

Host genus and rainfall drive the population dynamics of a vascular epiphyte

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Abstract. Vascular epiphytes constitute up to 25% of tropical plant diversity and play an important role in providing food, water, and shelter to many organisms. However, the factors that drive their population dynamics, including the influence of their host plants (phorophytes) and of climatic factors, are still poorly understood. We provide the first test of whether host tree genus can affect population dynamics of an epiphytic species, and assess the interactive effects of host tree and rainfall. We carried out a five-year study of the demography of >1000 plants of the endemic bromeliad, *Tillandsia macdougallii* L. B. Sm, growing on pine and oak trees in a Mexican montane forest. We tested for differences in vital rates and used integral projection models to test whether these scaled up to differences in long-term population growth rates between the two host genera and as a function of rainfall. *T. macdougallii* survival and growth were higher on pines than on oaks for larger plants but not for seedlings. The probability of producing capsules was higher for *T. macdougallii* on oaks than on pines. Increasing dry season rainfall was significantly correlated with increased survival of individuals, but not of ramets, growing on both oaks and pines. The probability of clonal reproduction increased significantly with increasing dry season rainfall for *T. macdougallii* growing on oaks, but not on pines. Projected long-term population growth rates, λ , for *T. macdougallii* on pines were higher than on oaks. λ increased steeply as a function of dry season rainfall for *T. macdougallii* populations on both host tree genera, but the increase was steeper for populations on oaks, likely because the former are deciduous. Our results show that host tree genus can affect the long-term dynamics of epiphyte populations and suggest that these effects may depend on rainfall. The high sensitivity of this species to changes in dry season rainfall suggests that a better understanding of how rainfall may drive vascular epiphyte populations will be critical for understanding the effects of climate change on species persistence.

Key words: Bromeliaceae; climate change; environmental drivers; host preference; integral projection models; interactive effects; life table response experiment; *Pinus*; population dynamics; *Quercus*; *Tillandsia*; vascular epiphytes.

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INTRODUCTION

Vascular epiphytes constitute an estimated 9% of global vascular plant diversity, up to 25% of tropical plant diversity (Nieder et al. 2001, Zotz 2013), and play important roles in the maintenance of biodiversity. Vascular epiphytes provide food, water, and shelter for many organisms

including birds, insects, and microorganisms (Nadkarni and Matelson 1989, Ellwood and Foster 2004, Díaz et al. 2012, Brandt et al. 2016). In addition, given the ability of many vascular epiphytes to store water and capture nutrients directly from the atmosphere, they can also alter biogeochemical processes in some ecosystems (Van Stan and Pypker 2015).

Epiphytes live on other plants, and although they do not take nutrients directly from them, they are intimately linked to their host trees (phorophytes). Very few epiphytic species require a specific host (Ackerman et al. 1989, Tremblay et al. 1998), and most are generalists (Benzing 1990). However, most epiphytes appear to demonstrate a preference for particular hosts in that they are more frequently found and usually are more abundant on certain species than on others (e.g., Mehltreter et al. 2005, Bergstrom and Carter 2008, Köster et al. 2011).

The factors that shape epiphyte preference are thought to be a result of various different host characteristics. For example, rough and/or fissured bark permits the attachment of epiphyte seeds, while smooth bark tends to be poorly colonized by epiphytes (Benzing 1978, Zimmerman and Olmsted 1992, Bergstrom and Carter 2008). Hosts with high bark-peeling rates are less colonized by epiphytes than those with more stable barks (López-Villalobos et al. 2008). Hosts that have bark with a greater capacity for water retention also tend to have more epiphytes (Castro-Hernández et al. 1999, Callaway et al. 2002, Mehltreter et al. 2005). Branch size and inclination can also influence the abundance of epiphytes: Hosts with bigger branches (more surface area for colonization) and with smaller inclination angles (lower effects of gravity) promote the presence of epiphytes (Benzing 1990). Other factors that may influence the abundance of epiphytes include the density of canopy foliage—and therefore the amount of light available to epiphytes (Callaway et al. 2002), and the presences of exudates of resin or allelopathic substances (Frei et al. 1972, Valencia-Díaz et al. 2010). The age and size of the hosts can also influence the presence of epiphytes, as bigger and older hosts usually have more epiphytes (Andersohn 2004, Benavides et al. 2006, Flores-Palacios and García-Franco 2006).

Most studies that have examined host preference have assessed how the richness and abundance of epiphytes vary with particular host characteristics. A few studies have directly measured the effect of nutrient concentration of the throughfall of hosts (Schlesinger and Marks 1977) on the growth of epiphytes (Callaway et al. 2002). Other studies have compared the effect of different hosts on specific life-cycle stages, typically

on seed germination and seedling survival (Frei et al. 1972, Benzing 1978, Callaway et al. 2002, López-Villalobos et al. 2008).

However, this information is still limited as differences in one life-stage, such as germination, seedling survival, or adult seed production, may have little or no effect on long-term population growth rates (Caswell 2001). No studies have tested whether and how hosts with differing sets of characteristics may affect epiphytes over their whole life-cycles: that is, if individuals growing on different host genera or species exhibit differing rates of growth, survival, and reproduction throughout their life-cycles, and most importantly, if these differences actually scale up into differences in long-term population growth rates. Furthermore, the effect of host identity on epiphyte demography may depend on climatic or environmental conditions that change over time (Wagner et al. 2015). Epiphytes can be heavily limited by the availability of both light and water (Benzing 1990, Pereira-Dias and Santos 2015), and a host with a growth habitat that allows high levels of light for its epiphytes may also expose them to greater levels of desiccation during a dry year or season. Understanding these relationships is central to developing a better understanding of what drives the dynamics of epiphyte populations in tropical forests, especially in the context of a changing climate. This information can also provide insight into how changes in the composition of forest trees, through successional processes, or anthropogenic disturbances such as logging and climate change, may affect the distribution, abundance, and viability of epiphyte populations.

We provide the first test of whether and how host genus can affect the long-term population dynamics of epiphytes through a case-study of the bromeliad, *Tillandsia macdougallii* L. B. Sm in Mexico. In tropical montane forests, pines (*Pinus* spp.) and oaks (*Quercus* spp.) represent two of the most common tree genera. The species within each genus share many of the traits expected to influence epiphyte populations, including similar bark types, branching, and other structural characteristics. *T. macdougallii* is an endemic species that grows on both pines and oaks in montane forests of Oaxaca. We track the fate of 1000 *T. macdougallii* plants over 5 years to address the following questions:

1. Do *T. macdougallii* individuals growing on oak trees have higher rates of germination, growth, survival, and capsule production, than those on pine trees?
2. Are long-term population growth rates of *T. macdougallii* greater on oak trees than on pine trees?
3. How does variation in rainfall affect the vital rates and long-term population growth rates of *T. macdougallii* growing on oaks and pines?

We hypothesized that *T. macdougallii* individuals would have (1) lower survival on pines than on oaks, as pines have a higher rate of bark peeling than oak (Schlesinger and Marks 1977, Callaway et al. 2002), and dislodgement is one of the main causes of mortality for epiphytes in general (Hietz et al. 2002, Mondragón et al. 2004a); (2) faster growth on oak than on pine, due to the higher mineral concentration of throughfall and litterfall on oaks (Liu et al. 2001, Pérez-Suárez et al. 2009); and (3) higher capsule production on oaks than on pines. Reproduction in bromeliads can be limited by nutrients (Lasso and Ackerman 2013) and light (Cervantes et al. 2005, Scrok and Varassin 2011), and oaks have higher mineral concentration of throughfall and litterfall, and are deciduous and therefore likely allow more light penetration during the dry season. We also expected that (4) vital rates of *T. macdougallii* would be more sensitive to differences in rainfall on oaks than on pines, because oaks lose their leaves during the dry season (November–April), which may make epiphytes growing on oaks more susceptible to desiccation. Finally, we expected that (5) differences in *T. macdougallii* long-term population growth rates between oaks and pines would depend on rainfall.

METHODS

Study area and species

This study was conducted in the Petenera, municipality of Santa Catarina Ixtepeji, located in the Sierra Norte region of the state of Oaxaca (17°12'29" N and 96°35'29" W, elevation 2547 m a.s.l.), Mexico. The mean annual temperature and precipitation are 17°C and 900 mm, respectively (INEGI 2000). The dominant vegetation consists of pine forest (*Pinus teocote* Schltdl. and Champ. and *Pinus oaxacana* Mirov) with scattered oaks (*Quercus*

castanea Née, *Quercus crassifolia* Hump. and Bonpl and *Quercus obtusata* Bonpl) and some madrones (*Arbutus xalapensis* Hbk) (Zacarias-Eslava and Del Castillo 2010). At our study site, pines are taller than oaks (mean adult height 17.8 ± 3.0 m [*n* = 10] vs. 8.3 ± 1.1 m for oaks [*n* = 10]) and also have larger trunks (mean diameter at breast height 1.1 ± 0.4 m vs. 0.4 ± 0.1 m for oaks; mean first ramification 7.8 ± 1.1 m, vs. 3.3 ± 1.3 m). The oak species have similar rough bark, but the pines on which *Tillandsia macdougallii* grows have similar fissured and exfoliating bark. The pines exude a resin, while the oaks do not. The oak species are deciduous and drop their leaves during the dry season. The main differences between species within each genus relate to the length of the leaves and the size of the fruit/cones. Epiphytic species at our site include a wide variety of orchids, ferns, and bromeliads. Other bromeliad species reported at this site include *Tillandsia prodigiosa* (Lem.) Baker, *Tillandsia carlos-hankii* Matuda, *Tillandsia macdougallii* L. B. Smith, and *Tillandsia bourgaei* Baker (Mondragón et al. 2006).

Tillandsia macdougallii is an atmospheric bromeliad (i.e., it does not form a tank, and most water and nutrient absorption occurs by trichomes that cover the plant) endemic to Mexico. It grows in oak and pine–oak montane forests from 1800 to 3200 m elevation (Smith and Downs 1977, McVaugh 1989). It is an ideal species to address our research questions because (1) it is relatively abundant; (2) unlike most bromeliads, its seedlings and juveniles can be identified to the species level in the field as the large number of trichomes on the leaves is a distinctive characteristic of the species; and (3) as it is endemic and also harvested in some areas, understanding the drivers of long-term demographic rates is of conservation interest.

Tillandsia macdougallii plants grow up to 20 cm tall and consist of a compact rosette of narrow leaves, 10–25 cm long and covered with cinereous spreading scales. The inflorescence is pendulous, with pink bracts and purple petals. Fruits are narrow capsules with plumed seeds. An experiment on the breeding system of *T. macdougallii* revealed that 53.8% of flowers that were self-pollinated, and 69.4% of those that were outcrossed, produced capsules (Mondragón and Ramírez 2008). Flowers are pollinated by hummingbirds (D. Mondragón, *personal observation*). Offshoots (ramets) are produced within the outer leaves of the mother.

Demographic censuses

In February 2005, we tagged 1000 *T. macdougallii* rosettes on 17 pine and eight oak trees. With the exception of a few plants that were on branches too fragile to reach safely, all *T. macdougallii* rosettes on those trees were labeled. For each rosette, each year through 2010, we measured rosette height (from rosette base to the tip of the uppermost leaf), counted the number of capsules and offshoots, and recorded survival. Because we modeled the demography of the rosettes (i.e., the ramets, as opposed to the genets), and because rosettes die after flowering, we considered rosettes that had flowered the previous year as dead the following year, and any new rosettes they produced as new ramets (clonal reproduction). For all rosettes >1.5 cm that died, we recorded the cause of death (flowering, desiccation (desiccated but present on branches, with no signs of other sources of mortality such as pathogens), dislodgement, or herbivory). Desiccated rosettes eventually get dislodged, but except for the smallest plants (excluded from our analysis), this process typically takes longer than 1 yr, and therefore, it is unlikely that desiccated rosettes would have fallen before our recensus. Over the five-year period, we did not observe mortality from pathogens and <2% of rosettes suffered herbivory. We also labeled and measured all the new seedlings each year.

In May 2010, we carried out an experiment to test whether there are differences in *T. macdougallii* seed germination on oaks vs. pines. The month of May coincides with the start of the hurricane season and is when germination in the field naturally begins. We haphazardly selected five oak and five pine trees, and on each of them placed 20 *T. macdougallii* seeds at approximately 1.3 m high on the trunk. We made four groups of five seeds each and twisted the comas of the seed so that they were separated from each other. Each group was then stuck to the tree with a drop of glue (Benzing 1978, Mondragón and Calvo-Irabién 2006). Every week for 2 months, we checked the seeds for germination.

Data analyses

We tested for differences in individual (rosette) level survival, growth, and reproduction on oak vs. pine trees, as well as differences in the probability of dislodgement (falling) and of desiccation,

using generalized linear mixed models (GLMM). We considered rosette nested within host as random effects. Initial height (log-transformed), host species (oak vs. pine), ramet (yes or no), annual rainfall, and dry season (November through February) rainfall were fixed effects. Quadratic terms were added where necessary based on checks of model residuals. We used Akaike's information criterion (AIC) to determine whether to drop or retain a given fixed-effect term, retaining factors that reduced the AIC value of the model. Full models were reduced in a backwards stepwise process, sequentially dropping the fixed-effect term in the model that increased AIC the most. We used binomial GLMMs to model the probability of survival, germination, reproduction (sexual and clonal), desiccation, and falling; and a Poisson GLMM to model the number of capsules produced. To model growth (height at $t + 1$), we used Gaussian error structure with an exponential variance structure, where the variance increases as an exponential function of initial height (Zuur et al. 2009). We modeled the probability of sexual and clonal reproduction for plants >8 cm high, which was the minimum size observed for both kinds of reproduction. We modeled the probability of desiccation and of dislodgement for plants >1.5 cm high only, as it was impossible to identify the cause of mortality for smaller plants. To test whether the number of *T. macdougallii* rosettes and reproductive rosettes was higher on oaks or pines, we used a GLMM with log-transformed total number values. Analyses were carried out using the nlme and glmmADMB packages in R version 3.1.1.

Population growth rates

We used integral projection models (IPMs, Easterling et al. 2000, Ellner and Rees 2006) to project the long-term population growth rates (λ values) of *T. macdougallii* growing on oaks vs. on pines, and as a function of rainfall. Integral projection models are built from continuous functions that describe size-dependent growth, survivorship, and fecundity (Merow et al. 2014) and, as such, represent an advance over traditional matrix models, where individuals are classified into size or stage-classes. Our IPM model took the form:

$$n(y, t + 1) = \int_{\lambda} [p(x, y) + f(x, y) + c(x, y)] n(x, t) dx$$

where the $p(x, y)$ kernel represents transitions of a rosette of size x to size y attributable to size-dependent survival, $s(x)$, and growth $g(x, y)$, $p(x, y) = s(x)g(x, y)$. The fertility kernel $f(x, y)$ represents the production of new seedlings of size (x) produced from rosette of size (y) . This was calculated for rosettes of reproductive size (>8 cm height) as: $f(x, y) = s(x)f_n(x)p_E f_d(y)$, where $s(x)$ is the survival of rosettes of size (x) , $f_n(x)$ is the probability of producing capsules for rosette size x multiplied by the number of capsules/rosette size x ; p_E is the number of new seedlings per capsule; and $f_d(y)$ is the size distribution of new seedlings. For each host genus, p_E was calculated as the number of new seedlings observed in the field divided by the total number of capsules produced. This produced the best estimate of seedling recruitment, because although we were able to estimate germination rates experimentally, it was impossible to accurately estimate the number of seeds/capsule and dispersal rates. Consistent with other bark dwelling epiphytes, there is no evidence that this species has a seed bank (D. Mondragón, unpublished data).

The vegetative reproduction function $c(x, y)$ represents the production of new ramets and was calculated as: $c(x, y) = s(x)f_c(x)c_E f_c(y)$, where $s(x)$ is the survival of rosettes of size x , $f_n(x)$ is the probability of producing ramets for rosette size x ; c_E is the number of ramets per rosette (=1 maximum for this species); and $c_d(y)$ is the size distribution of new ramets.

We built the growth, survival, and reproduction (sexual and clonal) functions based on the above statistical analyses of vital rates, where dry season rainfall and annual rainfall (which were not correlated) were covariables in all full models (see Results, Table 1). Annual rainfall was eliminated in the model reduction process for all vital rates except for clonal reproduction. However, as dry season rainfall had a similar, but much stronger effect, and as dry season rainfall was significant in two of the other three models, we chose to build our IPM using dry season rainfall only. The size distribution of new seedlings and new ramets was calculated directly from our field data.

We constructed IPMs for *T. macdougallii* growing on both pines and oaks, as well as for two sets of hypothetical populations: one for plants growing only on oaks and one for those growing only on pines. We numerically integrated the

demographic kernel over the range of sizes Ω , using the midpoint rule (Ellner and Rees 2006) to generate IPMs across the range of dry season rainfall for plants growing on oaks and on pines. We calculated the long-term asymptotic projected population growth rate (λ) for each IPM using the popbio package in R (Stubben and Milligan 2007).

Life table response experiments

To identify which vital rates contributed most to differences in population growth rates of *T. macdougallii* on pine vs. oak trees, we carried out life table response experiments (LTREs) (Caswell 2001) at two contrasting levels of dry season rainfall: 20 and 80 mm. These values spanned the range observed over our study period (19.4–84.0 mm) and represented two ends of the spectrum observed over the past 55 years (0.5–112.1 mm) (CONAGUA 2010). We designated oak as the reference matrix so that positive contributions represented differences in vital rates that contributed to the higher population growth rates on pine:

$$\lambda^p - \lambda^o = \sum (x_i^p - x_i^o)(\partial\lambda/\partial x_j)|A^m$$

where x_i^o is a vital rate of stage j in the oak matrix, x_j^p is the vital rate of stage j in the pine matrix, and $\partial\lambda/\partial x_j$ is the sensitivity of λ to the vital rate of stage j evaluated at the midway matrix A^m . We used midway sensitivities based on matrices constructed from the mean vital rates of the matrices being compared.

RESULTS

Differences in *T. macdougallii* vital rates on oak vs. pine

There were no significant differences in germination of *T. macdougallii* seedlings on oak vs. pine trees ($\beta = -0.466$, SE = 0.297, $z = -1.577$, $P = 0.12$). Seeds on both genera of host started germinating 1 month after planting, when the heavy rains began, and although germination on oak was initially higher than on pine, this difference disappeared by the end of the experiment, when 67% \pm 15% of seeds germinated on oaks vs. 57% \pm 16% on pines. There were no differences in survival of the germinated seedlings on oaks vs. pines (90% and 93% respectively, $\beta = -3.9$, SE = 0.515, $z = -7.6$, $P = 0.45$).

Table 1. Estimated coefficients from mixed-effect models of the probability of survival, growth, probability of producing capsules, probability of clonal reproduction, and mean size of new ramets for *Tillandsia macdougallii* plants growing on oaks and pines†.

Fixed effects	Estimate	SE	Z value	P value
Probability of surviving to $t + 1$				
Intercept	0.508	0.314	1.62	0.106
Size at start‡	0.867	0.197	4.40	<0.001
Size at start ² ‡	-0.372	0.055	-6.80	<0.001
Species (pine)	-0.07	0.329	-0.22	0.823
Clone	0.286	0.335	0.85	0.394
Rain	0.016	0.003	5.40	<0.001
Size at start × pine	0.327	0.144	2.25	0.024
Pine × clone	-0.671	0.320	-2.10	0.036
Rain × clone	-0.011	0.006	-1.91	0.057
Size at $t + 1$ of surviving individuals§				
Intercept	0.360	0.035	10.09	<0.001
Size at start	0.855	0.016	51.39	<0.001
Species (pine)	-0.05	0.037	-1.44	0.151
Clone	1.49	0.066	22.49	<0.001
Size at start × pine	0.033	0.018	1.86	0.062
Size at start × clone	-0.600	0.027	-20.22	<0.001
Rain	-0.001	0.000	-5.08	<0.001
Probability of producing capsules at time t (for individuals ≥ 8 cm)				
Intercept	-2.70	0.319	-8.51	<0.001
Species (pine)	-0.742	0.382	-1.95	0.051
Capsules produced per reproductive plant at time t ¶				
Intercept	-1.14	1.04	-1.05	0.291
Size	0.903	0.405	2.14	0.032
Probability of clonal reproduction (for individuals ≥ 8 cm)††				
Intercept	-13.82	2.52	-5.47	<0.001
Size at start	4.15	0.959	4.33	<0.001
Species (pine)	0.541	0.444	1.22	0.223
Clone	5.2	2.48	2.10	0.036
Rain	0.011	0.05	2.29	0.022
Size at start × rain	-0.035	0.018	-1.97	0.049
Size at start × clone	-1.75	0.954	-1.84	0.066
Rain × pine	-0.018	0.009	-1.94	0.052

† Coefficients and standard errors were obtained from the final models (see *Methods*).

‡ Height of plant (log-transformed).

§ Variance around the growth curve, $\sigma^2 = 0.182 \times \exp(-0.163 \times \text{starting size of seedling})$.

¶ Variance around seedling size, mean = 0.481, $\sigma^2 = 0.05$.

†† Variance around the new ramet size, mean = 4.9 and 5.1, $\sigma^2 = 4.6$ and 9.3 for ramets on oak and pine, respectively.

Survival of *T. macdougallii* rosettes increased with size and was higher on pines than on oaks, except for the smallest seedlings (rosettes < about 2 cm high; Table 1 size × pine interaction, Fig. 1a). Higher dry season rainfall increased survival of individuals on both host genera, but not of ramets (Table 1). Growth of *T. macdougallii* was slightly lower on pines than on oaks for small individuals and slightly higher on pines than on oaks for large individuals (>about 12 cm height). Ramets growing on both host genera grew faster than individuals when plants were small (<about

12 cm height), but slower when they were larger (Table 1, Fig. 1b). Higher dry season rainfall was correlated with decreased growth for *T. macdougallii* on both oaks and pines (Table 1).

Tillandsia macdougallii plants become reproductive at a minimum size of 8 cm high. For plants of reproductive size, the probability of *T. macdougallii* capsule production was greater on oaks than on pines and did not increase as a function of rosette size (Table 1). In contrast, for those plants that produced capsules, the number of capsules produced per rosette increased with size, but there

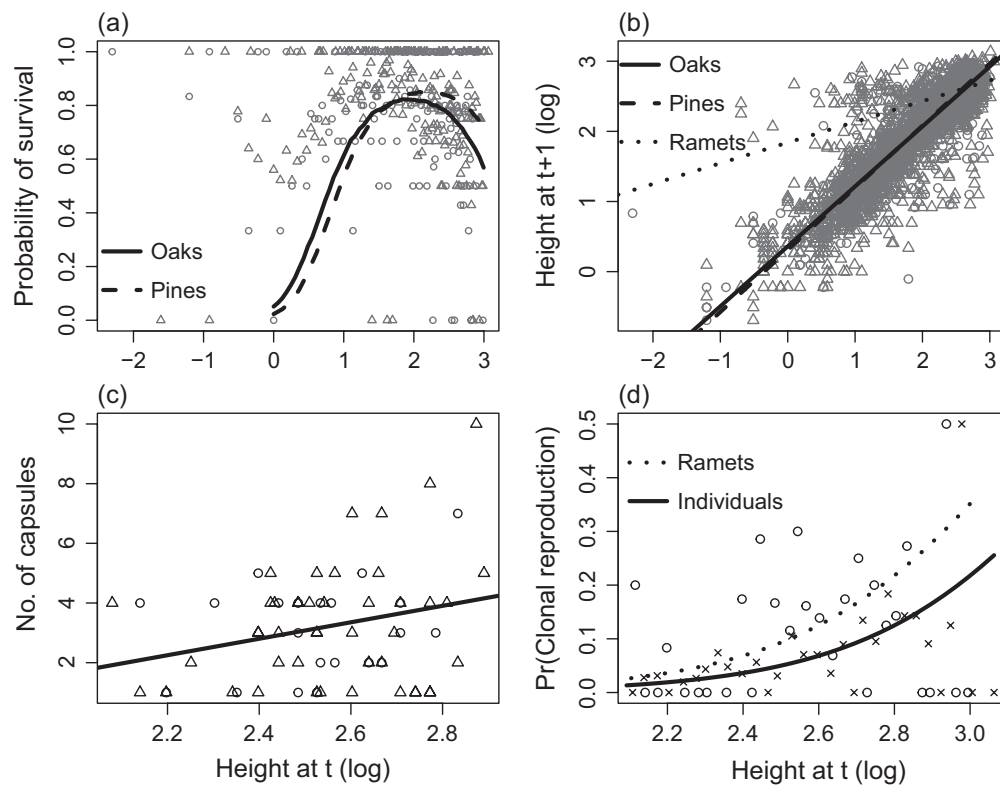


Fig. 1. Survival (a), growth (b) as a function of size, for *Tillandsia macdougallii* growing on oak trees (solid line, circle points) vs. pine trees (dashed line, triangle points). Growth of ramets (dotted line) does not differ between oaks and pines. For those plants that produced capsules, the number of capsules per rosette varies as a function of size (c) but does not differ between plants growing on oak vs. pine. Clonal reproduction (d) of ramets (dotted line, circle points) differs from that of individuals (solid line, cross points) for both oaks and pines. For (a) and (d), points represent the probability of survival and clonal reproduction, respectively, for plants binned into 0.5 cm height classes.

was no difference between *T. macdougallii* on oaks vs. pines (Table 1, Fig. 1c). The number of *T. macdougallii* rosettes per tree was higher on pines than on oaks ($\beta = 0.61$, $SE = 0.22$, $t = 2.76$, $P = 0.01$), which are also much taller and wider, but there was no difference in the number of reproductive rosettes on the two host genera ($\beta = 0.38$, $SE = 0.34$, $t = 1.11$, $P = 0.28$), nor of the number of flowers per rosette of the same size ($\beta = -0.04$, $SE = 0.33$, $t = -0.36$, $P = 0.72$). The number of new seedlings observed per capsule produced was low for *T. macdougallii* growing on both hosts, but was greater on pines than on oaks (0.38 vs. 0.12 new seedlings/capsule produced, respectively, over the five-year study period, Table 1).

The probability of clonal reproduction was higher for ramets than for individuals, and increased with size for all rosettes, but less so

for ramets than for individuals (Table 1, Fig. 1d). The probability of clonal reproduction increased with higher dry season rainfall, but this increase was greater for rosettes growing on oaks than on pines (Table 1). The increase in the probability of clonal reproduction with size was lower with higher dry season rainfall.

The probability of mortality due to desiccation decreased with size for rosettes on both hosts, but was significantly lower for *T. macdougallii* growing on pines than on oaks (Table 2). For plants growing on oaks, the probability of desiccation decreased with increasing dry season rainfall, but dry season rainfall had no effect on plants growing on pine. The probability of dislodgement decreased significantly with increasing *T. macdougallii* size and with increasing rainfall during the dry season (Table 2).

Table 2. Estimated coefficients from mixed-effect models of the probability of desiccation and of falling for *Tillandsia macdougallii* plants >1.5 cm high growing on oaks and pines.

Fixed effects	Estimate	SE	Z value	P value
Probability of desiccation				
Intercept	-1.152	0.64	-1.80	0.072
Size at start†	-0.898	0.173	-5.18	<0.001
Species (pine)	-1.467	0.634	-2.31	0.021
Rain	-0.039	0.02	-1.93	0.054
Rain × pine	0.041	0.021	1.96	0.05
Probability of falling				
Intercept	0.144	0.348	0.41	0.679
Size at start†	-2.058	0.441	-4.67	<0.001
Size at start ² †	0.454	0.130	3.48	<0.001
Rain	-0.019	0.004	-4.95	<0.001

† Size of plant (log-transformed).

Differences in *T. macdougallii* population dynamics on oaks vs. pines

Tillandsia macdougallii population growth rates (λ) were greater on pine than they were on oaks (Fig. 2). Lambda values for populations on both oaks and pines increased with increasing dry season rainfall, but the rate of increase was steeper on oaks than on pines. For populations on both oaks and pines, $\lambda < 1$, indicating long-term population decline.

Life table response experiments showed that under both low and high dry season rainfall scenarios, higher survival of reproductive-size individuals (>8 cm height) contributed most to the

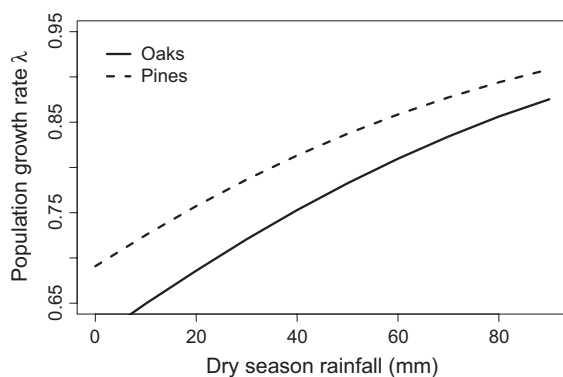


Fig. 2. Projected long-term population growth rates (λ) for *Tillandsia macdougallii* growing on oaks (solid line) and pines (dashed line), and as a function of dry season rainfall.

higher λ values for populations on pines (Fig. 3). Growth (including vegetative reproduction) was second in importance of LTRE contributions. Patterns of LTRE contributions were similar in both rainfall scenarios, except that in the high rainfall scenario, higher survival and growth of smaller individuals also contributed to the higher λ values for populations on pines.

DISCUSSION

Our results illustrate that demographic rates for *T. macdougallii* rosettes vary significantly between pine and oak hosts and as a function of dry season rainfall and that these can scale to differences in long-term population growth rates. As such, they provide new insight on drivers of vascular epiphyte dynamics in tropical forests.

Differences in *T. macdougallii* vital rates between hosts

Our hypothesis that *T. macdougallii* survival would be higher on oaks than on pines was not supported, as survival was higher on oaks for the smallest individuals (<2 cm) only. This may be due to several factors. Higher mortality on oaks can be partially attributed to the higher probability of desiccation of plants on oaks. This is a consequence of the deciduous nature of oaks: Oaks shed their leaves during the dry season, which likely exposes epiphytes to hotter, drier conditions than those growing on pines. Einzmann et al. (2015) showed that survival and growth of epiphytes tend to be lower on deciduous than on evergreen species, likely due to the sunnier and drier microclimates that characterize deciduous species, which also tend to have a lower density and diversity of vascular epiphytes. That the probability of mortality due to desiccation decreased significantly with increasing dry season rainfall for rosettes on oaks, but not on pines, supports this explanation. The probability of desiccation also decreased, and the overall probability of survival increased, as a function of rosette size. This finding is consistent with other studies on epiphytes, which have shown that mortality is higher for smaller individuals and that the greatest cause of mortality is water stress (Hietz 1997, Mondragón et al. 2015). Although *T. macdougallii* is not a tank bromeliad, as plants grow, the cavities between leaves grow, and therefore, the capacity to store water increases.

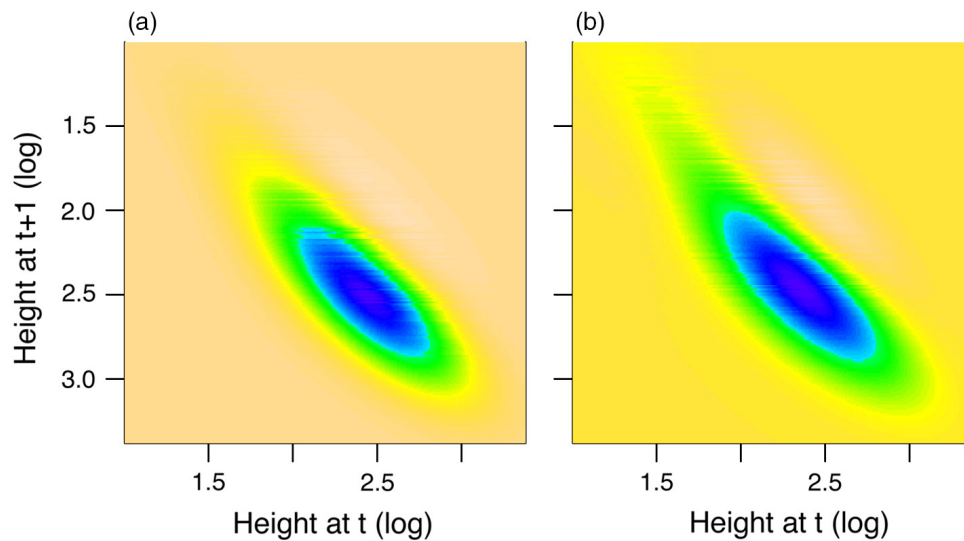


Fig. 3. Life table response experiment contributions for *Tillandsia macdougallii* plants growing on pines vs. oaks under (a) low dry season rainfall (20 mm) and (b) high dry season rainfall (80 mm). Darker colors represent life-history transitions that make greater contributions to higher λ values observed on pines. Values across the diagonal represent contributions from survival, and those below the diagonal represent contributions from growth and vegetation reproduction.

Higher mortality of rosettes on *T. macdougallii* on oaks is also partly a consequence of the significantly higher probability of reproduction on oaks than on pines, as rosettes die after they flower. The higher probability of reproducing on oaks could be related to greater access to resources. Throughfall on oaks has been reported to have higher concentrations of potassium (Johnson-Maynard et al. 2005) and phosphorous (Schlesinger and Marks 1977) than that on pines. Increases in these nutrients are associated with increased reproductive output in other species of *Tillandsia* (Benzing and Renfrow 1971). In addition, the greater light availability on oaks at least during the dry season may increase the probability of reproduction (Cervantes et al. 2005, Scrok and Varassin 2011). However, for those rosettes that flowered, the number of flowers and capsules produced per rosette did not differ between plants on oaks and pines.

Our finding that survival of individuals, but not of ramets, increased with higher dry season rainfall is likely due to the fact that ramets are partially protected against desiccation due to the translocation of water and nutrients from their mother plants. Although translocation has not been studied in *T. macdougallii*, it is important in

other vascular epiphytes (Yong and Hew 1995, Lu et al. 2015).

The probability of dislodgement of *T. macdougallii* plants did not differ between pines and oaks, despite the fact that pines have higher rates of bark peeling than oaks (Schlesinger and Marks 1977, Callaway et al. 2002). However, of those plants that died, a greater proportion died due to dislodgement on pines than on oaks (47.6% vs. 37.7% over the five-year study period). The decrease in dislodgement of larger plants is likely due to the fact that smaller plants are often found on thin twigs that are more easily broken (Hietz 1997, Mondragón et al. 2004a), that as plants grow, root systems develop and provide them with more stability (Hietz 1997), and that the branches they are on grow and become less susceptible to breaking (Einzmann et al. 2015). The decrease in dislodgement with increasing dry season rain may be due to the increase in twig fall rates during dry periods (Macinnis-Ng and Schwendenmann 2015).

Growth rates of *T. macdougallii* growing on pines and oaks were similar, but were slightly higher for larger individuals (>12 cm height) growing on pines. Higher adult growth rates on pines may be partly explained by the greater

probability of *T. macdougallii* capsule production on oaks. Individuals on oaks may be investing the extra resources they gain into reproduction as opposed to growth. These tradeoffs have been illustrated in epiphytic orchids (Zimmerman and Aide 1989, Ackerman and Montalvo 1990, Calvo and Horvitz 1990), but have not been investigated in semelparous bromeliads.

The probability of clonal reproduction increased as a function of size for individuals, but this increase was lower for ramets, and lower in wetter dry seasons. The translocation of resources from mothers to ramets, as well as more rain in the dry season, would allow for higher availability of water and nutrients. Higher water stress on oaks than on pines during the dry season may explain why clonal reproduction increased with increasing dry season rainfall for *T. macdougallii* growing on oaks but not on pines.

Differences in population growth rates between hosts

Our results suggest that host identity can affect long-term dynamics: *T. macdougallii* population growth rates were higher on pines than on oaks, largely as a result of higher rates of survival and growth in the larger sizes. They also suggest that the influence of host on population dynamics depends on climatic conditions. The negative effect of decreasing dry season rainfall on long-term growth rates was greater for *T. macdougallii* populations growing on oaks than on pines. However, our results also show that regardless of host, *T. macdougallii* population growth rates are very sensitive to decreases in dry season rainfall. We modeled the range of rainfall observed over our study period, which was representative of the range observed over the past 55 years (see *Methods*). However, climate models predict increased aridity for this region, including both lower annual rainfall and longer dry seasons (SEMARNAT 2010). This indicates that *T. macdougallii* populations may be at high risk in a drying climate. Other studies of epiphytic bromeliads have shown that increases in long-term population growth rates may be driven by increased precipitation (Mondragón et al. 2004a, Zotz and Schmidt 2006), although other abiotic and biotic factors can play important roles (Zotz et al. 2005).

As we calculated λ values for *T. macdougallii* on pine and oak trees separately, these values

represent what the long-term growth population growth rates would be for *T. macdougallii* in the context of a forest of only pines, or of only oaks. In reality, as is the case of our study site, this species exists in forests with both species. When the population dynamics of *T. macdougallii* growing on both oaks and pines are modeled together, the λ values for low rainfall scenarios are almost identical to those on pine, and under high rainfall scenarios, they are slightly lower than those on pine (Appendix S1). This is likely because pines are more abundant in Mexico's montane pine-oak forests, and so, our sample included four times as many rosettes on pines as on oaks. Although the higher probability of capsule production of *T. macdougallii* on oaks (which translated into higher mean capsule production per rosette) did not translate into higher long-term population growth rates when rosettes on oaks and pines were modeled together, it may still play an important role in enhancing colonization, something we could not capture in our study. As has been proposed for other epiphytes, *T. macdougallii* may function more as a meta-population, with individuals on each tree making up a distinct population so that persistence depends on the relative rates of survival, colonization, and extinction of populations, which can be quite dynamic (Laube and Zotz 2007, Winkler et al. 2009, Valverde and Bernal 2010). The higher mean capsule production on oaks may increase the probability of colonization. This is something that can be tested in future work.

Finally, the patterns we found for the population dynamics of *T. macdougallii* on both oaks and pines are similar to that of other epiphytic bromeliads, where lambda values are low and changes in adult survival have the largest impacts on population growth rates (Mondragón et al. 2004b, 2015, Winkler et al. 2007, Mondragón and Ticktin 2011). The low lambda values found for this and most other epiphytic bromeliads may reflect in part, harsh environmental conditions faced by epiphytes. However, they may also be underestimated resulting from sampling strategy: As is common due to the difficulty of accessing and sampling tree canopies, we sampled trees with relatively high densities of *T. macdougallii* and population growth rates on these trees may not be fully representative of the whole population. Laube and Zotz (2007) found evidence that

population growth rates declined with increasing population sizes for eight species of vascular epiphytes (Laube and Zotz 2007). A sampling strategy that includes trees with a range of colonization times and that uses a metapopulation approach could be used in future work.

To date, research on host preference has focused on specific life-stages or on the richness and abundance of epiphyte communities. Our research indicates that the long-term dynamics of epiphyte populations may also vary as a function of host genus and of climatic factors. Recent research has highlighted the importance of understanding interactions among drivers of plant population dynamics (Mandle et al. 2015). Further research that tests the contributions of different host genera and other potentially interacting drivers, including rainfall, to the viability of vascular epiphyte populations and metapopulations, is needed and especially in the context of climate change.

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