than terrestrial ones as measured by both MPD_{func} and $MNTD_{func}$ (two-sided *t*-test, both $P < 0.001$). Functional diversity increased along the gradient for both terrestrial and epiphytic communities when measured with MPD_{func} (linear model, $R^2 = 0.72$, $P < 0.001$), but not $MNTD_{func}$. Epiphytic communities were more phylogenetically clustered than terrestrial communities overall when measured using $MNTD_{phy}$ (two-sided *t*-test, $P < 0.001$) but not MPD_{phy} ($P = 0.258$; Fig. 7). No significant trend was detected in phylogenetic community structure with elevation in either terrestrial or epiphytic communities (Fig. 7). Spatial autocorrelation was not detected in any of the linear models for the community diversity metrics (Table S4).

Discussion

Our study reveals a striking duality in the phylogenetic and functional diversity of fern epiphytes. On one hand, we find that fern epiphytes are consistently smaller than terrestrial species at both the species and community level (Table 4, Fig. 6), and that epiphytic communities are phylogenetically clustered (Fig. 7). At the same time, we find that epiphytic fern communities are significantly more diverse functionally compared to terrestrial communities (Fig. 7). Collectively, these results suggest that environmental filtering plays a strong role in limiting plant size, while simultaneously supporting functional diversity across other trait axes in epiphytic ferns.

Convergence in sporophyte size and gametophyte morphotype in fern epiphytes

Epiphytes are markedly smaller than terrestrial species as measured by stipe and frond length, frond width, and rhizome diameter at both the species and community level (Table 4, Fig. 6), supporting both hypotheses (convergence in epiphytic traits and reduced functional diversity of epiphytic communities). These results are corroborated by Testo & Sundue (2018), who similarly observed abrupt size reduction associated with epiphytic growth in a globally sampled fern phylogeny. What might explain such consistent and convergent reduction in fern sporophyte size when transitioning into the canopy? An obvious answer is that water limitation in the canopy exerts strong selective pressure to maintain small size. In spite of similar and predictable leaf-level economic tradeoffs between angiosperms and ferns (Karst & Lechowicz, 2007), fern leaves are limited in their hydraulic flexibility as they rely wholly on primary xylem that feeds into laminar tissues with reduced leaf venation. Stipe length and structure in particular are critical for regulating whole leaf hydraulic conductance in ferns (Pittermann *et al.*, 2013). Species growing in water-limited habitats like those in the canopy are expected by biomechanical necessity to decrease stipe length to minimize resistance (Watkins *et al.*, 2010). Our results support previous studies that identified a prevalence of short stipes among epiphytic ferns (Watkins *et al.*, 2010; Creese *et al.*, 2011). However, given that stipe and frond length, frond width, and rhizome diameter were correlated in our study, and similar traits have previously been shown to co-vary (Arcand *et al.*, 2008; Creese *et al.*, 2011), careful experimental manipulations are required to distinguish the role of each trait in facilitating epiphytism.

Another clear pattern to emerge from our study supporting the hypothesis of convergence is the association between epiphytism and the prevalence of non-cordate (e.g., elongate or filamentous) gametophyte morphotypes. Gametophyte morphotype was previously observed to correlate with life history and habitat in ferns: terrestrial species tend to have short-lived (< 1 yr), cordate morphotypes that establish following disturbance and rapidly produce sporophytes, whereas epiphytic species tend to have non-cordate gametophytes that persist over multiple growing seasons and produce sporophytes more slowly (Watkins *et al.*, 2007a; Farrar *et al.*, 2008). The complex, three-dimensional structure of non-cordate gametophytes may serve two important functions. Complex thallus morphology can slow drying rates, and slow dehydration is correlated with the ability to recover from drought in gametophytes—likely a critical adaptation to drought-prone epiphytic habitats (Watkins *et al.*, 2007b; Pittermann *et al.*, 2013). Non-cordate thallus morphology may also promote outcrossing through the formation of long-lived gametophyte banks that can persist in epiphytic but not in more disturbance-prone terrestrial habitats (Watkins *et al.*, 2007a; Farrar *et al.*, 2008). Our study is the first to our knowledge to demonstrate that the correlation between non-cordate morphology and epiphytism in ferns is significant across broad phylogenetic scales.

Unexpected diversity in non-size related traits of epiphytes

Despite the apparent constraints on size and the recurrence of non-cordate gametophytes exhibited by epiphytes, we observed greater morphological diversity among epiphytic versus terrestrial communities for several traits. These results do not support the hypothesis that fern epiphytes have reduced functional diversity. For example, although epiphytes demonstrated less dissected fronds at the species level (Table 4), they exhibited much greater variation in this trait relative to terrestrial ferns at the community level (Fig. S2). It is likely that the high diversity of this trait reflects different physiological adaptations to various canopy niches. For instance, filmy ferns (Hymenophyllaceae), which depend on desiccation tolerance to survive dry conditions, have extremely thin, highly dissected fronds. Bird's nest ferns (e.g., *Asplenium nidus* L.), in contrast, avoid desiccation by capturing detritus and water in the bases of their simple, rosette leaves. At low-elevation sites on Moorea where these ferns co-occur, filmy ferns frequently grow in more humid portions of trees

including near the main trunk, whereas bird's nest ferns often grow higher in the canopy and on more exposed, drought-prone branches (J. Nitta, pers. obs.). Similar predictable patterns of niche partitioning at the local scale have been reported in neotropical epiphtyic ferns as well (Hietz & Briones, 1998; Tausz *et al.*, 2001). This distribution may reflect alternative water-usage strategies aligned to specific microhabitats in the canopy (desiccation tolerance vs. water capture; Hietz & Briones, 1998). Such hypotheses need to be carefully tested with additional quantitative investigation, including more finely examining microclimatic variation and species composition across the canopy.

Another trait that defied simple classification into epiphytic or terrestrial groups was specific leaf area (SLA; Fig. 6, Table 4). Specific leaf area is part of the leaf economic spectrum (LES), which posits that leaf traits including SLA, N and C content, and leaf life span vary along well-defined axes such that plants generally fall into one of two categories: fast-growing species with high SLA, low nutrient content, and short life spans vs. slow-growing species with low SLA, high nutrient content, and long life spans (Wright *et al.*, 2004; Díaz *et al.*, 2015). We expected that epiphytes would exhibit lower SLA, given their more extreme growing conditions. In contrast, we observed overlapping, wide ranging SLA values in both terrestrial and epiphytic communities, with only slightly lower values in epiphytes when taking elevation into account (Fig. 6). This may reflect adaptations to specific niches that are not captured by a binary categorization of growth habit. For example, the following species ranked among those with the five lowest SLA values (i.e., thick, well-protected leaves) on Moorea: *Davallia anderssonii* Mett. (a twig epiphyte), *Acrostichum aureum* L. (a terrestrial mangrove specialist), and *Paesia divaticatissima* (Dryand.) Copel. (a terrestrial species occurring on high-elevation ridges) (Table S2). Each of these species is likely to experience prolonged periods of drought-stress. In-depth characterization of such microhabitats was beyond the scope of our study and should be investigated further in the future.

We did not find that gemmae production in gametophytes was linked with epiphytism. Rather, occurrence of gemmae strongly reflects phylogeny, appearing concentrated in filmy ferns (Hymenophyllaceae) and vittarioid ferns (Vittarioideae) (Fig. 4). Gemmae are asexual propagules occurring primarily in non-cordate gametophytes that allow gametophytes to persist over multiple

growing seasons and attain large population sizes, and have been hypothesized to be associated with harsh environmental conditions (Farrar *et al.*, 2008). In particular, gemmae production should be useful in an epiphytic context because they may allow gametophytes to increase their boundary layer and hedge against population loss during extreme drying (Farrar *et al.*, 2008). Gemmae can also function sexually by producing antheridia in the presence of antheridiogen secreted by other gametophytes (Emigh & Farrar, 1977), which may confer a selective advantage in the epiphytic environment by enabling outcrossing (Dassler & Farrar, 2001). As with our results summarized above, it is possible that the diversity of gemmae and non-gemmae producing epiphytic species reflects undetected niche variation in the canopy. Interestingly, when we classified gametophytes as 'independent' if they occurred beyond the elevational range of conspecific sporophytes using the data of Nitta *et al.* (2017), we found that gemmae production is correlated with independent growth (log likelihood dependent model = -51.9, log likelihood independent model = -58, $P = 0.016$, Pagel's test of correlated evolution), echoing a pattern observed in Japan of non-cordate gametophytes frequently occurring independently of their conspecific sporophytes (Ebihara *et al.*, 2013).

Finally, the presence of hairs and glands in gametophytes also exhibit high phylogenetic signal (i.e., greater than expected under Brownian motion; Table 3), and these traits are concentrated in certain taxonomic groups (e.g., hairs, grammitid ferns (Grammitidoideae); glands, Thelypteridaceae; Stokey, 1951; Nayar & Kaur, 1971). Although hairs have been hypothesized to reduce rates of drying and increase water uptake after desiccation (Kappen & Valladares, 2007), and glands may affect rates of osmosis by modifying lipid concentrations (Crow *et al.*, 2011), we did not detect a correlation between hair or gland production and epiphytic growth. Given their high phylogenetic signal, it is possible that these traits are unrelated to environment but rather reflect phylogenetically conserved developmental pathways (Johnson *et al.*, 2012). Alternatively, the possibility remains that some epiphytic species rely on hairs or glands to prevent or slow drying depending on their niche within the canopy (e.g., hair-bearing grammitid gametophytes at mid to high elevation).

The dual roles of the canopy as both a filter and promoter of community diversity

Our results demonstrate that the canopy is far more dynamic with regard to fern epiphytism than has been previously appreciated. On the one hand, the canopy appears to have served as a potent barrier to entry, strongly selecting for small size. Furthermore, the results of our phylogenetic community structure analyses partially support the hypothesis of decreased phylogenetic diversity in epiphytic communities due to filtering: we observed that epiphytic fern communities were more phylogenetically clustered for $MNTD_{phy}$, but not MPD_{phy} (Fig. 7). This makes sense given that most epiphytes have radiated within a limited number of clades (Schuettpelz & Pryer, 2009); each epiphytic community we sampled tends to include closely related species from two or more epiphytic clades, but exhibits a similar overall degree of phylogenetic diversity as terrestrial communities.

However, while the canopy clearly acts as a filter, we also find that it simultaneously functions as a promoter of functional diversity. This is evident in our analyses of MPD_{func} and $MNTD_{func}$, which both indicate that epiphytic communities are more functionally diverse compared to terrestrial species (Fig. 7), thus contradicting our hypothesis of decreased functional diversity in epiphytic communities. Additional analyses using different trait combinations support the role of non-size related traits driving this pattern (Fig. S1). We propose that the high functional diversity of epiphytic fern communities is maintained by previously undetected niche partitioning within epiphytic habitats as follows. The canopy is generally drier than terrestrial habitats, exerting strong selection for small size. At the same time, microclimatic conditions in trees vary rapidly over short distances with height and distance from the trunk (Hietz & Hietz-Seifert, 1995; Cardelús & Chazdon, 2005), contributing to greater environmental variation per unit area than terrestrial habitats (Rojas-Hernández *et al.*, 2018). This vertical and horizontal diversity of niches is occupied by different fern species (Watkins *et al.*, 2006a; Cardelús, 2007; Parra *et al.*, 2009; Acebey *et al.*, 2017). Thus, when analyzed together, epiphytic fern communities encompass a wider range of morphological variation than terrestrial communities on average. Assuming that the traits we measured reflect physiological strategies of epiphytes, this high morphological diversity likely derives from physiological adaptations to a variety

of within-canopy niches. Clearly, fine-grained characterization of canopy niches and associated adaptations of epiphytic ferns occupying them is an important goal for future research.

The primacy of growth habit in determining fern community composition as indicated by modeling

The primary role of growth habit, in combination with temperature, in structuring fern communities is supported by the full-subsets model analysis (Fig. 5). It is somewhat puzzling that VPD did not contribute significantly to any models, as we hypothesized that this would be important for epiphytes that are frequently subjected to water stress. Previous studies have shown marked variation in air water potential across epiphytic habitats, with Watkins & Cardelús (2009) reporting a *c.* 40 MPa shift along the trunks of emergent canopy trees. Our epiphytic dataloggers only showed slightly greater VPD relative to those on the ground, with this difference largely dissipating at high elevations (Fig. 2). One reason for such low observed variation could be due to environmental conditions at our study site and placement of dataloggers: Moorea is a generally wet site overall (average annual rainfall 325 cm), and we placed the epiphytic dataloggers on tree trunks, not in the higher emergent portions of the canopy. Therefore, these measurements should be interpreted as reflecting the minimum amount of difference between terrestrial and canopy environments. Future studies characterizing within-canopy niches of epiphytic ferns should include placement of dataloggers at multiple sites throughout the canopy, which will allow for more detailed tests of the hypothesis that epiphytic fern diversity is maintained by niche partitioning.

Conclusion and future directions

Recent studies (e.g., Sundue *et al.*, 2015; Testo & Sundue, 2016, 2018; Lehtonen *et al.*, 2017) have called into question the scenario of rapid Cretaceous radiations of epiphytic ferns posited by Schuettpelz & Pryer (2009) by failing to detect increased rates of diversification associated with epiphytic growth. Our study provides a fresh perspective on this issue. Here, we demonstrate that epiphytism is likely a complex trait, and almost certainly requires the evolution of multiple associated and dependent traits. We propose that the timing and order of the evolution of such traits are related to the conflicting diversification dynamics observed in these studies. Another possibility raised by our

results is that fern epiphytes have radiated morphologically without corresponding species-level diversification (Givnish, 2015). Future research investigating the tempo and mode of the evolution of epiphytism in ferns should seek to better partition this morphological diversity when exploring hypotheses of exceptional species diversification.

Small size appears to be a prerequisite for epiphytic growth, as indicated both by our results and by Testo & Sundue (2018). However, we have shown that size appears to be the exception, not the rule, when it comes to trait diversity of epiphytic communities: although epiphytes are generally small, our data suggest they are diverse in numerous other traits. This emphasizes that fern epiphytes should not be treated as a single, static entity, but rather encompass a wide range of adaptive forms. Our results suggest new targets for future studies of fern ecology and evolution. We hope future global phylogenetic studies will build on our results by analyzing traits involved in epiphytic growth other than plant size (e.g., gametophyte morphotype, frond dissection, SLA, and hair and gland presence) to dissect how each may relate to diversification and growth habit. Additionally, future community ecological studies should focus on determining in more detail how niche space is partitioned within epiphytic vs. terrestrial habitats, which is clearly a major dividing line for ferns.

Acknowledgements

Author Contribution

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Table S1 List of ferns from Moorea, French Polynesia included in this study

Table S2 Trait values of ferns on Moorea, French Polynesia

Table S3 Analysis of covariance (ANCOVA) for differences between climatic variables measured with dataloggers placed on the ground (terrestrial growth habit) vs. mounted at 2 m on trees (epiphytic growth habit) on Moorea, French Polynesia, with elevation as a covariate

Table S4 Best-fitting linear models explaining climate and community diversity metrics of ferns on Moorea, French Polynesia by elevation and growth habit

Table S5 Phylogenetic signal in binary traits of ferns on Moorea, French Polynesia, strict dataset excluding any species whose traits were scored based on taxonomy

Table S6 Pagel's (1994) test of correlated evolution between binary traits of ferns on Moorea, French Polynesia, strict dataset excluding any species whose traits were scored based on taxonomy

Table S7 Best-fitting general additive models explaining community diversity metrics of ferns on Moorea, French Polynesia by climate and growth habit selected using full-subsets analysis

Table S8 Output of spatial generalized linear mixed model for community-weighted mean specific leaf area of ferns on Moorea, French Polynesia predicted by elevation and growth habit

Fig. S1 Correlation plot comparing functional diversity of fern communities on Moorea, French Polynesia calculated using different sets of traits as input

Fig. S2 Comparison of community-weighted standard deviations (CWSD) in traits of epiphytic and terrestrial fern communities on Moorea, French Polynesia

Fig. 1 Examples of fern traits used in this study. **(a)** Sporophyte traits. All sporophyte traits were quantitative, including frond length and width, stipe length, rhizome dia., number of pinnae pairs (in this example, nine) and degree of lamina dissection (in this example, once-pinnate). Specific leaf area (ratio of area to mass of leaf lamina) not depicted. **(b)** Gametophyte traits. Morphotype was defined as a binary trait, either cordate or non-cordate. Examples of non-cordate morphotypes include ribbon (thallus elongate and two-dimensional) and filamentous (thallus single lines of cells). Other gametophyte traits (gemmae, hairs, and glands) were scored as present or absent. Arrows point out instances of each binary trait. Scalebars 1 mm except for glands, which is .1 mm. Photographs by J. H. Nitta.

Fig. 2 Selected microclimatic variables of study plots along an elevational gradient from 200 m to 1200 m on Moorea, French Polynesia. Relative humidity (RH) and temperature were recorded every 15 min with dataloggers from July 7, 2013 to July 29, 2014. Vapor pressure deficit (VPD) was calculated from relative humidity and temperature as described in the methods, and overall means calculated for daily mean, minimum, maximum, and standard deviation (SD). 'Epiphytic' dataloggers were placed at *c.* 2 m on trees, and 'terrestrial' dataloggers placed at ground level. Color indicates growth habit: epiphytic dataloggers in green, terrestrial dataloggers in brown. Trendlines fit using

linear models (see Methods); all trendlines significant at $P < 0.05$. Asterisks indicate statistical significance of linear model; *** = $P < 0.001$; ** = $P < 0.01$. Partially transparent colors indicate outliers excluded from the models (see Methods).

Fig. 3 Principal components analysis (PCA) of traits related to epiphytic growth in ferns from Moorea, French Polynesia. **(a, b)** PC loadings. **(c, d)** species scores. **(a)** and **(c)** are standard PCA, **(b)** and **(d)** are phylogenetic PCA. Epiphytes in green, terrestrial species in brown. Quantitative traits only, including only species with no missing observations for any traits (n = 103 spp.). Trait abbreviations as follows: dissection, degree of frond dissection; length, frond length; width, frond width; pinna, number of pinnae pairs; rhizome, rhizome diameter; stipe, stipe length; SLA, specific leaf area.

Fig. 4 Time-calibrated phylogenetic tree of ferns from Moorea, French Polynesia with growth habit and associated traits mapped on the tips. Tree obtained from Nitta *et al.* (2017). Relative value of quantitative (sporophyte) traits shown by heat gradient: low values are lighter, high values are darker. Stipe length and rhizome diameter were log-transformed prior to scaling. States of qualitative (gametophyte) states and growth habit indicated by colors in key. Grey indicates missing data or non-applicable trait states. Values for three leaf size traits (stipe length, frond length, and frond with) were correlated, so of these, we only present stipe length. Species missing data for six or more traits not shown. For a summary of traits, see Table 1. Major epiphytic radiations identified by Schuettpelz & Pryer (2009) labeled on tree in green: H, Hymenophylloideae; T, Trichomanoideae; V, Vittarioideae; A, *Asplenium*; E, *Elaphoglossum*; P, Polypodiaceae; taxonomy follows Pteridophyte Phylogeny Group I (2016). Scale in millions of years (my).

Fig. 5 Variable importance scores from a full-subsets analysis using general additive models exploring the effect of climate and growth habit (terrestrial vs. epiphytic growth) on community diversity of ferns on Moorea, French Polynesia. Predictor variable abbreviations: VPD, vapor pressure deficit; SD, standard deviation. Response variable abbreviations: MPD_{phy}, standard effect size (SES) of mean phylogenetic distance; $MNTD_{phy}$, SES of mean nearest taxon distance; MPD_{func}, SES of mean functional distance; $MNTD_{func}$, SES of mean nearest functional distance; SLA, specific

leaf area. All trait names refer to community-weighted mean values. Community-weighted means of frond length, frond width, stipe length, and rhizome diameter were correlated (Pearson's correlation coefficient > 0.9), so of these we only show stipe length.

Fig. 6 Change in community-weighted mean (CWM) values of epiphytic and terrestrial fern communities along an elevational gradient on Moorea, French Polynesia. Response variable abbreviations: SLA, specific leaf area. Epiphytic communities in green, terrestrial communities in brown. Error bars are each one standard deviation (values below zero not shown). Trendlines and R^2 shown for significant relationships as determined by a linear model at $P < 0.05$ (R^2 not shown for SLA, which was fit with a spatial generalized linear mixed model; see Methods). t shown for significant differences between means of CWMs by growth habit as determined by a two-sided t-test at $P < 0.05$; *** = $P < 0.001$. Results for frond width were very similar to frond length and not shown.

Fig. 7 Functional and phylogenetic diversity of epiphytic and terrestrial fern communities along an elevational gradient on Moorea, French Polynesia. Epiphytic communities in green, terrestrial communities in brown. Response variable abbreviations as follows: MPD_{phy}, standard effect size (SES) of mean phylogenetic distance; $MNTD_{phy}$, SES of mean nearest taxon distance; MPD_{func}, SES of mean functional distance; $MNTD_{func}$, SES of mean nearest functional distance. Trendlines and R^2 shown for significant relationships as determined by a linear model at $P < 0.05$. Boxplots show median values (bold lines) by growth habit. Lower and upper hinges correspond to first and third quartiles, and whiskers extend to values within $1.5 \times$ the interquartile range. Asterisks indicate statistical significance of two-sided t-test; *** = $P < 0.001$; ** = $P < 0.01$.

Table 1 Fern traits used in this study

	Data type (unit)	Functional significance	Reference(s)
Sporophyte traits			
Stipe Length	Continuous (cm)	Shorter stipes compensate for low conductivity	Watkins *et al.* (2010)
Frond Length	Continuous (cm)	Smaller leaf size reduces evapotranspiration	Vogel (1968)
Frond Width	Continuous (cm)	Smaller leaf size reduces evapotranspiration	Vogel (1968)
Rhizome Diameter	Continuous (cm)	Scales with overall plant size	Creese *et al.* (2011)
Frond Dissection	Ordinal	Less divided laminae reduce evapotranspiration	Kluge & Kessler (2007)
Pinna number	Integer	Less divided laminae reduce evapotranspiration	Kluge & Kessler (2007)
Specific Leaf Area	Continuous (m^2 kg^{-1})	Species in more stressful environments invest in thicker leaves	Wright *et al.* (2004)
Gametophyte traits			
Morphotype	Binary (cordate vs. noncordate)	Noncordate morphology reduces drying rates by holding	Watkins *et al.* (2007b),

		external water in crevices and folds	Pittermann *et al.* (2013)
Gemmae	Binary (present/absent)	Enable asexual reproduction, thereby overcoming local extinction due to drying	Farrar *et al.* (2008)
Glands	Binary (present/absent)	Lipids exuded by glands may regulate osmotic balance	Crow *et al.* (2011)
Hairs	Binary (present/absent)	Hairs reduce drying rates by holding external water and increasing boundary layer thickness	Watkins *et al.* (2007b)

Noncordate gametophyte morphotypes include ribbon, strap and filamentous.

Table 2 Phylogenetic signal in continuous traits of ferns from Moorea, French Polynesia

	K	$P(K)$	λ	$P(\lambda)$
Stipe length	0.28	0.001	0.75	< 0.001
Frond length	0.50	0.002	0.92	< 0.001
Frond width	1.10	0.001	0.99	< 0.001
Rhizome diam.	1.31	0.001	1.00	< 0.001
SLA	0.26	0.001	0.74	0.007
Pinna no.	0.21	0.003	0.24	0.018
Frond dissection	0.38	0.001	0.90	< 0.001

K, Blomberg's *K* (Blomberg *et al.*, 2003); λ, Pagel's λ (Pagel, 1999). Values of λ or *K* greater than 1 indicate traits evolving according to Brownian Motion (BM); values of λ or *K* near 0 indicate random distribution of traits.

Table 3 Phylogenetic signal in binary traits of ferns from Moorea, French Polynesia

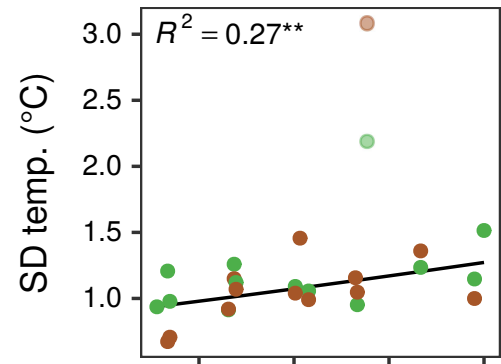|	Number of presences	Number of absences	*D*	*P*(rnd)	*P*(BM)
Epiphytic growth	72	56	- 0.11	< 0.001	0.694
Gemmae	95	25	- 1.24	< 0.001	1
Glands	72	38	- 0.57	< 0.001	0.972
Hairs	103	7	- 0.37	< 0.001	0.757
Cordate morphotype	52	76	- 0.53	< 0.001	0.987

D, Fritz and Purvis' *D* (Fritz & Purvis, 2010); *P*(rnd), probability of random distribution of traits; *P*(BM), probability of traits evolving under Brownian motion (BM). Values of *D* 0 or less indicate evolution according to BM; values near 1 indicate random trait distribution.

Table 4 Results of phylogenetically independent contrasts analysis of quantitative (sporophyte) traits related to epiphytic growth in ferns from Moorea, French Polynesia

	Num. constrasts	Num. pos. constrasts	t	P
Stipe length	17	1	-3.23	0.005
Frond length	17	5	-1.95	0.068
Frond width	17	3	-2.53	0.022
Rhizome diam.	16	3	-2.09	0.054
SLA	17	5	-1.68	0.113
Pinna no.	17	2	-2.32	0.034
Frond dissection	17	4	-3.01	0.008

All trait contrasts were made by subtracting epiphytic values from terrestrial values; thus, a positive contrast indicates greater values for terrestrial clades.

Table 5 Pagel's (1994) test of correlated evolution between binary traits in ferns from Moorea, French Polynesia

	LogL(independent)	LogL(dependent)	Likelihood ratio	P
Gemmae	-68.6	-65.1	7.1	0.133
Glands	-87.7	-84.0	7.2	0.123
Hairs	-72.2	-68.7	7.0	0.134
Cordate morphotype	-103.0	-95.3	15.3	0.004

LogL, log-likelihood. Each gametophyte trait was coded as a binary trait and tested for correlated evolution with growth habit (epiphytic vs. terrestrial growth). Traits with a significantly higher (i.e., less negative) log likelihood for the dependent model are correlated with growth habit.
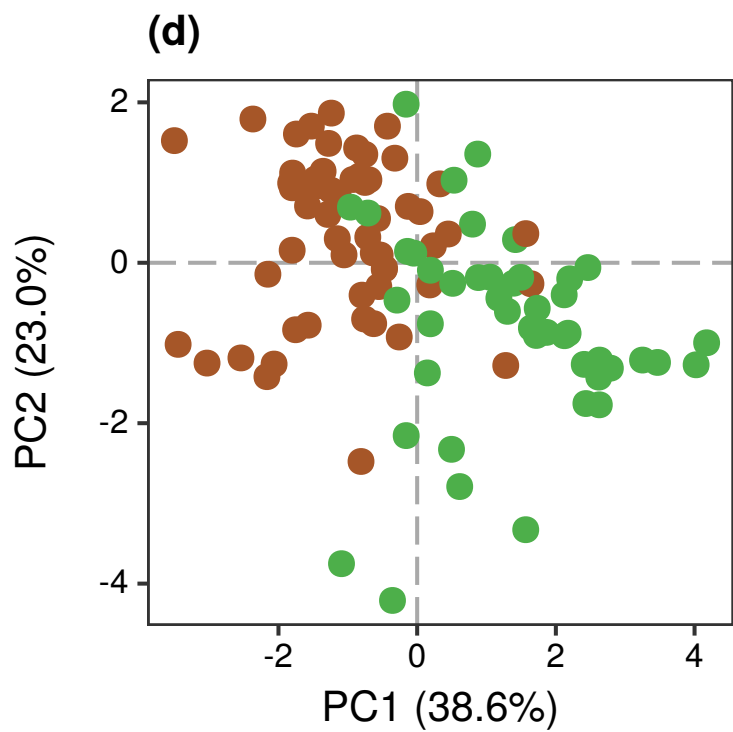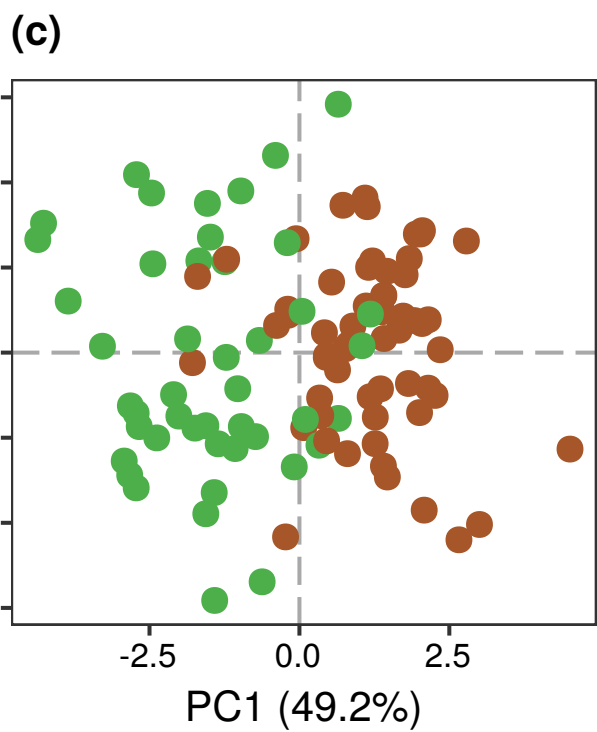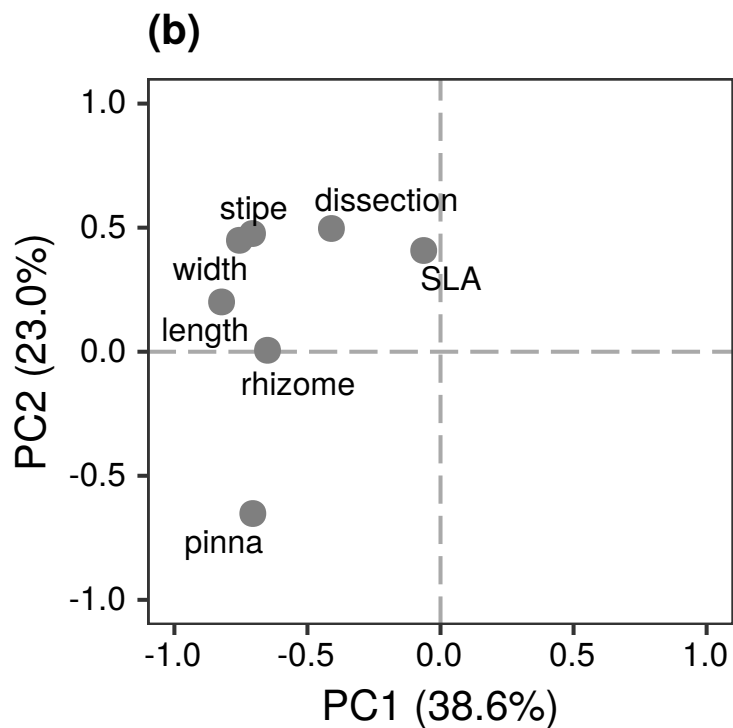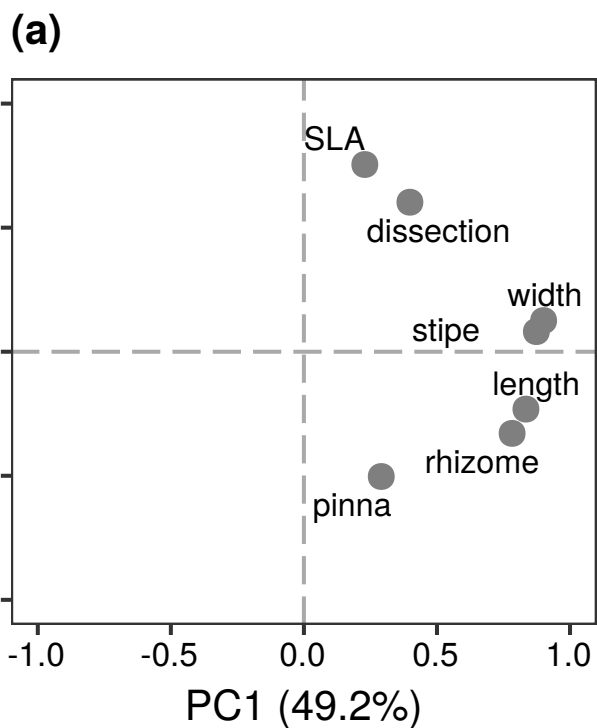
(a)

Frond Width

Frond Length
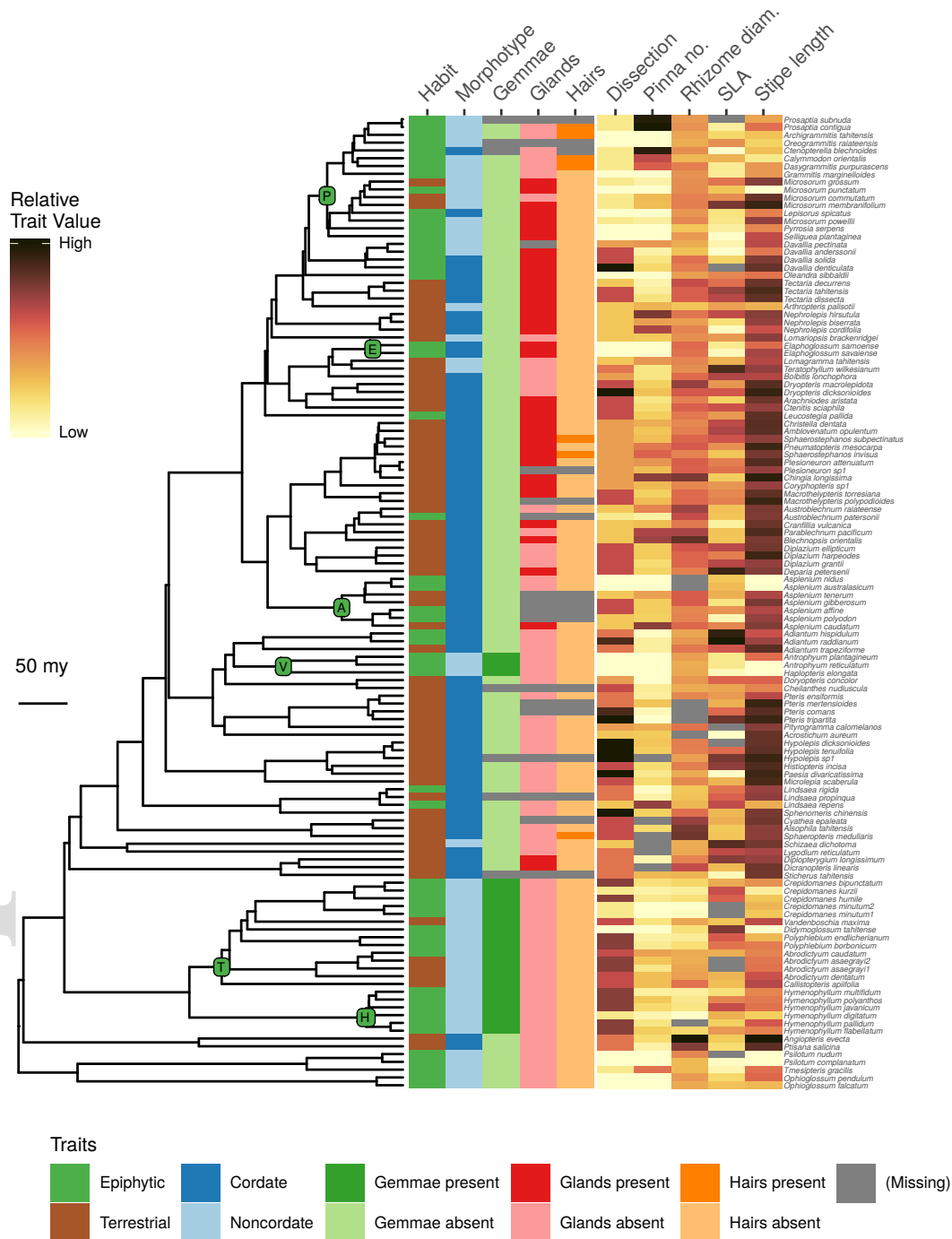
Stipe Length

Pinna num.

Rhizome Dia.

(b)

Morphotype

non-cordate

cordate

Hairs

Gemmae

Glands
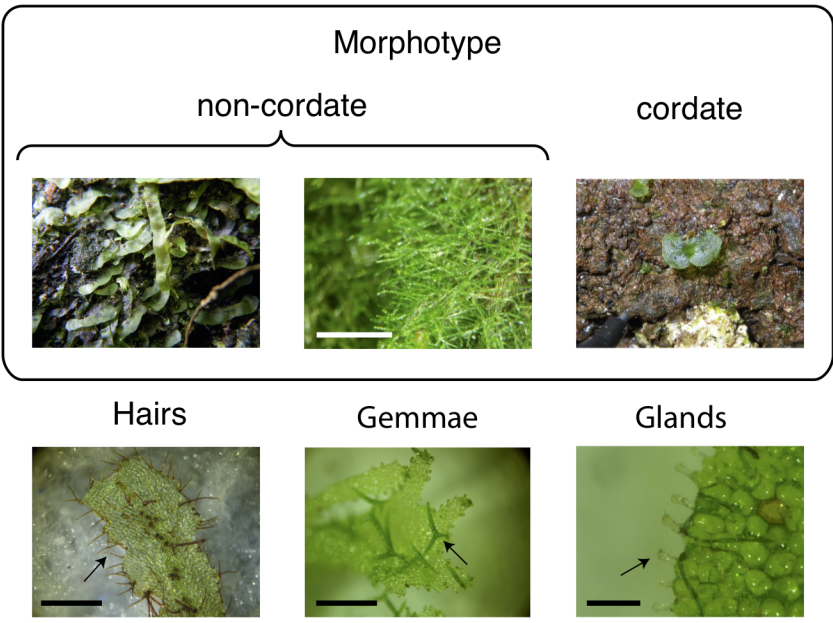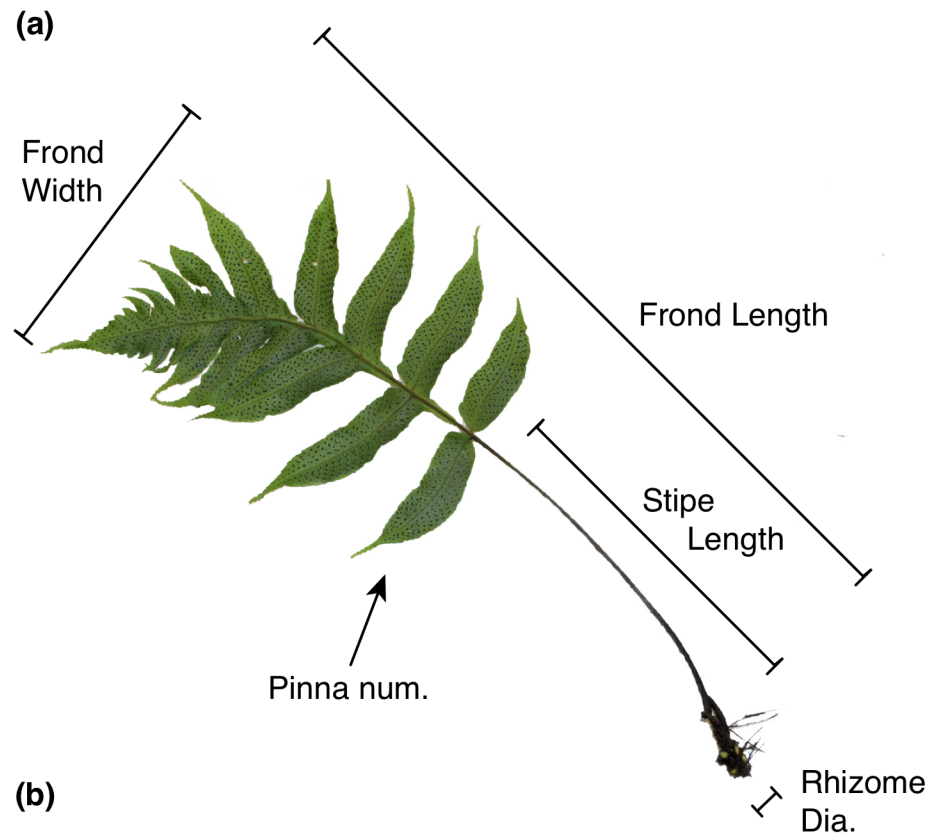
nph_16607_f1.tiff

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(a)

SLA

dissection

width

stipe

length

rhizome

pinna

PC2 (21.2%)

PC1 (49.2%)

(b)

stipe dissection

width SLA

length

rhizome

pinna

PC2 (23.0%)

PC1 (38.6%)

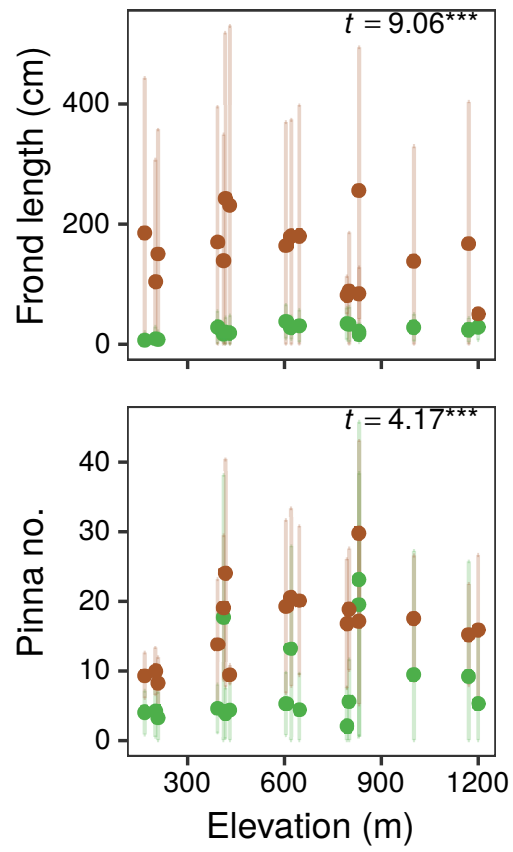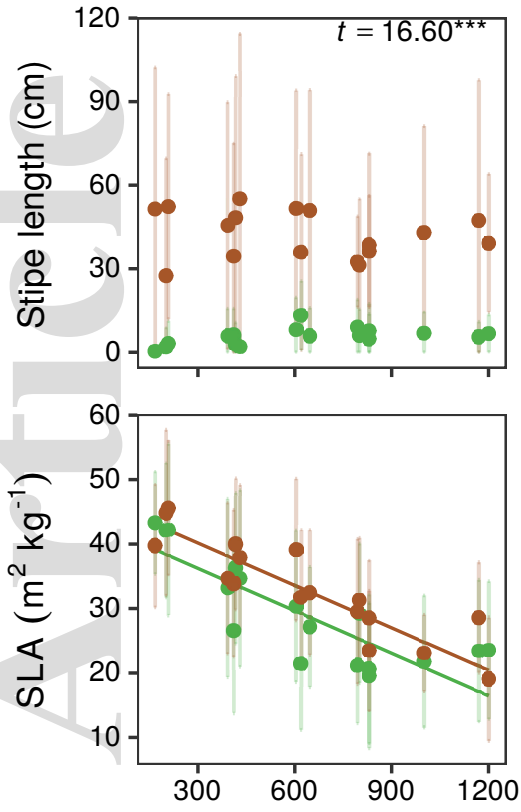**(c)**

PC2 (21.2%)

PC1 (49.2%)

(d)

PC2 (23.0%)

PC1 (38.6%)
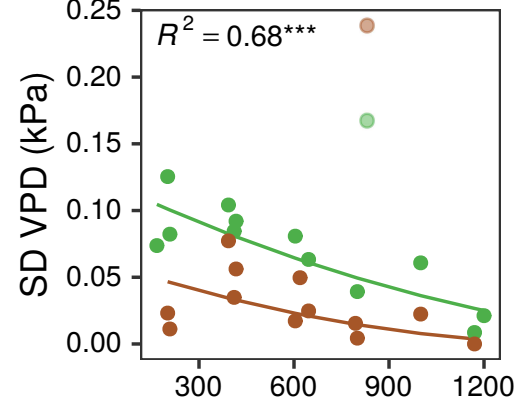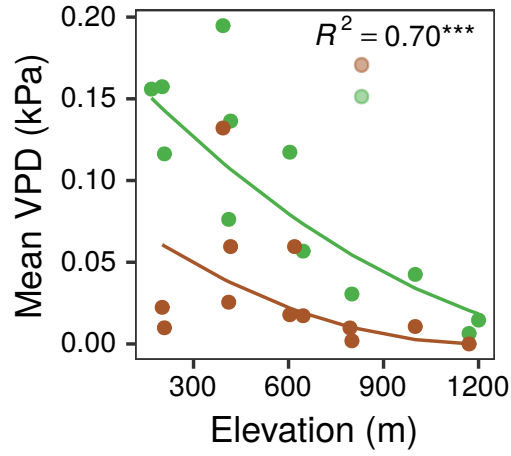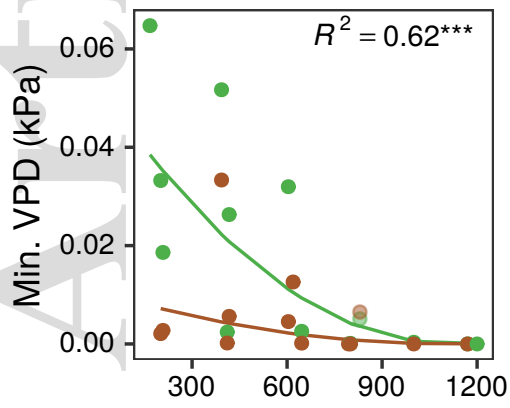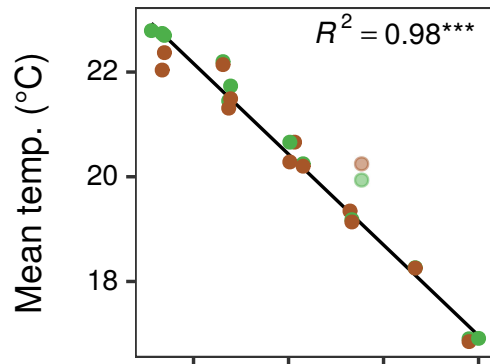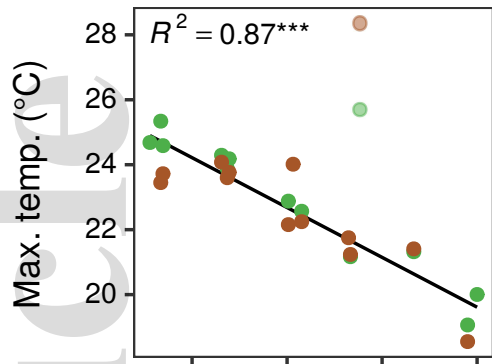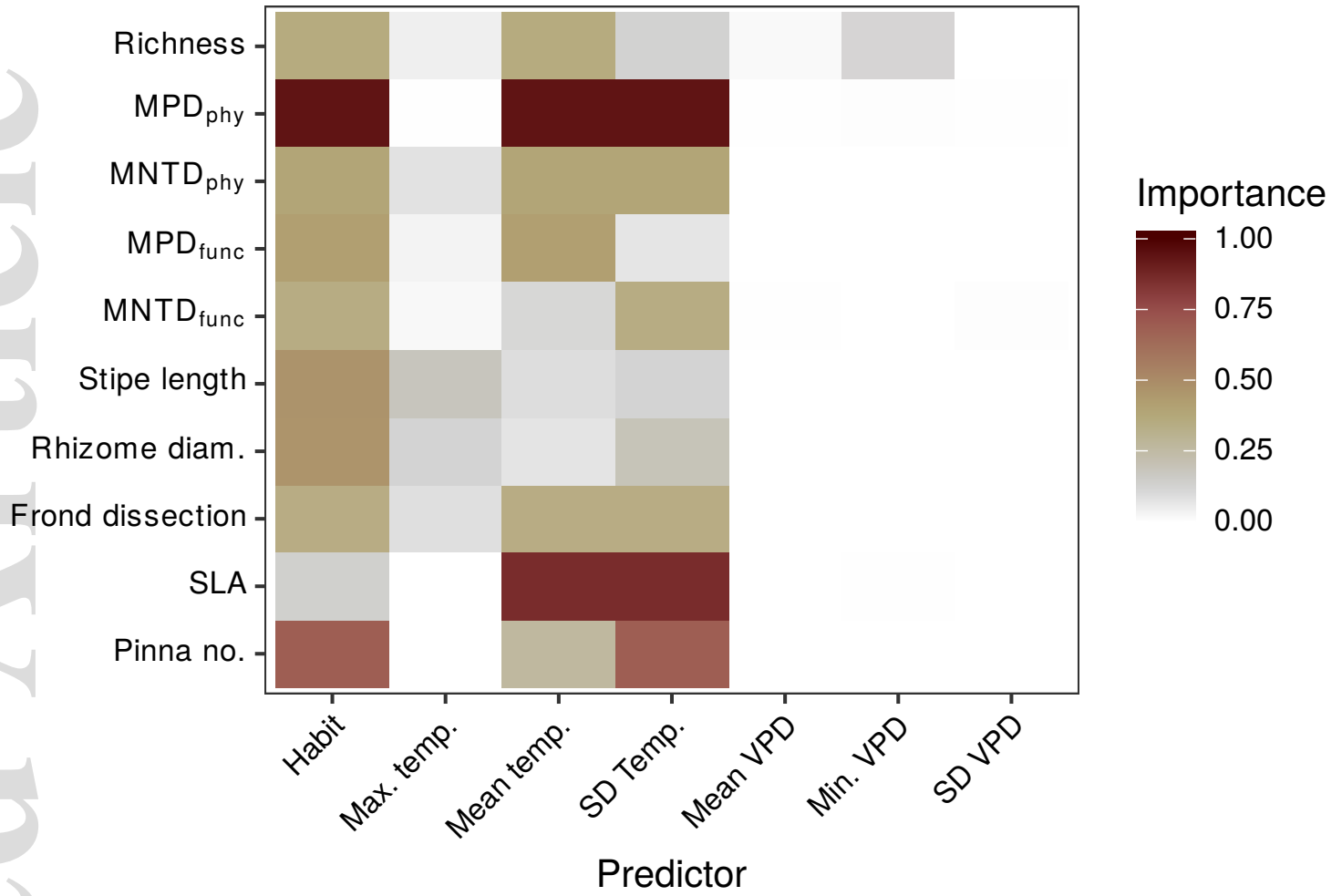
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