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Crossing the Divide: An Exploration of Functional Traits in Ferns that Grow Across Terrestrial, Epipetric, and Epiphytic Habitats

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ABSTRACT.—Plants are characterized by their marked plasticity and ability to alter their functional biology to partition ecological niches. However, there are limits to functional trait exploration especially in complex and stressful habitats. Highly specialized traits may control a species ability to explore within and across habitats. Such may be especially true of epiphytes, whose array of unique traits may constrain their ability to cross establish in epiphytic and terrestrial habitats. In the case of ferns, there are few reported examples of species that can grow across these habitats with regularity. However, this study reports and explores species that exhibit great ecological flexibility growing across a wide range of habitats and growth forms. Specifically, we examine species that grow as 1) terrestrially rooted and epiphytic individuals, 2) nest and non-nest-forming epiphytes; and nest-forming terrestrially rooted individuals, and 3) species that grow as terrestrial, epiphytic, and epipetric individuals. We use natural abundance foliar stable isotope ratios (SIR) of N^{15} and C^{13}, and %N, to explore intraspecific variation in mineral nutrition and water relations across and within niches. Our results reveal the 1) unreported ability of some species to grow across the epiphytic/terrestrial divide, 2) surprising ability of some species to explore these habitats with little to no shift in functional traits; 3) a potentially new function for the nest in nest-forming epiphytes. Finally, our work highlights the need to consider intraspecific trait variation more carefully when studying ferns that occur across a wide range of habitats.

KEY WORDS.—epiphyte, epipetric, niche partitioning, water and nutrient relations, functional biology

As ecosystems evolve and niches fill, organisms are faced with the need for increased functional diversity to more carefully partition their environments. Life form evolution may be one response to niche partitioning and ultimately allows for diverse species coexistence. For example, as angiosperms diversified in the Cretaceous (144 - 65 MYA), they altered global rainfall and climate. This change resulted in the rapid diversification of many plant groups (Heimhofer *et al.*, 2005). Such diversification is thought to have put pressure on niche space and increased the movement of plants from terrestrial ancestors into the epiphytic niche (Schneider *et al.*, 2004; Benzing, 2008; Schuettpelz and Pryer, 2009). Perhaps nowhere is this more obvious today than in wet tropical forests that are structurally and microclimatically complex. Such

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diverse systems create an array of complex habitats for epiphytes to explore and exploit; however, the tropical epiphytic environment is functionally different from the terrestrial environment, the former typically being hotter, brighter, drier, and less nutrient rich than the terrestrial environment (Cardelús and Chazdon, 2005; Cardelús and Mack, 2005; Cardelús *et al.*, 2009). The magnitude of these differences can increase with height in the canopy such that high canopy epiphytes experience a distinct environment when compared to plants rooted in the understory soil. Even a slight increase in height through the understory can result in potentially biologically significant shifts in light and humidity (Cardelús *et al.*, 2009). The contrast between these habitats provides differing selective pressures, and as a result, epiphytic plants are physiologically, and often morphologically unique from their terrestrial colleagues (Rada and Jaimez, 1992; Watkins, Rundel, and Cardelús, 2007; Zotz, 2016; Zhang *et al.*, 2018). Pressures acting across epiphytic and terrestrial may select for highly specialized traits that ultimately lock species into each habitat, reducing their ability to radiate across habitats.

Given the confines of their niche, epiphytes have developed a suite of diverse functional characteristics to enhance water and nutrient acquisition, conservation, and use, including thick, long lasting leaves (Holbrook and Putz, 1996), pendulous vellum coated roots of orchids (Zotz and Winkler, 2013), resource sharing among different ramets of the same rhizome (Lu *et al.*, 2015), symbiotic relationships with insects (Watkins, Cardelús, and Mack, 2008), tank, and nest-forming morphologies that trap leaf litter and water to buffer the plant from drought and nutrient scarcity and inconsistency (Schmidt and Zotz, 2001), and many more fascinating morphologies.

In a review of epiphyte physiological ecology, Zotz and Hietz (2001) concluded that while broad generalizations warrant more research, epiphytes are often limited by water and can be subject to nutrient limitation. Such observations have been supported by more recent work (Lasso and Ackerman 2013; Gora and Lucas 2019) and while these two variables strongly influence epiphyte ecology, this is not the case for all taxa. In a more recent survey on accidental epiphytes, Hoeber and Zotz (2021) found that primarily terrestrial species growing as accidental epiphytes exhibited higher leaf-level nutrient concentrations and showed no evidence of water limitation. For ferns specifically, it has long been known that epiphytic species exhibit myriad adaptations to conserve water. Hietz and Briones (1998) demonstrated that ferns in a wet Mexican cloud forest exhibit increasingly strong water conservation adaptations such as shifts in stomatal traits and increased incidence of CAM higher into the canopy. Campany *et al.* (2021) found that epiphytic ferns exhibit strong drought avoidance adaptations (lower stomatal density, reduced xylem area, thicker leaves, etc.) when compared to terrestrial species. Like sporophytes, fern gametophytes also boast a range of fascinating adaptations to the relatively dry epiphytic environment, including long lifespans and desiccation tolerance (Watkins *et al.*, 2007; Pitterman, Brodersen, and Watkins, 2013). Together, these studies, and many others, reveal significant functional differences between plants growing in epiphytic and terrestrial habitats, yet suggest that there may be a great deal of plasticity in functional response.

In spite of some of the more predictable trends in functional trait combinations within and across habitats, plants respond in different ways to the same stressors. Thus, it is unlikely that a single trait combination spells success, even in the same habitat. Marks and Lechowicz (2006) used a genetic algorithm to model the survival and growth 34 species of co-occurring tree seedlings and found that interspecific variation in physiological traits was greater than that predicted by variation in the environment, indicating that there is more than one optimal combination of traits for a single environment. Their findings are supported by studies which range from tropical to subarctic environments and show that co-occurring plant species exhibit high trait variation and have settled into different optimal trait combinations for the same environment (Cavender-Bares, Kitajima, and Bazzaz, 2004; Wright *et al.*, 2004; Ackerly and Cornwell, 2007). Such high trait variation commonly occurs within individuals of the same species and is especially apparent if a plant ontogeny is considered (Hietz and Wanek, 2003; Testo and Watkins 2012). Tank-forming bromeliads can drastically change their water and nutrient uptake strategies across ontogeny in response to changing needs: young plants invest more in the capture of atmospheric nutrients while larger plants rely on their tanks for internal nutrient cycling (Schmidt and Zotz, 2001; Zotz, Hietz, and Schmidt, 2001; Laube and Zotz, 2003; Reich *et al.*, 2003). Testo and Watkins (2012) found that the non-nest forming epiphytic fern *Asplenium auritum* showed changes in physiological traits across plant size, shifting from drought tolerance in small plants to drought avoidance in large plants.

In addition to changes that occur with ontogeny, some species exhibit functional trait shifts with changes in life form. For example, hemiepiphytic strangler figs change leaf-level functional traits (Holbrook and Putz, 1996) and some fundamental aspects of their cellular-level physiology (Zhang *et al.*, 2009) as they move from epiphytic to terrestrial individuals. Similar functional trait shifts have been observed between strictly epiphytic and terrestrial orchids (Zhang *et al.* 2015) and ferns (Sulaiman and Cicuzza, 2021). Excluding the relatively rare examples of hemiepiphytic species, few fern species have the ability to grow in both habitats. Watkins *et al.* (2006) found only a single species of *Elaphoglossum* out of 264 fern species across 60 genera that could grow as both a high canopy exposed epiphytic and as understory terrestrial individuals on the Barva Transect in Costa Rica. A similar paucity of reciprocal occurrence has been reported in the series of papers by Kluge and Kessler (2007, 2011, and references therein) who completed transects on the same elevational gradient. There are many reports of fern species occurring in both epiphytic and terrestrial habitats and obviously these studies do not say cross occurrence never occurs, yet few fern species can be found in the extremes, i.e., high canopy or highly exposed epiphytic conditions and growing in the mineral soil. Cases where species cross these boundaries, for example primarily understory epiphytes apparently growing in understory soil, are usually facilitated by habitat heterogeneity and the occurrence of rocks and/or rotting logs (Canestraro, Moran, and Watkins, 2014). Much more work must be done to understand mechanistic parameters and to quantify the extent to which fern species actually exhibit reciprocal establishment across these habitats. Reports on floristic assemblages and keys rarely distinguish between occurrence and establishment and frequently confuse accidental occurrences with the more typical state of species. All of this taken together suggests that shifts in functional traits, changes in physiology, and general rarity of individual species that can explore epiphytic and terrestrial habitats suggest habitat fidelity.

This paper aims to explore inter and intraspecific variation in physiological traits of ferns across an array of niches and life forms *in situ*. Specifically, we examine percent nitrogen (%N), the ^{15}N:^{14}N stable isotopic ratio (SIR) ($\delta^{15}N$), and ^{13}C:^{12}C SIR ($\delta^{13}C$) of: 1) two species of the genus *Elaphoglossum*, *E. eximium* (Mett.) Christ and *E. erinaceum* T. Moore, that grow across terrestrial, epipetric, and epiphytic niches and 2) two species in the Polypodiaceae that grow as nest-forming epiphytes and terrestrials, *Niphidium crassifolium* (L.) Lellinger and *Serpocaulon fraxinifolium* (Jacq. A.R.Sm.) as both epiphytic and terrestrial plants. We chose to examine these traits because they are well studied and related to water and nutrient relations, two aspects that are likely to be critical to plants growing on such disparate substrates such as soil, rocks, and trees. Given the complex nature of epiphyte ecophysiology and the differences between and even within co-occurring species, we predict that each species will exhibit a unique response to growth across different niches: epiphytic, epipetric, and terrestrial.

MATERIALS AND METHODS

Study sites.—Samples were collected from Las Cruces Biological Station (8° 47′ 7" N, 82° 57′ 32" W) in Puntarenas Province, Costa Rica and along the river that passes through the Savegre Lodge property (9° 33′ 12" N, 83° 48′ 23" W) in San José Province, Costa Rica (permit nos. No PI-R-072-2018 to J. E. Watkins Jr). The Las Cruces Biological Station is in a mid-elevation (1000 m elevation) tropical wet forest that has a mean total annual rainfall typically around 3500 mm, with wet seasons in May and September-October, and a pronounced dry season in December-March. January is the driest month during which only 50 mm of rainfall occur on average (www.ots.ac.cr). The collection site was characterized by high light and low canopy cover due to its juxtaposition with young secondary rainforest.

The Savegre Lodge property is in a premontane (2200 m elevation) wet cloud forest that has a mean total annual rainfall of 3600 mm, with wet seasons in May and September-October, and a dry season in December-March. February receives only 70 mm of rainfall (en.climate-data.org). The study site was characterized by low light, high humidity, with evidence of flooding during the wet season.

A total of 101 samples from four epiphytic fern species across three genera were collected at two study sites. Sampling was equal with approximately 10 samples per treatment per species. Primarily epiphytic species were observed and collected as 1) low trunk, non-nest forming epiphytes (within 2.5 m of the soil), 2) low trunk nest-forming epiphytes, 3) terrestrially rooted plants (with and without a nest), and as 4) epipetric (growing on rocks) plants. Species collected at Las Cruces include *Niphidium crassifolium* (epiphytic, nest-forming epiphytic, and terrestrial), and *Serpocaulon fraxinifolium* (epiphytic and terrestrial) (Fig. 1). Species collected at Savegre include *Elaphoglossum eximium* and *Elaphoglossum erinaceum*. Both *Elaphoglossum* species lie within the *E. subulata* clade (Rouhan *et al.* 2004) and were collected as epiphytic, epipetric, and terrestrial individuals (Fig. 2).

A word on isotopes.—There is a dizzying array of plant functional traits that have been cited and measured across a remarkable diversity of studies. In fact, the TRY Plant Trait Database now lists over 2,091 separate traits from 280,000 plant taxa (Kattge *et al.* 2020). Of these 2,091 traits, there is little consensus as to the most important traits one should use. Much of this is context dependent and often based on what the investigator has the capacity to carry out. Nitrogen content is related to metabolism and among other things, there is typically an increased capacity for photosynthesis with more %N. Dawson *et al.* (2002) wrote an excellent review on the use of stable isotopes in ecology useful in understanding the use of isotopes. The application of stable isotopes is largely based on the idea that normal metabolic reactions abhor heavy isotopes and "avoid" them in a process known as biological isotope fractionation. For example, carbon exists as three isotopes C^{12}, C^{13}, C^{14} that vary in their overall concentration in our atmosphere with C^{12} being the most abundant (approximately 99% of atmospheric C) and the radioactive C^{14}, thankfully, being the rarest (Boutton, 1991). When we think of photosynthesis, CO_2 is taken in through the stomata and enters the dark reactions through the catalyzing nature of RuBisCO (Ribulose-1,5-bisphosphate carboxylase-oxygenase). RuBisCO has a natural affinity for the lighter isotope C^{12} and will discriminate against C^{13} and C^{14}. This act of discrimination allows scientists to evaluate certain aspects of the water relations of a plant (Farquhar, Ehleringer, and Hubick, 1989). Typically, internal leaf spaces become filled with CO_2 gas and if the stomata are open, a larger proportion of $C^{13}O_2$ and $C^{14}O_2$ diffuses from the leaf as RuBisCO reacts more readily with $C^{12}O_2$. However, if a plant must close its stomata to conserve water, no new CO_2 gas can enter, and RuBisCO will continue to preferentially deplete $C^{12}O_2$ in the substomatal cavity. This increases the internal ratio of $C^{13}O_2$ to $C^{12}O_2$ eventually causing the plant to use more $C^{13}O_2$ and $C^{14}O_2$. In this case, the leaf will become enriched in the heavier isotopes (compared to a plant with open stomata and high stomatal conductance) and in general terms, one can assume that a leaf with an enriched C isotope signal may close its stomata (or have lower stomatal conductance) more often than a less water use efficient leaf. Thus, a plant with a higher $\delta^{13}C$ SIR has greater water use efficiency (WUE). Nitrogen isotopes are perhaps more difficult to summarize as many biological processes play a part in altering the ratio of N isotopes; however, one interpretation of a plant's natural N^{15} abundance is nitrogen source. As total

Fig. 1. Las Cruces species *Niphidium crassifolium* (A-C) and *Serpocaulon fraxinifolium* (D-E) growing across epiphytic and terrestrial habitats. *N. crassifolium* develops a nest over time as its fronds get wider and dead fronds accumulate at the bottom of the plant. The nest morphology may allow for the capture of water and leaf litter. *S. fraxinifolium* has a long creeping rhizome. Photo credit: Robbin C. Moran, picture (B).

Fig. 2. Savegre Lodge species *Elaphoglossum eximium* (A-C) and *Elaphoglossum erinaceum* (D-F) occurring abundantly on soil (A&D), rocks (B&E), and trees (C&F).

nitrogen (a combination of the N^{14} and N^{15} isotopes) passes through an ecosystem, metabolism again discriminates against the heavier isotope. So, a plant that obtains nitrogen from N-fixing bacteria, which convert N_2 directly from the atmosphere, will be depleted in N^{15} relative to a plant that absorbs nitrogen from decaying leaf litter. Nitrogen found in leaf litter has undergone more biological fractionation. Interpretation of $\delta^{15}N$ SIR data can be controversial, but in this paper, we use $\delta^{15}N$ SIR data as a possible indicator of where plants obtain nitrogen.

Sample preparation for isotopic and nutrient analyses.—Air dried field samples were taken to the lab and oven dried at 60 °C, pulverized into a fine powder with a Wiley Mill (Thomas Scientific Model 3383-L10), and weighed and rolled inside tin capsules (5 by 9mm Costech pressed tin capsules).

Prepared samples were analyzed for %N and δ^{15}N and δ^{13}C SIRs at the Cornell Stable Isotope Laboratory (COIL) (Ithaca, NY, USA) using a Finnigan Matt Delta Plus IRMS. Leaf isotope numerical values are expressed in delta notation (δ) and are relative to the standard PDB (Pee Dee Belemnite) and air, for both C and N.

Statistical Analysis.—Our data met the normality assumptions of parametric statistical tests as per Shapiro-Wilk tests for each variable (%N, δ^{15}N, and δ^{13}C SIRs) by site ($\alpha = 0.05$). To avoid the confounding effects of site differences, comparisons were never made across sites. Comparisons between species were only made with closely related species – *Elaphoglossum eximium* and *E. erinaceum* – growing in the same habitat. When two groups were compared, two-sample t-tests were used to determine if groups exhibited significant differences ($\alpha = 0.05$). If variances between groups were unequal via a Welch F-test, then Welch's two-sample t-test (unequal variance) was performed instead. When three groups were compared, analysis of variance (ANOVA) followed by post-hoc Tukey Honest Significant Difference tests were used to determine significant differences among groups ($\alpha = 0.05$). Comparisons include: 1) two-sample t-test between terrestrial and epiphytic *S. fraxinifolium*; 2) analysis of variance between epiphytic, epiphytic nest-forming, and terrestrial *N. crassifolium*; 3) two-sample t-test between *E. eximium* and *E. erinaceum* within habitat; 4) analysis of variance between epiphytic, epipetric, and terrestrial individuals of *E. eximium* and *E. erinaceum*, treated separately. All statistical analyses were performed in R version 4.0.2: packages 'base' (R Core Team, 2020) and 'dplyr' (Wickham *et al.*, 2020). All graphs were plotted using 'ggplot2,' (Wickham, 2016) 'ggpubr,' (Kassambara, 2020) 'ggsignif,' (Ahlmann-Eltze, 2019) and 'rstatix' (Kassambara, 2020) packages.

RESULTS

Global results.—Across all 101 samples taken, plants exhibited a wide range of %N, δ^{15}N, and δ^{13}C SIR values. Sampled plants exhibited %N values ranging from 0.8% to 2.7% with a mean of 1.8%. δ^{15}N values ranged from highly depleted (less processed) (-5.9) to enriched (more processed) (2.3) with a global mean value of -1.7. δ^{13}C values ranged from enriched (high WUE) (-28.9) to depleted (low WUE) (-35.8) and averaged -32.7 across all samples.

Serpocaulon fraxinifolium grew abundantly as an epiphyte in the low canopy (Fig. 1D) and scattered as terrestrial individuals along the forest floor (Fig. 1E). Morphologically, the species did not differ obviously between life forms, except that the rhizome grew horizontally across the soil when found as a terrestrially rooted plant and vertically up tree bark when epiphytic. Curiously, we found no significant differences between the epiphytic and terrestrial individuals in either %N ($t_{10.5} = -0.256$, $p = 0.80$), δ^{15}N SIR ($t_{10.9} = -0.873$, $p = 0.40$), or δ^{13}C SIR ($t_{11.9} = 0.437$, p-value $= 0.67$) (Fig. 3A-C).

Mature *Niphidium crassifolium* (Fig. 1A-C) individuals were found growing abundantly in the understory as large plants with well-developed nests. Immature individuals (2-6 fronds, Fig. 1A) were also found as epiphytes, but

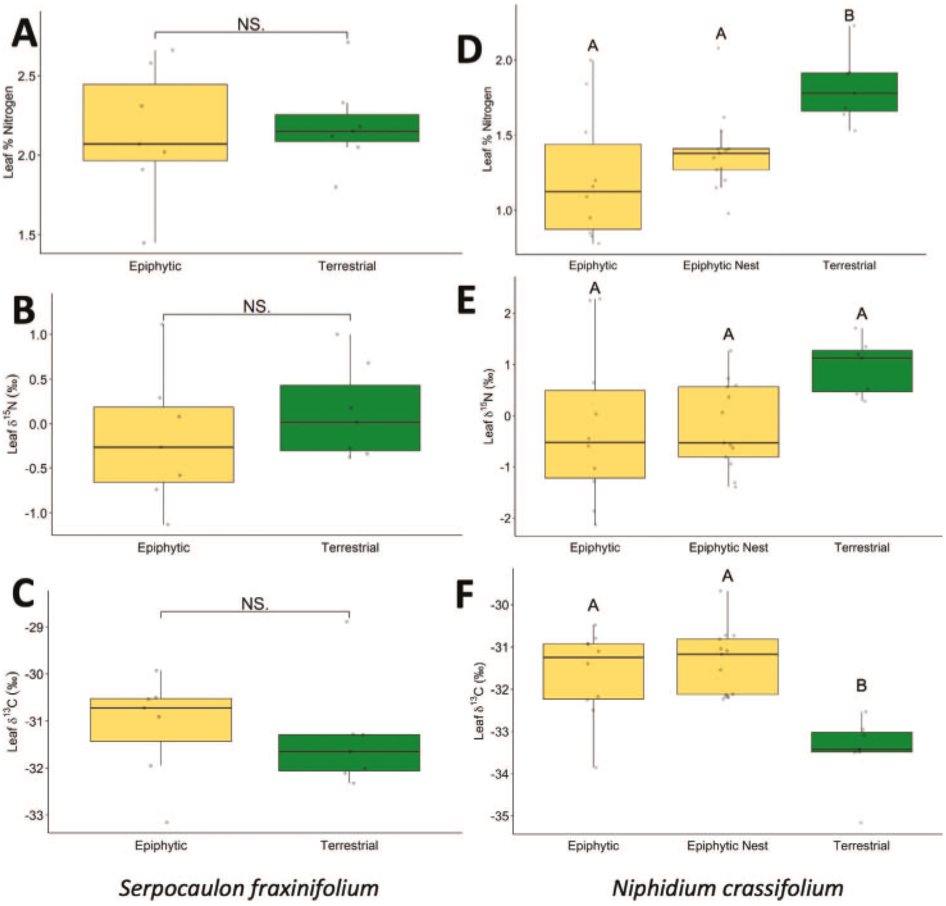

Fig. 3. Boxplots of trait values for Las Cruces species *Serpocaulon fraxinifolium* (A-C) and *Niphidium crassifolium* (D-F) compared across epiphytic and terrestrial habitats *in situ*. Boxes represent the interquartile range and lines represent the median. Whiskers represent the highest and lowest values within 1.5 times the interquartile range. Each individual sample is denoted by grey dots. Significant differences are denoted by NS., *, **, *** corresponding to >0.05, <0.05, $<.01$, and $<.001$ p-values respectively as determined by T-tests. Uppercase letters denote significant differences determined from ANOVA and post hoc Tukey tests ($p < 0.05$). Colors correspond to habitat (yellow = epiphytic, green = terrestrial).

lacked a fully-formed nest morphology (Fig. 1B-C). Fully mature, fertile, and seemingly healthy ferns growing rooted in the mineral soil were also observed. At this site, we never observed young plants recruiting on the soil, so we assumed that these terrestrial plants represented fallen individuals. In all sampled cases, these plants were solidly rooted in the mineral soil, having fallen long ago. Terrestrial *N. crassifolium* were relatively abundant, though not as abundant as epiphytic *N. crassifolium*. Terrestrially rooted *N. crassifolium* had a higher %N than both epiphytic life forms ($F_{2,27} = 7.08$, p

< 0.01): nest epiphytic ($p = 0.03$), and non-nest epiphytic ($p < 0.01$) (Fig. 3D). δ^{15}N SIRs did not differ among life forms ($F_{2,27} = 3.005$, $p = 0.06$), while δ^{13}C SIRs did ($F_{2,27} = 13.47$, $p < 0.001$) (Fig. 3F). Terrestrially rooted *N. crassifolium* had more depleted δ^{13}C values (less WUE) than conspecific non-nest epiphytes ($p < 0.001$) and nest epiphytes ($p < 0.001$) (Fig. 3F).

Elaphoglossum eximium and *Elaphoglossum erinaceum* grew abundantly in the low canopy on the tree trunks (Fig. 2C&F), on large and small boulders (Fig. 2B&E), and rooted in the rocky mineral soil (Fig. 2A&D). Individuals were collected along the Rio Savegre at the bottom of a ravine within 10-20 m of the river side. The area was wet and showed evidence of recent flooding such as the presence of silt covering the lower trunks of trees. The river is known to flood this ravine frequently (Felipe Chacón Vargas pers. comm.) %N varied by life form ($F_{2,25} = 7.39$, $p < 0.01$), with epipetric *E. erinaceum* having greater %N compared to conspecific epiphytic individuals ($p < 0.01$) with terrestrial individuals exhibiting intermediate %N to epipetrics ($p= 0.18$) and epiphytes ($p = 0.14$) (Fig. 4A). Surprisingly, *E. erinaceum* δ^{15}N SIRs did not respond to different growth substrates ($F_{2,25} = 0.116$, $p = 0.89$) (Fig. 4B); while δ^{13}C SIRs did differ among substrates ($F_{2,25} = 4.26$; $p = 0.03$). According to a post hoc Tukey, epiphytic *E. erinaceum* individuals were more water use efficient (more enriched in C^{13}) than terrestrially rooted individuals ($p = 0.02$), but did not differ from epipetric individuals ($p = 0.30$). Epipetric and terrestrial individuals did not differ from one another ($p = 0.44$) (Fig. 4C).

Elaphoglossum eximium exhibited no response to substrate in either leaf tissue %N ($F_{2,26} = 1.74$, $p = 0.20$), or δ^{13}C SIR ($F_{2,26} = 1.518$, $p = 0.24$) (Fig. 4A&C). However, leaf tissue δ^{15}N SIR was correlated by life form in *E. eximium* ($F_{2,26} = 4.587$, $p = 0.02$). Epipetric individuals utilized less processed nitrogen than epiphytic individuals ($p = 0.02$), but were not different from terrestrial individuals ($p = 0.39$). Terrestrial and epiphytic individuals also did not differ ($p = 0.18$) (Fig. 4B).

We also tested for differences between these two closely related species growing on similar substrates to investigate the possibility of niche partitioning in nutrient and water acquisition and use. Using Welch's t-tests, no differences in %N were detected between *E. eximium* and *E. erinaceum* growing on trees ($t_{16.1} = 0.656$, $p = 0.64$), rocks ($t_{12.5} = -2.38$, $p = 0.10$), or soil ($t_{18} = 1.02$, $p = 0.64$) (Fig. 4A). *E. erinaceum* utilized less processed nitrogen than *E. eximium* while growing on trees ($t_{17.1} = -3.40$, $p = 0.01$), but the species were not different while growing on rocks ($t_{12.2} = -0.297$, $p = 0.77$) or soil ($t_{9.5} = -2.09$, $p = 0.13$) (Fig. 4B). Interestingly, *E. eximium* had at least marginally ($p < 0.1$) higher WUE than *E. erinaceum* across all substrates: trees ($t_{10.4} = 1.82$, $p = 0.01$), rocks ($t_{13.2} = 2.24$, $p = 0.09$), and soil ($t_{13.4} = 3.05$, $p = 0.03$) (Fig. 4C).

DISCUSSION

Epiphytic ferns are often presented as growing at their physiological limits, surviving on the edge, disconnected from the soil, and in highly competitive

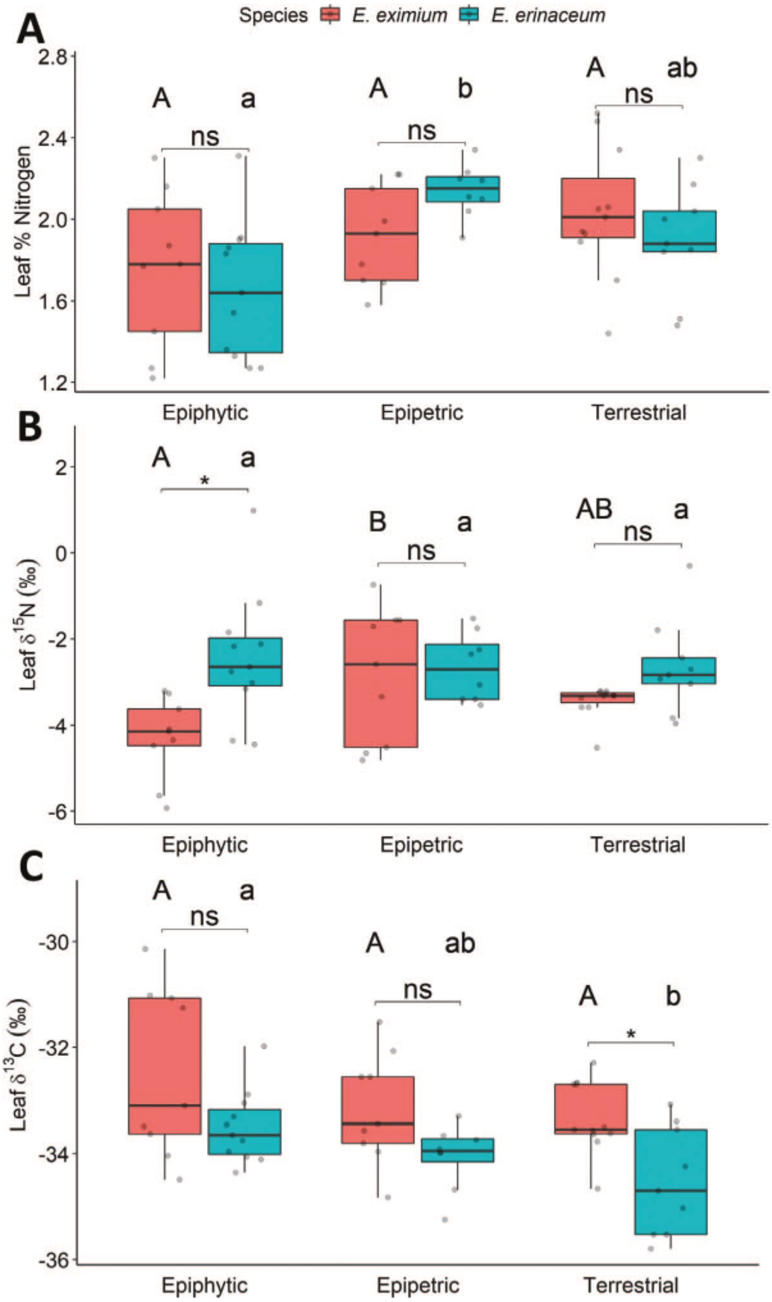

Fig. 4. Boxplots of %N (A), δ^{15}N (B), or δ^{13}C SIRs (C) for Savegre species *Elaphoglossum eximium* and *Elaphoglossum erinaceum*. Boxes represent the interquartile range and lines represent the median. Whiskers represent the highest and lowest values within 1.5 times the interquartile range. Each individual sample is denoted by grey dots. Significant differences are denoted by NS., *, **, *** corresponding to >0.05, <0.05, <.01, and <.001 p-values respectively as determined by T-tests. Uppercase and lowercase letters denote significant differences determined from ANOVA and post hoc Tukey tests performed across habitats and within species ($p < 0.05$). Colors correspond to species.

environments (Hsu *et al.*, 2012; Ding *et al.*, 2016; Santiago *et al.*, 2017). In stressful habitats, plants have a limited range of functional trait values available to them. For this reason, epiphytes are often treated as a single functional group, adapted under a similar set of limitations that produce a predictable set of morphological and physiological adaptations (Stewart *et al.*, 1995; Watkins, Rundel, and Cardelús, 2007; Mardegan *et al.*, 2011; Nitta, Watkins, Jr., and Davis, 2020). While such classifications often come from large comparative studies and have reasonable applications when comparing across habitats, they may be overly simplistic. This concept is not entirely new as some studies have suggested that there can be significant *intra*specific variation in epiphyte functional traits and such variation may surpass interspecific variation reported in some species (Petter *et al.*, 2015; Hurtado *et al.*, 2020); however few studies have carefully examined such traits in tropical epiphytic ferns. The goal of the current study is to take a closer look at inter and intraspecific trait variation in fern taxa that can grow across multiple habitats.

At the Savegre site, *Elaphoglossum eximium* and *Elaphoglossum erinaceum*, both species of the *Elaphoglossum subulata* (subulate scales) clade, grow in close proximity often intermixed on soil, rocks, and trees (Fig. 2). Morphologically, the two species are similar, and they inhabit similar niches, however their N content and δ^{15}N SIR can often differ, even when growing on the same substrate (Fig. 4B-C). The range of intraspecific and interspecific trait values suggests that the two co-occurring *Elaphoglossum* species are highly plastic and simultaneously limited by some resources and unaffected by discrepancies in others, depending on the substrate. The work of Cardelús and Mack (2009) on epiphyte mineral nutrition produced similar results: inter- and intraspecific variation in δ^{15}N SIR across an elevational gradient was high and did not correlate with differences in the mineral nutrition of the host tree or elevation, leading the authors to conclude that resource partitioning among epiphytes may contribute to high diversity in the epiphytic niche. Marks and Lechowicz (2006) describe a similar phenomenon among temperate tree species: trait values reach different optimums within a relatively homogenous niche which suggests that there is not a single combination of traits that spells success for any given habitat. Corresponding patterns have been found in non-ferns and Albert *et al.* (2011) caution that intraspecific trait variation is often incorrectly ignored in many analyses and should be incorporated more often.

The charismatic nest forming ferns characteristic of the paleotropics are nearly absent in the neotropics and those present never quite reach the size and ecological importance of old world *Asplenium* and *Platycerium*. *Niphidium crassifolium*, a neotropical species, comes in a distant third with its ability to form moderately large nests, especially in older plants (Fig. 1B). We were particularly interested in this species as 1) we suspected that nest-forming plants would be physiologically different from non-nest plants and 2) at Las Cruces, it is not uncommon to find large healthy plants firmly rooted and thriving in terrestrial mineral soil. This provided us with yet another opportunity to evaluate an epiphytic/terrestrial species with the potential addition of a nest influence. Surprisingly, we found no differences between young, non-nest forming epiphytic individuals of *Niphidium crassifolium* and older, epiphytic nest-forming individuals (Fig. 3D-F). This was quite unexpected as the non-nest forming plants were significantly smaller and likely younger than those with litter-trapping nests. At this site, Las Cruces, it was only the large plants that formed noticeable nests. Nests can typically provide benefits to epiphytes and act to store water and enhance nutrient capture (Benzing, 1989; Watkins *et al.*, 2008; Jian *et al.*, 2013). While similar but not functionally equivalent to nests, Hietz and Wanek (2003) found bromeliad species that shift from atmospheric to tank-forming morphologies exhibited a positive relationship between $\delta^{15}N$ and a negative relationship between $\delta^{13}C$ SIRs and plant size, indicating changes in N source and WUE with size, a finding reinforced by Reich *et al.* (2003). Testo and Watkins (2012) found similar size mediated changes in physiology in the non-nest forming fern *Asplenium auritum* Sw. There is evidence that both size and nest formation can influence physiology, yet we did not detect this in *N. crassifolium*.

One particularly intriguing aspect of the biology of *Niphidium crassifolium* at this site was its ability to survive and flourish on the forest floor. We discovered dozens of large plants rooted in the mineral soil and in all cases, these plants were quite large. When we compared these rooted plants to epiphytic ones, they were significantly less water use efficient (WUE), had higher foliar %N, and generally, although not significantly, utilized more highly processed N sources (Fig. 3D-F). Both patterns reflect what is typically expected in terrestrial/epiphytic comparisons. Even though these plants were rooted in the soil, their nests were still filled with fallen leaves, twigs, and other organic matter, all of which likely supplement the nitrogen and water relations of these plants. It was notable that we found no small plants growing on soil. From this, we believe that these terrestrial plants represent fallen individuals and not plants that originally established on the forest floor. In most cases, fallen epiphytic ferns that land on soil rarely survive long and typically exhibit rapid decline (J.E. Watkins pers. obs.). Yet, *N. crassifolium* frequently seems to thrive in such conditions. While most have viewed nests as an adaptation for nutrient capture and water storage (e.g., Freiberg, 1997; Turner and Foster, 2006; Suhaimi and Cicuzza, 2020), epiphytes eventually fall, and it is possible that nests serve a role in the survival and terrestrial establishment of these plants perhaps by buffering them from changes in their new microenvironment. We have also observed the phenomenon in tropical forests in Australia, where is it not uncommon to find bird's nest *Asplenium* growing on the forest floor.

Perhaps one of the most unexpected results of this work was our failure to detect a consistent difference between soil rooted and epiphytic plants of *Serpocaulon fraxinifolium*. This species is a somewhat weedy epiphyte with a green, creeping rhizome that is abundant in secondary forests. Plants did not differ with life form in any of the variables tested (Fig. 3A-C). In all cases, we carefully traced the rhizomes to their point of rooted origin and were sure that we sampled from epiphytic or terrestrial individuals and not simply from scrambling plants. This could suggest that 1) there is not an elevated level of water stress or shift in N source associated with these niches, or that 2) *S. fraxinifolium* is particularly flexible and has optimized other traits that we did not measure to offset niche differences, or that 3) unlike terrestrial and canopy habitats, the biotic and abiotic differences between the low trunk epiphytic and terrestrial niches may not be distinct enough to produce more obvious differences at this site.

The epiphytic niche is unusual in many ways and is characterized by nutrient and water poverty, comparatively higher temperatures, and brighter light than terrestrial habitats (Cardelus and Watkins 2007; Nitta, Watkins, and Davis, 2020). Combined, these conditions select for a complex set of traits in species that inhabit the epiphytic niche of tropical rainforests. It is for this reason that few species can live equally as both true epiphytic and terrestrial individuals. Overall, our paper demonstrates the dynamic nature of some taxa as they explore these habitats and is one of the few to carefully examine individual species that can cross the epiphyte/terrestrial divide. Some species like those we studied in *Elaphoglossum* and *Niphidium* reflect many of the expected functional traits reported from several studies cited above. While intraspecific functional trait exploration is limited to some degree in our data, what is notable about these taxa is their flexibility to grow in both habitats and to take on functional traits that reflect the different selective pressures of each growing condition. Perhaps more surprising is *Serpocaulon,* which, at this site, was able to grow in both habitats with little evidence of trait shifts. However, it is likely that this species exhibits other responses to these disparate environments and our ability to detect these was limited by the traits we chose. In spite of this possibility, it is noteworthy that this taxon has consistent nitrogen content and isotopic ratios across habitats, as these traits typically differ with habitat.

Taken together, the results of this study suggest that the epiphytic niche is not necessarily a stressful environment as some species can cross establish with few physiological consequences; a confirmation of the hypothesis put forth by Zotz and Heitz (2001). This niche is partitioned by different species, functional groups, and even individual plants in myriad ways, creating the conditions for hyperdiversity in a liminal habitat (Woods, Cardelús, and DeWalt, 2015; Nitta, Watkins, and Davis, 2020). Though cross establishment of ferns between epiphytic and terrestrial habitats may be uncommon, especially in seasonal lowland tropical forests (Canestraro, Moran, and Watkins, 2014), our study suggests that species found in both habitats can sometimes exhibit few measurable physiological differences between habitats, as in the case of *S. fraxinifolium*, or exhibit marked plasticity but still thrive across habitats as in the case of *Elaphoglossum* spp. Our results may have implications in understanding the functional evolution of fern epiphytes. While some have implicated the "hemiepiphytic bridge" hypothesis to explain the evolution of vascular epiphytes from terrestrial ancestors (Lagomarsino, Grusz, and Moran, 2012; Watts, Moran, and Watkins, 2019), or of hemiepiphytes from epiphytic and climbing ancestors (Testo and Sundue, 2014), our results suggest that in some lineages, radiation into the canopy may have been possible through, 1) an understory-epiphyte and/or 2) an epipetric bridge. This is perhaps especially true in wet, dark understories and less seasonal forests where the physiological barriers to cross establishment may not be as great as movement directly into the high canopy. Our data are also intriguing in their support of the potential role of the epiphytic nest in the survival and establishment of fallen epiphytes. It is possible that, in capturing fallen organic matter, nests create their own soil and have roots pre-disposed to absorbing nutrients from the mineral soil.

An important and unresolved question of this work is that of establishment. We believe it unlikely that *Niphidium* establishes on the forest floor, but we cannot say the same of *Serpocaulon*. Further investigation of the gametophyte and young sporophyte ecology of these species (and of tropical ferns in general) is required before more clear determinations can be made. However, it is clear from the sheer numbers that *Elaphoglossum eximium* and *E. erinaceum* establish across the three habitats we observed. Other biological interactions at the spore and gametophyte level such as gametophyte physiology, form, reproductive ecology, gametophyte interactions with bryophytes, etc. may limit the cross establishment of epiphytic and terrestrial ferns (Watkins and Moran, 2019; Harrington and Watts, 2021). However, more research must be done as an increasing number of studies have recently demonstrated that gametophytes often extend beyond the range of their sporophyte counterparts, possibly to explore novel habitats (Farrar, 1967; Ebihara, Farrar, and Ito, 2008; Kuo *et al.*, 2017, reviewed in Pinson *et al.*, 2017). Thus, in order to fully understand the evolution of niche partitioning across and within habitats, gametophyte ecology should not be overlooked. Overall, our study encourages us to rethink the traditional notion of the exclusive epiphytic niche and suggests that, in light of a growing body of literature, a more nuanced, species/functional group perspective be taken in future studies on epiphytes.

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