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Host tree species effects on long-term persistence of epiphytic orchid populations

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The destinies of epiphytic orchids (about 70% of all orchids) are linked to their host trees. However, there is little information on if differences in host trees characteristics can affect the long-term persistence of orchid populations, and how this might vary under different climatic conditions. We compared the population dynamics of two epiphytic orchid species, *Alamania punicea* and *Oncidium brachyandrum* growing on two host trees with contrasting leaf phenologies: the deciduous *Quercus martinezii* and the semideciduous *Q. rugosa*, over 3 years with varying levels of rainfall, in a montane tropical oak forest in Oaxaca, Mexico. Using data from > 500 individuals growing on 63 host trees, we applied linear mixed effects models, Integral Projection Models, and Life Table Response Experiments to identify the effects of host tree on orchid vital rates and population growth rates. For both orchid species, survival and growth did not differ between host species during wettest year. However, during the driest year both vital rates were higher on the semi-deciduous host *Q. rugosa* than on the deciduous *Q. martinezii*. Host species did not affect fecundity for *A. punicea*, but for *O. brachyandrum* fecundity was higher on the deciduous host. For *A. punicea*, λ values were similar between hosts during the wettest and intermediate years, but significantly lower ($\Delta\ \lambda$ = 0.28) on the deciduous than on the semi-deciduous host during the driest year. This was due primarily to lower survival on the deciduous host. For *O. brachyandrum*, λ was slightly higher ($\Delta\ \lambda$ = 0.03) on the deciduous than the semideciduous host during the wettest year, due to higher growth and reproduction. However, during the intermediate and driest years, λ values were significantly higher on the semi-deciduous than on the deciduous host ($\Delta\ \lambda$ = 0.13 and 0.15, respectively). This was due to higher survival and growth. *A. punicea* populations appear more vulnerable to dry conditions than *O. brachyandrum,* likely due to its smaller pseudobulbs, and hence lower water-storing capacity. Our results show that host tree species can both influence the vital rates and the long-term dynamics of orchid populations, and these effects vary across orchids species and over time. Our results highlight the importance of maintaining a diversity of host trees to ensure long-term population persistence.

KEYWORDS

Orchidaceae, population dynamics, host preference, integral projection models, life table response experiment, *Quercus*, *Oncidium*, *Alamania*

Introduction

The orchid family is comprised of 850 genera with more than 30,000 species, and 50% of these species are concentrated in tropical areas of the world (Chase et al., 2015). In Mexico, there are approximately 1,200 species of orchids. Nearly 40% of Mexican orchids are endemic. Some species of Mexican orchids, including epiphytes, are very attractive to horticulturists, collectors, and public, and are extracted from their natural habitats and sold illegally, which can lead to them being threatened or extirpated (Halbinger and Soto, 1997; Merritt et al., 2014).

For vascular epiphytes, the presence of their host trees is essential for the establishment and permanence of their populations. However, due to differences in host traits, not all trees offer the same conditions for the establishment and development of epiphytic orchids (Wagner et al., 2015). For example, rough bark texture can affect the capture of seeds [rugose and scaly barks favor seed adherence compared to smooth barks (Adhikari and Fischer, 2011; Gowland et al., 2013; Timsina et al., 2016)], while an ability to retain and release water can favor the germination of seeds [barks with higher water retention capacity and slower release rates favor seed germination (Callaway et al., 2002; Einzmann et al., 2015)]. Similarly, the presence of allelopathic compounds in the bark of trees can limit seed germination and establishment of epiphytes (Callaway et al., 2002; Harshani et al., 2014); the rate of bark exfoliation and the fragility of branches can lead to differential mortality rates as a result of epiphyte falls (López-Villalobos et al., 2008); and the nutrient quality of stemflows and throughfalls could affect growth and fertility of the epiphytic orchids (higher amounts of nutrients could increase growth and fecundity rates). Finally, the leaf phenology of the host trees can affect the demography of epiphytes (Einzmann et al., 2015; Ticktin et al., 2016). In addition, these and other host trees characteristics can not only influence epiphytes directly, but also indirectly by providing different microclimatic conditions for the mycorrhizal fungal community, which are indispensable for the germination of the orchid seeds. Different trees may possess different communities of fungi that may or may not favor the germination of orchids (Otero et al., 2007; Rasmussen et al., 2015).

Although there is a large literature on the effects of host traits on orchid germination, establishment and survival, there is little information on whether differences in vital rates may scale up across the life cycle to differentially affect population persistence. Similarly, if and how these differences may shift with climatic conditions is largely unexplored. For example, annual variation in climatic conditions can influence the demographic behavior of epiphytes (Mondragón et al., 2004; Ticktin et al., 2016). Populations of epiphytes growing on host species that allow for higher humidity due to their phenology, architecture or bark water holding capacity might perform better during dry years, but not during average or wettest years. The one epiphyte study that has assessed this showed that the vital rates and population growth rates of an epiphytic bromeliad were different when growing on perennial pine vs. deciduous oak host trees (Ticktin et al., 2016). Populations on oaks had higher fecundity, but those on pines had higher survival and growth. Growth rates of populations on both host genera increased with increasing dry season rainfall, but the effect was larger for populations on oaks. The authors concluded that the presence of both pine and oak trees is very important for long-term conservation of these bromeliad populations.

Although we are unaware of other studies that have addressed this question for orchids, it is of great importance for developing conservation and management plans. Like many other wild species, populations of orchids are threatened by habitat loss and conversion to monocultures of timber species or other types of plantations (Boelter et al., 2011; Mondragón Chaparro et al., 2015), where diversity of host tree species is considerably diminished, for such as reforestation with pine species only (Jiménez-Bautista et al., 2014), or substitution of native shade trees from coffee or cocoa plantations by *Inga* spp. trees (Peeters et al., 2003; Valencia et al., 2016). These changes, in combination with changes in distribution of preferred hosts of species of epiphytes due to climate change (Hsu et al., 2012), could present problems for the long-term persistence of epiphytic orchid populations.

We carried out a demographic study to provide the first test of whether and how host species can affect the population dynamics of epiphytic orchids. We focus on two epiphytic orchid species *Alamania punicea* Lex. in La Llave and Lex. and *Oncidium brachyandrum* Lindl, growing on two congeneric

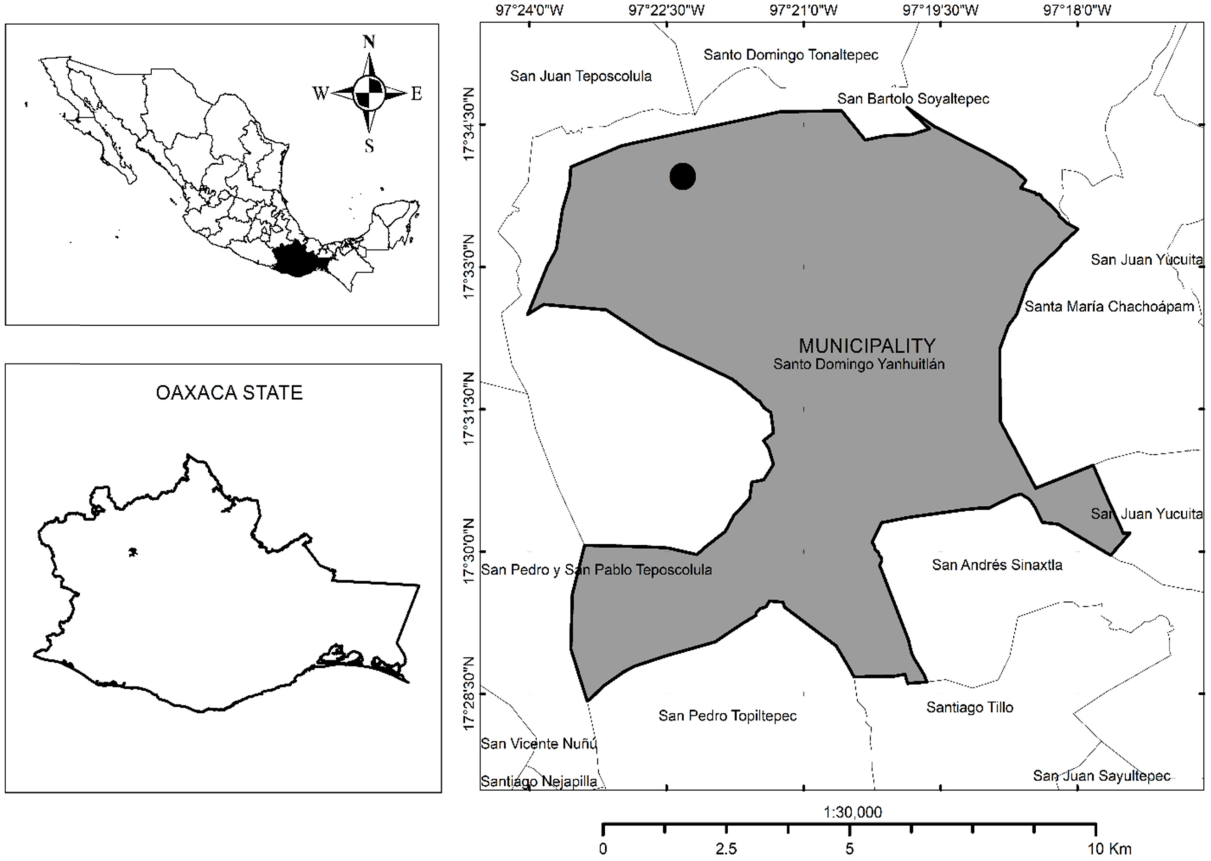

FIGURE 1
Geographic location of the study area within a seasonal oak forest in the municipality of Yanhuitlán, Oaxaca, Mexico.

host trees: the fully deciduous *Q. martinezii* Neé and the semi deciduous *Quercus rugosa* Neé. We addressed the following questions:

i) Do orchid vital rates (survival, growth, reproduction) vary between host tree species?
ii) Do differences in vital rates translate into differences in population growth rates?
iii) Do differences in vital rates and population growths rates vary with inter-annual climatic variation?

We hypothesized that:

(1) Survival and reproduction would be higher for both orchids on semi-deciduous *Q. rugosa* than fully deciduous *Q. martinezii*, due to lower light penetration and higher humidity in their treetops of the former, which can help orchids avoid photoinhibition (de la Rosa-Manzano et al., 2014; Einzmann et al., 2015) and increase flowering (Cervantes et al., 2005). In addition, we expected that branch fall, one of the main causes of mortality in epiphyte populations (Mondragón Chaparro et al., 2015; Cortes-Anzures et al., 2017), would be lower on *Q. rugosa* due to its thicker branches.
(2) Higher survival of individuals on the semideciduous *Q. rugosa* would translate into higher population growth rates (λ values), since population growth rates of long-lived species are highly sensitive to differences in survival (Franco and Silvertown, 2004). We also expected that the difference in λ values may be greater in drier years than in wettest years.

Materials and methods

Study area and species

This study was carried out in an oak forest in Tooxi, municipality of Yanhuitlán, Oaxaca, Mexico located in the Sierra Madre del Sur physiographical province (17°33′57.34″ N and 97°22′19.28″ W, elevation 2,579 m a.s.l; **Figure 1**) that encompasses the Mixteca Alta UNESCO Global Geopark

TABLE 1 Precipitation patterns in Tooxi, Yanhuitlán, Oaxaca from 2018 to 2020.

Year	Annual precipitation (mm)	Dry season (November–April) total/ average dry season monthly precipitation (mm/month)	Range: minimum/month-maximum/month during dry season (mm/month)
2018	1058	264.8/44.1 ± 24.2	14.9–84.7
2019	947	103.1/17.28 ± 4.3	10–22.3
2020	1041	125.2/20.9 ± 15.1	4.3–48.2

(García-Sánchez et al., 2021). Mean annual precipitation is 753 ± 152 mm, with a dry season average of 86 ± 67 mm. The mean temperature of the dry season is 14.4 ± 1.3°C, and the average maximum and minimum temperatures are 23.3 ± 1.8°C and 7.0 ± 2.9, respectively (INIFAP, 2021; **Table 1**). Tree vegetation includes deciduous, semi-deciduous and evergreen trees and is comprised mainly of *Quercus candicans* Neé, *Q. castanea* Neé, *Q. crassifolia* Humb. and Bonpl., *Q. rugosa* Neé, *Q. martinezii* C.H. Müll., *Juniperus flaccida* Schltdl., and *Arbutus xalapensis* Kunth. The epiphytic vegetation includes *Tillandsia bourgaei* Baker, *T. macdougallii*, *T. plumosa* Baker, *T. prodigiosa* (Lem.) Baker, *T. recurvata* (L.) L., *T. usneoides* (L.) L., *Pleopeltis conzatti* (Weath.) R. M. Tryon and A.F.Tryon, *Polypodium martensii* Mett., *Echeveria nodulosa* (Baker) Otto, *O. brachyandrum* and *A. punicea*.

We selected two species of tree hosts, *Q. rugosa* and *Q. martinezii* (**Table 2**) for this study. *Quercus rugosa* is distributed from Texas and Arizona, in the USA, to the Sierra Madre de Chiapas in Guatemala. Its populations are abundant in mountainous areas of western and central Mexico in temperate sub-humid climate, between the 1,800 and 2,800 m a.s.l. *Quercus martinezii* is endemic to Mexico and distributed in the states of Aguascalientes, Guanajuato, Hidalgo, Guerrero, Jalisco, Nuevo Leon, Nayarit, Puebla, Queretaro, San Luis Posoti, Tamaulipas, Veracruz, and Oaxaca from 2,000 to 2,500 m a.s.l (Valencia-A, 2004). The other species that hosted orchids (*Q. crassifolia* and *Q. candicans, J. flaccida* and *A. xalapensis*) had few individuals on them.

We focused on the two most abundant orchid species out of the three present at the study site. In addition, *Alamania punicea* is listed in CITES Appendix II, is the only species of a monotypic genus endemic to Mexico, and nothing is known about the demography of this species that could help to establish management and conservation strategies. *Oncidium brachyandrum* is harvested commercially species in Tlaxiaco, Oaxaca which is close to the study site (Ticktin et al., 2020). Nothing is known about the demography of this species; there is only one demographic study on another species of the genus (*Oncidium poikilostalix* Kraenzl.) M.W. Chase and N.H. Williams but in coffee plantations. We describe each orchid species as follows:

> *Alamania punicea* Lex. is an epiphytic perennial orchid, 3–6 cm high including the inflorescence; ovoid pseudobulbs, slightly elongated, covered by translucent papyrus sheaths, 7–10 mm long; leaves 2, rarely 3, at the apex of the pseudobulb, elliptic to oblanceolate sheets, 1–4 cm long, 5–10 mm wide; flowers 7–14, red to pinkish reddish. Fruits are capsules with dust-like seeds. There is no report of *A. punicea* breeding system. Stpiczyńska et al. (2005) suggest that given its floral morphology, it could be pollinated by hummingbirds. *Alamania punicea* is an endemic species prevalent in cool and seasonally dry *Quercus-Pinus* forests on the *Trans*-Mexican Volcanic Belt and the Sierra Madre Oriental above 1,900 m a.s.l. (where oaks are dominant; García-Cruz et al., 2003; Soto Arenas, 2005; UNEP-WCMC, 2020).

> *Oncidium brachyandrum* is an epiphytic perennial orchid, up to 20 cm high with clustered pseudobulbs, ovoid to ellipsoid or subglobose, somewhat laterally compressed, 2–3 cm long; 2 or 3 lateral leaves; flowers 2 or 3, simultaneous, showy, 25–30 mm in diameter, sepals, and petals brown or yellow with irregular brown spots and yellow lip. Fruits are capsules with dust-like seeds. This species probably is pollinated by oil-collecting or bombini bees and might be self-incompatible as reported for other members of the genera (Damon and Cruz-López, 2006; Pemberton, 2008). This orchid is distributed in Honduras, Guatemala, and in Mexico in the states of Durango, Guerrero, Jalisco, Michoacán de Ocampo, Morelos, Nayarit, Sinaloa, Zacatecas, and Oaxaca. It grows mainly in oak forests elevations of 2,000–2,500 m a.s.l. (Jiménez et al., 1998).

Precipitation, the most limiting factor for epiphytes (Zotz and Hietz, 2001; Laube and Zotz, 2003), varied across our three study years, especially during the dry season (**Table 1**). Although precipitation in all 3 years was above the mean of the past 20 years (**Supplementary material**), we refer to these years as the wettest year (2018), driest year (2019) where dry season precipitation was less than half that of the wettest year–and intermediate year (2020).

TABLE 2 Host traits of two *Quercus* species in a seasonal oak forest in Yanhuitlán, Oaxaca, Mexico.

Trait	*Quercus martinezii*	*Quercus rugosa*
Leaf phenology	Deciduous	Semi-deciduous
Leaf area (cm^2)*	39.96 ± 4.61^{b}	59.70 ± 11.94^{a}
Tree height (m)§	9.69 ± 1.43^{a} ($n = 21$)	7.74 ± 2.05^{b} ($n = 42$)
Diameter at breast height (cm)	36.11 ± 12.59^{ns} ($n = 21$)	29.09 ± 17.72^{ns} ($n = 42$)
Bark roughness (cm)†	5.87 ± 0.39^{ns} ($n = 10$)	5.53 ± 0.59^{ns} ($n = 10$)
Water holding capacity of bark (ml/cm^3)	0.28 ± 0.07^{ns} ($n = 5$)	0.33 ± 0.09^{ns} ($n = 5$)
Canopy openness (%)		
Dry season	30.74 ± 6.74^{ns}	33.10 ± 8.91^{ns}
Wettest season	38.07 ± 5.81^{ns}	38.07 ± 2.24^{ns}
Relative humidity (%)		
Dry season	75.49 ± 15.96^{ns}	80.38 ± 14.04^{ns}
Wettest season	71.44 ± 10.32^{ns}	76.99 ± 9.30^{ns}
Mean temperature (°C)		
Dry season	14.17 ± 0.57^{ns}	14.52 ± 0.95^{ns}
Wettest season	13.76 ± 1.56^{ns}	13.47 ± 1.79^{ns}
Concentration of phosphorus in throughfalls (mg/l)	0.16 ± 0.03^{ns} $n = 5$	0.15 ± 0.05^{ns} $n = 5$
Concentration of potassium in throughfalls (mg/l)	2.56 ± 1.06^{ns} $n = 5$	2.76 ± 1.16^{ns} $n = 5$

Values are means ± SD for each tree species. Superscript lower-case letters indicate significant differences (ANOVA: $P < 0.05$, Tukey HSD).

§Significant differences across tree species [$F_{(1,62)} = 15.30$, $p = 0.0002$].

*Significant differences across tree species [$F_{(1,39)} = 47.52$, $p = 0.0001$].

†Information taken from Hernández-Álvarez (2021).

We selected 21 *Q. martinezii* and 42 *Q. rugosa* trees within a 1 ha plot and tagged and measured all the orchids of our study species on them. We selected a higher number of *Q. rugosa* trees since they had lower densities of orchids: on average there were 14 ± 11 *O. brachyandrum* plants/tree on *Q. martinezii* versus 6 ± 6 on *Q. rugosa*; these values were 8 ± 6 plants/tree vs. 7 ± 6, respectively, for *A. punicea.* For each of 3 years (2017–2020), we recorded plant status (alive, dead), size, and fecundity (number of capsules), and recorded the number of new seedlings. For both species of orchid, we measured height and width of the largest pseudobulb and counted the number of pseudobulbs. We also recorded causes of mortality distinguishing broadly between desiccation (the entire dead plant was still attached to the tree) and falling (the plant was missing). Although individuals that die due to desiccation are susceptible to falling, our monthly checks ensured that we were able to ascertain the correct cause of mortality. We did not include herbivory as a cause of death since we did not observe orchid plants attacked by herbivores at our study site. This is consistent with findings from other studies that rates of herbivory are mostly low in epiphytes (Benzing, 1990; Zotz, 1998; Winkler et al., 2005). Finally, we measured host characteristics on a subsample of individuals of each host species and tested for differences between hosts using ANOVAs (**Table 2**; Ramírez-Martínez, 2022).

Data analyses

Host effects on demographic rates (vital rates)

We tested differences in survival, growth, and reproduction of orchid individuals on the different *Quercus* species using generalized linear mixed models (GLMMs). Initial size (log-transformed), host species (*Q. martinezii* vs. *Q. rugosa*), and year were fixed effects and individual orchid nested within individual host tree were random effects. We used regression analyses to identify which measure of size (e.g., number of pseudobulbs, size of the pseudobulb, etc.) was the best predictor of growth, reproduction, and survival. We used Akaike's information criterion (AICc) to compare model fit. We found that for *A. punicea*, the best predictor was an index of number of leaves times area of the longest leaf (calculated with the formula for an oval). For *O. brachyandrum,* the best predictor was pseudobulb area (calculated with the formula for an oval).

To model the probability of survival, reproduction, and probability of mortality due to desiccation, we used binomial distributions, and to model the number of capsules, we used a negative binomial model. To model growth (size at $t + 1$), we used Gaussian error structure with an exponential variance structure, where the variance increases as an exponential function of initial size (Zuur et al., 2009). We modeled the probability of reproduction with the minimum size observed for plant reproduction (sizes: *A. punicea* $\geq$ 1.44 cm^2, and *O. brachyandrum* $\geq$ 0.79 cm^2). We selected the best fit model based on the lowest Akaike (AICc). All analyses were performed using the glmmTMB package in R v. 4.1.1.

Host effects on population growth dynamics

Integral projection models

We used integral projection models [IPMs (Easterling et al., 2000)] to project the long-term (asymptotic) population growth rates (λ values) of each orchid species growing on each of the two host species. The IPMs are constructed from continuous functions that describe size-dependent growth, survivorship, and fecundity. The IPM kernel is the sum of two functions. One describes the survival, probability and growth (or shrinkage) of survivors (*p* kernel), and the second is the reproductive contribution of each individual and the size distribution of the new seedlings (*f* kernel). Our IPM took the form:

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

For both orchid species, the $p(x,y)$ kernel was represented by the survival probability of individuals 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 $f(x,y)$ denotes the production of new seedlings of size (x) produced from plants of size (y). This was calculated for plants of reproductive size as: $f(x,y) = s(x)\ f_n(x)\ p_E f_d(y)$, where $s(x)$ is the survival of plants of size (x), $f_n(x)$ is the probability of producing capsules for plant size x times the number of capsules per plant size x; p_E is the number of new seedlings produced per capsule, and $f_d(y)$ is the size distribution of new seedlings. For each host species, p_E was calculated as the number of seedlings observed in the field divided by the total number of capsules produced. We calculated the asymptotic projected population growth rate (λ) for each IPM using the popbio 2.7 package in R (Stubben and Milligan, 2007) and obtained 95% confidence intervals by bootstrapping ($N = 100$).

We used life table response experiments (LTREs) (Caswell, 2001) to identify which vital rate contributed most to the observed differences in population growth rates between hosts, for each orchid species and year.

Results

Host effects on vital rates

Alamania punicea

Survival

For individuals on both host species, survival increased as a function of size and was highest during the wettest year and lowest during the driest year (**Table 3** and **Figure 2A**). The best fit model included an interaction between host species and year such that difference in survival between individuals on semideciduous *Q. rugosa* and the deciduous *Q. martinezii* was least during the wettest year. The probability of mortality due to desiccation decreased significantly with (log) size ($\beta = -0.69$, SE = 0.09, $z = -7.35$, $p < 0.001$) but did not differ significantly between host trees.

Growth

For individuals on both species, growth was lowest in the driest year and highest in the intermediate year. During the dry year, growth was higher on the semi-deciduous *Q. martinezii* than on the deciduous *Q. martinezii* (**Table 3** and **Figure 2B**).

Reproduction

Plants began to reproduce once they reached 1.08 cm^2 size (number of leaves times area of the longest leaf). Only 1.4% of plants flowered and 100% those produced capsules. The probability of reproduction increased as a function of size, as did the number of capsules produced by reproducing plants (**Table 3**).

TABLE 3 Estimated coefficients from mixed-effect models of the probability of survival, growth, reproduction, and probability of producing capsules for *Alamania punicea* plants growing on two *Quercus* species.

Fixed effects	Estimate	SE	*Z* value	*P*-value
Probability of surviving to *t* + 1[†]				
Intercept	1.6513	0.4654	3.548	0.000388
Size at start	0.5076	0.1049	4.837	$1.32e-06$
Year 2 (2018–2019)	−1.3216	0.4157	−3.179	0.001477
Year 3 (2019–2020)	−1.0069	0.4871	−2.067	0.038704
Host species (*Q. rugosa*)	0.4296	0.6309	0.681	0.495931
Year 2 × *Q. rugosa*	1.1342	0.6219	1.824	0.068194
Year 3 × *Q. rugosa*	−0.5589	0.6066	−0.921	0.356817
Size at *t* + 1 of surviving individuals (growth)[§]				
Intercept	0.30439	0.10874	2.80	0.00512
Size at start	0.83544	0.02640	31.65	< 2e-16
Year 2 (2018–2019)	−0.52526	0.11704	−4.49	$7.2e-06$
Year 3 (2019–2020)	0.39822	0.12676	3.14	0.00168
Host species (*Q. rugosa*)	−0.06609	0.12641	−0.52	0.60110
Year 2 × *Q. rugosa*	0.33882	0.16004	2.12	0.03425
Year 3 × *Q. rugosa*	−0.11524	0.17310	−0.67	0.50557
Probability of producing capsules at time *t* (for individuals ≥ 35 cm)[†]				
Intercept	−4.8208	0.7344	−6.564	$5.23e-11$
Size at start	0.5040	0.1692	2.980	0.00289
Year 2 (2018–2019)	0.5833	0.6006	0.971	0.33141
Year 3 (2019–2020)	0.4047	0.7060	0.573	0.56647
Host species (*Q. rugosa*)	0.9169	0.6554	1.399	0.16183
Year 2 × *Q. rugosa*	0.0587	0.7462	0.079	0.93730
Year 3 × *Q. rugosa*	−20.3430	7179.93	−0.003	0.99774
Capsules produced per reproductive plant at time *t**[*]				
Intercept	−0.7825	0.4918	−1.591	0.111585
Size at start	0.4162	0.1160	3.590	0.000331
Host species (*Q. rugosa*)	0.5830	0.3702	1.575	0.115327

[†] Binomial (logit) GLMM.

[§] GLMM with Gaussian error structure and an exponential variance structure.

[*] Negative binomial GLMM.

Oncidium brachyandrum

Survival

For plants on both host species, survival increased as a function of plant size. There was no difference in survival between host species during the wettest year, but survival on the semi-deciduous *Q. rugosa* was higher than on the deciduous *Q. martinezii* during the dry and intermediate years (**Table 4** and **Figure 3A**). The probability of mortality due to desiccation decreased significantly with (log) size ($\beta = -0.64$, SE = 1.07, $z = -6.00$, $p < 0.001$) and was significantly higher in the intermediate year than in the wettest year ($\beta = -1.63$, SE = 0.57, $z = -2.89$, $p = 0.004$). It did not differ significantly between host trees.

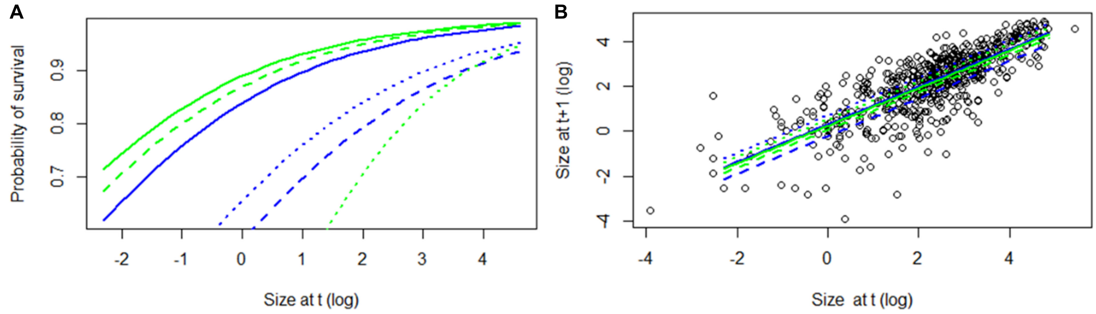

FIGURE 2

(A) Survival and **(B)** growth as function of size, for *Alamania punicea* plants growing on two oak species *Quercus martinezii* (blue) and *Q. rugosa* (green). Solid lines indicate year 2017–2018, dashed lines year 2018–2019, and dotted lines year 2019–2020.

TABLE 4 **Estimated coefficients from mixed-effect models of the probability of survival, growth, reproduction, and probability of producing capsules for *Oncidium brachyandrum* plants growing on two *Quercus* species.**

Fixed effects	Estimate	SE	*Z* value	*P*-value
Probability of surviving to $t + 1$[†]				
Intercept	2.021234	0.363086	5.567	$2.59e-08$
Size at start	0.404343	0.078653	5.141	$2.74e-07$
Year 2 (2018–2019)	−0.500072	0.275850	−1.813	0.0699
Year 3 (2019–2020)	−0.357534	0.331662	−1.078	0.2810
Host species (*Q. rugosa*)	−0.009813	0.598163	−0.016	0.9869
Year 2 × *Q. rugosa*	1.320310	0.661457	1.996	0.0459
Year 3 × *Q. rugosa*	2.523453	1.119749	2.254	0.0242
Size at $t + 1$ of surviving individuals (growth)[§]				
Intercept	−0.27854	0.05545	−5.02	$6.08e-07$
Size at start	0.74661	0.02133	35.01	< 2e-16
Year 2 (2018–2019)	0.26731	0.08206	3.26	0.00112
Year 3 (2019–2020)	0.82965	0.08549	9.70	< 2e-16
Host species (*Q. rugosa*)	−0.06476	0.11067	−0.59	0.55847
Year 2 × *Q. rugosa*	0.42201	0.159992	2.64	0.00832
Year 3 × *Q. rugosa*	0.45812	0.16220	−2.82	0.00474
Probability of producing capsules at time t (for individuals $\geq$ 35 cm)[†]				
Intercept	−3.4918	0.4120	−8.476	< 2e-16
Size at start	1.5336	0.2978	5.150	$2.62e-07$
Host species (*Q. rugosa*)	−0.8107	0.4413	−1.837	0.0662
Capsules produce per reproductive plant at time t[*]				
Intercept	−0.02442	0.27662	−0.088	0.9297
Size at start	0.36621	0.19401	1.888	0.0591

[†] Binomial (logit) GLMM.
[§] GLMM with Gaussian error structure and an exponential variance structure.
[*] Negative binomial GLMM.

Growth

For plants growing on both host species, growth was higher in dry and intermediate years than in wettest year. Growth was higher on the semi-deciduous *Q. rugosa* than on the deciduous *Q. martinezii* only during the dry year (Table 4 and Figure 3B).

Reproduction

Plants began to reproduce once they reached 0.78 cm^2 (pseudobulb area); 14% of plants flowered and 100% of these produced capsules. The probability of reproduction and the number of capsules produced per reproductive plant both increased as a function of size (Table 4). Host species was included in the best fit model for the probability of reproduction, with reproduction higher on the deciduous *Q. martinezii* than the semideciduous *Q. rugosa* (Table 4).

Host tree effect on population dynamics

Population growth rates of *A. punicea* on the two host species were similar in the wettest year and the intermediate years (Δ λ between hosts = 0.01). However, population growth rates were significantly higher on the semideciduous host than the deciduous host during the driest year ((Δ λ = 0.28; Figure 4A). For *O. brachyandrum*, λ was slightly lower on *Q. martinezii* than on *Q. rugosa* during the wettest year (Δ λ = 0.03). However, the reverse was true during the driest and intermediate years, where λ values were significantly higher on *Q. rugosa* than on *Q. martinezii* (Δ λ = 0.15 and 0.13, respectively) (Figure 4B). For *O. brachyandrum*, λ values were higher in the dry and intermediate years, than in the wettest year.

LTRE analyses

For *A. punicea*, the higher λ value observed for populations on *Q. rugosa* in the driest year was mainly due to higher survival on that host tree. For the wettest and the intermediate rainfall year, there was little differences in λ values across hosts, but differences were due to higher survival on *Q. rugosa* during the wettest year growth, and higher growth on *Q. martinezii* during the intermediate year (Figures 5A–C). For *O. brachyandrum* higher growth and reproduction contributed the most to the higher λ value of *Q. martinezii* in wettest year. The higher λ

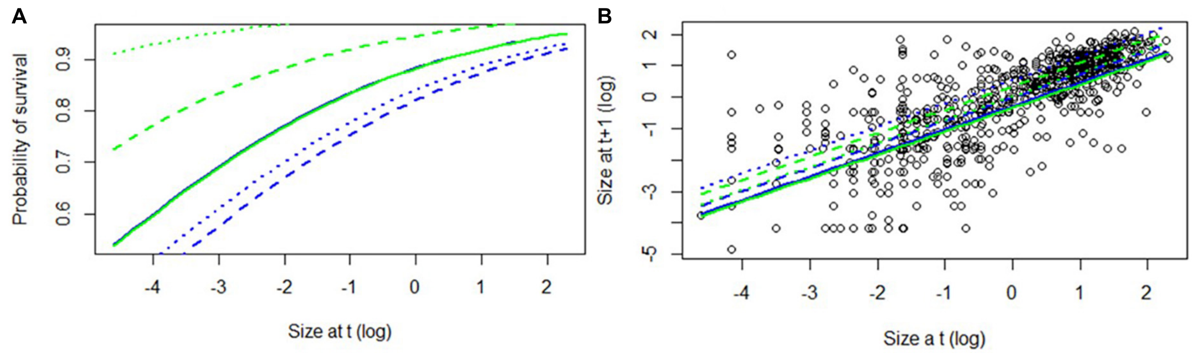

FIGURE 3
(A) Survival and **(B)** growth as function of size, for *Oncidium brachyandrum* plants growing on two oak species *Quercus martinezii* (blue) and *Q. rugosa* (green). Solid lines indicate year 2017–2018, dashed lines year 2018–2019, and dotted lines year 2019–2020.

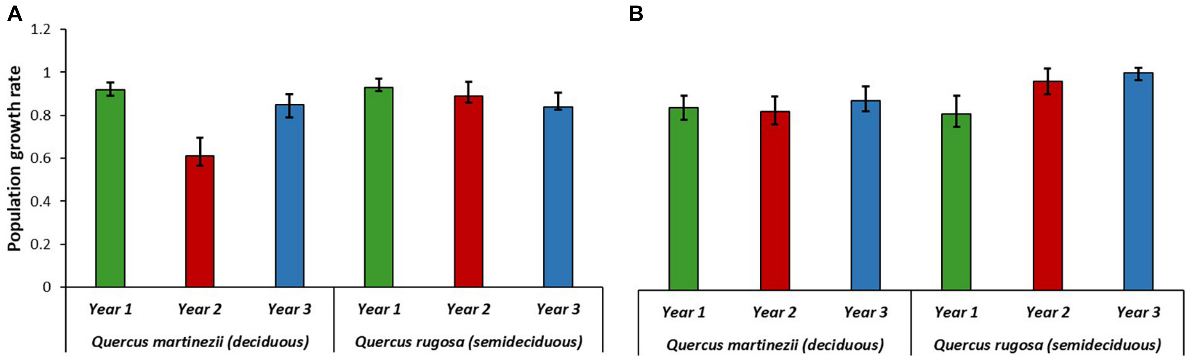

FIGURE 4
Population growth rates (λ values) of **(A)** *Alamania punicea* and **(B)** *Oncidium brachyandrum* growing on two *Quercus* species, from 2018 to 2020 in an oak forest in Oaxaca, Mexico. Error bars represent 95% confidence intervals.

values observed for populations in *Q. rugosa* during the two drier years was due to higher growth (driest year), and higher survival (intermediate year) (**Figures 5D–F**).

Discussion

The aim of our paper was to test if and how host species can affect the population dynamics of epiphytic orchids. Our results show that rates of survival, growth and reproduction of epiphytic orchids can vary across host tree species, and this can translate into difference in population growth rates. They also suggest that the direction and magnitude of these differences appears to depend on climatic conditions.

Our finding that both orchid species had higher growth and survival on the semi-deciduous host than on the deciduous host, during the driest year, but not during the wettest year, is consistent with other studies. Einzmann et al. (2015) found higher growth and survival rates of two epiphytic species growing on perennial trees than on deciduous trees, due to the sunnier and drier microclimates during dry season on the latter, which increased mortality due to desiccation. The same has been reported for an epiphytic bromeliad, where individuals growing on perennial pines had higher survival and growth rates that those growing on deciduous oak (Ticktin et al., 2016). Similarly, Callaway et al. (2002) reported higher growth rates of epiphytic individuals growing on their preferred host and attributed it to the higher water holding capacity its bark. Species with greater water holding capacity provide a more humid environment, and allow epiphytes access to water for a longer period. Humidity is recognized as the more limiting factor within epiphytism (Benzing, 1990; Laube and Zotz, 2003; Zotz, 2013).

Our results suggest potential lag effects of drought, since for the semi-deciduous host, a higher number of orchid individuals died the year after the driest year (intermediate year), than during the driest year itself. According to Zotz and Tyree (1996) there can be long-term drought stress effects on the physiology of orchids that can be perceived afterward forcing plants to show die back on some of their parts (like leaves), and finally die.

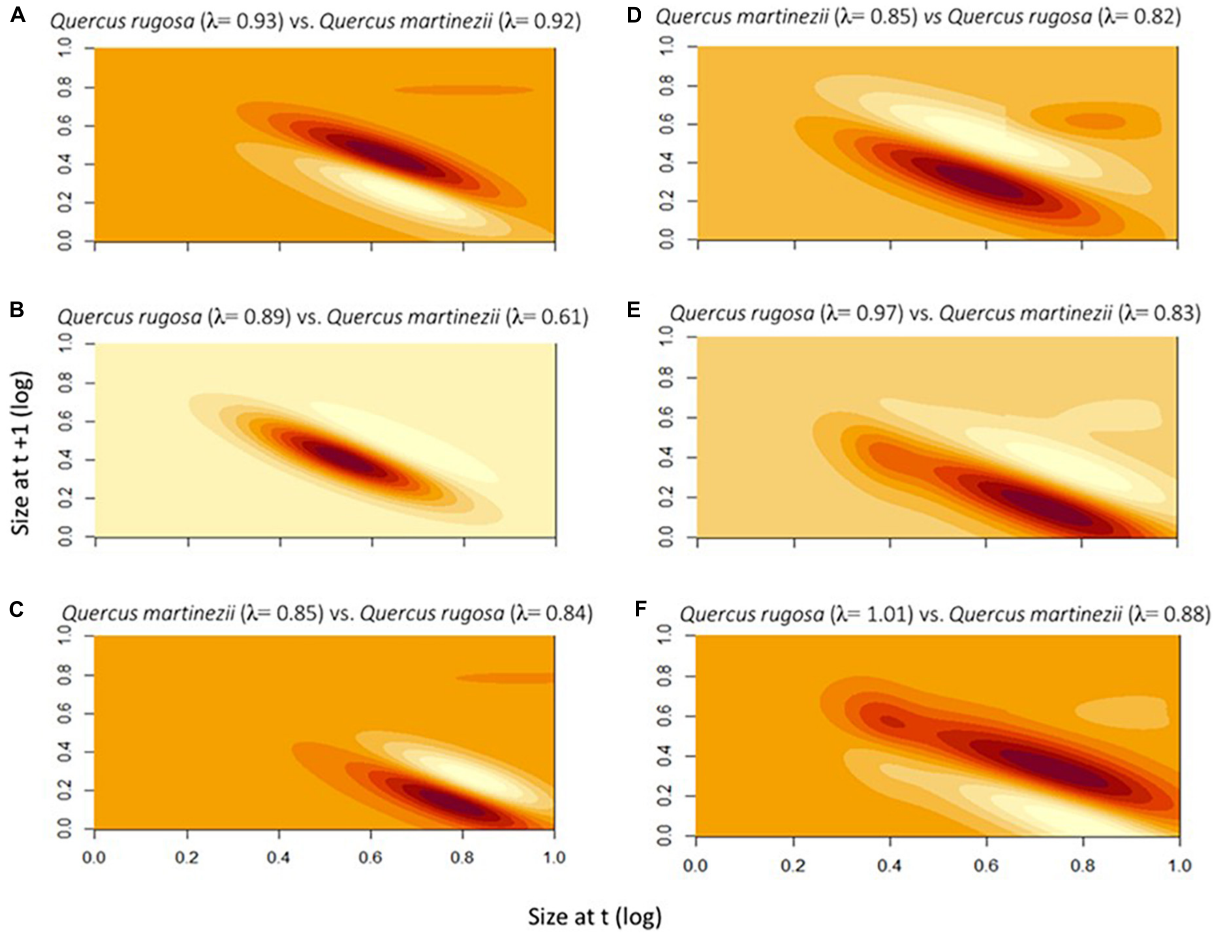

FIGURE 5
Life table response experiment contributions for *Alamania punicea* **(A–C)** and *Oncidium brachyandrum* **(D–F)** plants growing on two *Quercus* species. Darker colors represent life-history transitions that make greater contributions to higher λ values observed. Values across the diagonal represent contributions from survival, and those below diagonal represent contributions from growth. Fecundity contributions are represented in the top right corner.

Our finding that fecundity of *O. brachyandrum* was also higher on the deciduous host could be related to the low photosynthetic efficiency of epiphytic orchids due to drought adaptation (Sahagun-Godinez, 1996); they therefore need higher light (as in deciduous trees in our case) to perform photosynthesis efficiently and produce photosynthates for flower production. The lack of effect that we observed for *A. punicea* could be related to sample size, since very few individuals flowered during our study. The low probability of flowering is typical for many epiphytic orchids (Tremblay, 2006).

The differences we found in vital rates scaled up to differences in population growth rates, with λ values much lower on the deciduous host during the dry years than in the wettest year. Our finding that Δ λ between the wettest and dry year was greater for *A. punicea* than for *O. brachyandrum* is likely related to differences between the species in adaptation related with drought tolerance. *A. punicea* has thick leaves and cuticles, and small pseudobulbs (7–10 mm long), while *O. brachyandrum* has thin leaves and pseudobulbs 2–3 cm long. These represent two of the main strategies of orchids for drought tolerance (Stancato et al., 2001; Yang et al., 2016): thick cuticles avoid water loss, while pseudobulbs store water. In our study, the species with pseudobulbs better buffered the effect of host tree on its growth and survival rates. Pseudobulbs play an important role in the growth and survival of epiphytic orchids since they not only store water but are also responsible for the partition of assimilates, carbohydrate and minerals and can perform photosynthesis (Ng and Hew, 2000). Further research is needed to identify how morphological and physiological variation in epiphytic orchids (Dressler, 1993; Yang et al., 2016; Zhang et al., 2018) shapes demographic responses. In addition, translocation experiments could further disentangle differences in demographic rates across hosts.

Our results highlight the importance of preserving tree species diversity to foster the long-term persistence of populations of vascular epiphytes. This is especially true if we consider that vascular epiphytes function as metapopulations (Winkler et al., 2009; Valverde and Bernal, 2010), where individuals growing on one host tree represent a sub-population interconnected with other sub-populations (on other host trees) by seed dispersal, and where trees that support growing sub-populations determine the growth of the metapopulation (Winkler et al., 2009). Thus, metapopulation growth may be maximized when there is a diversity of host species that allow for growth under varying climatic conditions. In addition, variation among genotypes of the same tree species could potentially affect demographic rates, given that Zytynska et al. (2011) found a positive correlation between the genetic distances among host trees and similarity among the community vascular epiphytes growing on them. Further research is needed to better understand how host tree traits shape the persistence of populations of epiphytic orchids. On the ground, working with local communities to help identify land-use options that maintain tree diversity will be key.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AR-M conducted fieldwork and wrote most of the manuscript. DM conceived the study, provided the advice, financial support, conducted fieldwork, and contributed to the manuscript. TT provided the advice, helped with data analyses, contributed to the manuscript, and reviewed the English. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.1059136/full#supplementary-material

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