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RESEARCH ARTICLE

Source height and contact with terrestrial soil drive transplanted epiphyte performance

Michelle Elise Spicer[1,2] | **Josué Ortega**[3,4]

[1]Yale School of the Environment, Yale University, New Haven, Connecticut, USA

[2]Department of Earth & Environmental Sciences, Lehigh University, Bethlehem, Pennsylvania, USA

[3]Smithsonian Tropical Research Institute, Panama, Panama

[4]Fundación Yaguará Panamá, Panama, Panama

Correspondence
Michelle Elise Spicer
Email: michelle.elise.spicer@gmail.com

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Abstract

1. Epiphytes are characterized by their ability to survive without a root connection to the ground, but many basic life-history traits and ecological trade-offs of this unique aerial growth habit remain largely uncharacterized. Mortality causes are still not well understood, but falling from the host tree has been suggested as a leading cause of epiphyte mortality and community dynamics. Little empirical evidence exists for *why* epiphytes do not survive when forced to become terrestrial, and few studies exist that transplant epiphytes between high- and low-forest strata to test trade-offs between thriving in canopy environments and survival in the forest understorey.
2. Here, we experimentally test two hypotheses regarding the drivers of epiphyte mortality in a cloud forest of central Panama. We test whether simple contact with terrestrial soil is deleterious to epiphytes, preliminarily testing the epiphyte enemy escape hypothesis, and test the vertical niche differentiation hypothesis, wherein epiphytes are specifically adapted for microsites throughout the vertical forest strata. By monitoring survival, leaf loss and health status of 270 transplanted epiphytes for a year and a half, we pinpoint the extent to which soil contact and height of origin regulate epiphyte performance.
3. We found that contact with terrestrial soil itself was detrimental to epiphytes in situ, providing some of the first empirical data to explain why falling onto the ground, versus falling into the understorey, is particularly fatal to epiphytes. However, we also found that mortality rates vary substantially among taxonomic groups and among epiphytes that originally came from different height strata.
4. *Synthesis*. Plants that are adapted for the canopy experience a trade-off with higher mortality when in contact with terrestrial soil. Follow-up studies should explore the role of terrestrial soil microbes and physiological constraints as potential drivers of decreased grounded epiphyte survival.

KEYWORDS
aroids, bromeliads, enemy release hypothesis, ferns, leaf retention, mortality, niche, orchids, soil enemies, survival, tropical cloud forest

1 | INTRODUCTION

Vascular epiphytes contribute greatly to tropical diversity and forest function, comprising approximately 20% of the Neotropical vascular flora, mediating water and nutrient cycles and providing resources to fauna and humans alike (Coxson & Nadkarni, 1995; Gentry & Dodson, 1987a; Spicer et al., 2020; Van Stan & Pypker, 2015). Yet many fundamental ecological and life-history questions remain unanswered in epiphytes, in part due to the difficulty in accessing organisms that spend their life high in the vertical forest strata (Mondragón et al., 2015; Nakamura et al., 2017; Zotz, 2005; Zotz & Hietz, 2001). This aerial growth form and adaptations to living up in the canopy is what makes epiphytes unique, but also confers certain ecological challenges and evolutionary trade-offs (Benzing, 1987). These trade-offs are hypothesized to explain, in part, the distribution of vascular epiphytes across the globe as well as across smaller scales within forest strata (Benzing, 1987; Lüttge, 2012; Spicer et al., 2020). For example, adaptations to tolerate desiccation, such as succulent leaves, may be poorly suited to cold temperature climates, which may contribute to the limitation of most epiphytic plants to frost-free areas (Lüttge, 2012; Nobel, 2005; Zotz, 2005; but see Godoy & Gianoli, 2013). Likewise, within a tree canopy, the energy balance advantage of gaining access to high canopy light confers the heightened risk of desiccation, as well as the risk of falling to the forest floor because of high winds or host branch breakage (Gotsch et al., 2015; Matelson et al., 1993; Sarmento Cabral et al., 2015).

These life-history trade-offs vary substantially among different epiphytic taxa. Like terrestrial plants, both theoretical expectations and empirical evidence exist for niche differentiation among species and functional groups in epiphytic communities (Kelly, 1985; Lyons et al., 2000; Reyes-García et al., 2012; Woods, 2017; Zimmerman & Olmsted, 1992). Many observational studies document spatial stratification of epiphytes, both across height in the host tree and among microsites in the canopy (Johansson, 1974; Woods, 2017; Woods et al., 2015; Zotz, 2007). Many epiphytic orchids, for example, reside primarily on high-strata branches, while ferns are more common in the shaded lower strata and trunks of trees (Johansson, 1974; Kelly, 1985). This spatial stratification within host trees is a well-documented pattern in epiphyte ecology across the world, from montane cloud forests in the Americas (Krömer & Kessler, 2006; Martinez-Melendez et al., 2008) to lowland tropical forests in Africa and Asia (Johansson, 1974; Wang et al., 2016). However, many open questions remain in epiphyte niche differentiation, including how strata-exclusive different epiphytic groups are, how these differences may vary across spatial scales and whether epiphytes could in fact succeed in other vertical strata if dispersed there. One hindrance to our understanding of niche differentiation in epiphytes is the paucity of experimental work.

Evolutionary explanations for epiphyte niche differentiation also exist, but have been scarcely tested (Gentry & Dodson, 1987b; Lüttge, 2012; Sundue et al., 2015). In addition to biogeography and founder effects contributing to the patterns of evolution of epiphytism on the global scale (e.g. Gentry & Dodson, 1987b), several hypotheses highlight biotic interactions as potential drivers of epiphyte differentiation (Baguette et al., 2020; Bermudes & Benzing, 1989; Dodson, 1975; Janzen, 1974; reviewed in Spicer & Woods, 2022). Epiphytism itself may have evolved in part to escape biotic enemies in the soil, rather than strictly for abiotic reasons such as access to light (Zotz, 2016), a proposal recently coined the epiphyte enemy escape hypothesis (Spicer et al., 2020; Spicer & Woods, 2022). If modern-day epiphytes are thus adapted to thrive in the absence of terrestrial soil pathogens, then contact with terrestrial soil would be detrimental to epiphytes *even in an absence of abiotic differences in habitat*. There is evidence from one transplant experiment in a temperate rain forest that contact with terrestrial soil degrades epiphyte performance (Nadkarni & Kohl, 2018). Likewise, Titus et al. (1990) compared the germination of tropical hemiepiphytic figs experimentally planted on terrestrial soil, petri dishes or in sterilized potting soil, and found the lowest germination rates in terrestrial soil; in fact, zero figs germinated when in contact with the live soil. The authors also noted that naturally occurring fig seedlings they observed in their study area all became infected with fungi and died during the time of their experiment (Titus et al., 1990). Recent comparisons of arboreal versus terrestrial soil microbial composition show distinct microbial communities (Cardelús et al., 2009; Gora et al., 2019; Pittl et al., 2010). Gora et al. (2019) found that bacteria and fungi that decompose organic matter change in abundance, diversity and community composition along a height gradient in tropical forests, with the strongest differences being between ground samples and just above-ground samples. However, the effects of these differences in soil microbial communities have never been directly tested on epiphytes.

Host branchfall is a common yet underappreciated driver of epiphyte mortality. In one study using repeated photographs to track epiphyte population dynamics, 28% of small branches <1 cm in diameter fell within a year; for some species that occur mostly on these small branches (e.g. twig bromeliads), these branchfall dynamics correspond to an estimated half of total annual mortality (Hietz, 1997). However, for larger individuals, or epiphyte species that preferentially occur on larger branches, mortality from other causes was much more common than branchfall (Hietz, 1997). Zuleta et al. (2016) also performed repeated epiphyte surveys across a broad environmental gradient and determined that mechanical factors such as branchfall, bark sloughing and wind removal accounted for more mortality in a year than non-mechanical factors. As such, the variation in susceptibility to branchfall could act as a filter at the population level (e.g. Sarmento Cabral et al., 2015), or contribute to epiphyte diversity and community dynamics by creating fine-scale opportunities for niche differentiation. Few reports on the long-term survival of fallen epiphytes on the forest floor exist, but one study demonstrated that more than 70% of fallen epiphytes died within a year (Matelson et al., 1993). This high mortality rate for grounded epiphytes could be due to abiotic conditions such as insufficient light, biotic pressures, such as fungal pathogens or herbivory, or a combination of both. To our knowledge, no study exists that attempts to parse apart the causes of fallen epiphyte mortality. Whole host treefall, although a relatively rare temporal occurrence (van der Meer & Bongers, 1996), could also be a strong driver of epiphyte mortality. This is because the very trees that are well established as hosts to the highest diversity and abundance of epiphytes—large, tall, old trees—may also be more susceptible to mortality via water stress, lightning and windthrow (Gora & Esquivel-Muelbert, 2021; Lindenmayer & Laurance, 2017; van der Meer & Bongers, 1996; Woods & DeWalt, 2013; Yanoviak et al., 2020). Although many epiphytes on fallen trees do die (Zimmerman & Aide, 1989; Zotz, 1998), they have also been found still thriving on fallen trees for at least 3 years post-treefall, likely much longer than if the epiphytes had fallen directly to the ground (Mondragón Chaparro & Ticktin, 2011; Nadkarni & Kohl, 2018; Spicer & Ortega, pers. obs.). Depending on the size of the gap created by the treefall, an epiphyte on a fallen tree that resides only a metre or less above-ground may not experience starkly different light or relative humidity conditions than being on the forest floor. Very small-scale temperature and humidity gradients (e.g. within the first few metres) are not well documented in tropical forests, but empirical evidence and models suggest the more dramatic abiotic gradients exist higher in the canopy (Barker, 1996; Goulden et al., 2006; Smith, 1973; but see Vinod et al., 2022). Thus, biotic factors may provide more parsimonious explanations for why contact with the ground per se is so detrimental to epiphyte survival.

Here, we provide an experimental test of fundamental aspects of these two hypotheses—epiphyte enemy escape and vertical niche differentiation—to better understand the processes underlying epiphyte ecology and evolution. Specifically, we transplanted 270 epiphytes from fallen trees to new host trees such that they were either in contact with the ground or separated from the ground by one or two metres. We predicted that epiphytes in contact with the ground would perform worse than epiphytes just above the ground, simulating epiphytes falling to the ground via branch break versus via treefall. To test whether vertical niche differentiation would drive subsequent survival, we recorded the height at which the epiphytes lived in the original host tree prior to falling. We predicted that epiphytes collected from higher strata would have higher post-transplant mortality rates than those collected from the understorey strata. Finally, because we had such a diverse cohort of collected epiphytes, we explored taxonomic differences in transplant survival. We monitored the survival, health status and leaf retention of these transplanted epiphytes for 77 weeks (1.5 years).

2 | MATERIALS AND METHODS

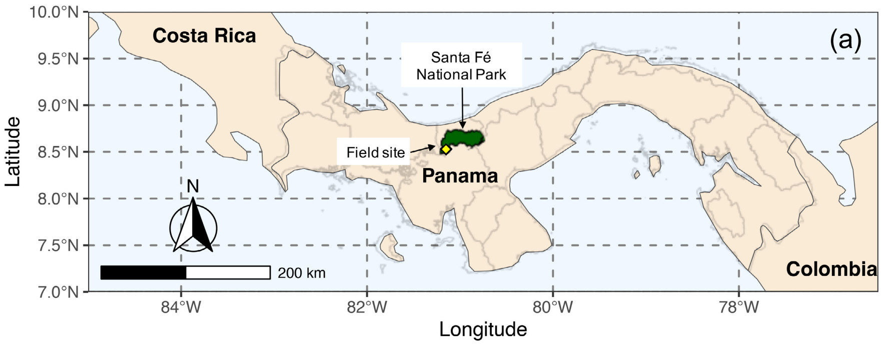
2.1 | Study site

We established our experiment in the Santa Fé National Park in Veraguas, Panama (8° 31.98′ N, 81° 9.03′ W), near the headwaters of the Santa María river. The field site is characterized by primary premontane tropical rain forest, with a highly diverse flora and fauna (ANAM, 2010, Angehr & Dean, 2010). Elevation in our plots range from approximately 750 to 820 masl and all plots are oriented on the Pacific slope of the Cordillera Central mountain range, just at the division of Atlantic–Pacific headwaters and Río Santa María (Figure 1). Heights of a subset of 30 climbable large canopy and emergent trees in the area were measured in 2017 with a laser rangefinder, and these tree heights ranged from 12 to 26 m (mean 20 m ± 0.5 m standard error); this is the closest approximation for canopy height of the study area that is available. The nearest weather station is in a cleared area in the town of Santa Fé (8° 30.64′ N, 81° 4.52′ W), at 463 m elevation and 11 km southeast of our field site; the reported mean annual temperature from 1956 to 2019 was 24.7°C (ETESA, 2019), mean annual precipitation of 2250 mm and mean annual relative humidity of 83% (ETESA, 2019; Macinnis-Ng et al., 2012, 2014). We placed an iButton datalogger (Thermochron DS1923, San José, CA) in the field site from January 2019 to January 2020, and recorded a mean of 20.8°C and mean relative humidity of 88% (Spicer et al., 2022). This datalogger was placed in the understorey near the focal plots to capture closed-canopy microclimatic conditions. Research was conducted under permit SE/AP-1-17 granted by the Republic of Panama Environmental Ministry (MiAmbiente).

2.2 | Source epiphytes

We collected adult vascular epiphytes for the experiment from four fallen trees in the study area ('donors'), of the species *Pouteria* sp. (35 cm diameter at breast height, DBH), *Siparuna* sp. (30 cm DBH), *Rollinia mucosa* (32 cm DBH) and one unknown tree species. All donor trees were recent single- or small-group treefalls, with no visible rotten areas on the trunk or inner wood. The three trees that were identified to genus or species still had some leaves, but the unknown tree species no longer had leaves on its branches. In total, we collected 270 epiphyte individuals, including holo-epiphytes (e.g. orchids and bromeliads with no root connection to the ground) as well as primary hemi-epiphytes and nomadic vines (e.g. aroids that at some point in their life cycle may have a root connection to the ground) (sensu Moffett, 2000). Epiphytes were carefully removed from fallen host trees to reduce root disturbance. All epiphytes were stored in ambient conditions in situ for less than a week between collection and experimental treatments. Although we do not know the exact date of when the host trees fell (and thus, how long the epiphytes were near to the ground prior to the experiment), all epiphytes appeared vibrant and undamaged at the start of experiment.

Plants were identified to family, separated into descriptive morphotypes (putative species groups) and photographed. We collected vouchers of nearby fertile specimens that corresponded to the morphotypes in the experiment throughout field seasons at the site in 2017–2019 and 2022, and deposited them in the University of Panama Herbarium (PMA) under MiAmbiente permits SE/AP-1-17, SE/AP-5-2018, SE/AP-6-19 and ARG-016-2022. Voucher specimens were identified by local experts and matched to the morphotypes via photos.



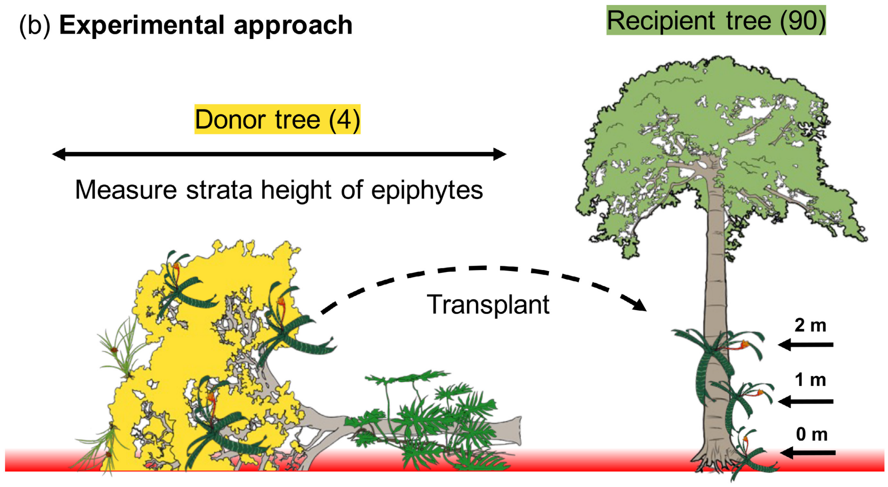


FIGURE 1 (a) Map of the study area. Santa Fé National Park is outlined in green, in the northern part of Veraguas province. The study site is marked with a gold diamond in the southwest section of the Park. (b) Experimental design of experiment, illustrated for one recipient tree. Two hundred and seventy epiphytes were collected from four fallen donor trees and experimentally transplanted to 90 standing recipient trees at heights of 0, 1 or 2 m from the forest floor.

When positive species or genera identifications were not able to be confirmed via photographs (e.g. distinguishing *Elleanthus* from *Sobralia* without an inflorescence), we kept the standardized morphotype name. We used 93 individuals in the Orchidaceae family (34% of the total number of epiphytes), 84 Bromeliaceae (31%), 51 Araceae (19%), 27 pteridophytes in various families (10%) and 15 Piperaceae (6%).

2.3 | Experimental design

To test whether contact with the ground per se mediates epiphyte survival and performance, we transplanted the fallen epiphytes onto new host trees ('recipients'). We placed the epiphyte on the trunks of recipient trees at one of three heights: in contact with the ground at 0 m, at 1 m or at 2 m above the ground (Figure 1b). We adhered the epiphytes to their new host trees with twine that degrades slowly over the course of a year. We set up the experiment in a nested spatial design to facilitate high-frequency data collection in a logistically challenging site. Fifteen recipients were haphazardly selected from within six accessible areas ('plots'), for a total of 90 trees. We selected only trees that already had at least three adult vascular epiphytes below 5 m on them, as a proxy for habitat suitability.

We tested the degree to which height niche differentiation could mediate transplant survival by recording the height at which the epiphytes were established on their original donor tree. We measured original heights in continuous 2-m bins (0–2 m, 2–4 m etc.), as well as categorized them into the Johansson zones 1–4 (Johansson, 1974). Johansson zones (JZ) are frequently used to account for differing total heights of the donor trees; the 'upper canopy' may be at 10 m when the overall canopy height is low, and 40 m in a taller canopy tree. The Johansson zones have been a useful tool to compare forests across many regions, but have also historically failed to characterize epiphytes on small trees and branches in the understorey (Zotz, 2007). We did not collect any epiphytes from small upper crown branches, so Johansson zone 5 (outer third of large branches) and small diameter branch epiphytes are not represented in our data (Table ST1).

2.4 | Data collection

Because there is very little literature on the in situ mortality of such a wide variety of epiphyte species, and over 70% of fallen epiphytes have been reported to survive less than a year (Matelson et al., 1993), we collected data on a weekly basis for the first 7 weeks. Thereafter, we decreased our frequency of data collection to once per 2–3 weeks until week 22. At this point, the rainy season precluded more frequent data collection and we collected data at three more time points, at week 36, week 58 and week 77, for a total of 16 data collection time points. At each time point, we visually inspected each transplanted epiphyte and categorically classified health status, with a score of zero for dead, one for damaged or unhealthy and two for appearing perfectly healthy and vibrant (Table ST2; Nadkarni & Kohl, 2018). We also counted the total number of living leaves.

2.5 | Statistical analyses

2.5.1 | Cumulative effects of transplant height, source height and taxonomic group on epiphyte performance

We first built a set of generalized linear mixed models using only the data from the final census (77 weeks). These models allowed us to test whether our three predictors of interest drove *cumulative* epiphyte performance across the whole year and a half of the experiment. All models included the main effects of the three predictors, as well as random effects of plot to represent our experimental design and avoid pseudoreplication (Hurlbert, 1984). We did not have sufficient replication of epiphytes within all taxonomic groups to include any three-way interactions, but included the two-way height-by-taxonomic group, transplant height-by-original height and original height-by-taxonomic group interactions in the models where possible. Each model is described below and reported in Table 1 and Table ST3. The three response variables we ran in final analyses were epiphyte survival (binary: alive or dead), health status (ordinal: dead<unhealthy<healthy) and change in leaf abundance (continuous: number of live leaves gained or lost throughout the whole experiment). Data and errors were modelled as suggested in Bolker et al. (2009) and Zuur et al. (2009): Survival was modelled as a binomial distribution with a logit link function, health status as multinomial with a logit link function and net leaf abundance as binomial (leaf gains as wins and leaf losses as losses, weighted by total number of leaves) with a log link (R Core Development Team, 2019). The three analyses (survival, health status and leaf abundance) were run with all 270 epiphytes included. Post hoc pairwise comparisons were run using the *emmeans* function in the *emmeans* package when we found statistical differences among our predictor transplanted height groups or taxonomic groups (Lenth et al., 2018). When significant interactions were found in the main analyses, we separated into subgroups and reran follow-up models without the interactions.

2.5.2 | Survival rates through time

Next, we ran a complementary set of survival analyses, including data from all 16 data collection time points; these analyses tested the *rate* of change, rather than the ultimate cumulative differences after 77 weeks. We created survival curves from the Kaplan–Meier formula and tested whether the survival curves differed among the three transplant heights, binned original heights and the taxonomic groups with a Cox hazards model, including epiphytes that were still alive at 77 weeks as censored data points (Andersen & Gill, 1982; Kaplan & Meier, 1958).

All analyses were run with R version 3.4.2.0 (R Core Development Team, 2019) in the R Studio platform. GLMMs were run with the package *lme4* version 1.1–21 (Bates, 2016) and Type-II ANOVA results interpreted with the *Anova* function in the *car* package version 3.0–12 (Fox & Weisberg, 2019). Multinomial analyses for ordinal health status data were modelled in the *ordinal* package version 2022.11–16 (Christensen, 2022). Longitudinal survival analyses were run in the package *survival* version 3.3–1 (Therneau, 2023) and visualized with the package *survminer* version 0.4.9 (Kassambara et al., 2020). Figures were

TABLE 1 Results of statistical tests of the effects of experimental transplant height, height in the original source tree (pre-transplant), epiphyte taxonomic group and their interactions on transplanted epiphyte performance metrics, as measured at the end of the experiment (77 weeks). Estimates of the coefficients and errors for each variable are provided in Table ST3.

	Dependent variable								
	Survival			**Health status**			**Leaf abundance change**		
Predictor	**Chisq**	**df**	***p*-value**	**Chisq**	**df**	***p*-value**	**Chisq**	**df**	***p*-value**
Transplant height (height)	6.03	2	0.049*	6.89	2	0.032*	8.49	2	0.0003***
Source height (source)	3.57	1	0.059.	3.23	1	0.073.	8.48	1	0.0047**
Taxonomic group (taxa)	9.98	4	0.041*	8.26	4	0.082.	39.1	4	<0.0001***
Height*Source	0.27	2	0.867	0.51	2	0.777	8.23	2	0.018*
Height*Taxa	4.70	8	0.789	5.90	4	0.207	32.9	8	—
Source*Taxa	3.77	4	0.439	9.91	8	0.207	18.6	4	0.0045**
Random *Var*		0.35			0.30			1.13	
Random *StDev*		0.59			0.55			1.01	
Observations (*N*)		270			270			270	
Log likelihood		−156.1			—			−426.1	
Akaike Inf. Crit. (*AIC*)		358.2			—			882.3	
Bayesian Inf. Crit. (*BIC*)		440.9			—			936.2	
R^2_m (†McFadden)		0.33			0.06†			0.44	
R^2_c (†Nagelkerke)		0.40			0.13†			0.77	

Significance symbols: *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001; †specifies type of R^2 value.

created using version 4.2.0 of the *graphics* package (R Core Development Team, 2019) and version 3.3.6 of *ggplot2* (Wickham, 2016).

3 | RESULTS

3.1 | Preliminary test of the epiphyte enemy escape hypothesis

We found some support for our predictions of the epiphyte enemy escape hypothesis, wherein epiphytes transplanted in contact with the ground performed worse than epiphytes transplanted just a few metres above them. Epiphytes at 0m had a 14% higher chance of being found dead at 77weeks in comparison to epiphytes transplanted at 1m or at 2m (Figure 2a, Table 1). Notably, post hoc tests showed that the survival was marginally higher at both 1 and 2m when compared to epiphytes at 0m, but did not differ between 1 and 2m epiphytes. Transplant height also had a significant overall effect on health status (Figure 2d, Table 1; see Table ST4 for health status of just surviving epiphytes). Post hoc tests showed epiphytes at 1m had a higher health status than epiphytes on the ground, and epiphytes at 2m had marginally higher health status than epiphytes on the ground, but health of epiphytes at 1 and 2m did not differ at the end of the experiment. Overall, 66% of the epiphytes lost leaves over the year and a half (179/270); 24% gained leaves (64/270) and 10% had no net change in leaf abundance throughout the experiment

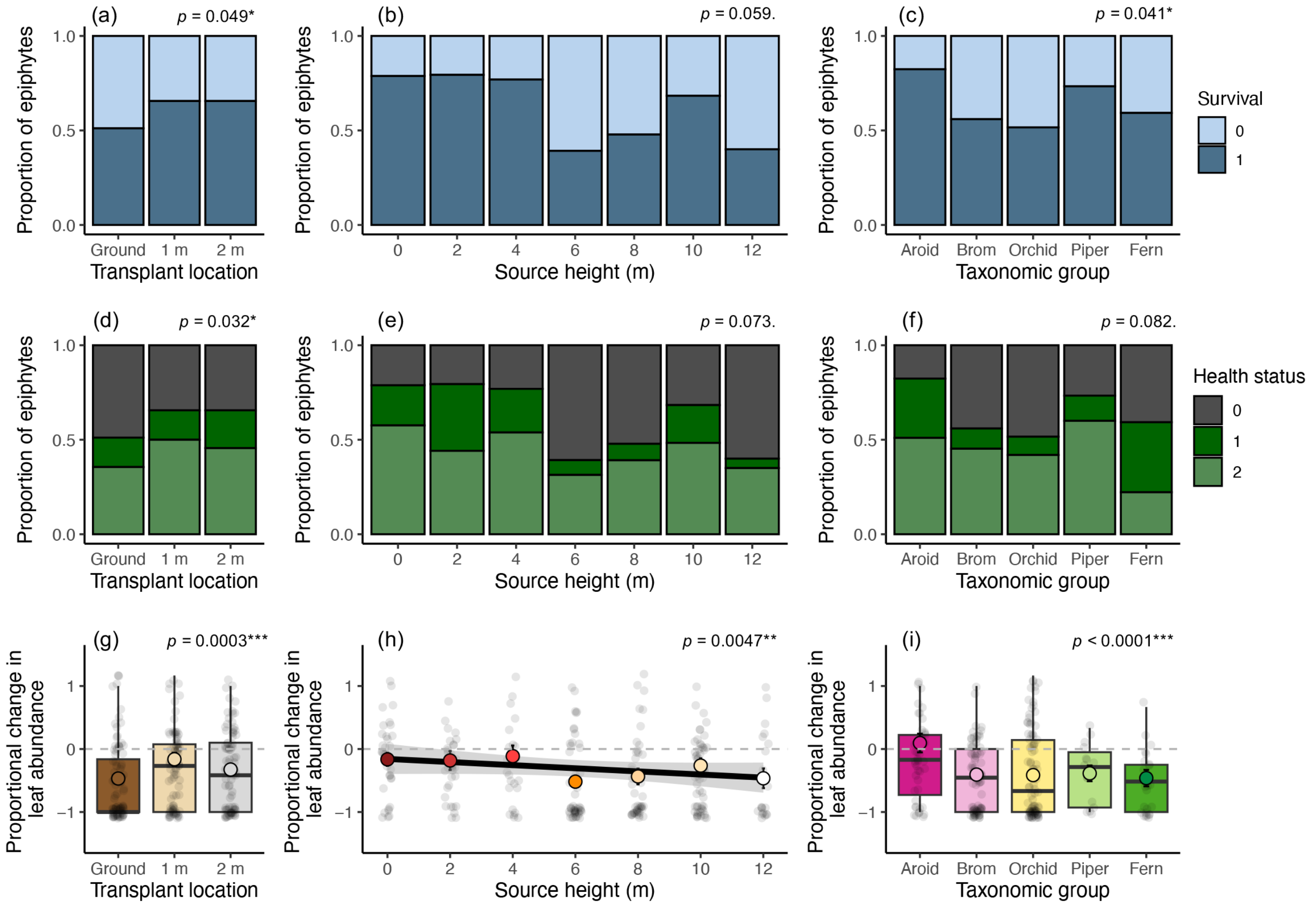


FIGURE 2 Main effects of transplant height, source height and taxa on transplanted epiphyte performance at 77weeks, with binary and ordinal data displayed as stacked bars. Epiphyte responses to (a, d, g) transplanting to 0m (in contact with the ground), 1m or 2m high in the recipient tree (separated from the ground); (b, e, h) to source height (where the epiphyte was collected in the original host tree); and (c, f, i) among epiphytic taxonomic groups (Aroid = Araceae, Brom = Bromeliad, Orchid = Orchidaceae, Piper = Piperaceae and Fern = Pteridophyta). Responses displayed are, from top panel to bottom: (a–c) Survival, as a proportion of all epiphyte individuals (90 per treatment height; $N = 270$); (d–f) Health status of plant, where a higher number indicates better leaf condition, as a proportion of epiphytes in each group ($N = 270$); and (g, h, i) Proportional change in leaf abundance, calculated as the difference between the number of leaves present at 77weeks and the number of leaves present at the first survey, divided by the number of leaves present at the first survey. Zero line indicates the epiphyte retained the same number of leaves throughout the whole experiment ($N = 27$), >0 indicates net leaf gains ($N = 64$), and <0 indicates net leaf losses ($N = 179$). Open circles denote group means, and error bars represent standard error, as calculated numerically to illustrate main effect group differences. Data points that lie outside of 1.5 times the interquartile range in (g–i) are omitted for clarity, but all data points were included in analyses. Raw data for all response variables are shown in Figure SF2. Details of statistical tests are reported in Table 1 and Table ST3, and significant interactions for (g–i) are displayed separately in Figure SF1.

(27/270). Epiphyte leaf loss or gain depended on the interacting effects of transplant height and source height (Table 1). Although epiphytes that were transplanted to 1 m or 2 m consistently retained more leaves than those transplanted to the ground, epiphytes that originated from low in the forest strata did comparatively better when transplanted to 1 m than high-canopy epiphytes transplanted to 1 m (Figure 2g, Figure SF1A). In other words, source height only mediated the gain or loss in leaves for epiphytes at 1 m, but not for 0 m or 2 m (Figure SF1A). Longitudinal survival rates through time did not significantly differ among epiphytes transplanted at different heights, although the survival rates were ordered as expected (Figure 3a). This is likely due to loss of statistical power in the longitudinal study (discussed below).

3.2 | Test of the vertical niche differentiation hypothesis

We also found some support for the vertical niche differentiation hypothesis. The measured original height of the epiphytes in source trees was a marginally significant negative predictor of both mortality (Figure 2b, Table 1) and health status (Figure 2e, Table 1). Source height also had interacting effects on leaf retention with transplanted height (as discussed above, Figure 2h, Figure SF1A, Table 1), as well as with taxonomic group (Figure 2h, Figure SF1B, Table 1). Mortality rates, when analysed longitudinally across all the census points, differed among epiphytes from various heights in the donor trees (Figure 3b,c). Regardless of whether we categorized the source

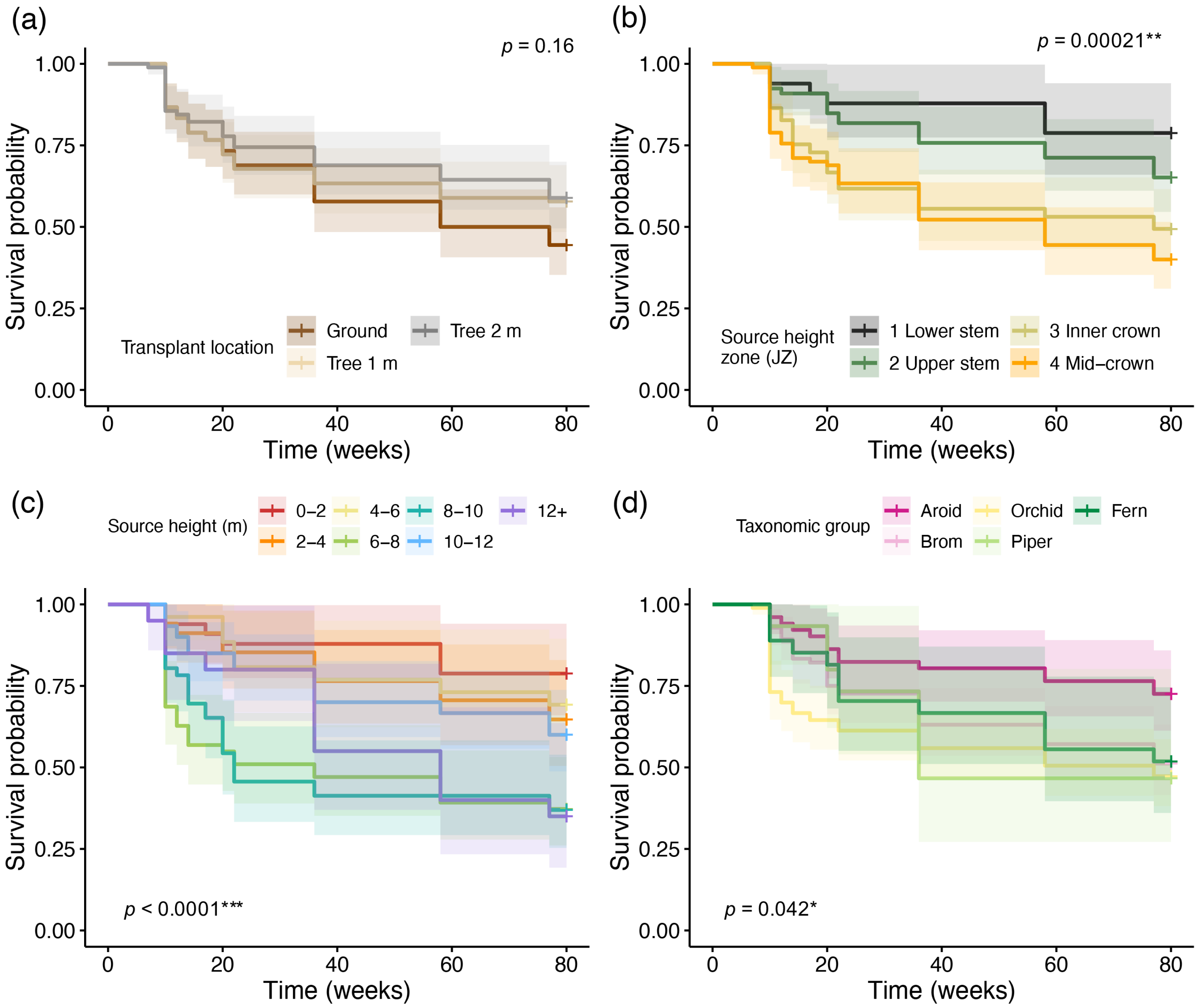


FIGURE 3 Survival curves for epiphytes throughout the 77 weeks of the experiment. All epiphytes that were still alive during the last survey were coded as truncated at 80 (+ signs). Epiphytes are grouped by (a) transplant height, (b). height strata in the original donor tree, categorized into four Johansson zones (1 = Lower stem, 2 = Upper stem, 3 = Inner crown, 4 = Mid-crown; we did not collect any epiphytes from JZ5, the outer crown), (c) height in the original donor tree, measured in 2 m height bins and (d) taxonomic grouping (Aroid = Araceae, Brom = Bromeliaceae, Orchid = Orchidaceae, Piper = Piperaceae, and Fern = Pteridophyta).

heights into Johansson zones (Figure 3b) or left them in measured 2m bins (Figure 3c), high-canopy epiphytes died faster than low-canopy epiphytes. When categorized into Johansson zones to account for differing maximum height of tree, mortality rates were ordered exactly as expected, with epiphytes from zone 1 (lowest) having the shallowest curve, then zone 2, zone 3 and finally zone 4 (highest) with the steepest mortality curve.

3.3 | Taxonomic variability in transplanted epiphyte performance

Taxonomic groups varied in their performance throughout the experiment as well. Overall survival rates over the 77 weeks of the experiment were Araceae (82%), Piperaceae (73%), Pteridophyta (59%), Bromeliaceae (56%) and Orchidaceae (52%) (Figure 2c, Table 1). There were also marginal differences in final health status across taxa (Figure 2f, Table 1); Araceae generally were healthier than Pteridophytes and orchids by the end of the experiment. As mentioned above, the epiphytes varied along taxa, source height and transplant location for leaf retention (Figure 2i, Figure SF1B); this model also explained a high amount of variance in the data (Table 1). Longitudinal epiphyte mortality differed among taxa as well, with orchids and bromeliads dying off slightly quicker than the other groups (Figure 3d).

4 | DISCUSSION

Fallen epiphytes have only been the focus of a few ecological studies, even though mechanical failure may cause the majority of adult epiphyte deaths (Matelson et al., 1993; Nadkarni & Kohl, 2018; Zuleta et al., 2016). As aptly noted in Sarmento Cabral et al. (2015), fallen epiphytes thus provide an overlooked opportunity to probe a variety of ecological questions, from population dynamics to ecosystem services. We found that contact with terrestrial soil itself was detrimental to epiphytes in situ, providing some of the first empirical data to show that falling onto the ground, versus falling into the understory, is particularly fatal to vascular epiphytes. However, we also found that mortality rates vary substantially among taxonomic groups and among epiphytes that originally came from different height strata.

4.1 | Some support for the epiphyte enemy escape hypothesis

Like in terrestrial plants, light and water availability are strong drivers of epiphyte dynamics (e.g. Laube & Zotz, 2003). In the spatial scale of only a few metres within the understorey, the microclimatic abiotic conditions likely vary little, and they may play a comparatively smaller role in structuring epiphyte communities (Barker, 1996; Goulden et al., 2006; Smith, 1973), but see Vinod et al. (2022). Microbial communities are distinct between terrestrial and epiphytic habitats (e.g. Cardelús et al., 2009; Looby et al., 2019; Vance & Nadkarni, 1990), likely even over small distances (Gora et al., 2019). As has often been proposed for invasive species that can flourish when released from their native enemy predators, herbivores, competitors or pathogens (e.g. Keane & Crawley, 2002; reviewed in Mlynarek et al., 2017), the epiphyte enemy escape hypothesis suggests that epiphytism could confer the advantage of no longer interacting with enemies in the terrestrial soil. In turn, relaxed selection on defensive traits could leave epiphytes more susceptible to terrestrial enemies. We hypothesized that the *net effect* of terrestrial soil on epiphytes would be negative, both because of the evolutionary separation of the microbes and epiphytes (e.g. Lehnert et al., 2017), and because we assumed pathogenic soil microbes would outweigh effects of beneficial microbes.

Our results were consistent with the terrestrial soil playing some role in the decline in vigour of the epiphytes. In our experiment, epiphytes in contact with the ground experienced 14% higher mortality rates over a year and a half. Similar to what Nadkarni and Kohl (2018) demonstrated in bryophytic epiphytes in a temperate rainforest, epiphyte vitality ('health status') was also lower for epiphytes in contact with the ground, and our experiment showed higher leaf loss for the ground epiphytes. However, epiphyte mortality rates through time did not differ significantly between transplant height, indicating relatively slow dynamics or individual (intraspecific) differences in mortality rates. Indeed, we started the experiment re-surveying epiphytes on a weekly basis, expecting high mortality immediately. The detrimental effects of soil contact may have been stronger had we continued the experiment for longer; many tropical vascular epiphytes have relatively tough, long-lived leaves and relatively slow life cycles. Ultimately, we collected 16 data points in which only the last few had any noticeable differences between groups. Future studies may consider less frequent, but longer term, surveys to better allocate resources in similar wet premontane epiphyte communities. Soil enemies are also likely to be most deleterious to epiphytes at an earlier, more vulnerable, life stage than what we used in our experiment. Titus et al. (1990) and Zotz (2016) reported complete mortality of young epiphytes in live soils (hemiepiphytic *Ficus* seedlings, and *Clusia uvitana* plantlets, respectively), both suggesting soil pathogens as the cause of death.

Our experiment only scratches the surface of addressing the epiphyte enemy escape hypothesis. For the first time, we compared the effect of soil contact, as would happen for an epiphyte falling off the tree to the ground, with the effect of microclimate changes. The differences we show in decreased epiphyte performance on the ground support the initial assumption of the epiphyte enemy escape hypothesis: that terrestrial soil per se is detrimental to epiphytes. Because we neither surveyed the microbial community nor experimentally manipulated the soil microbes, we cannot extend our results to the mechanisms behind mortality. Moreover, additional mechanisms for high mortality on the terrestrial soil, such as competition, soil-dwelling herbivores or lack of tolerance to rooting in such moist conditions are alternate explanations for the advantages of becoming epiphytic (or the exclusion of being on the ground) (Zotz, 2016). We leave this exciting work for future research.

4.2 | Experimental evidence for niche differentiation among epiphytes

We also found support for the niche differentiation hypothesis among epiphytes; as predicted, high-canopy epiphytes performed worse than low-strata epiphytes when transplanted to the understorey. Even considering the interactions, all three main metrics had overall negative correlations with source height (Figure 2h, Figures SF1 and SF2). Although stratification of many epiphytes among vertical forest layers has been well documented (e.g. Johansson, 1974; Zotz, 2007), here we focus on the survival implications of this stratification. The patterns we found are consistent with epiphytes being adapted for certain height strata and experiencing trade-offs; physiological constraints of high-canopy epiphytes such as adaptations to desiccation, high light requirements or roots adapted for adhesion rather than water absorption may preclude them from succeeding on the forest floor (summarized in Zotz, 2016 table 1.1). We did not quantify physiological traits of the epiphytes, but this would be a fruitful future study. Recent epiphyte functional trait studies (e.g. Hietz et al., 2022; Petter et al., 2016) and open databases of epiphyte traits (e.g. EpIG-DB; Mendieta-Leiva et al., 2020) will continue to facilitate further mechanistic analysis of life-history trade-offs.

4.3 | Taxonomic variability in epiphyte transplant success: Implications for tropical forest management

Understanding which epiphytes perform well post-transplant (Figures 2c,f,i and 3d) could eventually contribute to better biodiversity conservation practices in managed tropical forests. Little information exists on survival of epiphytic ferns, aroids or Piperaceae even though these three groups make up approximately 21% of epiphytic species diversity (Zotz, 2013). We provide mean survival rates of these three understudied taxonomic groups as well as the hyperdiverse orchid and bromeliad families (see Section 3), and demonstrate >50% survival rates in all five groups of transplanted epiphytes. Moreover, little ecological information exists for the epiphyte species in Santa Fé National Park (listed in Table ST5). Aroids did particularly well, with mean survival rates of >80% in all three transplant locations. Aroids are most frequently found in the understorey and are well suited for the humid, low-light conditions near the forest floor, even post-transplant. We did not specifically subdivide aroids into hemi-epiphytes, holo-epiphytes and nomadic vines (see discussions in Bautista-Bello et al., 2021; Zotz et al., 2021), but it seemed that almost all aroids recovered from being removed and transplanted to new trees, including nomadic vines. The most common of the aroid species in our experiment was *Anthurium vallense* Croat, a species that in our site occurs primarily as a holoepiphyte, but is listed on GBIF as also occurring terrestrially (GBIF Secretariat, 2022). Intraspecific flexibility in growth form could contribute to overall high performance when transplanted. Even orchids, which are frequently, but not always, categorized as high-canopy epiphytes (e.g. Johansson, 1974), had survival rates of over 50% overall, despite being moved to the shaded understorey. Although we cannot directly compare to repeated ground surveys due to differing experimental designs, our mortality rates of just the subset of epiphytes in contact with the ground was 51% at approximately 1 year (58 weeks), substantially lower than the 70% mortality rate of fallen epiphytes reported over a year from a cloud forest in Costa Rica (Matelson et al., 1993).

Transplanting epiphytes fallen to the ground, like we did in our experiment, could offer biodiversity conservation and socioeconomic co-benefits. Many epiphytes, especially orchids and bromeliads, are valued as commercial species. Although wild harvesting of epiphytic species can provide social benefits and sometimes be sustainable, concern is growing that overharvesting also threatens many epiphyte populations (Elliott & Ticktin, 2013). Unfortunately, although many countries have consequently banned trade and sale of wild-harvested orchids and bromeliads (e.g. CITES species), collection still occurs (Flores-Palacios & Valencia-Díaz, 2007). Collection of wild epiphytes for profit from *fallen* trees or from the ground may be a more sustainable alternative to harvesting off of live trees. Practitioners could also partner with industries such as coffee or palm production, which already remove and discard epiphytes (Acuña-Tarazona et al., 2015; Prescott et al., 2015; Toledo-Aceves et al., 2013, 2014). Simple re-attachment of fallen epiphytes to nearby trees could potentially provide a cheap, time-efficient method to enhance epiphyte populations, decrease ecological impacts in degraded landscapes and in some locales, contribute to sustainable local ecotourism. In Santa Fé, for example, rural ecotourism is a relatively new industry, but the tourism cooperative has already highlighted orchids as a natural attractor to the area (IICA, Instituto Interamericano de Cooperación para la Agricultura, 2014). Although our study area forest was intact, this methodology could potentially be particularly useful in secondary forests, which, unaided, may take several decades to accumulate dense and diverse epiphyte assemblages similar to old-growth forests, yet are important reservoirs of epiphyte propagules (Acuña-Tarazona et al., 2015; Hietz et al., 2012; Woods & DeWalt, 2013).

4.4 | Caveats and limitations

There are several limitations to our study, which should be taken into consideration when extending our results to other systems or designing follow-up experiments. First, we did not directly test whether the microbial community in the terrestrial soil caused the difference in epiphyte performance among the three transplant heights, because we did not have reciprocal transplants of soil to the higher heights (1 and 2 m). This would be an excellent way to parse apart the contribution of the soil from the potential contribution of other abiotic differences in microhabitat within the small height gradient (0–2 m). In addition, fine-scale measurements of abiotic factors such as relative humidity, temperature and light may have added explanatory power to the models, as well as directly confirmed our assumption of relatively small abiotic gradients along our height gradient. It is also possible that the epiphytes we used in the experiment had already been somewhat filtered for survival after the experimental changes by the treefall; that is, particularly sensitive species or individuals may have already died before we harvested the epiphytes. Ideally, opportunistic treefall experiments should attempt to minimize the time between the treefall and the survey of the epiphyte community. Finally, because of the high variability of the epiphyte performance among taxonomic groups, 270 individuals was not a sufficient sample size to test all the interactions among the factors of interest. A higher overall replication would have allowed us to better characterize the relative strength of soil contact, abiotic conditions and taxonomic group on the performance of the transplanted epiphytes. In addition, a functional trait or phylogenetic approach would be complementary in the future to provide evolutionary context and to identify physiological trade-offs underlying the taxonomic patterns we found.

5 | CONCLUSIONS

Here, we experimentally tested drivers of fallen epiphyte performance across a broad taxonomic range. Our research provides basic mortality rate data for many epiphytic species previously not studied, as well as tests two key hypotheses regarding the ecological trade-offs of epiphytism and the distribution of these diverse communities along vertical forest strata. We suggest that future research further parses apart the mechanisms by which terrestrial soil is detrimental to epiphytes; in particular, we suggest probing the extent to which soil microbial communities may drive epiphyte mortality. This area of research could shed much-needed light on several fundamental questions remaining in epiphyte ecology and evolution.

AUTHOR CONTRIBUTIONS

Michelle Elise Spicer and Josué Ortega conceptualized the research and performed the fieldwork and data collection. Michelle Elise Spicer entered, analysed and visualized the data and wrote the original manuscript draft. Both authors contributed to editing the manuscript.

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CONFLICT OF INTEREST STATEMENT

None.

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DATA AVAILABILITY STATEMENT

Data and R code are deposited in Dryad at the link: https://doi.org/10.5061/dryad.k6djh9wcd (Spicer & Ortega, 2023).

ORCID

Michelle Elise Spicer https://orcid.org/0000-0003-0613-415X
Josué Ortega https://orcid.org/0000-0001-9690-989X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure SF1. A. Original source height-by-transplanted height interactive effects on epiphyte leaf abundance (net gains or losses of leaves).

Figure SF2. Main effects of transplant height, source height, and taxa on transplanted epiphyte performance at 77 weeks.

Table ST1. Height zone categorizations for donor trees.

Table ST2. Health status categorizations.

Table ST3. Model coefficients and error estimates.

Table ST4. Health status analyses for subset of epiphytes that survived the whole experiment.

Table ST5. List of epiphytes.

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