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Source: The Journal of the Torrey Botanical Society, 149(1) : 86-97

Published By: Torrey Botanical Society

URL: https://doi.org/10.3159/TORREY-D-21-00038.1

Journal of the Torrey Botanical Society 149(1): 86–97, 2022.

Substrate texture and natural removal processes mediate vascular epiphyte establishment: Experimental evidence from a Panamanian cloud forest[1, 2]

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Abstract. Epiphytes are a unique group of plants that live nonparasitically on other plants ("hosts") and constitute approximately one-fifth of Neotropical vascular plant diversity. However, the processes governing early epiphyte community assembly are poorly understood and have scarcely been experimentally tested. Here, we use an *in situ* experiment in the cloud forest of Santa Fé, Panama, to evaluate the extent to which host substrate texture regulates early epiphyte establishment. We experimentally varied the surface roughness of native wood substrates, applied bromeliad and orchid seeds to the substrates, and monitored emergence of epiphyte seedlings and their persistence for a year. Rougher substrates facilitated higher initial abundance of epiphyte seedlings; after two months, 81% of the 1,934 total germinated epiphytes occurred on the substrates with experimentally added roughness. Via photo analysis, we also show that epiphytes disproportionately established early on in the experimental grooves, wherein 71% more epiphytes per unit area occurred within 1.5 mm of the grooves than on nearby smooth surfaces. While epiphyte cohort survival rates differed between rough and smooth substrates in the first six months, more than 99% of all seedlings died after one year, regardless of experimental roughness treatment. Only 10 seedlings survived through the end of the experiment. Our results suggest that while substrate texture explains some variation in early epiphyte emergence, roughness alone is not sufficient to explain epiphyte persistence to adulthood. Moreover, our results highlight the importance of removal processes (*e.g.,* wind, rain, animals) in structuring early epiphyte community assembly. Variation in substrate texture may contribute to differences in epiphyte diversity and community composition within- and among-host tree species, but more experiments are needed to disentangle removal processes from substrate-mediated host affinity.

Key words: Bromeliaceae, community assembly, epiphytes, establishment, germination, microhabitat, niche, Orchidaceae, rugosity, tropical cloud forest

Epiphytes, or plants that live nonparasitically on other plants ("hosts"), constitute approximately one-fifth of Neotropical vascular plant diversity (Spicer *et al*. 2020, Zotz 2013) and can account for the majority of all vascular plant species in montane forests (Kelly *et al*. 1994). They mediate ecosystem function by enhancing water capture per unit forest area, increasing nutrient retention, and contributing to aboveground biomass (Nadkarni 1984, Coxson and Nadkarni 1995, Holwerda *et al*. 2010, Van Stan and Pypker 2015). Epiphytes increase forest heterogeneity by providing structural complexity and fine-scale microclimatic variability (Ortega-Solís *et al*. 2017, Borst *et al*. 2019). They facilitate high arthropod diversity and abundance (Stuntz *et al*. 2002, Ellwood and Foster

[1] We thank Chefín and Fletcher of Santa Fé, Panama, for their assistance in the field, Rodolfo Flores for identifying host trees, and Orlando Ortiz and Bonarge Rodríguez for identifying epiphyte specimens. Initial design of the project in 2016 was aided by critique from Gerhard Zotz and Joe Wright. We thank the Republic of Panama and MiAmbiente for permitting us to do research in Santa Fé National Park, and the PNSF guardabosques for logistical support. We thank Yusan Yang, Sergio Ramos, Gerhard Zotz, and several anonymous reviewers for comments that improved the manuscript. Funding for the research came from the The Beverly Schnitzer Endowment via a Smithsonian Tropical Research Institute Short-term Fellowship to MES and the University of Pittsburgh Center for Latin American Studies (Fabiola Aguirre Fellowship to MES). This article was edited while MES was supported by the NSF Postdoctoral Research Fellowship in Biology under Grant #1907190.

[2] Supplemental material for this article is online at http://dx.doi.org/10.3159/TORREY-D-21-00038.s1.

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doi: 10.3159/TORREY-D-21-00038.1

Received for publication October 29, 2021, and in revised form January 31, 2022; first published March 28, 2022.

2004, Díaz *et al*. 2012, Angelini and Silliman 2014, Rogy *et al*. 2019), provide novel breeding habitat that is otherwise limiting to some species of amphibians and birds (Nadkarni and Matelson 1989, Scheffers *et al*. 2014), and can create climate refuges for animal species (Scheffers *et al*. 2014, Seidl *et al*. 2020). Despite their clear ecological importance, the ecology of epiphytic plant communities is much less well-understood than terrestrial plant ecology.

The processes and mechanisms driving epiphyte community assembly and development remain largely debated and rarely tested experimentally (Burns 2007, Mendieta-Leiva and Zotz 2015, Woods 2017, Spicer and Woods 2022). A recent study that monitored vascular epiphyte community composition and diversity over more than a decade showed strongly directional changes, providing some of the first evidence for deterministic, niche-based mechanisms as the dominant driver of vascular epiphyte assembly (Mendieta-Leiva *et al*. 2021). In nonvascular epiphytes and epiphytic lichens, several observational studies and a few experiments show an important role of dispersal limitation (*e.g.,* Sillett *et al*. 2000), environmental filtering based on species traits (Gjerde *et al*. 2012, Schei *et al*. 2012), and epiphyte-epiphyte biotic interactions in shaping community assembly (reviewed in Ellis 2012, Sillett and Antoine 2004, Spicer and Woods 2022). For both epiphytic and terrestrial plants, the earliest life stage transitions are key bottlenecks to individual survival and community development (Harper 1977, Ackerman *et al*. 1996, Zotz and Vollrath 2002, Mondragon and Calvo-Irabien 2006, Victoriano-Romero *et al*. 2017).

Epiphytes face the unique challenge of adhering to their arboreal substrate. Because epiphytes need specific arboreal microclimatic conditions to germinate, and cannot survive on the ground if they fall, they must adhere well to arboreal substrates early in their life cycle (Madison 1977, Matelson *et al*. 1993, Goode and Allen 2009, Mondragón *et al*. 2015, Jiménez-Salmerón *et al*. 2017, Ji *et al*. 2018). Thus, host bark characteristics can be vital to epiphyte establishment and subsequent community development. For example, bark that absorbs water may reduce moisture stress for epiphytes (Callaway *et al*. 2002, Mehltreter *et al*. 2005, Mondragón *et al*. 2015). Rough bark can also host more diverse and abundant nonvascular epiphytes (Sillett and Antoine 2004, Gradstein and Culmsee 2010) and epiphytic lichens (Lamit *et al*. 2015), which could further reduce water stress for vascular epiphytes or facilitate vascular epiphyte succession (Jarman and Kantvilas 1995, Nadkarni 2000, Callaway *et al*. 2001, Ellyson and Sillett 2003). Bark exfoliation and allelopathic compounds, on the other hand, may inhibit germination, seedling growth, or survival (Valencia-Díaz *et al*. 2007, 2010; López-Villalobos *et al*. 2008; Cortes-Anzures *et al*. 2017). Several observational studies have identified a positive association between bark roughness and epiphyte abundance or diversity of epiphytes (Callaway *et al*. 2002, Wyse and Burns 2011, Adhikari, H. S. Fischer *et al*. 2012). However, Vergara-Torres *et al*. (2010) and Boelter *et al*. (2014) found that bark texture was less important to epiphyte diversity than larger-scale variables such as nearby hosts and soil nutrients. In epiphytic lichens, Sillett *et al*. (2000) showed that propagule sources were more important than bark texture, and that experimentally sown propagules established just as much on smooth-barked substrates as on rough-barked substrates. Nonetheless, the results to date remain equivocal, mainly because observational studies cannot simultaneously separate the effects of bark texture from other correlated host plant traits such as age, size, and nearby epiphyte source populations (reviewed in Wagner *et al*. 2015). In one experimental study of epiphyte seed adherence to naturally varying bark roughness, epiphyte adherence increased with roughness up to a certain point, but seed adherence did not relate to natural relative abundance of epiphytes (Einzmann and Zotz 2017). More experimental work is needed *in situ* to identify the independent contributions of host traits to epiphyte assembly (Wagner *et al*. 2015).

Here, we test the hypothesis that substrate texture (roughness) regulates both vascular epiphyte germination and persistence using an *in situ* replicated experiment in a Neotropical cloud forest. We predict higher initial establishment of epiphytes on rougher substrates as well as a positive relationship between roughness and epiphyte persistence, wherein epiphyte seedlings survive longer on rougher substrates in comparison to smoother substrates (Fig. 1). Our experiment is unique because we sourced all substrates from the same tree, thereby controlling for both intra- and interspecific variation in host trees. We also experimentally manipulated substrate roughness,

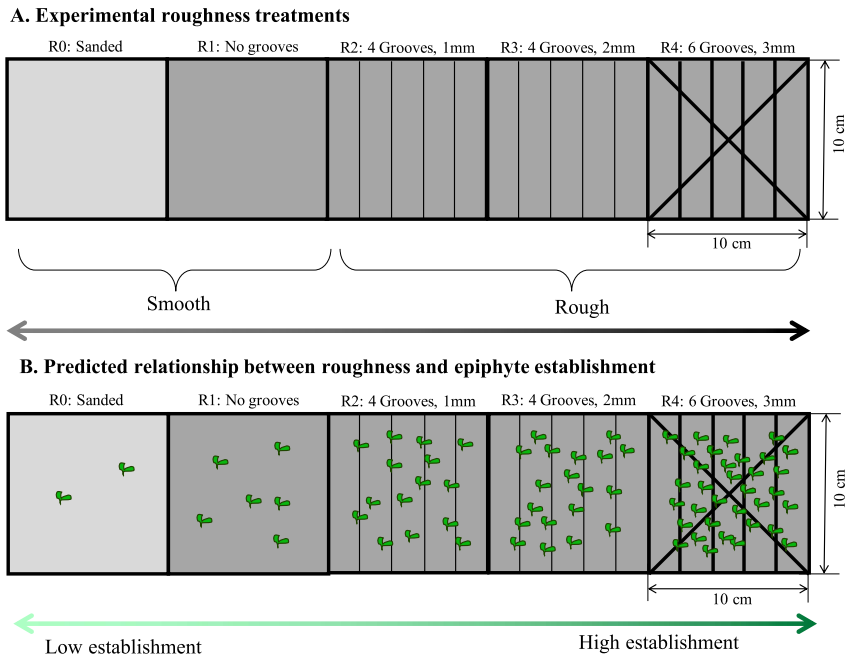

FIG. 1. Experimental design and predictions for one plot. One of five roughness treatments, in random order, were applied to each 10 × 10 cm subplot of salvaged native wood (A). We used a standardized protocol to artificially wind-disperse seeds onto all substrates and predicted higher epiphyte abundance on rougher substrates because the epiphytes would gather in the experimental grooves (B). Substrates with treatments R0 and R1 were categorized as "Smooth" and substrates with treatments R2–R4 were categorized as "Rough" for supplemental analyses.

allowing us to separate independent effects of substrate texture from host bark traits *per se*. By pairing field abundance measurements at the subplot scale (10 × 10 cm) with image analyses at the microhabitat scale (3 mm grooves), we sample epiphyte dynamics at spatial scales relevant to their natural history—on very small branch habitats. Moreover, we tracked cohort survival of epiphyte seedlings every two months for a year, providing important temporal resolution and a medium-long term component to our *in situ* experiment.

Materials and Methods. STUDY SITE. We set up our experiment in the premontane cloud forest of Santa Fé National Park, Veraguas, Panama (8°31.98′N, 81°9.03′W) at an elevation of approximately 750 m a.s.l (Fig. S1). Santa Fé National Park, established in 2001, is a 72,636 ha National Park located in the mountainous Cordillera Central region of Panama (Ministro de Economia y Finanzas 2001, Corporación de Desarrollo Ambiental *et al.* 2013). The park contains old-growth premontane, montane-tropical cloud forest, and lowland tropical seasonal forest with sparse human development (ANAM 2010, Cáceres-González 2013). We set up an iButton datalogger (Thermochron DS1923; Maxim Integrated, San José, CA) at our research site in 2019 because there is no weather station in Santa Fé National Park. The average temperature between January 2019 and 2020 was 20.8 °C and mean relative humidity was 88%. The broader Santa Fé region has a distinct dry season from January through April, wherein mean monthly rainfall ranges from 25–73 mm (Macinnis-Ng *et al.* 2012, 2014; ETESA 2019). Higher elevations, such as at Altos de Piedra (858 m elevation, 6 km from our field site), are much foggier and receive more precipitation than the town of Santa Fé (Macinnis-Ng *et al.* 2012). We observed rainfall or heavy mist frequently in our field site during repeated visits throughout the "dry season" from January–May in 2017–2019.

ARTIFICIAL SUBSTRATE CONSTRUCTION. We tested the impact of substrate texture on epiphyte establishment by constructing substrate platforms with varying roughness (Fig. 1, S2C). Each

platform was salvaged from the debarked trunk of a native recently fallen tree of the genus *Pouteria* (donated via permit #SE/AP-1-17). We cut the nine platforms to approximately 10 × 15 × 110 cm (depth × width × length), and divided each platform into two halves (*plots*), with at least a 2.5 cm buffer between each half and around all edges. Each plot was then subdivided into five 10 × 10 cm *subplots*, which was the unit of replication for each experimental treatment (Fig. 1A). Thus, there were five treatments in each of 18 plots for a total of 90 subplots.

We manipulated substrate texture by hand-sawing grooves to create five experimental levels of increasing roughness (Fig. S2C). The smoothest subplot (R0) was created using sandpaper to decrease the chainsaw cut texture; the second-most smooth subplot (R1) had no additional grooves because we used the grain created by the original chainsaw cut of the wood. Similar board-substrates have been used as controls in host tree bark peeling experiments (Jiménez-Salmerón *et al*. 2017). We created the next two treatments (R2 and R3) by hand-sawing four equidistant parallel grooves running the entire length of the subplot. Grooves on R2 were approximately 1 mm deep and grooves on R3 were approximately 2 mm deep. The roughest subplot (R4) also had four parallel hand-sawn grooves of approximately 3 mm deep, had two additional grooves sawn from corner-to-corner, and had five 3 mm-deep holes drilled in the center and corners to mimic animal excavation (Fig. 1A). The five roughness treatments were randomly allocated to each subplot. We quantified the variation in the roughness of our experimental treatments by measuring *rugosity* via the straight-chain method (Luckhurst and Luckhurst 1978). Rugosity in this context was the length of a fine-chain laid across the surface (encompassing all the surface topography) divided by the straight-line distance (as measured by a ruler). Rugosities in our experiment ranged from 1.0 (as measured, perfectly smooth) to 1.46. Our experimental rugosities fell within the range of rugosities of nearby tree bark; measured tree branch bark rugosities for 10 individuals across four tree species ranged from 1.0 to 1.9. We confirmed that the five rugosity treatments increased in measured rugosity (Fig. S3), although R0 and R1 did not statistically separate (see note below in Statistical Analyses).

We suspended and leveled all platforms 1.3 m above the ground throughout the forest using shark-grade fishing line tied to nearby trees, at least 50 m from each other. Although the platforms were in the same general area as the fallen source tree, we located the plots at least 50 m away from the treefall, under closed canopy forest. We did not expect the light conditions caused by the treefall to affect our experiment. To decrease the potential for establishment of microorganisms or juvenile plants prior to epiphyte seed application (see below), we sanitized the surface of all boards with a 50/50 mix of bleach and water. In a separate study, we found that epiphytes readily established on bleached wood substrates in the absence of seed addition (Spicer unpublished data). Notably, our experimental substrates were oriented horizontally, so were modeled after branch substrates rather than vertical tree trunk substrates. We chose a horizontal substrate orientation to reduce seed loss during the experiment and thereby increase replication.

Collection of Epiphyte Seeds. We opportunistically collected local seed capsules from seven different epiphyte species, using one or two individuals of each species (permit SE/AP-1-17). Four individuals were bromeliads (two of *Guzmania sprucei*, one *Guzmania calamifolia,* and one unidentified bromeliad species), and six were orchids (two of *Miltoniopsis roezlii* and *Sobralia leucoxantha,* and one each of *Prostechea vespa* and *Sobralia decora*). Seed capsules were kept in ambient conditions for less than two months until we used them in the experiment. It is unlikely that storage under ambient conditions would have decreased their viability (Correa and Zotz 2014), and we documented abundant germination on our substrates. All adult epiphyte individuals were found in the understory (< 2 m above the ground). Seeds were collected during the dry season (February–April) and experimentally dispersed (see below) near the end of the dry season (May). Although we do not have much information about the phenology of these species specifically in this region, many epiphytes are adapted to disperse seeds at this time of year (Mondragón *et al*. 2015, Victoriano-Romero *et al*. 2017). We assume that the timing of our experiment was close to the natural cycle of epiphyte seed development and dispersal at our study site.

Application of Epiphyte Seeds and Data Collection. All epiphyte seeds were removed

from capsules and mixed thoroughly. For each subplot, one level teaspoon of the seed mix was measured with a measuring spoon and deposited by hand on a flat glass plate held parallel and flush immediately adjacent to one of the 10 × 10 cm subplots. We then used five puffs of air from an infant ear-cleaner to "wind disperse" the seeds onto the subplot. Counted infant ear-cleaner puffs has been used in other fields as a standardized method of applying air force (*e.g.,* invertebrate behavior; Sweeney *et al*. 2013, Settepani *et al*. 2015). The glass plate was washed with water and dried between each application. We applied all seeds in only a few hours when it was not raining, but the substrates were damp from morning rain, which matches typical ambient conditions. We did not add any water, nutrients, or growth hormones (*cf*. laboratory germination experiments; Arditti 1967; Arditti and Ghani 2000; Mondragon and Calvo-Irabien 2006). We also did not affix the seeds to the subplot, unlike other seed field experiments (Mondragon and Calvo-Irabien 2006, Hietz *et al*. 2012, Ruiz-Cordova *et al*. 2014, Shao *et al*. 2017, Vergara-Torres *et al*. 2018) because our goal was to expose the epiphytes to *in situ* processes. Glue can also diminish the germination of seeds (Ruiz-Cordova *et al*. 2014). Notably, the local community and Indigenous peoples in the Santa Fé region regularly propagate orchids the way we did, without any added nutrients or adhesion (Spicer and Ortega, personal communication). We censused all subplots for epiphytes at approximately two-month intervals for 12 months. We included only epiphyte seedlings that were within the 10 × 10 cm subplots in the census. We noted, but did not count, seedlings that established outside of the 10 × 10 cm subplot (or were moved there) but that were still attached to the sides of the substrates (Fig. S4).

PHOTO ANALYSIS. To complement our branch-scale experimental field approach (10 × 10 cm subplots), we also analyzed the relationship between substrate texture and epiphyte abundance on the microhabitat scale using Preview version 11.0. We took photos of each subplot four months after experimental dispersal and created 1.5 mm buffer zones on each side of the experimental grooves and holes. In each photo, we counted the epiphyte germinants, coding all vascular epiphytes that visibly crossed the buffer zone as "in groove" and all epiphytes outside of the buffer zone as "out of groove." Epiphytes that were found within 1.5 mm of the border of the plot or within 1.5 mm of the corner subplot marker nails were not included (Fig. S5). To standardize area sampled, we calculated the area of "in groove" and "out of groove" space for each treatment; epiphyte microhabitat densities are reported as abundance divided by this area calculation (in cm^2). We believe this is a conservative estimate of whether the epiphyte got caught in the experimental grooves because we observed epiphyte germinant roots to be longer than 3 mm.

STATISTICAL ANALYSES. To accurately reflect the original experimental design, we report results from all five rugosity treatments, even though only four of the five treatments statistically separated (Fig. S3). However, we also re-ran the analyses binning the two "Smooth" rugosity treatments that did not statistically separate (no experimental grooves; R0 and R1) and all the "Rough" treatments (with experimentally added grooves; R2, R3, and R4; for results, see Fig. S6). Results from the reported five-treatment subset align with those from the two-category binned treatments.

First, we tested whether roughness of the substrate predicted the abundance of germinated epiphytes at the first time point, two months after applying seeds. All of our statistical analyses followed recommendations from Bolker *et al*. 2009 and Zuur *et al*. 2009. We ran a generalized linear mixed model (GLMM) using each subplot's (10 × 10 cm) categorical roughness treatment to predict the abundance of epiphytes. We included a random blocking factor with plots nested within the nine platforms, which is recommended for split-plot designs, and modeled the count data with Poisson error distributions and a log link function (Bolker *et al*. 2009, Zuur *et al*. 2009). Second, we tested whether the substrate roughness drove changes in epiphyte persistence by comparing the epiphyte abundance across all time points with a longitudinal GLMM. In this model, we used the ordinal time points, the categorical roughness treatments, and their interaction as fixed factors to predict epiphyte abundance. We included random blocked plot and pair factors as above, as well as the individual subplot IDs as random factors to account for the repeated measures in this longitudinal analysis. Because we did not individually mark seedlings, we excluded subsequent recruitment (increases in total epiphyte abundance) that occurred after the first survey. Finally, we used a GLMM to assess whether being in or out of an

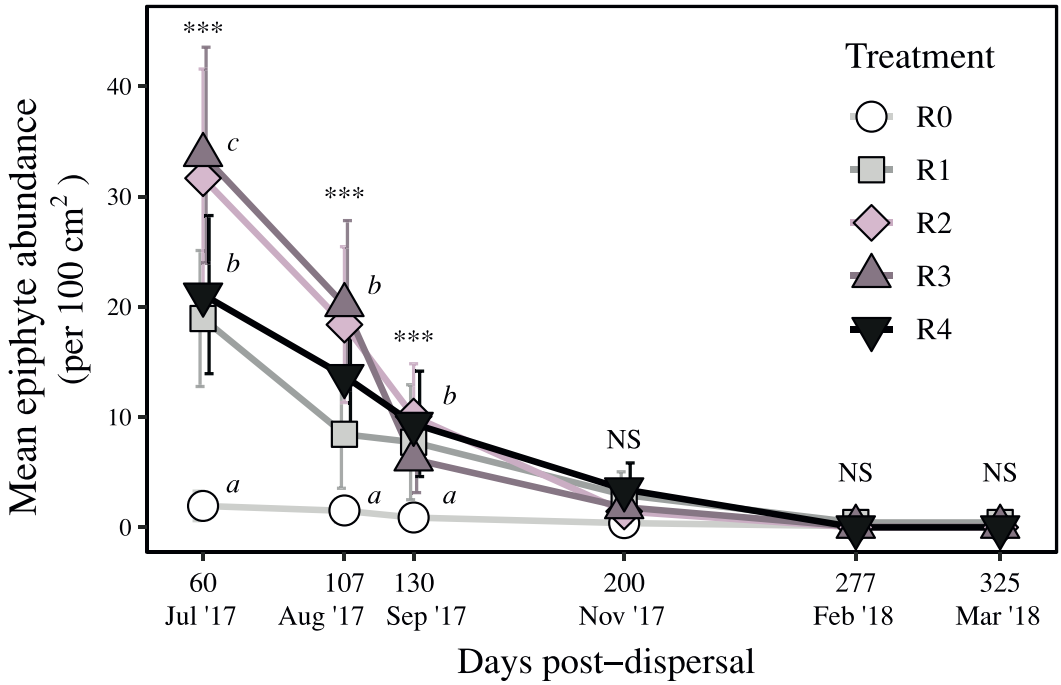

FIG. 2. Cohort epiphyte abundances through time. After two months, rougher rugosity treatments had higher epiphyte establishment than the smoothest substrate ($X^2 = 351.35$, $p < 0.0001$). Maximum mean epiphyte abundance at two months was found at the mid-levels of roughness (R2 and R3). Letters refer to statistical difference from posthoc Tukey's HSD tests, run within time point. (Mean number of epiphyte seedlings and standard errors at time point 1, 60 days: R0 = 2 ± 1, R1 = 19 ± 6, R2 = 32 ± 10, R3 = 34 ± 10, R4 = 21 ± 7; $N = 18$ per treatment). Almost all epiphytes were removed from the substrates or died in one year, but epiphytes on rougher substrates survived longer than those on the smoothest substrates (Time: $X^2 = 2825$; Roughness: $X^2 = 33$; Time × Roughness: $X^2 = 61$; all $p < 0.0001$). Note that the last two abundance values are both above zero (11 and 10 total epiphytes, respectively).

experimental groove determined epiphyte abundance (per cm^2 substrate surveyed) in our photo analysis, and included a subplot-level random factor (nested within plot and site) to account for the paired nature of the photo analysis. This GLMM had a log link with a Gaussian distribution to characterize the data distribution appropriately. All analyses were run in R version 3.6.0 and models were run using the lme4 package (Bates *et al*. 2014, R Core Development Team 2019). We calculated the pseudo-R^2 conditional and marginal coefficients for the GLMMs with the package MuMIn (Barton 2019). Results of GLMMs are presented in Table S1, and follow-up tests (Tukey's HSD) are presented in Table S2.

Results. We found a total of 1,934 epiphyte seedlings across all plots after two months. Mean epiphyte seedling abundance per 10 × 10 cm subplot was 21 (± 3.5 *SE*), and ranged from 0 to 173. At two months, the higher roughness treatments caused higher epiphyte abundance, wherein all roughened substrates hosted 93% more epiphytes than the smoothest substrate on average (Table S1, Table S2, Fig. 2). The third-roughest substrates hosted the highest abundance of epiphytes at two months, with a mean of 34 (± 10 SE) epiphytes, whereas the smoothest substrates hosted the lowest, with a mean of 2 (± 1 SE) epiphytes (Table S2, Fig. 2). Approximately 56% of the smooth substrates were empty by two months; in contrast, on roughened substrates, only 17% of the subplots were empty (Fig. S7). At the microhabitat scale, our photo analysis showed that epiphyte density (abundance per cm^2) was 71% higher in the experimental grooves than outside of the grooves (Table S1, Fig. 3). Epiphyte seedlings, therefore, "stuck" more where there was experimental roughness. Over time, almost all epiphyte seedlings were dislodged or died on all treatments,

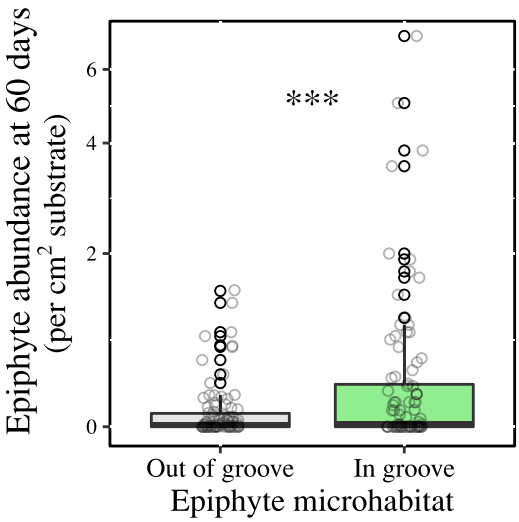

FIG. 3. Epiphyte abundance, per cm^2, within a 1.5 mm buffer zone of experimental grooves, in comparison to epiphyte abundance on smooth surfaces farther than 1.5 mm away from the grooves. Epiphyte seedlings were 71% more abundant per unit area in experimental grooves in comparison to outside the grooves ($X^2 = 49$, $p < 0.0001$). Data shown are epiphyte abundance from photos taken approximately four months after experimental dispersal and are relative to the amount of area of each type of substrate within plots (see Fig. S5). Data are plotted on a log10 scale. Means and standard errors: Groove: 0.5 ± 0.1 epiphytes/cm^2, $N = 90$; NoGroove: 0.1 ± 0.03 epiphytes/cm^2, $N = 90$.

but this was delayed by months on the higher-rugosity substrates (a significant Time × Treatment interaction; Table S2, Fig. 2, Fig. S8). Comparing the abundance of epiphytes at two months to subsequent surveys, 60% of epiphytes survived at four months, 35% survived halfway through the experiment, 12% survived at seven months, and 0.5% survived at a year.

Discussion. Early ontological transitions are common bottlenecks to community assembly in plants; here we tested this concept in tropical vascular epiphytes. Our study revealed two key insights to epiphyte dynamics in natural conditions. First, epiphyte emergence depended on the texture of their substrate. Epiphyte seedlings were more abundant on rougher substrates in comparison to smoother substrates after two months. Second, differences in epiphyte *emergence* did not carry into successful *establishment* to adulthood. Ultimately, seedling mortality was very high regardless of substrate texture: almost 100% of the epiphytes disappeared within a year. Thus, the effects of substrate texture on epiphyte abundance were no longer detectable after approximately six months.

SUBSTRATE ROUGHNESS AS A REGULATOR OF EPIPHYTE EMERGENCE. Our results provide the first experimental evidence *in situ* of the direct connection between substrate rugosity and epiphyte emergence. As we predicted, higher rugosity substrates initially hosted more epiphytes than smooth substrates. Interestingly, the main difference we found was between the smoothest (sanded) substrate and all other rougher textures, suggesting that vascular epiphytes may need just a small amount of roughness to adhere and persist for several months. This contrasts with some data from epiphytic lichen experiments, which did not show a strong correlation to bark texture differences and establishment (*e.g.,* Sillett *et al*. 2000). The extent that the pattern or type of roughness enhances epiphyte establishment, and contrasts among different epiphyte groups, is not well-explored in the literature. Characterizations of bark traits is also a challenge; Jiménez-Salmerón *et al*. (2017) and Callaway *et al*. (2002) showed that visual categorization of bark texture (smooth, rugose, peeling, *etc*.), a common approach to characterizing epiphyte substrate (Migenis and Ackerman 1993, Vergara-Torres *et al*. 2010, Adhikari, A. Fischer *et al*. 2012), did not correlate well to the quantitative bark peeling rates of trees. Additional experiments with controls (such as in Jiménez-Salmerón *et al*. 2017), paired with quantitative measurements of host tree traits, could greatly advance our understanding of the factors limiting epiphyte establishment.

We are aware of only one other study that experimentally tested the effects of substrate microsite (and fungal inoculum) on epiphyte germination processes *in situ* and included unadhered treatments (Shao *et al*. 2017). The authors showed that germination and early establishment *required* added fungal inoculum as well as adhering seeds to substrates to protect seedlings from removal processes. If seeds were not adhered to substrates and provided inoculum, none germinated (Shao *et al*. 2017). Thus, our experiment complements the work of Shao *et al*. 2017 and serves as a proof-of-concept for *in situ* epiphyte germination experiments; in natural conditions, without human-aided fungal inoculation, adher-

ence, or pretreatment, bromeliad and orchids seedlings can germinate on experimental substrates (Fig. S2B). Although our results are relatively intuitive, the natural germination dynamics of epiphytes have not been rigorously established in scientific literature. More detailed field population studies with individually tracked seedlings are needed to address questions of natural epiphyte establishment dynamics. Regardless, our study suggests that host–epiphyte interactions are likely important at this early ontogenetic stage.

Epiphyte Seedling Mortality and Potential Removal Processes. We also found that epiphytes survived longer on the rougher substrates, and this difference persisted for almost six months (Fig. 2). Our results were somewhat conservative; the experimental roughness only captured the lower range of measured rugosity at the site (30% of maximum). In natural or secondary succession, bryophytic epiphytes would likely establish prior to vascular epiphytes (Nadkarni 2000, Lu *et al*. 2020), providing additional complexity to the substrate and potentially facilitating the establishment of vascular epiphytes (Ellyson and Sillett 2003, Jarman and Kantvila 1995; reviewed in Spicer and Woods 2022). Survival rates likely would have been higher with these more realistic conditions included. Moreover, in a natural dispersal event where several thousand or millions of seeds may be present in a similarly small substrate area (Mondragón *et al*. 2015), a low survival rate would still result in true establishment (survival to adulthood) of some epiphytes. In that case, differences in substrate roughness could result in population- or community-wide differences in epiphyte abundance or diversity, as observed in several systems (Callaway *et al*. 2002, Wyse and Burns 2011, Adhikari, H. S. Fischer, *et al*. 2012).

Although substrate texture explained some of the variation in early epiphyte survival, it was not sufficient to allow for long-term persistence of seedlings. After a year, seedling mortality was almost 100% on all substrates. While it is possible that some of our epiphyte germinants may have been blown or washed onto other viable substrates, the likelihood they survived if they landed on soil or litter is exceedingly low; even larger adult epiphytes have high mortality rates in such situations (Matelson *et al*. 1993). Thus, our findings highlight mortality prior to adulthood as a neglected aspect of epiphyte ecology. In seasonally dry or dry tropical forests, drought was a major cause of annual epiphyte mortality (Winkler *et al*. 2005, Benzing 2008, López-Villalobos *et al*. 2008, Werner and Gradstein 2008, Zotz 2016; but see Cascante-Marín *et al*. 2008). At our site, we speculate that rainfall, particularly heavy downpours, contributed to high mortality more than drought (Fig. S4), because light rain and mist occurs almost daily year-round and humidity remains high. Results from regions where typhoons are common show that high winds and associated heavy rainfall can drive epiphyte community dynamics (Rodríguez-Robles *et al*. 1990, Oberbauer *et al*. 1996, Robertson and Platt 2001, Hsu *et al*. 2018). Even in dry tropical forests, epiphyte seed dispersion can be hampered by seasonal rainfall, and many epiphyte species are hypothesized to be adapted to disperse their seeds at the driest time of the year for this reason (Victoriano-Romero *et al*. 2017). Apart from drought and heavy rainfall, epiphyte-epiphyte competition, microbial enemies, seed or seedling removal via ants, and other inhospitable abiotic conditions can contribute to epiphyte mortality (Mondragón *et al*. 2015, Vergara-Torres *et al*. 2018, Spicer and Woods 2022). Only ant depredation has been explicitly considered in any previous study of epiphyte establishment (Vergara-Torres *et al*. 2018). Epiphyte-epiphyte competition has been shown in nonvascular plants and lichens (*e.g.,* Antoine and McCune 2004, Mikhailova 2007), but there is little established support for competition among vascular plants (reviewed in Spicer and Woods 2022). Relay floristics (*sensu* Egler 1954), wherein early colonizing species preempt later successional species, may also be at play, although this has not been tested. Several epiphyte mortality agents are likely mediated by both height in the canopy and substrate angle, but these factors have yet to be well explored experimentally (Mendieta-Leiva and Zotz 2015, but see Zotz and Vollrath 2002). Because our experimental substrates were all horizontal and placed in the understory, we cannot extrapolate how important removal processes would be higher in the canopy or on more steeply angled substrates such as tree trunks.

Conclusions. Our findings contribute to understanding mortality dynamics in an understudied yet ecologically important group of tropical plants. Our work is a proof-of-concept demonstrating that simply adding propagules of epiphytes to sub-

strates in the field can lead to relatively high densities of seedlings (over 170 seedlings/100 cm^2). In addition, by observing high mortality rates over a year, our research highlights the importance of removal processes in mediating early epiphyte community assembly. These processes have likely been overlooked, particularly in aseasonal forests. Thus, we demonstrate that a minimal degree of roughness promotes epiphyte emergence and early persistence, but is insufficient to guarantee survival to adulthood.

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