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“Host tree effect on demography and phenology of epiphytic species”

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RESUMEN

Las epífitas, conocidas como plantas que viven en otras plantas, dependen en gran medida de sus árboles hospederos o forofitos para sobrevivir; por lo que su desempeño y destino están íntimamente relacionados con los rasgos de los árboles, los cuales varían en función de la especie. El efecto de los forofitos sobre la abundancia y riqueza de epífitas está bien documentado, pero se sabe poco acerca de sus efectos sobre las tasas vitales y la fenología de las epífitas vasculares. En este estudio analizamos el efecto de diferentes especies de árboles hospederos sobre la fenología y demografía de diferentes especies epífitas, esta información es fundamental para tener una mejor comprensión de los posibles promotores de la distribución y abundancia de epífitas en los bosques tropicales y para establecer futuras estrategias de conservación y manejo para epífitas y sus árboles hospederos. Para tal fin, seleccionamos tres especies de encino con diferentes rasgos y carga de epífitas (*Quercus martinezii, Q. castanea* y *Q. rugosa*). Las epífitas estudiadas fueron: *Oncidium brachyandrum*, *Alamania punicea*, *Echeveria nodulosa*, *Tillandsia prodigiosa* y *T. plumosa*. En diciembre de 2017, marcamos individuos de cada especie de epífita en 21 árboles de *Q. martinezii*, 17 de *Q. rugosa* y 42 de *Q. castanea*. Para cada especie de árbol, estimamos la capacidad de retención de agua de sus cortezas, el contenido mineral de las escorrentías foliares, la apertura del dosel, la humedad relativa y la temperatura de sus copas. Para el estudio de fenología monitoreamos mensualmente individuos adultos desde marzo de 2018 a febrero de 2020 (24 meses) y registramos el estado reproductivo de las plantas, seleccionamos las siguientes fenofases: formación de inflorescencias, floración, fructificación y dispersión de semillas. Para el procesamiento de datos, calculamos el índice de actividad (IA) para facilitar la descripción de la fecha de inicio, duración y frecuencia. Adicionalmente, determinamos la estacionalidad de las fenofases aplicando estadística circular, además utilizamos Modelos Aditivos Generalizados para Ubicación, Escala y Forma (GAMLSS) para estudiar la posible correlación entre los parámetros ambientales con la presencia de las fenofases para cada especie epífita creciendo en diferentes especies de árboles. Para el estudio demográfico, medimos a los individuos anualmente durante tres años consecutivos (diciembre de 2017 a 2020) y registramos su supervivencia, estado reproductivo y la presencia de nuevas plántulas. Los análisis de datos incluyeron Modelos de Proyección Integral (MIP) para ver el efecto del árbol hospedero en la dinámica poblacional a largo plazo (en términos de la tasa de crecimiento de la población [λ]) y Experimentos de respuesta de la tabla de vida (LTREs) para determinar que tasas vitales, provocan la variación en los valores de λ en poblaciones creciendo en diferentes especies de árboles hospederos. Nuestros resultados muestran que existe un efecto del árbol hospedero sobre la fenología de las epífitas vasculares y que dicho efecto varía entre las especies epífitas y las fenofases evaluadas. Para las especies de bromelias, la fenofase de formación de inflorescencias pareció más sensible al efecto del forofito, sobre todo en un adelanto de la fecha de inicio; en tanto que las especies de orquídeas presentaron una menor variación en el IA. Las condiciones microambientales dentro de las copas de los árboles mostraron un ligero efecto sobre la fenología de las epífitas. Encontramos que el efecto del forofito sobre la supervivencia, el crecimiento y la reproducción depende de la epífita vascular estudiada y que este efecto varía entre años. De acuerdo con los valores de λ, los árboles de *Q. castanea* son hospederos más estables para *T. prodigiosa* pero su idoneidad mostró ligera variación interanual. Para las especies de orquídeas, los árboles de *Q. rugosa* promueven la supervivencia, pero su efecto cambió con el tiempo, posiblemente por la interacción con otras condiciones micro y macroambientales. Las diferencias en las tasas de crecimiento poblacional entre las especies de hospederos generalmente se debieron a cambios en el crecimiento o supervivencia de los individuos adultos jóvenes y reproductivos; y en algunos casos la fecundidad. Nuestro estudio, evidenciamos claramente un efecto de árbol hospedero en la fenología y demografía de las epífitas vasculares.

ABSTRACT

Epiphytes, known as plants that live on other plants, depend strongly on their host trees for survival. Their performance and fate are intimately linked with their host tree traits that vary as a function of the host species. The influence of host trees on epiphyte abundance and richness is well documented, but little is known about their impact on their vital rates and phenology. In this study, we estimated the effect of host tree species on the phenology and demography of different epiphytic species. This information is central to understanding possible drivers of distribution and abundance of epiphytes in tropical forests and establishing future conservation and management strategies for epiphytes and their host trees. We selected three oak species with different traits and high epiphyte loads (*Quercus martinezii, Q. castanea,* and *Q. rugosa*). Epiphytes comprehended *Oncidium brachyandrum*, *Alamania punicea*, *Echeveria nodulosa*, *Tillandsia prodigiosa* and *T. plumosa* growing on all host tree species. In December 2017, we tagged individuals of each epiphyte species on 21 trees of *Q. martinezii*, 17 of *Q. rugosa*, and 42 of *Q. castanea*. For each tree species, we estimate the water holding capacity of their barks, mineral content of throughfalls, canopy openness, relative humidity, and temperature of their crowns. For the phenology study, we monthly monitored adult individuals from March 2018 to February 2020 (24 months) and registered the reproductive status of the plants; we observed the following phenophases: inflorescence formation, flowering, fruiting, and seed dispersal. We calculated the Activity Index (AI) to facilitate the description of the onset date, duration, and frequency for data processing. Additionally, we determined the seasonality of phenophases with circular statistics; we also applied Generalized Additive Models for Location, Scale, and Shape (GAMLSS) to correlate environmental parameters with the presence of phenophases each epiphyte species growing on different host trees. For the demography study, we measured individuals annually for three consecutive years (December 2017 to 2020) registered their survival, reproductive status, and the presence of new seedlings. Data analyses included Integral Projection Models (IPMs) to see the effect of host tree on long term population dynamics (in terms of the population growth rate [λ]) and Life Table Response Experiments (LTREs) to determine which vital rates promote variations on λ values of populations of epiphytes growing on different host species. Our results showed a host tree effect on the phenology of vascular epiphytes, but this effect differs across epiphytic species and phenophases evaluated. For bromeliad species, the inflorescence formation phenophase seemed more sensitive to host effect, especially in early-onset dates, while orchid species showed a minor variation on AI. Microenvironmental conditions within host tree canopies showed a slight impact on epiphyte phenology. We found that the host tree effect on survival, growth, and reproduction depends on the vascular epiphyte studied, and this effect also varies over the years. According to λ values, trees of *Q. castanea* seemed more stable hosts for *T. prodigiosa*, but their suitability showed interannual variation. For orchid species, *Q. rugosa* trees enhanced survival but their effect changed over time, possibly interacting with other micro and macroenvironmental conditions. Differences in population growth rates across host species usually were given by the growth or survival of juvenile and reproductive adult individuals, and in some cases, fecundity. Our study evidences a host tree effect on phenology and demography of vascular epiphytes.

CHAPTER I. GENERAL INTRODUCTION

Vascular epiphytes comprise 10% of all global plant species (Zotz, 2013) and more than 25% of all tropical vascular plants (Nieder et al., 2001). They play essential roles in the ecosystems since they increase the structural complexity of forests, change patterns of rainfall interception and atmospheric nutrient capture (Van Stan & Pypker, 2015; Hargis et al., 2019; Mendieta-Leiva et al., 2020); also they facilitate food, water, and shelter to several species of insects, birds, reptiles, mammals, across others (Boechat et al., 2019; Borst et al., 2019; Seidl et al., 2020).

Since epiphytes need a host for the establishment, they depend on their host plant's features. Therefore, host characteristics have important consequences on the richness and abundance of epiphytes. For example, larger, older trees with cracked and non-exfoliating bark tend to have greater wealth and abundance of epiphytes (Cortés-Anzúres et al., 2020; Woods et al., 2015). The effect of host traits also has been documented for some life-cycle stages of epiphytes. For example, trees with rugose barks with high water absorption capacities and no secondary metabolites production enhance epiphyte seeds germination and seedling survival (Callaway et al., 2002; López-Villalobos et al., 2008; Harshani et al., 2014). However, since the trees´ features are related to their taxonomic identity, it could be expected that epiphytic individuals growing on different hosts species will present different demographic and phenological behaviors, as shown by the study of the demography of *Tillandsia macdougalli* L.B.Sm. growing on trees of different genera (Ticktin et al., 2016).

Since epiphytes are considered one of the most vulnerable plant groups due: 1) since they live on other plants or "phorophytes" are especially susceptible to forest deforestation and fragmentation, which represent and noticeable loss of habitat (Mondragón et al., 2015); 2) reforestation practices with non-native tree species and implementation of monocultures which change the habitat quality for epiphytes species and promote, for most sensitive species, a richness decline (Boelter et al., 2011; Ceballos, 2020). 3) Over collecting of species with anthropogenic value (Emeterio-Lara et al., 2021; Toledo-Aceves et al., 2014); 4) climate change due: a) to their dependence for atmospheric sources of water and nutrients (Zotz, 2016), and b) to the possible change in the distribution ranges of their host plants (Jump & Peñuelas, 2005; Hsu et al., 2012; Köster et al., 2013); so, understanding the effect of host trees on epiphyte demography and phenology is critical information to develop robust programs to maintain or restore population of epiphyte species and to a have a more profound comprehension of the host-epiphyte relationship.

For those reasons, in this study, we test the effect of three *Quercus* species on the demography and phenology of a vascular epiphyte community in a seasonal oak forest in Yanhuitlán, Oaxaca. We addressed the following questions: 1) Do host tree traits influence phenology patterns on vascular epiphytes? 2) Do host tree traits influence the demographic parameters on vascular epiphytes?

Background

Vascular epiphytes

Epiphytes are plants that live on other plants but do not feed on them and represent close to 10 % of the total vascular flora of the world, with 27,614 species described representing 913 genera and 73 families (Zotz, 2013). These kinds of plants are common in tropical, subtropical, and temperate forests.

The high taxonomic diversity of vascular epiphytes allows finding differences across species like growth forms, way of nutrients, and water acquirements, across others (Benzing, 1978, 2000; Zotz, 2016); but in other cases, some epiphytic taxa shared salient characteristics as their wind-dispersed seeds (*e.g.,* dust-like in Orchidaceae) and animal-pollinated flowers (*e.g.,* insects for Orchidaceae members or birds for some Bromeliaceae) (Madison, 1977; Gentry & Dodson, 1987; Zotz, 2016).

Threats for vascular epiphytes

a) *Host tree loss*

As epiphytes depend on host trees for support, the increase in deforestation, habitat fragmentation, and climate change could have significant implications in their distribution, abundance, and diversity (Zotz, 2016). In modified landscapes (including secondary forests and monocultures), vascular epiphyte richness has been demonstrably lower when compared to that of primary forests, and this is due to lower phorophyte diversity and drier microclimates (Boelter et al., 2011; Ceballos, 2020).

Worldwide, including Mexican regions, primary forests are being replaced for monoculture crops of economic value (Evans 1997). This practice could have severe consequences on epiphytes populations since Ticktin et al. (2016) have demonstrated that various host tree species maintain epiphytic population functionality within the ecosystems. For example, in wet periods, epiphytic bromeliad *T. macdougalli* has a better performance in wet periods on deciduous trees (oaks); in contrast, in dryer periods, evergreen trees (pines) act as buffers to maintain populations.

Another serious issue is the introduction of non-native tree species in reforestation practices. These types of trees compete for resources like light, water, and nutrients; and in some cases also produce secondary metabolites that impede the seed germination and growth of native plant species (Calviño-Cancela et al., 2012; Chu et al., 2014), including epiphytes (Harshani et al., 2014; Valencia-Díaz et al., 2010), and also impede the development of organisms associated like orchid mycorrhizal fungi (Gowland et al., 2013). For example, reforestation programs used pine species in Mexican regions for their high productivity, wide adaptability, and rapid economic returns (Pedraza and Williams-Linera, 2003). However, some of them are reported to produce allelopathic compounds, which negatively influence epiphyte richness and abundance patterns (da Silva et al., 2015).

b) Climate change

Most epiphytes depend on atmospheric nutrient and water sources, making them vulnerable to potential climate change effects like rising temperatures, lower precipitations, and an increase in carbon dioxide (Zotz, 2016). Some studies support reducing atmospheric humidity promotes higher mortality of individual epiphytes (Mondragón et al., 2015). Also, a combination of higher temperatures, higher evapotranspiration, and excessive exposure to solar radiation may cause CAM-idling, a variation in CAM metabolism, which implies that plants may survive but not grow (Benzing, 1998), affecting the population dynamics of vascular epiphytes.

Climate change may limit the incidence of fog in mountainous areas affecting the survival and growth of epiphytes. Nadkarni & Solano (2002) observed under drier atmospheric conditions higher leaf mortality and lower leaf longevity and production. These environmental conditions may sooner or later result in the death of many epiphytes, thus driving a drastic change in the composition and dynamics of the canopy community.

Although, responses to changes in climate parameters may depend on epiphyte species traits since they may acclimate in specific ways (Campbell et al., 2007; Wagner & Zotz, 2018) given the great variety of growth forms (*e.g.,* atmospheric vs. tank species), morphological (*e.g*., cuticles, trichomes, etc.) and physiological adaptations (*e.g*., photosynthetic pathways) (Benzing, 1990; Zotz, 2016).

Climate change may also affect epiphyte phenological patterns since temperature and precipitation trigger many natural history traits (Fenner, 1998). Changes in flowering rhythms (*e.g.,* time of occurrence and duration) may lead to mismatches and affect the epiphyte-pollinator interactions as observed in other plant groups (Donnelly et al., 2011; Forrest, 2015). Mismatches occur when a synchronous partnership is disrupted in time, resulting in partial or complete decoupling (Stenseth & Mysterud 2002). Temporal phenological mismatches between plants and pollinators can significantly decrease pollination efficiency transfer for outcrossing plants (Kudo & Ida, 2013; Høye et al., 2014) and reduce their reproductive success, yet relatively little is known about their evolutionary and demographic implications (Miller-Rushing et al., 2010). Since not all species or phenophases may respond simultaneously to temperature increments, thus disrupting previously synchronized interdependent key life-cycle stages (Primack, 1987).

Climate change may cause shifts on distribution ranges of tree species to higher elevations and latitudes as the climate to which they are adapted will poleward. This phenomenon represents a severe threat to epiphytes since their distributions are highly correlated with certain forest types (Hsu et al., 2012). For example, in Mexican forests, it has been predicted that the current geographic distribution of oak forests will decrease up to 48% (Gómez-Mendoza & Arriaga, 2007); these shifts may affect epiphyte distributions since these kinds of forests are known to harbor a high richness and abundance of epiphytes (Espejo-Serna et al., 2007).

c) *Extraction*

Some epiphytes are extracted from their natural habitats by collectors or local people. Most pressure has been observed in species of Orchidaceae, Bromeliaceae, and Araceae families. In some countries, including Mexico, many local people have traditionally used some epiphyte species as ornaments, medicine, food, fiber extraction, and religious offerings (Aranda-Coello et al., 2012; Jiménez-López et al., 2019; Mondragón et al., 2016). In general, adult reproductive individuals are the targets of these collections, but few studies have tested the effects of adult extraction on population dynamics (Mondragón et al., 2015).

Site and study species

Study site

This study was carried out at an oak forest in Tooxi, municipality of Yanhuitlán, Oaxaca located in the Sierra Madre del Sur physiographical province (17°33′57.34″ N and 97°22′19.28″ W, elevation 2579 m a.s.l; Fig. 1) that comprehends the Mixteca Alta UNESCO Global Geopark (UNESCO, s/f). Accumulated annual precipitation is 804 mm with a monthly average of 67.02 ± 68.67 mm, with two peaks, the first in June and the second in September, with a dry season from October to April (Fig. 2); the mean temperature is 14.36 ± 1.34 °C, and the average maximum and minimum temperatures are 23.27 ± 1.75 °C and 7.02 ± 2.87, respectively (CONAGUA, s/f).

Tree vegetation comprises mainly of *Quercus candicans* Neé, *Q. castanea* Neé, *Q. crasifolia* Humb. & Bonpl., *Q. rugosa* Neé, *Juniperus fláccida* 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 & A.F.Tryon, *Polypodium martensii* Mett., *Echeveria nodulosa* (Baker) Otto, *Oncidium brachyandrum* Lindl., and *Alamania punicea* Lex. in La Llave & Lex.

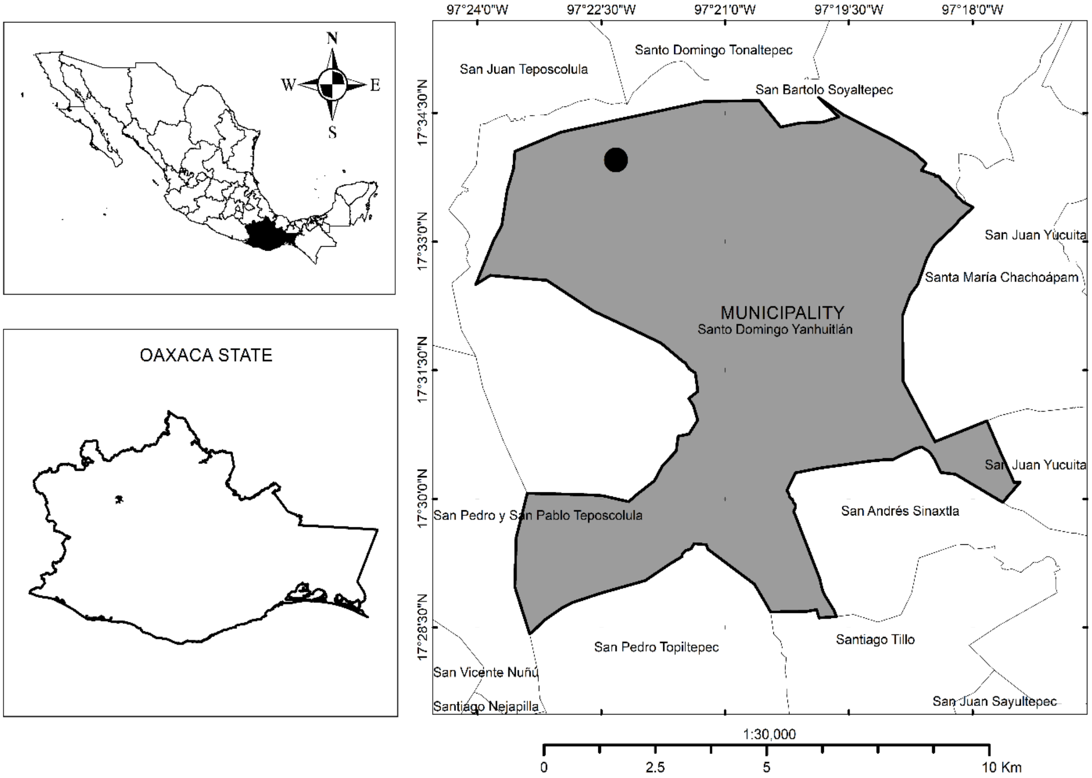

Figure 1. The study site is located in a seasonal oak forest in the municipality of Yanhuitlán, Oaxaca, Mexico.

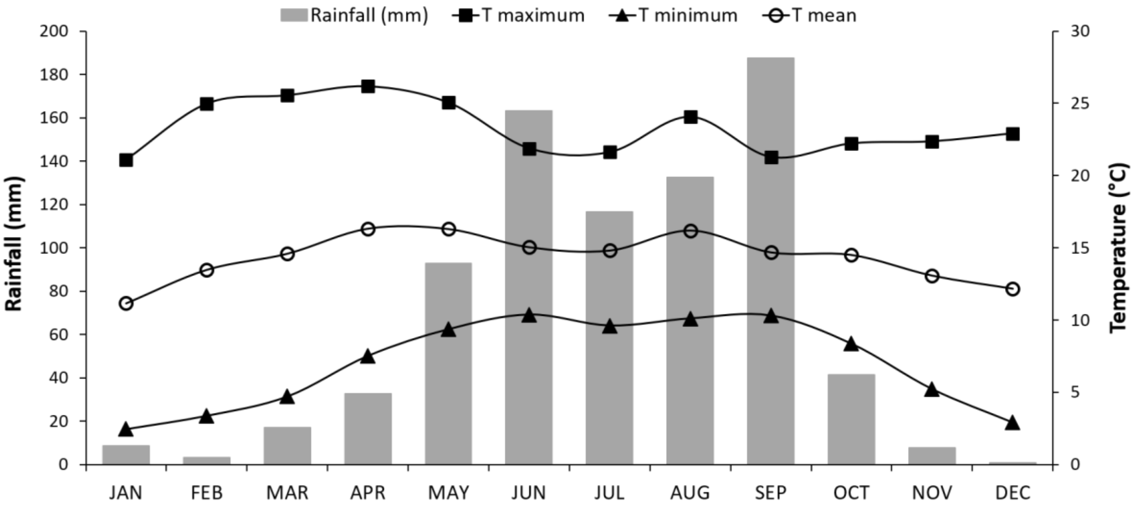

Figure 2. Monthly rainfall and temperatures in the municipality of Yanhuitlán, Oaxaca, Mexico.

Study species

a) Vascular epiphytes

We selected some bromeliad and orchid species from the community of vascular epiphytes present at Yanhuitlán since they have different growth forms and inhabit the study site.

i) *Tillandsia prodigiosa* is an epiphytic tank bromeliad. Rosettes reach up to 40 cm in height and are composed of 50–80 rigid leaves (Figure 3a). The reproductive stalk measures *ca.* 150 cm; it is a pendant with imbricate green broad bracteae at the base, which gradually becomes pink towards the tip. The inflorescence is cylindrical, and the spikes are short and stipitate. Flowers are tubular with pale green petals 5.2–5.7 cm long. Fruits are capsules that contain wind-dispersed plumose seeds (Smith and Downs, 1977; Espejo-Serna et al., 2004). *T. prodigiosa* is a monocarpic plant. It has a mixed breeding system, and its inflorescence and flower morphology suggest hummingbirds carry pollination (Escobedo-Sarti, 2008). This plant is endemic to Mexico, inhabits temperate forests dominated by *Quercus* spp and *Pinus* spp. in the states of Colima, Distrito Federal, Guerrero, Jalisco, Estado de Mexico, Michoacán, Morelos, Oaxaca and Puebla, at elevations of 450 – 2800 m a.s.l (Espejo-Serna et al., 2004).

ii) *Tillandsia plumosa* is an atmospheric epiphytic bromeliad. Its rosettes reach up to 18 cm and are composed of *ca*. 35 withe-gray leaves that don´t form a tank (Figure 3b). The reproductive stalk measures 5-9 cm long; it is sturdy covered with pinkish-gray-white bracts and pink spikes; flowers are tubular with pale green petals 1-1.5 cm long. *Tillandsia plumosa* is polycarpic. Floral morphology suggests cleistogamy (Gilmartin & Brown, 1985). This plant is endemic to Mexico and is distributed Guerrero, Estado de Mexico, Oaxaca, and Puebla in coniferous and *Quercus* forests, at 1200 to 2675 m a.s.l. (Hernández-Cárdenas et al., 2018).

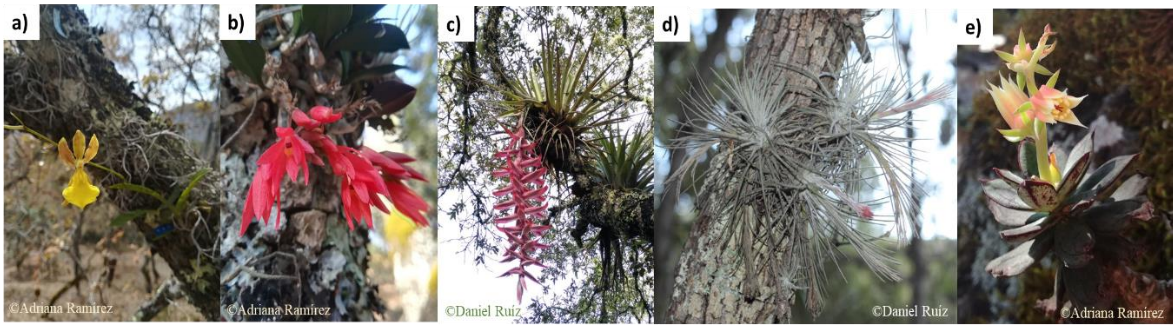

Figure 3. Epiphyte species a) *Oncidiun brachyandrum*, b) *Alamania punicea*, c) *Tillandsia prodigiosa*, d) *Tillandsia plumosa*, and e) *Echeveria nodulosa* (Fotos: Daniel Ruíz-Contreras c-d, and Adriana Ramírez-Martínez a, b, and e).

iii) *Alamania punicea* Lex. is an epiphytic perennial orchid, suddenly, 3 to 6 cm high including the inflorescence; ovoid pseudobulbs, slightly elongated, covered by translucent papyrus sheaths, 7 to 10 mm long; leaves 2, rarely 3, at the apex of the pseudobulb, elliptic to oblanceolate sheets, 1 to 4 cm long, 5 to 10 mm wide; flowers 7 to 14, red to pinkish reddish (Figure 3c). 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 could be pollinated by hummingbirds. This plant is endemic to Mexico and grows in oak, pine-oak, and cloud forests, at 1850- 2700 m a.s.l. (García-Cruz et al., 2003).

iv) *Oncidium brachyandrum* is an epiphytic perennial orchid, up to 20 cm high with clustered pseudobulbs, ovoid to ellipsoid or subglobose, somewhat laterally compressed, 2 to 3 cm long; 2 or 3 lateral leaves; flowers 2 or 3, simultaneous, showy, 25 to 30 mm in diameter, sepals, and petals brown or yellow with irregular brown spots and yellow lip (Figure 3d). Fruits are capsules with dust-like seeds. This species might be pollinated by oil-collecting or bombini bees and probably is self-incompatible as reported for other members of the genera (Dodson, 1962; Ackerman 1995; Tremblay et al. 2005; Damon and Cruz-López, 2006, Pemberton, 2008). This orchid is endemic to Mexico and grows in oak forests at an elevation of 2000 to 2500 m a.s.l. (Jímenez et al., 1993).

v) *Echeveria nodulosa* is a perennial herbaceous plant with green leaves (sometimes with red spots), succulent, simple, whole, obovate-wedged, and spiral phyllotaxy. Its inflorescence is lateral, and axillary composed of a floral stem or peduncle that supports the flowers and bracts in the form of a cluster. The orange flowers are arranged in a spiral along the peduncle, each on the pedicel found in the armpit of a bract. The pedicels have two bracteoles. This species is probably pollinated by hummingbirds since they were observed visiting these plants at the study site (Per. obs). *Echeveria nodulosa* is endemic to Mexico and grows in different environments, although precise information about its distribution is still scarce (Jímenez et al., 1993).

We marked 23 *Echeveria nodulosa* plants growing on four *Q. martinezii* trees and one on *Q. rugosa*. Since the sample size was too small, we could not test the host tree effect for this species, but we wrote a scientific note about their phenology and population structure (see Miscellaneous paper section in page 82).

b) Host species

We selected the following tree species because they were abundant at the study site and had different loads of vascular epiphytes.

i) *Quercus martinezii* C.H. Müll.

This tree is a deciduous species. Trees are 6 to 25 m in height and 3 to 13 m in diameter with brown-scaly bark. Leaves are oblong to oblanceolate of 5 to 20 cm long and 3 to 13 cm wide.

Flowers in April and mature fruits in one year. It is endemic to Mexico and it distributes in Guerrero, Jalisco, Mexico, Nayarit and Oaxaca; from 800-2700 m a.s.l (Arizaga et al., 2009) .

ii) *Quercus castanea* Neé

This is a deciduous specie. Trees are 5 to 20 m in height and from 30 to 60 cm in diameter with dark gray, smooth bark. Leaves are ovolanceolate, lanceolata or ovoid of 2.5 to 15 cm long and 1.3 to 5 cm wide. Flowers from May to June and fruits from October to January. It distributes from Mexico (Colima, Chiapas, Mexico, Michoacan, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Morelos, Nayarit, Oaxaca, Puebla, San Luis Potosi, Sinaloa, Sonora, Tamaulipas and Veracruz) to Guatemala; from 800 - 2600 m a.s.l (to 3500 m a.s.l in Guatemala) (Arizaga et al., 2009).

iii) *Quercus rugosa* Née.

This is a semideciduous species, sizes range from 3 to 25 m in height and from 10 to 80 cm in diameter, with bark dark brown, scaly, rough, and relatively thin. Leaves are thick and very coriaceous, generally concave-convex, from 4 to 17 cm long and 1.8 to 10 cm wide. Flowers in April, fruits are produced from October to February. It distributes in the United States, Mexico, and Guatemala, from 1200 to 3200 m a.s.l (Arizaga et al., 2009).

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CHAPTER II. HOST TREE TRAITS

Introduction

Epiphytes are structurally dependent on their host plants for the establishment and are influenced more or less by certain host traits (Wagner et al., 2015). Some epiphytes exhibited host preferences for certain tree species (Bernal et al., 2005; Toledo-Aceves et al., 2017; Ramírez-Martínez et al., 2018) that have been related to differences in host trees architecture, physical and chemical characteristics of the bark, mineral sources, and tree phenology (Callaway et al., 2002; Einzmann et al., 2014). Also, It has been reported that the presence of non-vascular epiphytes "facilitate" the survival of vascular epiphyte seedlings and change the chemical composition of throughfalls and stem flows (Knops et al., 1996; Nadkarni, 2000; Cascante-Marín et al., 2008; Scheffknecht et al., 2010) that are essential sources of nutrients for vascular epiphytes (Marler, 2018).

Host traits' characteristics influence all life cycle stages of epiphytes from germination, seedling survival, growth, and reproduction (Mondragón et al., 2015; Wagner and Zotz, 2020). Different host species may exhibit different traits; for example, *Quercus* species have different leaf morphologies, barks types, phenologies, and types and quantity of secondary metabolites production (Gailing et al., 2012, 2018). Therefore, each oak species could have different effects on epiphyte population dynamics. This has been partially tested in the Ticktin et al. (2016) study, which demonstrated the influence of pines and oaks (without distinguishing between species) on the population dynamics of atmospheric *Tillandsia macdougalli*.

As part of this dissertation, we measured several traits of three *Quercus* species that harbor different richness and abundance of epiphytes in a seasonal oak forest in Yanhuitlán, Oaxaca, to detect differences or similarities across them and use this information for subsequent chapters of this manuscript.

Background

Tree species differ in many traits, and these differences could affect their suitability as phorophytes for epiphytes. This section will describe those that are more relevant for epiphyte demography and phenology (Fig. 4).

a) Substrate stability

This variable depends on several tree traits like bark stability and branch diameter distribution. Every tree species exfoliate their barks in minor or higher frequency throughout their life (Callaway et al., 2002). This trait and branch fall are two leading causes of dislodgement of individual epiphytes from their phorophytes (Mondragón et al., 2004, 2015). Usually, branch falling has been related to branch diameter, and thinner branches have generally higher probabilities of braking (Hietz 1997).

The number of thin branches and the degree of bark exfoliation can differ depending on tree species and longevity. It seems that bark exfoliation augments with age since young trees (resembling thin branches) often have smooth, unbroken bark but will usually roughen as trees age. This phenomenon has been approached by López-Villalobos et al. (2008), who studied the bark peeling rate of *Bursera fagaroides* (Kunth) Engl. in a tropical dry forest of the central coastal zone of Veracruz, Mexico. These authors found the highest bark peeling rate on the trunk and decreased towards the branches and twigs. The growing season of trees also could influence the number of thin branches of the trees and probably change the probabilities of epiphyte seed capture.

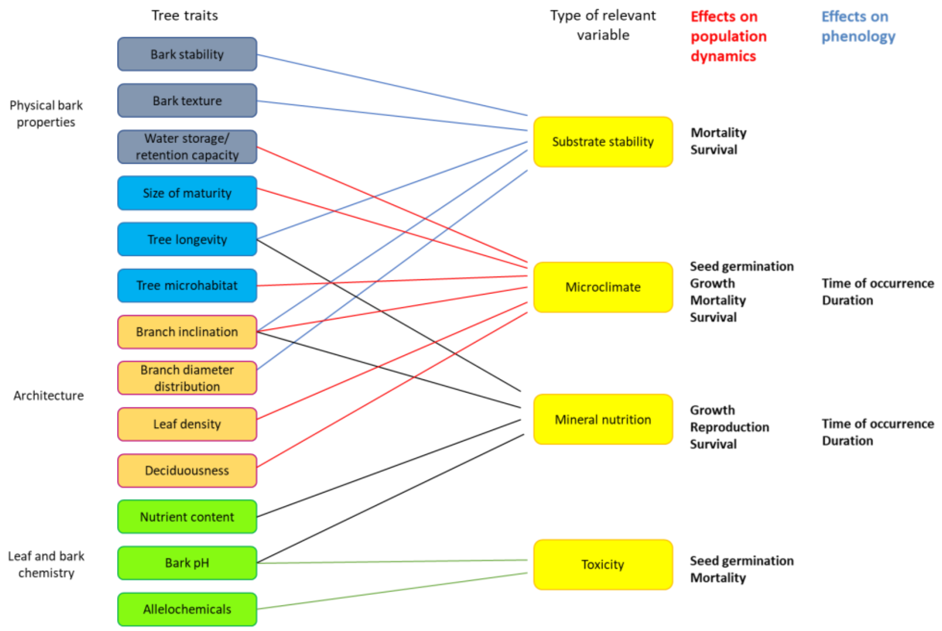

Figure 4. Tree traits related to host preferences and their main influence on four types of variables relevant to epiphyte performance and their link with demography and phenology. Modified after Wagner et al. (2015).

Thicker branches offer a higher landing area for epiphyte seeds. And their positive influence can be enhanced if they are horizontal since seeds cannot be washed easily by stem flow caused by heavy rains (Cascante-Marín et al., 2008; Mondragón et al., 2004). Also, horizontal branches accumulate more canopy soil and augment the nutrients available for epiphytes (Marler, 2018). Finally, horizontal branches could reduce the intensity of stemflows and influence the relation of stemflow to total precipitation (Wagner et al., 2015).

Bark texture also plays a vital role in population dynamics since it has been observed that rough and fissured bark types allow a better anchorage for epiphyte seeds, whereas smooth barks do not facilitate tree colonization(Bernal et al., 2005; Wagner et al., 2015). Although atmospheric bromeliads can attach even in tree trunks and branches with smooth barks (Chaves et al., 2016), epiphyte orchids can occur on the smooth-barked host species if they are in association with a moss clump (Wyse & Burns, 2011). Trees with rough and fissured barks are highly preferred by epiphyte orchids (Callaway et al., 2002; Otero et al., 2007; Timsina et al., 2016; Segovia-Rivas et al., 2018).

Fissured barks probably receive a more continuous water supply as water is withheld longer within bark crevices and directly benefit epiphytes or their associated organisms like orchid mycorrhizal fungi (Harshani et al., 2014; Hernández-Pérez et al., 2018). In a recent study, Zarate-García et al. (2020) found that orchid species prefer lined decorated rhytidomes (bark surface) over those with flaky or plated bark because they probably improve stemflow of water and could modify other properties of the bark such as pH, which influences seed germination and orchid distribution (Adhikari & Fischer, 2011).

b) Microclimate

This variable depends on many tree traits like leaf density, which influences the amount of light that epiphytes receive. Dense foliage may buffer temperature and vapor pressure fluctuations but decrease the light intensity within canopies. These conditions may favor mesic species and certain life cycle stages like epiphyte seed germination and seedling survival, but in some cases, they can impede the establishment of new seedlings due to lower availability of light (Mondragón et al., 2015; Rasmussen et al., 2015).

On the other side, an increment in the amount of light available for epiphytes could benefit atmospheric species which have some adaptations to support these conditions. For example, atmospheric bromeliad *Tillandsia brachycaulos* Schltdl. individuals that received a lesser photon flux density (PFD) due to their position within the canopy produce fewer flowers than those located in the most exposed microhabitats (Cervantes et al., 2005).

In seasonal environments, during the leafless phase of trees, which usually coincides with the dry season, epiphytes experience more extreme microclimates on deciduous than evergreen trees (Einzmann et al., 2014). However, the effect of deciduousness may depend on the epiphyte species since dry-adapted species could exploit the resource of light and increment their photosynthetic capacity, growth, and reproduction (Cervantes et al., 2005; Reyes-García et al., 2008), while mesic species could lower their growth rates and change their physiology (Einzmann et al., 2014).

As stated above, light is an essential resource for plants, same as water availability which influences the microclimate within the host trees. It has been tested that trees with barks with a high-water absorption and retention capacity may increase the humidity and benefit some epiphyte species that require these conditions (Callaway et al., 2002). The amount of water held by the bark (water-storage capacity [WHC]) depends on its porosity and thickness, so these traits can indirectly modify the water balance in forest ecosystems (Ilek et al., 2016) and the amount of water available for epiphytes (Mendieta-Leiva et al., 2020). Water availability is important during germination and seedling establishment of epiphytes, so barks with a high-water absorption and retention capacity may increase the quality of the phorophyte for species of epiphytes that require these conditions (Callaway et al., 2002).

c) Mineral nutrition

Epiphyte's nutrients come from external and internal sources. External suppliers of nutrients comprise dry depositions and precipitation (Nadkarni 1986, Stewart et al. 1995; Hietz et al. 1999). Internal sources include nutrient cycling via canopy soil (mixture of epiphyte and host tree litter [Nadkarni 1986, Stewart et al. 1995, Hietz et al. 1999]), host tree foliar, and bark leaching (Hietz et al. 2002), and throughfall. Host trees indirectly influence the quantity and quality of nutrients available for epiphytes since they modulate microclimate (*i.e.,* moisture and temperature) through their architecture (horizontal branches tend to accumulate more organic matter than vertical) and phenology (Einzmann et al., 2014). Thus, microclimate can influence the rates of organic matter decomposition since it regulates the presence of saprobic microorganisms (Cardelús, 2010). Also, host trees can directly influence nutrient cycling via host tree litter quality. Since litter chemical composition varies across tree species (Sedio et al., 2017), phorophytes could offer different litter nutrient sources for epiphytes.

Litter together with leaf and bark leachates (which vary across tree species) enrich throughfalls and stemflows (Cardelús & Mack, 2010). Further, throughfalls can be modified by the presence of other organisms like non-vascular epiphytes. For example, Knops et al. (1996) found that N concentrations of throughfalls increment with the presence of lichens.

Another host tree trait that might modify the availability of macro and micronutrients for epiphytes is host tree bark pH. Although, the effect of this trait on vascular epiphyte´s performance has not been tested. On the other side, bark pH has been strikingly often correlated to host preferences for non-vascular epiphytes (Löbel et al., 2006; González-Mancebo et al., 2003).

d) Toxicity

Some tree species exudate allelopathic substances, which are hypothesized to have inhibitory effects on germination and early stages (Valencia-Díaz et al., 2010; Harshani et al., 2014). Also, some non-vascular species exudate secondary metabolites and indirectly affect epiphyte seedling establishment (Callaway et al., 2001). Even though this is not a tree trait is essential to quantify the abundance of vascular epiphytes on host trees since it can give relevant information about host preferences.

Aim and objectives

Aim

Get information about some tree traits of three *Quercus* species that could affect the demography ad phenology of vascular epiphytes in a seasonal oak forest in Yanhuitlán, Oaxaca.

Objectives

1. Evaluate bark exfoliation rates of *Q. castanea, Q. rugosa* and *Q. martinezii*
2. Collect bibliographic information about bark texture of *Q. castanea, Q. rugosa,* and *Q. martinezii*.
3. Compare canopy openness, temperature, relative humidity, and water holding capacity and retention of the bark of *Q. castanea, Q. rugosa,* and *Q. martinezii*

4. Compare the mineral composition of throughfalls of *Q. castanea, Q. rugosa,* and *Q. martinezii*
5. Collect bibliographic information about pH and toxicity of *Q. castanea, Q. rugosa,* and *Q. martinezii*.

Materials and methods

For study site information, remit to Chapter I

a) Bark exfoliation rates

We selected five trees per host tree species and collocate pins to delimit a 20 x 20 cm^2 square (Jiménez-Salmerón et al., 2017). Monthly we took pictures to see if any portion of bark was missing inside those squares.

b) Microclimate indicators

1) *Canopy openness:* monthly hemispherical photographs were taken under each tree, from 1.3 m above the forest floor, with a smartphone with a 180° fisheye lens attachment, from 8:00 to 10:00 a.m. to avoid high light intensities. Digital images were instantly analyzed using Gap Light Analysis Mobile App version 3.0 (GLAMA 3.0; (Tichý, 2016).

2) *Temperature and relative humidity*: on five individuals per host tree species, we collocated one Krestel drop 2 data loggers (Krestel Intruments®) in the middle of tree crowns where most epiphytes were concentrated. These devices registered temperature (°C) and relative humidity (%) every hour at one-minute intervals. Data loggers were collocated in March of 2018, and we were able to register data until February 2020 before pandemic restriction.

3) *Barks ‘water holding capacity and water loss rates*: three bark samples were taken from the trunk, primary and secondary branches of five trees per oak species. Bark sections were cut into squares of 5 x 5 cm then we used them to determine bark water holding capacity (WHC; (Callaway et al., 2002). First, samples were cleaned of any moss or lichen, oven-dried for 48 h (50, °C), and weighed. Afterward, pieces were submerged in water for 30 min, and after a 5-min pause, we considered them again. This measure was taken as maximum WHC. Next, we calculated water loss rates by keeping the samples at a temperature of 26.5 ± 0.23 (µ± e.e) °C and relative humidity of 59 % ± 1 (µ± e.e) on a lab table. Next, we weighed samples at 2, 5, and 8 hours, calculated the water loss, and expressed it as a percentage of maximum WHC.

c) Mineral nutrition

Nutrient content of throughfalls: before the rainy season began, we selected five individual trees per species funnels (8 cm perimeter) covered with a net and adhered to a plastic bottle of 500 ml. Three funnels were collocated under each tree crown. After the samples were collected, we passed them through a filter paper to capture any solid particle and put them into a new plastic bottle, previously rinsed with deionized water. The new bottles with samples were sealed with parafilm, tagged, and stored in a refrigerator until their analysis at the Servicio Geológico Mexicano (SGM) laboratories.

Data of roughness, pH, and toxicity of barks were taken from Hernández-Álvarez (2021).

Statistical analyses

The data were rescaled when needed and then analyzed applying one-way ANOVAs. To test statistically significant differences, we apply a Tukey *pos occ* test (Zar, 2010). All analyses were performed in SPSS Statistics 22 (IBM Corp 2013).

Results

a) Bark exfoliation rate

We monitored bark peeling for 24 months and did not observe bark flaking in any phorophyte species.

b) Microclimate indicators

1) Canopy openness, temperature, and relative humidity

i) Canopy openness (CO): we monitored canopy openness for two years. In 2018 the mean ($P>0.05$, $F_{(2,79)}$ =0.977) and maximum CO ($P>0.05$, $F_{(2,79)}$ = 2.2785) were similar across host species while minimum CO was higher in *Q. martinezii* ($P<0.05$, $F_{(2,79)}$ = 4.0816). In 2019, mean ($P<0.05$, $F_{(2,79)}$= 3.6456) and maximum ($P<0.05$, $F_{(2,79)}$ = 12.7901) CO were higher in Q. *castanea*; minimum CO did not differ across host species ($P>0.05$, $F_{(2,79)}$= 0.6481, [Fig. 5]).

ii) Temperature and relative humidity: values did not differ statistically across host species and years (Fig. 6 and 7).

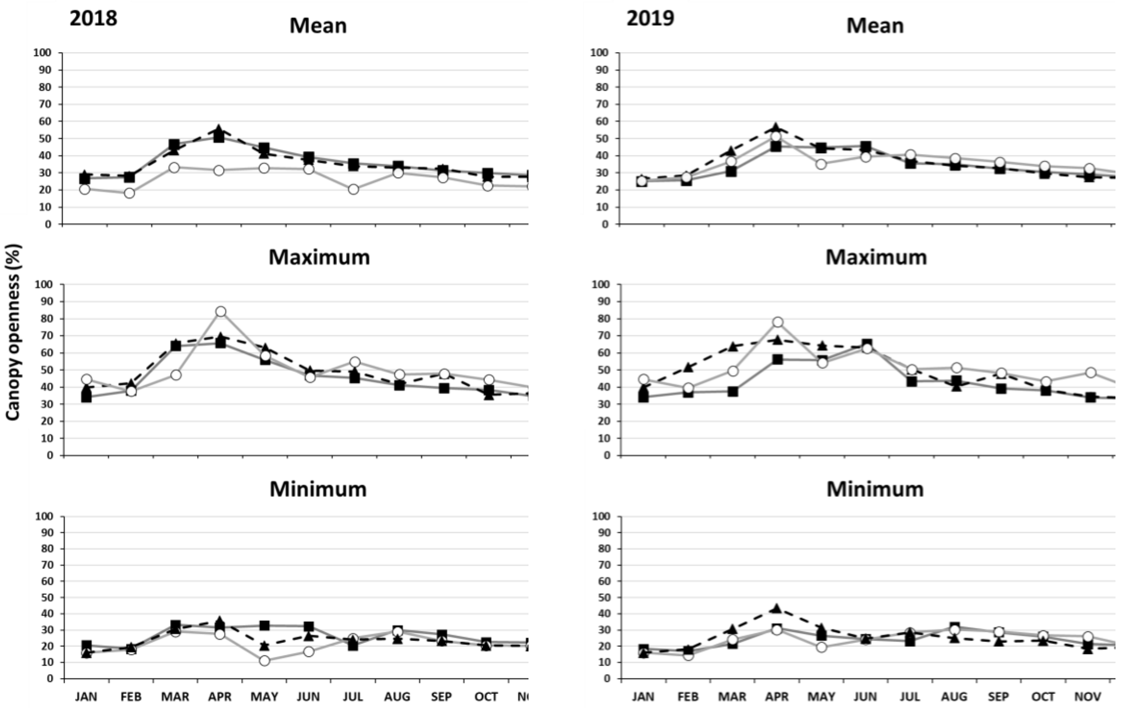

Figure 5. Monthly mean, maximum and minimum canopy openness for three *Quercus* species for two years in Tooxi Yanhuitlán, Oaxaca. Symbols indicate –■– *Quercus martinezii*, –▲–*Q. castanea*, and –○– *Q. rugosa*.

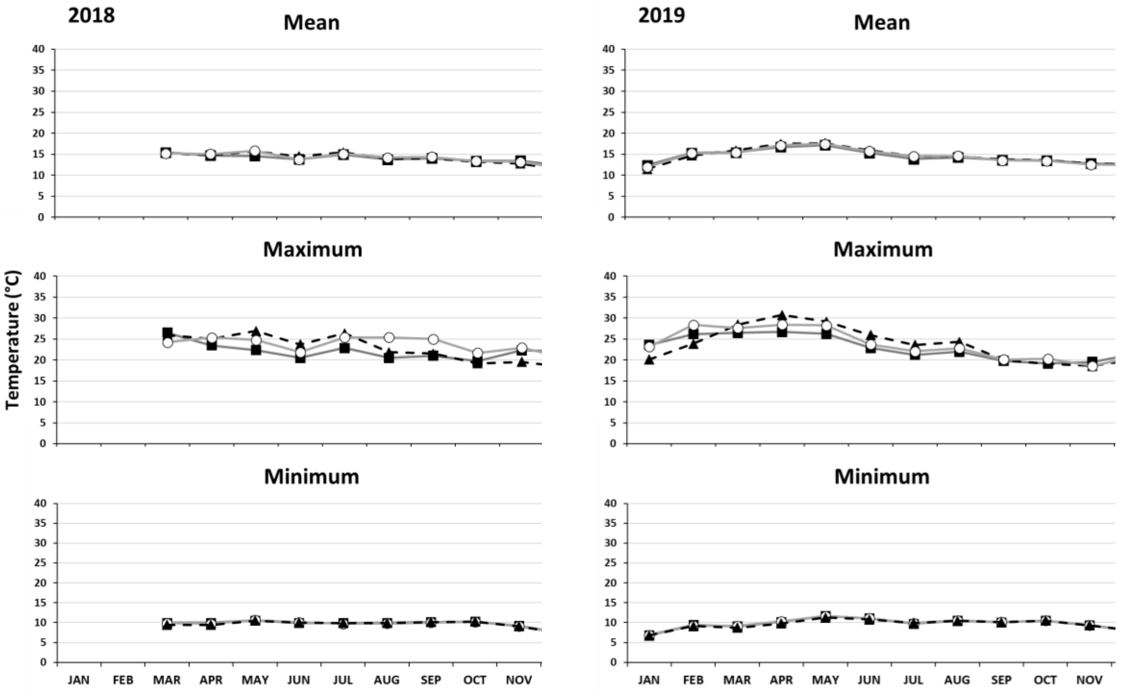

Figure 6. Monthly mean, maximum, and minimum temperature for three *Quercus* species for two years in Tooxi Yanhuitlán, Oaxaca. Symbols indicate –■– *Quercus martinezii*, –▲–*Q. castanea*, and –○– *Q. rugosa*.

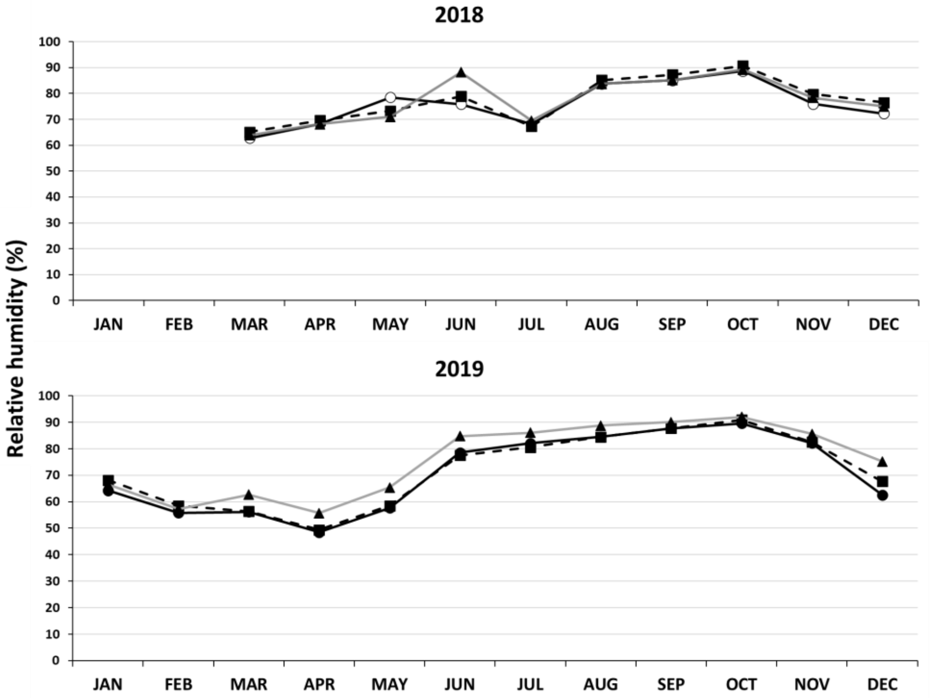

Figure 7. Monthly relative humidity for three *Quercus* species for two years in Tooxi Yanhuitlán, Oaxaca. Symbols indicate -■- *Quercus martinezii*, -▲- *Q. castanea*, and -○- *Q. rugosa*.

2) Water holding capacity of the bark

Primary and secondary branches absorb fewer volumes of water than trunk sections. Water holding capacity of trunk sections ($P< 0.05$, $F_{(2, 12)} =61.551$) and primary branches differed across phorophytes ($P< 0.05$, $F_{(2, 12)} = 6.362$). While secondary branches retained similar water volumes for all host tree species ($P> 0.05$, $F_{(2, 12)} = 3.122$, [Fig. 8A]).

Water loss of trunk ($P> 0.05$, $F_{(2, 12)} = 1.211$) and secondary branches sections ($P> 0.05$, $F_{(2, 12)} = 0.122$) did not vary significantly across host tree species. But primary branches of *Q. rugosa* lost water faster ($P<0.05$, $F_{(2, 12)} = 5.135$) than *Q. castanea* and *Q. martinezii* (Fig. 8B).

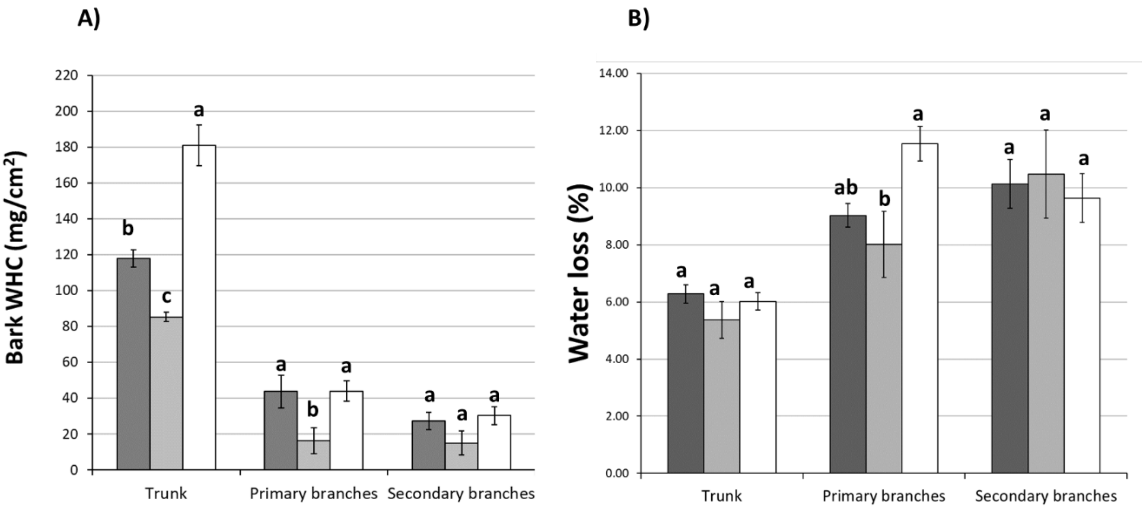

Figure 8. A) Bark water holding capacity (WHC) and B) Water loss (%) of three sections of *Quercus martinezii* (dark gray), *Q. castanea* (light gray), and *Q. rugosa* (white), in Yanhuitlán, Oaxaca. Error bars show one standard error, and different letters indicate significant differences at *P*< 0.05.

c) Mineral nutrition

The concentration on phosphorus ($F_{(2,14)}$= 4.013, p<0.05) and potassium($F_{(2,14)}$=10.068. p<0.01) differ across phorophytes. *Quercus castanea* had the lowest concentrations of phosphorus and potassium (Table 1).

Table 1. Concentration of phosphorus and potassium (± one standard error) in throughfalls of three *Quercus* species in Tooxi, Yanhuitlán, Oaxaca. Different letters indicate significant differences across the *Quercus* species.

Concentration (mg/l)	Phosphorus	Potassium
Quercus martinezii	0.18 ± 0.04^{a}	2.56 ± 1.06^{a}
Quercus castanea	0.12 ± 0.01^{b}	0.87 ± 0.41^{b}
Quercus rugosa	0.15 ± 0.04^{ab}	2.60 ± 1.11^{a}

As I mentioned before some information was taken from Hernández- Alvarez´s dissertation (Hernández-Álvarez, 2021). Next, I summarize that information. His results showed that *Q. castanea* has smoother bark than *Q. rugosa* and *Q. martinezii* (P< 0.01, F $_{(2,}$

$_{29)}$ =5.60). Also found that bark pH values are slightly acid (6.7-6.8) and there were not differences across host tree species ($p > 0.05$, $F_{(2, 29)} = 0.065$). In regard toxicity of powdered bark found higher values of catechins and gallic acid for *Q. castanea*.

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CHAPTER III. HOST TREE EFFECT ON VASCULAR EPIPHYTE REPRODUCTIVE PHENOLOGY

Introduction

Epiphytes represent approx. 10 % of vascular flora (Zotz, 2013) and play important functions within the ecosystems, influencing water and nutrient cycles, giving food, water, and shelter to different organisms (Díaz et al., 2012; Van Stan & Pypker, 2015; Brandt et al., 2017; Antonetti et al., 2021). These kinds of plants live on other plants, and although they do not feed directly from them, they are tightly linked to their host trees or phorophytes (Callaway et al., 2002; Einzmann et al., 2015; Wagner et al., 2015). The effect of the host tree over epiphyte has been shown at the communities level showing a variation of epiphytes abundance and richness over different host tree species (Bernal et al., 2005; de la Rosa-Manzano et al., 2014; Toledo-Aceves et al., 2017; Vergara-Torres et al., 2010); while at the population level, differences have been observed in demographic rates across epiphyte individuals growing on different host tree species (*e.g.,* germination, seedling survival, growth, reproduction, and mortality). Supporting the idea that host tree identity plays an important role on epiphytes performance (López-Villalobos et al., 2008; Ramírez-Martínez et al., 2018; Ticktin et al., 2016; Wagner et al., 2015).

Given this background, host trees are expected to influence most epiphyte's life-history traits, like their phenology. Phenology studies the timing of recurring reproductive and vegetative events in plants, influenced by abiotic and biotic factors (Lieth, 1974). It can be described and quantified in terms of several parameters (Newstrom et al., 1994). Some of those parameters are (1) the onset data, which includes the starting date of the earliest individuals and the date of peak activity event (2) the duration of the event; (3) the frequency of occurrence of the phenological event; and (4) the seasonality of the events.

Variations in phenology patterns could affect the fitness of the individuals. For example, delay or advanced flowering could trigger a mismatch with pollinators and dispersers and, sometimes, make more severe the damage caused by herbivores (Canela & Sazima, 2003; A. Cascante-Marín et al., 2009; Orozco-Ibarrola et al., 2015; Nunes et al., 2016). Therefore, it is very imperative to take into consideration their phenology to develop management and conservation plans.

Vascular epiphytes are considered one of the most threatened groups due to their dependence on host trees and atmospheric sources of nutrients and water (Benzing, 1998; Obregon et al., 2011; Zotz, 2016). As epiphytes depend upon host trees for habitat, deforestation, reforestation with non-native species, and habitat fragmentation affect their distribution, abundance, and diversity (Hietz, 1999; Hsu et al., 2012). Further, the implementation of monocultures that reduces the diversity of host tree species could have effects on their population performance; since populations fluctuate in specific parameters depending on the host tree they inhabit and the environmental conditions that change over time (Wagner et al., 2015; Ticktin et al., 2016; López et al., 2021). In addition, it has been predicted that climate change will promote vegetation shifts where some tree species would shift their distribution in response to changes in temperature and precipitation, affecting epiphyte´s fate directly (Hsu et al., 2012) since some limiting host tree species could dominate those forests.

Consequently, understanding the effect of host trees on the phenology of vascular epiphytes is fundamental to comprehend more deeply this relationship and develop robust programs to maintain or restore populations of species of conservation concern. For that reason, we explore the effect of *Quercus* species on the reproductive phenology of orchids and bromeliads, the two families with the most epiphytic members (Zotz, 2013). Therefore, we expected that *a)* Epiphyte species will show different phenology patterns (onset date, duration, frequency, and seasonality) between host species since it has been observed that host tree identity can affect growth and the probabilities of reproduction of epiphytic individuals (Einzmann et al., 2015; Ticktin et al., 2016) and this could be reflected in their phenologies and *b)* Phenology patters of epiphytes will be related to differences in temperature, relative humidity, and canopy openness of host tree species since these factors have been proved to affect epiphytes growth and performance (Einzmann et al., 2015; Wagner et al., 2015; Woods et al., 2015).

Background

For this section, we attached our already published review article.

Ramírez-Martínez, A., Chaparro, D. M. M., & García, R. R. (2021). Vascular Epiphytes: The Ugly Duckling of Phenological Studies. *Acta Biológica Colombiana*, 26(2), Article 2. https://doi.org/10.15446/abc.v26n2.83473

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ARTÍCULO DE REVISIÓN / REVIEW ARTICLE

BOTÁNICA

VASCULAR EPIPHYTES: THE UGLY DUCKLING OF PHENOLOGICAL STUDIES

Epífitas vasculares: el patito feo de los estudios fenológicos

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ABSTRACT

The phenology of vascular epiphytes, which account for about 10 % of the world's flowering plants and perform important ecological functions, has been just partially explored. Since phenology is a key tool for the management and conservation of species, the objective of this review was to synthesize the information published so far about the phenology of vascular epiphytes, detect gaps of knowledge, and suggest future lines of investigation to understand the underlying mechanisms. We conducted an online search for articles in Google Scholar and in the ISI Web of Science database from 1800 to 2020, with different combinations of keywords. 107 studies addressing the phenology of different holoepiphyte species were found; 88 % of the studies were performed in the Neotropic, especially in tropical and subtropical wet forests. The phenology of only ca. 2 % (418 spp.) of all reported holoepiphyte species has been explored. There is a bias toward the study of the flowering and fruiting phenology in members of the Orchidaceae (192 spp.) and Bromeliaceae (124 spp.) families. In general, the vegetative and reproductive phenology of epiphytes tends to be seasonal; however, there is a huge gap in our understanding of the proximate and ultimate factors involved. Future research should explicitly focus on studying those factors.

Keywords: environmental factors, dispersion, pollination, reproductive biology, seasonal development, vegetative biology.

RESUMEN

Las epífitas vasculares, que representan cerca del 10 % de la flora vascular y cumplen funciones ecológicas importantes, se han explorado poco desde el punto de vista fenológico. Dado que la fenología es una herramienta clave para el manejo y conservación de especies, el objetivo de este trabajo fue sintetizar la información publicada, detectar vacíos de conocimiento y sugerir líneas de investigación que permitan entender los mecanismos que regulan la fenología de este grupo. Se realizó una búsqueda de artículos en Google Académico y en la base de datos ISI Web of Science desde 1800 a 2020, con diferentes combinaciones de palabras clave. Se encontraron 107 estudios que abordan la fenología de especies holoepífitas, el 88 % de estos estudios se realizaron en el Neotrópico, principalmente en bosques lluviosos tropicales y subtropicales. Solamente se ha estudiado la fenología de ca. 2 % (418 spp.) del total de especies de holoepífitas reportadas; los trabajos se han enfocado principalmente en estudiar la floración y fructificación de miembros de Orchidaceae (192 spp.) y Bromeliaceae (124 spp.). La fenología vegetativa y reproductiva de las epífitas tiende a ser estacional. Sin embargo, existe un vacío enorme de los factores próximos y últimos implicados; los futuros estudios pueden enfocarse a elucidar qué factores detonan la fenología de epífitas vasculares.

Palabras clave: biología reproductiva, biología vegetativa, desarrollo estacional, dispersión, factores ambientales, polinización.

INTRODUCTION

Vascular epiphytes, which represent around 10 % of the world's flowering plants (Zotz, 2013), are an important part of ecosystems because they increase biodiversity by intervening in water and nutrients cycles, and by providing important sources of food, water, and shelter for numerous organisms (Díaz *et al*., 2012; Van Stan and Pypker, 2015; Brandt *et al*., 2017; Seidl *et al*., 2020). Given the complexity and quality they provide to their habitats; they are considered secondary foundation species (Angelini and Silliman, 2014).

Epiphytes have developed several adaptations, that allow them to survive in the canopy of trees, characterized by abrupt temperature changes and low availability of water and nutrients (Benzing, 1990; Zotz, 2016). Many of these adaptations are related to the capture, storage, and efficient use of water and nutrients since epiphytes are not in direct contact with the ground, which is the main reservoir of these resources for most plants. Alternatively, epiphytes are limited to the cortical and foliage runoffs of their host trees, rainwater, dew, and fog, as sources of water and nutrients (Benzing, 1990; Cardelús and Mack, 2010; Wu *et al*., 2018; Mendieta-Leiva *et al*., 2020). Given this strong correlation between epiphytes and the availability of water and atmospheric nutrients, different authors have pointed out that this life form will be among the most affected by the ongoing climate change (Lugo and Scatena, 1992; Benzing, 1998; Zotz and Bader, 2009).

Since 1990, phenology has been one of the most active disciplines to evaluate the effects of climate change on ecosystems (Piao *et al*., 2019). It is defined as the study of recurrent events during the life cycle of living beings, along with the causes of their occurrence concerning biotic and abiotic factors (Lieth, 1974). Phenological studies allow us to understand the effects of climate change as well as the availability of resources for pollinators and dispersers (Kebede and Isotalo, 2016; da Silva Freitas *et al.,* 2017), ecosystem productivity (Richardson *et al*., 2010; Chang *et al*., 2013), and ecological processes such as competition and herbivory (Ekholm *et al*., 2019; Hood *et al*., 2019), among others. Phenology is also important for the development of conservation plans because it allows the development of germplasm collection calendars for both *in situ* and *ex situ* conservation. Moreover, phenology also contributes to the development of management plans for ecosystems and agroecosystems, which ensure the continuous availability of resources for pollinators, thereby sustaining pollination ecosystem services, and which make possible the sustainable harvest of non-timber forest products, among other benefits (Morellato *et al*., 2016; Buisson *et al*., 2017).

Unfortunately, this area has been poorly studied on vascular epiphytes (Williams-Linera and Meave, 2002; Morellato *et al*., 2010; Sakai and Kitakima, 2019). This led us to conduct this revision in hope of encouraging the phenological study of this group of plants. Our purpose was to synthesize the existing information and detect gaps in knowledge, suggesting future lines of study with emphasis on the particularities of the epiphytic environment.

MATERIALS AND METHODS

We conducted an online search for indexed articles that included reports on reproductive phenology (flowering and fructification) and vegetative phenology (leaves and pseudobulb production) of vascular epiphytes. We only considered studies made on holoepiphytes (plants that develop their full life cycle on their hosts according to Zotz (2013)).

Our search considered phenological studies published between 1800 and 2020, using the Google Scholar search engine and the ISI Web of Science database. Both resources are updated regularly and offer results that include trustworthy scientific documents that have been cited by numerous authors. To narrow down our search we used the following keywords, both in English and Spanish: vascular epiphytes × phenology, orchids × phenology, bromeliads × phenology, phenology × (holoepiphyte genus) including pteridophytes, community × phenology, and life forms × phenology. Since studies on food availability for pollinators usually describe the phenology of the plants they forage on, we also included the following keywords in our search, related to groups which have been reported as epiphyte pollinators: floral resources × hummingbirds, floral resources × bats, floral resources × moths and floral resources × euglossine bees (Gentry and Dodson, 1987; Ackerman, 1989; Benzing, 1990). Regarding resource availability for dispersers, we only included the following families in our search: Cactaceae, Araceae, Ericaceae, Gesneriaceae, Piperaceae, and Bromeliaceae, this is because the majority of epiphytes are anemochorial (Madison, 1977; Zotz, 2016), and the mentioned families are those with the higher number of animal-dispersed epiphyte species. We used a combination of the name of the families with the words fruit resources as keywords (e.g Cactaceae × fruit resources). Lastly, our search also covered articles about breeding systems since they report phenological information on the evaluated species. To find these studies, we searched for the following keywords: breeding systems × vascular epiphytes, breeding systems × family with epiphytic members.

To identify omissions in the vegetation types where epiphyte phenology has been studied, we extracted the coordinates reported in each study and superimposed them over the world's biomes layer available at https://ecoregions2017.appspot.com/, using the ArcGis 10.3© software.

RESULTS AND DISCUSSION

We found 107 papers with phenological information on vascular holoepiphytes (Supplement 1). Of these, 92 (88 %)

were studies conducted in the Neotropic (Fig. 1), the area with the highest epiphyte diversity in the world; eight (7 %) reported data from Asia and the Pacific which hold the second place in terms of global epiphyte diversity, and four (4 %) were localized in Africa, the continent with the lowest epiphyte diversity (Madison, 1977; Benzing, 1990; Zotz, 2016), and one in Australia (1 %), where vascular epiphyte flora has partially been explored (Wallace, 1981). This totals 105 articles after excluding the studies by Barve *et al*. (2015) and Hietz (2010), since the first used herbarium data for all the Americas and therefore extends beyond the Neotropical area, and the latter is a report about xeric fern species from all around the world.

Most of the studies found in our search were conducted in wet (76 %) or dry tropical and subtropical forests (Fig. 1). These forests hold the highest diversity of vascular epiphytes and cover about 17 % of the world's total area (Zotz, 2016; Dinerstein *et al*., 2017). While some temperate forests could compare to tropical ones in terms of epiphyte diversity and biomass (Zotz, 2005), we only found four studies done in these kinds of ecosystems (one in Chile and three in Japan). One explanation for the scarcity of studies in these types of forests could be that vascular epiphyte communities in temperate forests are dominated by ferns and similar species, while most phenological studies have focused on the reproductive biology of epiphytes with flowers (Fenner, 1998; Williams-Linera and Meave, 2002), and ferns are rarely included in the extensive vegetative phenology studies that have been done in temperate zones (Polgar and Primack 2011; Müller *et al.,* 2019).

When it comes to taxonomic representation (Fig. 2) following the classification by Zotz (2013) for vascular epiphytes, we can see that only 33 % of the families with epiphytic members (24/73), 16 % of the genera (149/911), and *ca.* 2 % of the species (418/22 905) have been studied. Most of these studies focused on the Orchidaceae (46 %, 192 spp.) and Bromeliaceae (30 %, 124 spp.), showing an over-representation of these families which has also been reported for demographic studies of vascular epiphytes (Mondragón *et al*., 2015). Many reasons could explain this bias: *a)* These two families hold more than 75 % of all vascular epiphyte species (Kress, 1986; Zotz, 2013), *b)* Since epiphyte members of these families represent an important source of food for both birds and insects they get included in many foraging studies (Sazima *et al*., 1995; Sazima *et al*., 1996) and *c)* Many orchid and bromeliad species are widely collected for various purposes (ornamental, medicinal, etc.) which have caused them to become endangered, favoring their study over other non-endangered species (Bonato and Muraro, 2006; Parthibhan *et al*., 2015).

The study by Nevling (1971) was the oldest we found on epiphyte phenology. From then on, there has been a considerable increase in vascular epiphyte research, particularly in the last two decades that concentrate 69 % of all the studies we found. This recent rise matches the period when studies in tropical rain forests flourished, around the beginning of the 21st century (Williams-Linera and Meave, 2002; Piao *et al*., 2019). However, the incorporation of epiphytes in the mentioned studies has not been easy. For example, in one of the pioneer studies on tropical phenology, conducted at Barro Colorado Island, which included

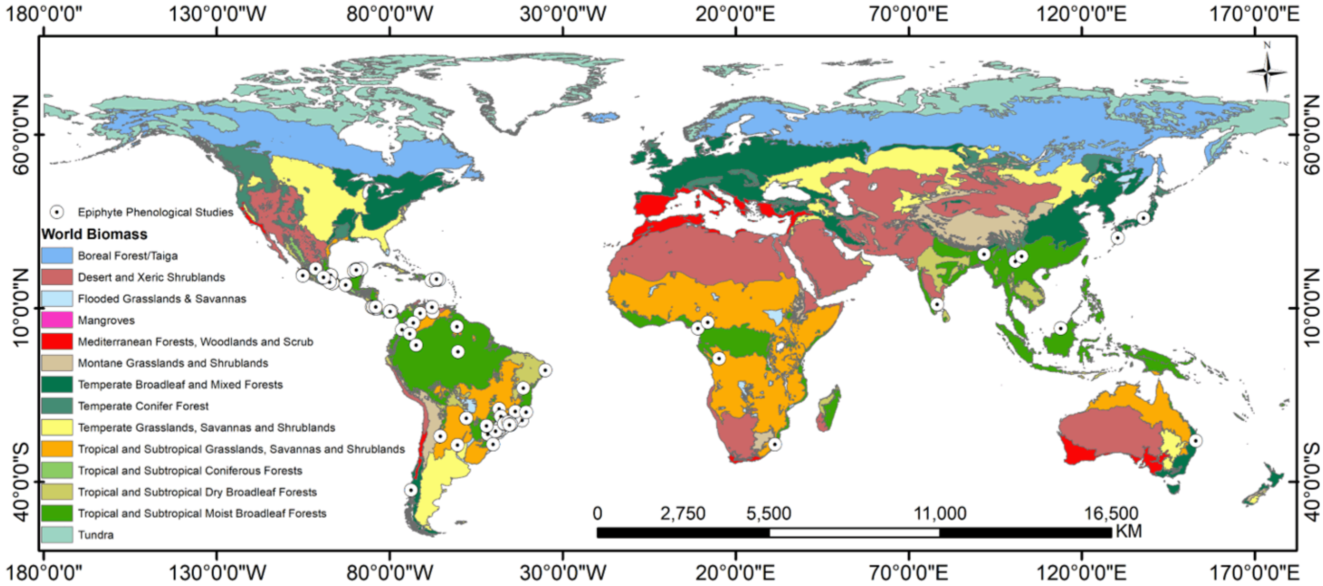

Figure 1. Geographic distribution of phenological studies that include vascular epiphytes and the biomes associated with these studies. Some points overlap because several studies were conducted at the same site.

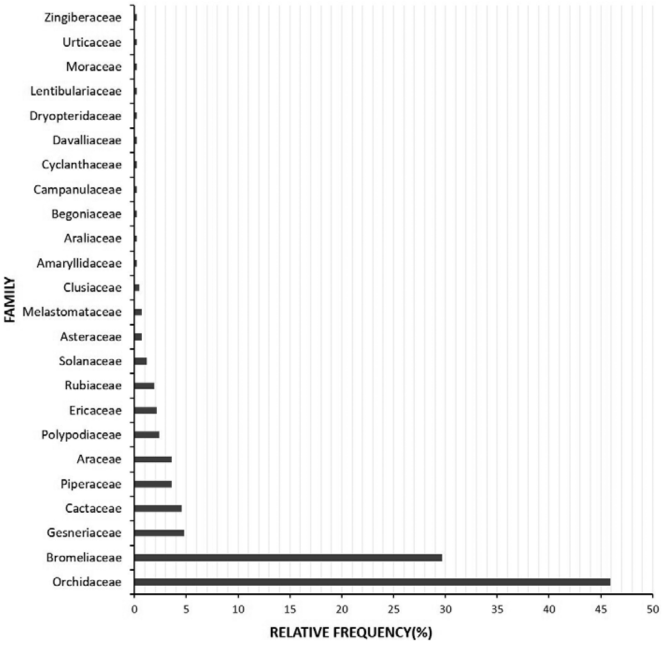

Figure 2. Representability of vascular epiphyte families in the phenological studies analyzed.

1181 species of plants -trees, shrubs, herbs, and climbing plants (Croat, 1969), no epiphyte species was considered. It was not until 1975, in his article *Phenological behavior of habitat and habitat classes on Barro Colorado Island*, where Croat analyzed the phenological patterns of 41 epiphyte species. This resistance to incorporate epiphytes in phenological studies persists to this day, much of it related to the logistical challenge involved in monitoring individuals that grow on trees, often at heights over 40 m off the ground (Sheldon and Nadkarni, 2015).

The studies that present information regarding the phenology of vascular epiphytes can be grouped in the following categories (Supplement 1):

a) *Studies about the reproductive biology of one or various species:* here we included studies regarding breeding systems, pollination biology, and germination. In this group of studies, the phenology of plants is reported as complementary information. Forty-six of the studies (43 %) we found can be included in this category. Examples of this are Borba and Braga (2003) and Bianchi and Vesprini (2014) with their work on breeding systems; Canela and Sazima (2003) and Aguilar-Rodríguez *et al.* (2016) on pollination biology; and Duarte *et al*. (2018) studying germination.

b) *Studies about resource availability for pollinators or dispersers*: in this kind of study, a yearlong investigation is done on the phenology of species that serve as resources for a specific group of animals. Sixteen of the studies we found were of this kind (15 %). As examples, we have the work by Sazima *et al*. (1995) and de Araújo *et al*. (2011) which evaluate resources for hummingbirds.

c) *Studies of the phenology of plant communities*: these studies follow the phenology of a group of species, generally including different life forms, to establish phenological patterns and then compare between them, evaluating possible factors to explain them. We found 24 studies that included epiphytes (22 %), but four of these, despite mentioning epiphytes in their methods, excluded them from their results and discussion or grouped them with hemiparasites, parasites, and climbers for their analysis. Examples of studies that clearly show variation between phenological patterns of epiphytes and other life forms include Nevling (1971) and Marques *et al*. (2004).

d) *Studies on vascular epiphyte phenology*: these track the phenology of one or various epiphyte species, aiming to point out the factors that might be triggering it. We found 21 studies of this nature (20 %), 20 of which evaluate reproductive phenology and only one that gives relevant information about vegetative phenology, focusing on ferns (Hietz, 2010).

A. Vegetative phenology of vascular epiphytes

Phenological plant studies can focus on vegetative or reproductive phenology. The former includes dormancy and events of leaf production and leaf falling, and the latter includes flowering, fructification, and seed dispersal (Williams-Linera and Meave, 2002; Guaraldo *et al*., 2013; Tang *et al*., 2016). For vascular epiphytes, we found that most studies (96 % of our search results) are related to the reproductive phenology of these plants. The scarce research done on epiphyte vegetative phenology could be related to the fact that most species are evergreen (Benzing, 1990) with constant production of leaves, thereby impeding the distinction and tracking of the beginning and end of vegetative phenophases (Denny *et al*., 2014). Even so, we did find five studies that tracked the vegetative phenology of deciduous epiphytes, particularly for orchids and ferns. In orchids, research has been done on the phenology of pseudobulb formation, which is tied directly to the formation of leaves on the lateral or superior side of the pseudobulbs once they reach their final size (Dressler, 1993). Foliar phenology has been monitored in epiphytic ferns where leaves (or frond) production is restricted to a certain part of the year. Fronds are the most conspicuous parts of these plants and are responsible for energy transfer and spore production, both of which contribute to fern growth, survival, and regeneration (Mehltreter and Sharpe, 2013; Lee *et al*., 2018). Nonetheless, the fact remains that phenological data on epiphyte ferns is very scarce and, up to 2020, we found information for only 14 (Lee *et al*., 2018) out of 2700 species of epiphytic ferns (Zotz, 2013).

A. Patterns of flowering phenology in vascular epiphytes

Just as with other life forms, vascular epiphytes present phenological variation at the level of individuals, populations, and communities (Texier *et al*., 2018). In their paper about phenological patterns, Williams-Linera and Meave (2002) mentioned that these phenological differences might be related to the physiological status or location of the plants in specific micro-habitats, also considering the effect of the genotype (Primack, 1980). The epiphytic environment presents a large variation in terms of possible micro-habitats, derived from a wide range of characteristics such as host tree species and position along the host tree (Johansson, 1974; Wagner *et al*., 2015; Rasmussen and Rasmussen, 2018). The diversity of microhabitats could favor phenological variation among epiphytic individuals. While this effect has not been measured on phenology itself, it has been proven that different micro-habitats cause variation in the growth, reproductive potential, and flower production of vascular epiphytes (Cervantes *et al*., 2005; Ticktin *et al*., 2016; Ramírez-Martínez *et al*., 2018).

At the population level, epiphytes have non-random flowering patterns (Johansson, 1974; Gardner, 1986; Sahagún-Godínez, 1996; Hietz *et al*., 2006; Machado and Semir, 2006; Texier *et al*., 2018). Individuals produce flowers within less than five months per year, and most of them flower around the same time, which is why they are considered to flower annually, following the classification by Newstrom *et al.* (1994), and they mostly have seasonal blooming. Some species bloom during rainy seasons (Sazima *et al*., 1995; Aragón and Ackerman, 2004; Stevenson *et al*., 2008), others in dry seasons (del Coro Arizmendi and Ornelas, 1990; de Araújo *et al*., 2011; Orozco-Ibarrola *et al*., 2015), while others during both seasons, usually at the end of the dry and beginning of the wet season (Sazima *et al*., 1996; Buzato *et al.,* 2000; Zimmerman *et al*., 2007).

There have been reports of variation in the duration or in the starting date of blooming among populations located in different regions. For example, in Machado and Semir's (2006) research about the flowering phenology of ornithophilic bromeliads in a tropical forest, they mentioned that eight of the fourteen monitored species had flowering periods that differed from those reported in other studies done in different areas of the same forest (Araujo *et al.*, 1994; Buzato *et al.,* 2000). This variation could be the result of temporal or micro-spatial differences among study sites. However, Texier *et al*. (2018) has reported the existence of phenological ecotypes in epiphytic orchids, in which their rhythms are genetically determined and are not influenced by habitat conditions.

At the community level, flowering in epiphytes tends to be continuous (Newstrom *et al*., 1994), meaning that throughout the whole year, different species can be found flowering, regardless of any possible peaks existing at the community level. For example, Johansson (1974) reported two flowering peaks for orchids during the dry season in eastern Africa, while Sahagún-Godínez (1996) mentioned that epiphytic orchids in western Mexico have a flowering peak at the beginning of the rainy season and another during the dry season. In the case of bromeliads, Machado and Semir (2006) reported they have sequential and continuous flowering with a peak during the rainy season.

When compared to other life forms, epiphytes shared similar flowering patterns with trees, shrubs, vines, and climbers (Croat, 1975; van Dulmen, 2001; Ramírez, 2002; Marques *et al*., 2004; Liebsch and Mikich, 2009), and in some cases also with terrestrial herbaceous plants (Marques *et al*., 2004; Cascante-Marín *et al*., 2017). Epiphytes might show marked flowering seasonality, similar to other life forms, but with shorter duration during the dry season (Croat, 1975; van Dulmen, 2001; Ramírez, 2002; de Freitas *et al*., 2013). Conversely, other epiphytes have shown low seasonality and extensive flowering, when compared to other life forms, as documented by two studies conducted north of the tropic of Capricorn, where seasonal differences were almost nonexistent (Smith-Ramírez and Armesto, 1994; Marques *et al*., 2004).

1. Determining factors on flowering phenology of vascular epiphytes

Plant phenology is commonly tied to abiotic (proximate factors) and biotic (ultimate factors) triggers (Lopezaraiza-Mikel *et al.*, 2013). Proximate factors include temporal variation in photoperiods, precipitation and temperature, among others, and ultimate factors are related to phylogenetic relations, biotic interactions such as competition among pollinators, and herbivore evasion (van Schaik *et al.*, 1993; Wright and Calderón, 1995; Lobo *et al.,* 2003).

From the 107 studies, we found only five that explicitly explore the correlation between flowering phenology and proximal factors considering: maximum temperature, minimum temperature, precipitation, relative humidity, and/or solar radiation (Lasso and Ackerman, 2003; Marques *et al.*, 2004; Ramírez and Briceño, 2011; Barve *et al.*, 2015; Cascante-Marín *et al.*, 2017). The possible effects of these correlations are only discussed in the Texier *et al.* (2018) study, while the effects of pollinators on flowering is only mentioned in the studies by Zimmerman *et al.* (1989) and Cascante-Marín *et al.* (2017).

The following sections were based on all the results obtained from our documental search. These can be broadly divided into studies that evaluate how proximate and ultimate factors might be regulating epiphyte phenology, and all the rest which include epiphytes, either directly in their discussions or indirectly through climographs (25 studies).

Proximate factors

In seasonal tropical environments, precipitation has been widely documented as a trigger for phenological events in numerous life forms (Sakai, 2001; Morellato *et al.*, 2013). Unlike terrestrial plants, epiphytes don't have access to either the water or the nutrients stored in the ground and depend on atmospheric sources to obtain them. Consequently, water availability is considered the most relevant abiotic restriction for epiphyte growth and survival (Benzing, 1990; Zotz and Hietz 2001; Mondragón *et al.*, 2015; Zotz, 2016). Taking this into consideration, one could expect vascular epiphyte phenology to be heavily influenced by precipitation availability, following the climate factor hypothesis (Wright and Calderon, 1995; Boulter *et al.*, 2006) or, in other words, epiphyte phenology might have evolved to coincide with the period with higher water availability, and, thus, increased humidity and nutrient availability (Cascante-Marín *et al.*, 2017).

However, although we find that in seasonal forests, *ca.* 47 % of epiphyte species flower during the rainy season, *ca.* 41 % do so in the dry season. This could be the result of various factors: *a)* According to the biological hypothesis, in which phenology is linked to the activity of pollinators (among other biotic interactions), the species that compete for pollinators tend to shift their flowering periods, thereby minimizing overlap and reducing competition. This would be the case for many epiphytes where, according to Ackerman (1986), one of the strategies adopted to handle the limitations imposed by their environments (individuals being far apart, few resources available to reward pollinators, and small size that limits their detectability) is to shift their flowering periods concerning other life forms, such as trees (Stiles, 1978). *b)* Phenophases are not disconnected from one another and involve compromises between them. This would mean that flowering during the dry season is more related to the fact that seeds benefit from being dispersed in seasons that favor germination and the establishment of seedlings (Primack, 1987). *c)* Restrictions due to growth forms. Zimmerman *et al.* (1989) mention how some species of the genus *Mormodes* Lindl. can flower during the dry season, when the population density of their pollinators is at its highest because their inflorescence emerges from pseudobulbs produced during the previous growing season. Meanwhile, *Catasetum viridiflavum* Hook., which shares the same pollinators with the *Mormodes* spp. mentioned, can't flower in the dry period because their inflorescence emerges from pseudobulbs produced during the same growing season, and this delays their flowering until newer pseudobulbs are formed, which happens around the middle and end of the rainy season.

In temperate environments, the temperature has been considered one of the main triggers for phenological events (Prevéy *et al.*, 2017; Flynn and Wolkovich, 2018; Reed *et al.*, 2019). However, in the tropics, where most epiphytes are found, attention is mostly turned to rain seasonality, ignoring changes in temperature and photoperiods because of their low annual variation (van Schaik *et al.*, 1993; Morellato *et al.*, 2000; Sakai, 2001). One of the few studies that evaluate factors that might affect the flowering phenophase in vascular epiphytes reported that an increase in solar radiation combined with a decrease in minimum temperature, are environmental cues that affect the floral phenology of *Werauhia sintenisii* (Baker) J.R. Grant (an epiphytic bromeliad growing in a cloud forest). However, the way these two factors influence floral induction remains unknown (Lasso and Ackerman, 2003).

Day duration has been associated with flowering induction in other life forms (Morellato *et al.*, 2000; Rivera and Borchert, 2001) and, although there is little annual variation in photoperiod in the tropics, it could be enough to influence epiphytes, as observed for other phenological events. However, we could not find any studies investigating the potential influence of day duration on epiphyte phenology. Lasso and Ackerman (2003), as well as Cascante-Marín *et al.* (2017), propose that solar radiation has a positive influence on flowering. This factor could influence the flowering phenology of epiphytes in seasonal forests given that, as pointed out by Sahagún-Godínez (1996), the drought-tolerating adaptations developed by these plants, make them photosynthetically inefficient, so that it is favorable for them to flower in the season with higher solar radiation when they can have higher photosynthetic rates and flower production. However, this hypothesis has yet to be proven.

Ultimate factors

Several authors have insisted on the importance of biotic factors as selective triggers, which have molded the periodicity of phenological events for plants in the tropics (Stiles, 1978; Augspurger, 1983; Marquis, 1988). The interactions that have received the most attention in this regard are herbivory, competition for pollinators, and diaspore dispersion (Fenner, 1998; Williams-Linera and Meave, 2002). In the case of vascular epiphytes, and according to our revision, interactions with pollinators have received the most attention and have been mostly studied in the Orchidaceae and Bromeliaceae families (Carranza-Quiceno and Estévez-Varón, 2008).

It has been hypothesized that competition between species for pollinators can be reduced by avoiding the overlap of their flowering periods ("Hypothesis of the shared pollinator"; Wright and Calderon, 1995), but this has barely been explored when it comes to vascular epiphytes. A study that stands out in this respect is the one by Sheldon and Nadkarni (2015) where they looked at the floral phenology of a community of vascular epiphytes in a tropical forest. Although they did not directly evaluate the competition for pollinators, they found asynchrony in the flowering periods among epiphyte groups that shared a common kind of pollinator. Species pollinated by insects had flowering peaks during the dry season, which is thought to be a mechanism used to maximize the presence of pollinators while reducing the competition for them (Talavera *et al.,* 2001). On the other hand, species pollinated by birds flowered at the end of the rainy season, which correlates with the migratory habits of the birds. Another relevant study is the one by Cascante-Marín *et al*. (2017) where they reported asynchrony in the flowering of some genera that shared a common pollinator, including *Monstera* Adans., *Peperomia* Ruiz & Pav., *Tillandsia* L. and *Werauhia* J. R. Grant. The authors emphasize that in order to prove the shared pollinator hypothesis, it is necessary to first establish that the group of species does share the same pollinator, and then evaluate the effect of pollinators on pollen deposition and fruit development.

Other studies show that asynchrony and sequential flowering in species that share pollinators not only reduces competition for them but also allows their pollinators to remain in the community for longer periods of time (Araujo *et al*., 1994; Machado and Semir, 2006; Marques and Lemos-Filho, 2008). This is the case for three species of *Vriesea* Lindl. that share the hummingbird *Ramphodon naevius* Dumont (1818) as their pollinator and bloom sequentially, thereby keeping the pollinator in the area for longer (Araujo *et al*., 1994).

Alternatively, to the flowering asynchrony mechanism to avoid competition, the flowering phenology of orchid species with pollination by deception (for food), could be conditioned by the flowering phenology of the species they mimic. For example, some epiphytic orchid species do not have floral rewards to attract pollinators, but they benefit from flowering synchronously with other plants that have similar flowers that produce pollinator rewards (Ackerman, 1983; Ackerman, 1986). Another example is *Warczewiczella lipscombiae* (Rolfe) Fowlie (Orchidaceae), which flowers synchronously with the terrestrial sympatric *Neurocarpum javitense* Kunth (Fabaceae), whose flowers produce floral rewards (Ackerman, 1983).

Another factor that has been poorly documented or avoided in phenological studies is phylogeny. According to Wright and Calderon (1995), flowering patterns will be influenced and, in some cases, limited by phylogeny, resulting in a tendency for similar flowering dates in taxonomically related species. This approach has only been explored for vascular epiphytes in the Texier *et al*. (2018) study where they found similar flowering patterns among genera of Orchidaceae. Johansson had already mentioned this in 1974, stating that there is a similarity in the flowering patterns of species of the same genus, setting them apart from the phenological patterns of other genera.

C. Fruiting and seed dispersal phenology of vascular epiphytes

In vascular epiphytes fructification happens mostly during the dry season, contrasting with trees, shrubs, and herbs that fructify mostly in the rainy season (de Freitas *et al*., 2013). Primack (1987) mentions how fruit maturation is strongly tied to the dispersal syndrome, so that species with fleshy fruits tend to mature once their dispersers are abundant. In the case of epiphytes, which seeds are mostly dispersed by wind (*ca*. 80 %, Madison, 1977), they tend to liberate them during the dry season.

1. Factors that determine fruiting and seed dispersal phenology in vascular epiphytes

While none of the articles explicitly discusses the factors that might influence these phenophases, it is known that anemochorous plants in seasonal tropical forests tend to disperse their seeds during the dry season (de Lampe *et al*., 1992; Morellato and Leitão-Filho, 1996; Cortés-Flores *et al*., 2019) since this dispersal syndrome is closely linked to wind speed and the surrounding vegetation (Augspurger, 1986). Dispersal during the dry season results more effective given the lack of foliage, facilitating the flow of wind currents and allowing the seeds to be carried over longer distances (García-Franco and Rico-Gray, 1991; Mondragón and Calvo-Irabien, 2006; Valverde and Bernal, 2010; Escobedo-Sarti and Mondragón, 2016). As occurs with flowering, fructification, and seed dispersal are influenced by other phenological phases (Primack, 1987) because, for instance, successful regeneration of a species does not only depend on seed dispersal, but also on seeds being dispersed over favorable areas during periods that allow them to germinate and establish as seedlings (Clark *et al*., 1999). The establishment and germination of epiphytes is a critical phase in their population dynamics (Benzing, 1981; Mondragón *et al*., 2015) since water availability is one of the main limiting factors for their germination (Benzing, 1978; Castro-Hernández *et al*., 1999; Toledo-Aceves and Wolf, 2008). This leads to the notion that the best time for dispersal to ensure seed germination and seedling establishment is during the last stretch of the dry season, or during the rainy season.

D. Suggestions for future phenological studies of epiphytes

A) To develop a standardized methodology to measure phenological events, facilitating the recognition of patterns, and interactions, while also enabling the comparison between populations and taxa (Bencke and Morellato, 2002; Miller-Rushing *et al*., 2010; Denny *et al*., 2014); *B)* To increase the taxonomic representation of other families besides orchids and bromeliads; *C)* To investigate the proximate and ultimate factors that trigger the phenology of this group; *D)* To assess the temporal and spatial variation of their phenological patterns.

Besides these initial and baseline suggestions, we also consider the following list as relevant to better understand the phenology of vascular epiphytes.

Tracking vegetative phenology

While most epiphytes are evergreen, there is also an important group of species that are not, including ferns and some orchids (Benzing, 1990; Hoeber *et al*., 2019). We suggest monitoring the production of leaves, pseudobulbs, and offspring in species where the phenophases can be set apart. This must be done considering that each phase needs to have a well-defined beginning and end date (Denny *et al*., 2014).

Host effect on epiphyte phenology

It is known that epiphytes have an intimate relationship with their host trees (Einzmann *et al*., 2015; Wagner *et al*., 2015; Ticktin *et al*., 2016; Ramírez-Martínez *et al*., 2018; Rasmussen and Rasmussen, 2018) so it is fundamental to understand how these hosts affect epiphyte phenology. If we consider a population as the group of individuals growing on the same tree (Overton, 1994), the effect of the host tree could be evaluated in two levels: *a)* interpopulation variation among populations on different hosts, and *b)* intrapopulation variation between individuals growing on the same tree. The first can be linked to the identity of the host, since each host offers different morphologies (*e.g.* stability and bark texture and angle and size of the branches), chemical environment (*e.g*. nutritional quality of the foliar and cortical runoffs, as well as the presence of allelopathic substances), and microclimatic conditions (*e.g*. light, temperature and humidity in the canopy) (Zimmerman and Olmsted, 1992; Valencia-Díaz *et al*., 2010; Einzmann *et al*., 2015; Taylor and Burns, 2016). At the intrapopulation level, variation can be caused by micro-climatic differences along the tree related to light and humidity gradients from the base to the crown (Johansson, 1974; Cervantes *et al*., 2005; Zotz, 2007), as well as substrate characteristics (*e.g*. tree barks retain more humidity than thin branches, while older branches that grow more horizontally retain more aerial soil) (Marler, 2018; Rasmussen and Rasmussen, 2018). The way human activities are causing changes in the composition and structure of forests influences the availability of host trees for epiphytes, thereby, directly affecting the fate of the epiphyte populations. Thus, evaluating the close relationship of epiphytes with their hosts is very important for the implementation of management practices and conservation plans (Hsu *et al*., 2012; Wagner *et al.,* 2015).

Study of phenological VARIATION among epiphytes with different growth forms

Different adaptations have developed among epiphytes allowing them to face the limitations posed by their habitats. In the case of bromeliad epiphytes, we can differentiate two large groups: tank bromeliads (those that accumulate water and debris between their overlapping leaves) and atmospheric bromeliads without tanks, which are densely covered by peltate trichomes (Benzing and Renfrow, 1974; Benzing, 2000). Both groups have quite different ways of capturing water and nutrients (Reyes-García *et al*., 2008; Cardelús and Mack, 2010; Wu *et al*., 2018). For example, bromeliad tanks capture and store water and debris between their leaves, providing a regular supply of resources and shelter for an array of organisms, which contribute nutrients from their debris (Benzing, 1990; Romero *et al*., 2010). On the other hand, atmospheric bromeliads absorb water and nutrients by pulses from atmospheric sources when they are available (Zotz and Hietz, 2001; Reyes-García *et al*., 2012). These differences not only influence the vertical distribution of these epiphytes on their hosts but might also produce variation in phenological patterns given their growth forms.

Another option for the further development of these studies could be to consider the Cardelús and Mack (2010) study as a reference. They found variation in the nutritional status of orchids, ferns, and bromeliads associated with differences in the way they acquire nutrients. Ferns and orchids have functional radicular systems and might depend more on nutrients coming from solid depositions and the aerial ground, whereas bromeliads would depend on runoffs and atmospheric sources. These differences might prompt phenological variation between these groups given that phenology is affected by the nutritional status of individuals, according to Williams-Linera and Meave (2002).

Effects of HERBIVORY on the phenology of VASCULAR epiphytes

Herbivory as an ultimate factor for epiphyte phenology has hardly been explored at all. Among epiphytes, herbivory is of low occurrence when compared to terrestrial plants (Benzing, 1990; Zotz, 2016) which could indicate that it does not have an important effect on their phenology. However, we need studies to confirm this idea, since there are reports of herbivore damage on reproductive structures of different orchid and bromeliad species, affecting flowers, peduncles, spigots, bracts, and fruits (Ackerman, 1989; Cascante-Marín *et al*., 2009; Orozco-Ibarrola *et al*., 2015; Palacios- Mosquera *et al*., 2019). This indicates that herbivores can have a direct effect on the loss of epiphyte reproductive tissue and an indirect effect on the behavior of pollinators (Canela and Sazima, 2003; McCall and Irwin, 2006; Cascante-Marín *et al*., 2009). Insects are the main consumers of reproductive structures (florivores) in vascular epiphytes (Canela and Sazima, 2003; Cascante-Marín *et al*., 2009; Orozco-Ibarrola *et al*., 2015; Nunes *et al*., 2016). This could lead one to expect that species affected by these florivores would delay or advance their phenology to avoid matching seasons with higher insect abundance.

In the case of ferns, where reproductive phenology is thought to be limited by proximate rather than ultimate factors (Rathcke and Lacey, 1985; van Schaik *et al*., 1993; Sharpe and Mehltreter, 2010; Müller *et al*., 2019), it is relevant to evaluate the effect of herbivory on reproductive phenology, given that their reproductive structures are found on their fronds (Ranker and Haufler, 2008). There is no available information on the effect of herbivory on the foliar phenology of epiphytic ferns, but on terrestrial ferns, with different growth forms, it has been observed that herbivory can determine the phenophase of leaf senescence (Mehltreter and García- Franco, 2008; Mehltreter and Sharpe, 2013).

Effect of climate change on epiphyte phenology

Given the strong correlation between epiphytes and both water and atmospheric nutrient availability, several authors have pointed out that these will be one of the most affected life forms by the ongoing climate change around the world (Lugo and Scatena, 1992; Benzing, 1998; Zotz and Bader, 2009). Climate change has already caused variation in the phenology of different species (Menzel *et al*., 2006; Mo *et al*., 2017) so one could expect epiphytes to be similarly affected.

Climate change is also related to current mismatches occurring between pollinators and the flowering of species (Rafferty *et al*., 2015; Gezon *et al*., 2016). Most vascular epiphytes have highly specialist pollinators (Madison, 1977; Ackerman, 1986; Zotz, 2016), and evaluating if this mismatch is occurring is important because it could affect the reproductive success and survival of both the epiphytes and their pollinators (Kudo and Ida, 2013).

CONCLUSIONS

The phenology of vascular epiphytes is just beginning to be explored when compared to other life forms. Thus, there is a vast universe of opportunities for research on their phenological patterns. Only by directing efforts to study these patterns will we be able to clearly understand the proximate and ultimate factors that drive them and the potential repercussions of climate change on vascular epiphyte populations.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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Aim, objectives, and hypotheses

Aim

Test the influence of three host tree species on the reproductive phenology of vascular epiphytes in an oak forest.

Objectives

- Describe the reproductive phenology of *Tillandsia prodigiosa* (Lem.) Baker, *Tillandsia plumosa* Baker, *Alamania punicea* Lex., *Oncidium brachyandrum* Lindl., and *Echeveria nodulosa* growing on *Quercus rugosa*, *Q. castanea* and *Q. martinezii* in terms of its (1) the frequency of occurrence (onset and peak date), (2) the time of occurrence; (3) the duration of the event; and (4) seasonality.

- Analyze if the host tree´s traits represent proximate causes for phenological events in each epiphyte species.

Hypothesis

We expected that:

- Epiphyte species will show different phenology patterns (duration, onset date, frequency, and seasonality) between host species since it has been observed that host tree identity can affect growth and the probabilities of reproduction of epiphytic individuals (Einzmann et al., 2014; Ticktin et al., 2016) and this could be reflected in their phenologies.

- Orchids will display more significant phenological patterns differences across host tree species since they absorb through their roots water and nutrients diluted in host trees stemflows while bromeliads depend mainly on wet and dry depositions since they have no functional roots (Benzing, 2000; Cardelús and Mack, 2010)

- Phenology patterns of epiphytes will be related to differences in temperature, relative humidity, and canopy openness of host tree species since these factors have been proved to affect epiphytes growth and performance (Einzmann et al., 2015; Wagner et al., 2015a; Woods et al., 2015).

Methods

a) Phenology monitoring

To test our hypothesis, we selected 21 trees of *Q. martinezii*, 17 of *Q. rugosa,* and 42 of *Q. castanea*. On each tree, we marked, with plastic tags, adult individuals of the two bromeliad species mentioned above and monthly monitored from March 2018 to February 2020 (24 months). Later we refer to period one from March 2018 to February 2019 and period two from March 2019 to February 2020. We did the same for orchids and echeveria species. Still, since they were scarce on *Q. castanea* (less than 10 adults individuals), we only tagged adult individuals growing on the other two host trees (Table 2). On each visit, we registered if these individuals were producing inflorescences (IF), flowering (FLO; taken as open flowers), fruiting (FRU; including seed development and maturation), or dispersing seeds (SD).

Table 2. Number of adult individuals of four epiphyte species monitored for 24 months on three *Quercus* species in a seasonal oak forest in Tooxi, Yanhuitlán, Oaxaca.

Epiphyte species	Host tree species		
	Quercus martinezii	*Quercus castanea*	*Quercus rugosa*
Tillandsia prodigiosa	**244** (32)	**157** (32)	**260** (35)
Tillandsia plumosa	**67** (21)	**26** (11)	**65** (28)
Alamania punicea	**63** (22)	-	**126** (126)
Oncidium brachyandrum	**262** (262)	-	**94** (94)
Echeveria nodulosa	**5** (2)		**2** (1)

Note: bold numbers indicate the total number of individuals monitored and inside parentheses the number of individuals that showed reproductive phenology.

b) Description of phenology patterns

Activity index

We calculated the Activity index (AI) for each phenophase. This parameter represents the proportion of individuals that exhibit the evaluated phenophase over time. Graphical representation of this analysis revel information and facilitate the description, comparison, and analysis of patterns (Bencke & Morellato, 2002) as described underneath:

- **Onset date:** it includes the starting date of the earliest individuals and the date of peak activity event (Bencke & Morellato, 2002).
- **Duration:** when phenophases showed an annual pattern, we classified them as *brief* (last < 1 month), *intermediate* (last 2-5 months), or *extended* (last > 5 months) (Newstrom et al. 1994).
- **Frequency:** based on AI, we classified the frequency of phenophases per species per host tree, adapting the classification proposed by Newstrom et al. (1994): *continual* (always reproductive with none or few brief interruptions up to 2 months between many reproductive episodes), *annual* (only one major cycle per year, 1-9 month of reproductive phase, which may show brief breaks up to 1-month non-reproductive interval inside the major cycle), or *sub-annual* (more than one event per year separated by intervals of 2-month or more between reproductive episodes).

To get an idea of which host tree promote an early start date and brief duration, we counted the number of times when there were variations on the start date for each phenophase, pointed out how many times epiphytic individuals started early the phenophases on each host tree, sum those values and obtain the percentage of that value for each host tree; for cases where individuals of two species start at the same time, we assigned one event at each of them. For the duration, we estimate de average and the standard deviation of the number of months of difference across the same event on individuals growing on different host trees.

Seasonality

We calculate **seasonality** with circular statistics. First, dates were converted to angles (Morellato et al., 2010). The count of individuals of each species per month was used to calculate the mean angle and length of the mean vector (*r*), which vary between 0 (all around the year, there are individuals in the phenophase evaluated, that means a lack of seasonality) and 1 (all individuals are in the same phenophase at the same time, which means a marked seasonality) representing the concentration of the data around the mean date; when we obtain values of *r* greater than 0.5 we apply the Rayleigh test (Zar, 1999) to assess seasonality. We used a Mardia-Watson-Wheeler test (*W*) to determine the variation in the seasonality of each phenophase evaluated between individuals of the same epiphyte species growing on different phorophyte species. This test compares $\bar{a}$ values of the different samples. A *p*-value > 0.05 means that the seasonality between samples is identical (null hypothesis), *p* values < 0.05 mean that there are differences between samples (alternative hypothesis). All analyses were performed with the software Oriana 4.0 (Kovach Computing Services (KCS), s/f) 2009).

Effect of microclimatic parameters

We selected temperature, relative humidity, and canopy openness since, according to the literature, they could influence epiphytes phenology (Ramírez-Martínez et al., 2021). To read about the methodology of microclimatic data collection, go to Chapter III.

We evaluated whether there was any association between the microclimate of host trees (mean, minimum, maximum temperatures, relative humidity, and canopy openness) and phenophases during their occurrence. We used The Generalized Additive Model for Location, Scale, and Shape (GAMLSS; [Rigby & Stasinopoulos, 2005]), with Poisson distribution and logarithmic link function, selecting the best model using the Akaike information criterion (AIC). We carried out these analyses considering the monthly values of the number of individuals for each phenophase as response variables and canopy openness (CO) mean (Tmean) and minimum (Tmin) temperatures, and relative humidity (RH) as explanatory variables. We did not include maximum temperature since it showed collinearity with relative humidity (Supplement 1).

Results

Since our goal was to evaluate the effect of the host tree identity over epiphyte phenology, rather than compare across epiphyte species, we show our results by epiphytes species and then assess the trends in general for all epiphyte species.

Since we found very few individuals of *Echeveria nodulosa*, we could not calculate AI, seasonality, and apply GAMLSS, so it was analyzed independently. The results were published in a scientific note about their phenology and population structure (see Miscellaneous papers section on page 82).

a) Phorophyte effect on Activity Index

Tillandsia prodigiosa: In Figure 9, we can see differences in onset and peak dates in most of the phenophases evaluated across individuals growing in different host tree species. Inflorescence formation phenophase presents variations in onset parameters: in period 1, individuals growing on *Q. martinezii* started one month earlier than those growing on *Q. rugosa* and *Q. castanea*; while during period 2, they started two and three months earlier than *Q. castanea* and *Q. rugosa*, respectively.

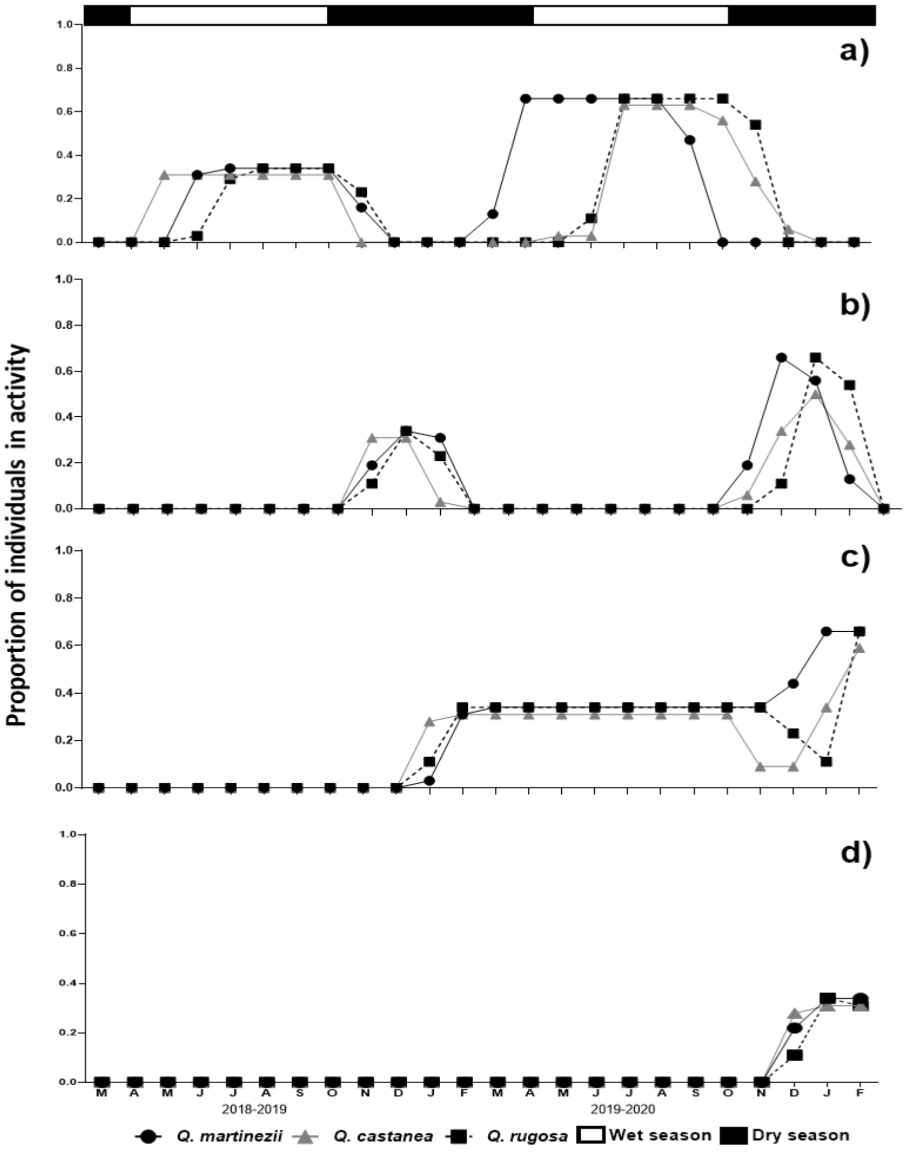

Figure 9. Activity Index for different phenophases of *Tillandsia prodigiosa*: a) Inflorescence formation b) Flowering, c) Fruiting, and d) Seed dispersal, of plants growing on three *Quercus* species in an oak forest in Yanhuitlán, Oaxaca.

There was also variation in duration during the period 2 in *Q. rugosa*, while the frequency was the same across periods and host tree species (Table 4). Flowering showed differences across host tree species in the second period in onset and peak dates (in *Q. martinezii* started one month early). At the same time, duration was shorter for *Q. rugosa* than for other hosts. For the first period in FRU, we could not capture the onset and peak dates, but in the second period, differences across phorophytes were perceived on the onset and peak dates.

Table 3. Main phenological parameters for *Tillandsia prodigiosa* growing on three *Quercus* species in a seasonal oak forest in Yanhuitlán, Oaxaca, México.

Phenophase	Parameter	Host tree species		
		Q. martinezii	*Q. castanea*	*Q. rugosa*
Inflorescence formation	Onset date	Jun / Apr	May / May	Jun / Jun
	Peak date	July / Apr	May /Jul	Aug / Jul
	Frequency	Annual	Annual	Annual
	Duration (months)	6 / 8	6 / 8	6 / 6
Flowering	Onset date	Nov /Oct	Nov /Oct	Nov / Nov
	Peak date	Dec / Nov	Dec/ Dec	Dec /Dec
	Frequency	Annual	Annual	Annual
	Duration (months)	3/ 4	3/ 4	3/ 3
Fruiting	Onset date	NA / Dec	NA / Dec	NA / Jan
	Peak date	NA / Mar	NA / Feb	NA / Feb
	Frequency	Annual	Annual	Annual
	Duration (months)	10	10	10
Seed dispersal	Onset date	Dec	Dec	Dec
	Peak date	NA	NA	NA
	Frequency	Annual	Annual	Annual
	Duration (months)	NA	NA	NA

Note: NA means not available since we could not capture the whole period of the phenophase. The first value before slash represents the values of the first year of sampling, and numbers after slash represent second year sampling.

Also, it was possible to see that the start date of the following fruiting event varied across host tree species beginning with individuals growing in *Q. martinezii*, followed by *Q.*

castanea, and at last individuals growing on *Q. rugosa*. For SD was not possible to capture the whole event, but the onset was similar in all phorophyte species.

Tillandsia plumosa: There was variation in the Activity index in all phenophases (Figure 10). Since when we started monitoring, the IF had already begun to form, we only could have information for one IF the whole event starting in September 2018, for individuals growing on *Q. rugosa*, we observed an advancement of IF on periods 1 and 2; we also detected a variation in the duration of the phenophase of IF (Table 4).

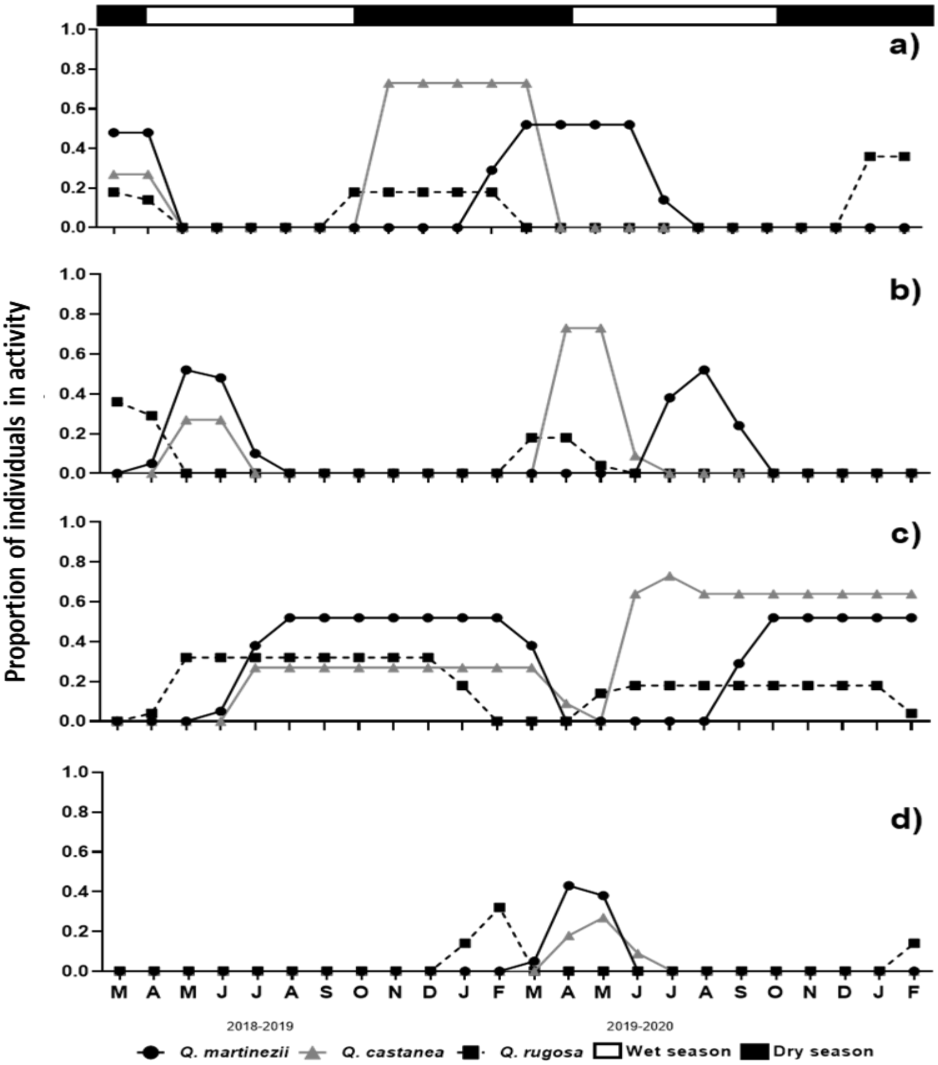

Figure 50. Activity Index for different phenophases of *Tillandsia plumosa*: a) Inflorescence formation b) Flowering, c) Fruiting, and d) Seed dispersal, of plants growing on three *Quercus* species in an oak forest in Yanhuitlán, Oaxaca.

Table 4. Main phenological parameters for *Tillandsia plumosa* growing on three *Quercus* species in a seasonal oak forest in Yanhuitlán, Oaxaca, México.

Phenophase	Parameter	Host tree species		
		Q. martinezii	*Q. castanea*	*Q. rugosa*
Inflorescence formation	Onset date	Feb (2019)	Oct (2018)	Sep (2018)
	Peak date	March (2019)	Oct (2018)	Sep (2018)
	Frequency	Annual	Annual	Annual
	Duration (months)	6	5	5
Flowering	Onset date	Apr / Jul	May / Apr	ND/Mar
	Peak date	May / Ago	May /Apr	Mar / Mar
	Frequency	Annual	Annual	Annual
	Duration (months)	4 / 3	2 / 3	NA / 3
Fruiting	Onset date	Jun / Sep	Jul /Jun	Apr /May
	Peak date	Ago / Oct	Jul / Jul	May /May
	Frequency	Annual	Annual	Annual
	Duration (months)	10	10	10
Seed dispersal	Onset date	March	Apr	Jan
	Peak date	Apr	May	Feb
	Frequency	Annual	Annual	Annual
	Duration (months)	3	3	2

Alamania punicea: star date, peak, and frequency of IF and FLO were the same for individuals growing in both host tree species (Figure 11, Table 5); only duration was brief for individuals growing on *Q. martinezii*. Differences were observed in period 2 for FRU, where individuals growing on *Q. rugosa* stared producing fruits before those growing on *Q. martinezii*. We could not register the SD of the previous year of our monitoring, only for *Q. martinezii* with a duration of 2 months, while during the second SD event, we recorded variation on peak dates and durations.

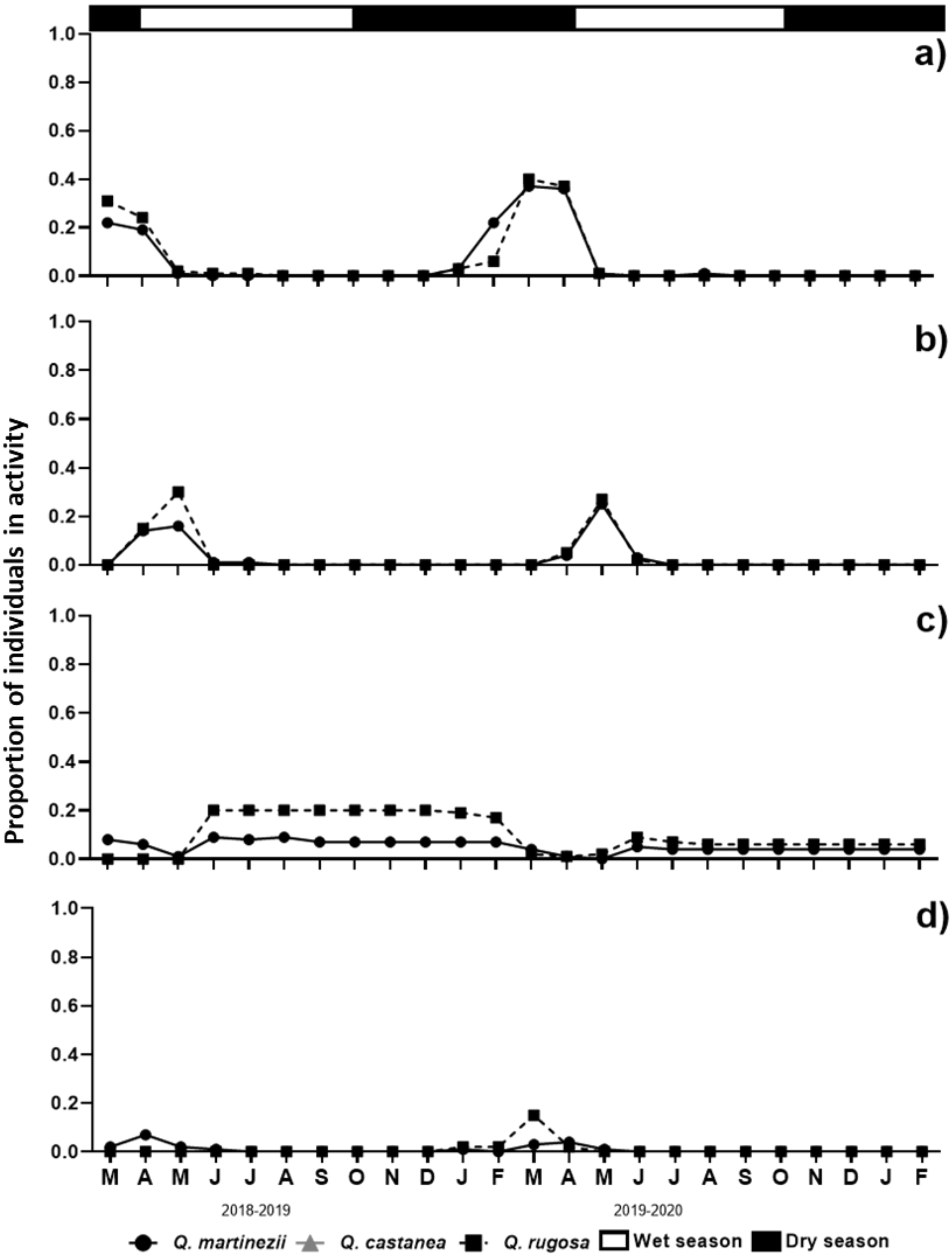

Figure 116. Activity Index for different phenophases of *Alamania punicea*: a) Inflorescence formation b) Flowering, c) Fruiting, and d) Seed dispersal, of plants growing on three *Quercus* species in an oak forest in Yanhuitlán, Oaxaca.

Table 5. Main phenological parameters for *Alamania punicea* growing on three *Quercus* species in a seasonal oak forest in Yanhuitlán, Oaxaca, México.

Phenophase	**Parameter**	**Host tree species**	
		Q. martinezii	***Q. rugosa***
Inflorescence formation	Onset date	NA/Jan	NA/Jan
	Peak date	NA/Mar	NA/Mar
	Frequency	Annual	Annual
	Duration (months)	NA/5	NA/5
Flowering	Onset date	Apr/Apr	Apr/Apr
	Peak date	May/May	May/May
	Frequency	Annual	Annual
	Duration (months)	4/2	3/3
Fruiting	Onset date	Jun / Jun	Jun / May
	Peak date	Jun / NA	Jun / NA
	Frequency	Annual	Annual
	Duration (months)	11/NA	11/NA
Seed dispersal	Onset date	NA/Jan	NA/Jan
	Peak date	NA/Apr	NA/Mar
	Frequency	Annual	Annual
	Duration (months)	NA/5	NA/4

Note: NA means data not available since we could not capture the whole period of the phenophase. The first value before slash represents the values of the first year of sampling, and numbers after slash represent second-year sampling.

Oncidium brachyandrum: IF start date was early for individuals growing on *Q. rugosa* (Fig. 12, Table 6), while the rest of the AI parameters were the same for this phenophase and FRU. FLO and SD were similar. For FLO, we detected variation during period 1 for peak date, while in period 2 on duration, where individuals growing on *Q. rugosa* present a brief FLO. For FRU, the peak date was early for individuals growing on *Q. rugosa* during period 1, while during period 2, individuals growing on *Q. martinezii* start producing fruits one more before those growing on *Q. rugosa*. SD start date was one month early on individuals growing on *Q. rugosa* during period 2 whit a duration of one month extra.

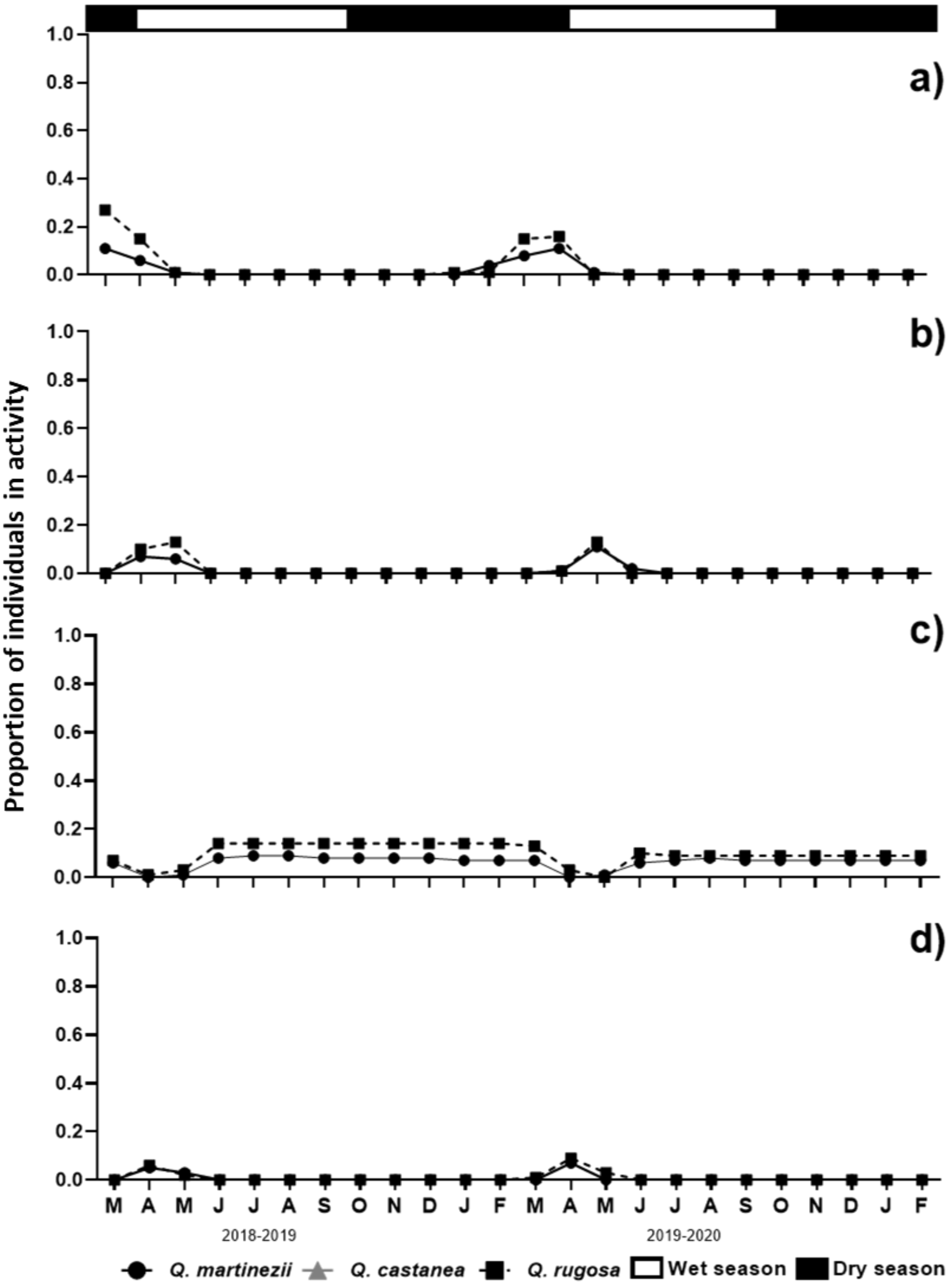

Figure 12. Activity Index for different phenophases of *Oncidium brachyandrum*: a) Inflorescence formation b) Flowering, c) Fruiting, and d) Seed dispersal, of plants growing on three *Quercus* species in an oak forest in Yanhuitlán, Oaxaca.

Table 6. Main phenological parameters for *Oncidium brachyandrum* growing on three *Quercus* species in a seasonal oak forest in Yanhuitlán, Oaxaca, México.

Phenophase	**Parameter**	**Host tree species**	
		Q. martinezii	***Q. rugosa***
Inflorescence formation	Onset date	NA/Feb	NA/Jan
	Peak date	NA/Apr	NA/Apr
	Frequency	Annual	Annual
	Duration (months)	NA/4	NA/4
Flowering	Onset date	Apr/Apr	Apr/Apr
	Peak date	Apr/May	May/May
	Frequency	Annual	Annual
	Duration (months)	2/3	2/2
Fruiting	Onset date	May / May	May / Jun
	Peak date	Ago / NA	Jun /NA
	Frequency	Annual	Annual
	Duration (months)	11/NA	11/NA
Seed dispersal	Onset date	Apr /Apr	Apr / Mar
	Peak date	Apr / Apr	Apr /Apr
	Frequency	Annual	Annual
	Duration (months)	2 / 2	2 /3

Note: NA means data not available since we could not capture the whole period of the phenophase. The first value before slash represents the values of the first year of sampling, and numbers after slash represent second-year sampling.

b) General patterns of host effect on Activity Index of vascular epiphytes

The only vascular epiphyte´s AI parameter that didn´t vary across host tree species and between periods was frequency, which always was annual (even FRU, fruit production was concentrated during a brief period after flowering, and it is fruit ripening that took many months). The rest of the parameters: star date, peak date, and duration, presented variation in all epiphytic species evaluated, both between periods and between phorophyte species. For IF 60% of the time, we observed variation across host tree species (five occasions), individuals growing on *Q. rugosa* started early to produce inflorescences; also, was in *Q. rugosa* where brief duration was more frequently observed approx. 66 % of the phenological event, on average 1 ± 1 month less than the duration of IF for individuals growing on other host tree species. For FLO, once again, individuals growing on *Q. rugosa* started early to bloom (50%, three occasions). Still, in *Q. castanea*, we observed the most significant variation for duration 2 ± 0 months less than the rest, meanwhile in *Q. rugosa* was only 1± 1 month of difference. For FRU one more time, individuals growing on *Q. rugosa* started early to produce capsules (50% of five occasions); in this phenophase, there wasn´t variation for the duration. Finally, for SD 100% of the occasions, we observed variation (just one occasion) for individuals growing on *Q. rugosa* that started first to liberate seeds.

c) Phorophyte effect on seasonality

Tillandsia prodigiosa: All the evaluated phenophases presented seasonality in both periods (Table 7-8, Values of the length of the mean vector (r) near to one and Rayleigh test $p < 0.05$), except for FRU that due to its duration (10 months) was not seasonal. For IF, seasonality did not vary between host tree species for period 1, but period 2 varied between *Q. martinezii* and *Q. castanea* (W=8.49, $p<0.01$) and *Q. martinezii* and *Q. rugosa* (W=6.97, $p<0.03$). FLO was highly seasonal and varied between *Q. martinezii* and *Q. castanea* (W=9.6, $p<0.01$) for period 1 and in the second period between *Q. martinezii* and *Q. rugosa* (W=6.5, $p<0.04$). FRU was not seasonal, and we could not calculate seasonality for SD for any period.

Tillandsia plumosa: All the evaluated phenophases presented seasonality in both periods (Table 7-8, Rayleigh test p < 0.05 values), except for FRU that due to its duration (10 months), presented a not seasonal pattern. IF seasonality for period 1 varied between *Q. martinezii* and *Q. castanea* (W=26.35, *p*<0.001) and in *Q. martinezii* and *Q. rugosa*. For period 2, due to sampling size, we only were able to test differences between *Q. martinezii* and *Q. rugosa* (W= 42.2, *p*<0.0001). Differences in FLO were found between *Q. martinezii* and *Q. rugosa* for periods 1 (W=6.5, *p*<0.001) and 2 (W=1.02, *p*<0.001) and between *Q. martinezii* and *Q. castanea* for period 2 (W=1.19, *p*<0.001). For SD, we were not able to perform de analyses due to small sample sizes.

Alamania punicea: All the evaluated phenophases presented seasonality for both periods (Table 7-8, Rayleigh test p < 0.05 values), except for FRU that due to its duration (11 and 12 months), presented a not seasonal pattern. Seasonality of IF (W=8.78, p<0.012) differed between *Quercus* species for period 1 and period 2 only FLO (W=47.49, p<0.001) and SD (W=6.323, p<0.042) varied between host species.

Oncidium brachyandrum: All the evaluated phenophases presented seasonality for both periods (Table 7-8, Rayleigh test p < 0.05 values), except for FRU that due to its duration (11 months), presented an unseasonal pattern. Differences in seasonality across host tree species were only observed for period 2 in IF (W=6.852, p<0.033), FLO (W=17.35, p<0.001), and SD (W=9.74, p<0.008).

d) General effects of host species on seasonality

Even when all the phenophases of all epiphytic species growing on species of trees presented a seasonal pattern (except FRU), there were statistical variations in values of seasonality across epiphytic individuals growing on different phorophytes, which means that the grade of concentration of individuals in the phenophase across the mean of the population varied, for example in *T. plumos*a for IF, *r* values ranged from 0.921 (high concentration around the mean) to 0.55 in *Q. rugosa* (more scattered distribution across the mean).

Table 7. Results of the circular analysis to determine the seasonality of the phenophases of two epiphytic bromeliads and two epiphytic orchids growing on three *Quercus* species, in Yanhuitlán Oaxaca, from March 2018 to 2019.

Epiphyte specie	Inflorescence formation			Flowering			Fruiting			Seed dispersal		
Tillandsia prodigiosa	*Q. martinezii*	*Q. castanea*	*Q. rugosa*	*Q. martinezii*	*Q. castanea*	*Q. rugosa*	*Q. martinezii*	*Q. castanea*	*Q. rugosa*	*Q. martinezii*	*Q. castanea*	*Q. rugosa*
Number of Observations	59	55	60	27	21	24						
Mean Vector (μ)	248.231°	266.259°	225°	4.600°	347.022°	5.104°						
Length of Mean Vector (r)	0.694	0.761	0.644	0.924	0.954	0.937						
Rayleigh test of uniformity(Z)	28.456	31.880	24.88	23.031	19.120	21.059						
Rayleigh test of uniformity (p)	< 1E-12	< 1E-12	1.57E-11	4.46 E-10	1.37E-08	2.55E-09						
Tillandsia plumosa												
Number of Observations	26	38	34	24	6	18	86	24	78			13
Mean Vector (μ)	94.792°	27.216°	26.932°	166.146°	165°	103.295°	318.4°	315°	261.239°			50.884°
Length of Mean Vector (r)	0.921	0.721	0.55	0.934	0.966	0.966	0.43	0.418	0.334			0.971
Rayleigh test of uniformity(Z)	22.043	19.741	10.271	20.926	5.598	16.809	15.868	4.199	8.684			12.258
Rayleigh test of uniformity (p)	1.02E-09	1.87E-09	163E-5	2.80E-09	0.00042	8.87E-08						134E-06
Oncidium brachyandrum												
Number of Observations	63		42	36		21	225		128			
Mean Vector (μ)	94.218°		99.465°	134.885°		137.192°	294.847°		304.423°			
Length of Mean Vector (r)	0.913		0.941	0.959		0.967	0.214		0.203			
Rayleigh test of uniformity(Z)	52.551		37.202	33.09		19.622	10.33		5.254			
Rayleigh test of uniformity (p)	< 1E-12		< 1E-12	< 1E-12		9.82E-09						
Alamania punicea												
Number of Observations	89		85	44		57	115		226	17		5
Mean Vector (μ)	86.314°		98.871°	139.373°		140.104°	294.462°		295.779°	119.478°		48.068°
Length of Mean Vector (r)	0.891		0.888	0.941		0.97	0.075		0.328	0.865		0.967
Rayleigh test of uniformity(Z)	70.649		66.965	38.947		53.606	0.643		24.384	12.706		4.678
Rayleigh test of uniformity (p)	< 1E-12		< 1E-12	< 1E-12		< 1E-12	5.25E-01			5.98E-07		0.003

Table 8. Results of the circular analysis to determine the seasonality of the phenophases of two epiphytic bromeliads and two epiphytic orchids growing on three *Quercus* species, in Yanhuitlán Oaxaca, from March 2019 to 2020

Epiphyte specie	Inflorescence formation			Flowering			Fruiting			Seed dispersal		
Tillandsia prodigiosa	*Q. martinezii*	*Q. castanea*	*Q. rugosa*	*Q. martinezii*	*Q. castanea*	*Q. rugosa*	*Q. martinezii*	*Q. castanea*	*Q. rugosa*	*Q. martinezii*	*Q. castanea*	*Q. rugosa*
Number of Observations	124	115	91	49	38	46	155	116	143			
Mean Vector (μ)	217.99°	264.91°	261.17°	342.20°	355.45°	9.91°	39.349°	123.126°	134.487°			
Length of Mean Vector (r)	0.638	0.732	0.744	0.914	0.906	0.947	0.139	0.121	0.054			
Rayleigh test of uniformity(Z)	50.511	61.603	50.383	40.952	31.194	41.266	2.995	1.71	0.42			
Rayleigh test of uniformity (p)	< 1E-12	< 1E-12	< 1E-12	< 1E-12	< 1E-12	< 1E-12						
Tillandsia plumosa												
Number of Observations	47	8	20	24	17	11	69	68	45	18	6	4
Mean Vector (μ)	139.409°	90°	45°	236.145°	137.505°	108.902°	2.789°	301.844°	275.867°	131.772°	144.896°	60°
Length of Mean Vector (r)	0.802	1	0.966	0.93	0.952	0.945	0.596	0.228	0.297	0.953	0.937	1
Rayleigh test of uniformity(Z)	30.232	8	18.66	20.737	15.395	9.815	24.483	3.549	3.969	16.35	5.265	4
Rayleigh test of uniformity (p)	< 1E-12	< 1E-12	2.12E-08	3.20E-09	2.23E-07	< 1E-12				1.15E-07	0.001	0.007
Oncidium brachyandrum												
Number of Observations	58		29	40		13	204		88	22		12
Mean Vector (μ)	110.139°		105.529°	154.265°		147.774°	311.088°		332.807°	121.31°		124.985°
Length of Mean Vector (r)	0.956		0.966	0.963		0.99	0.195		0.108	0.994		0.959
Rayleigh test of uniformity(Z)	53.051		27.06	37.124		12.753	7.724		1.02	21.744		11.035
Rayleigh test of uniformity (p)	< 1E-12		1.64E-11	< 1E-12		13E-6				1.94E-09		9.61E-07
Alamania punicea												
Number of Observations	100		99	43		43	53		81	10		21
Mean Vector (μ)	105.543°		104.803°	148.625°		147.945°	305.981°		287.243°	110.867°		92.761°
Length of Mean Vector (r)	0.947		0.963	0.969		0.973	0.139		0.201	0.945		0.988
Rayleigh test of uniformity(Z)	89.615		91.87	40.386		40.675	1.025		3.278	8.93		20.515
Rayleigh test of uniformity (p)	< 1E-12		< 1E-12	< 1E-12		< 1E-12				< 1E-12		5.29E-09

e) Factors explaining phenology of epiphyte species on different phorophyte species

Tillandsia prodigiosa: the GALMSS showed that different microclimatic factors affect the phenology of epiphytes on different host tree species. For example, IF in *Q. martinezii* and *Q. castanea* was influenced by mean temperatures (Tmean; when above 14 °C) while in *Q. rugosa* was by relative humidity (RH; when above 75 %). In *Q. martinezii*, FLO was affected by Tmean (when inferior or to 14 °C), in *Q. castanea* by canopy openness (CO; when inferior to 35%), and *Q. rugosa* by minimum temperatures (Tmin; when inferior to 9.5 °C). FRU was influenced Tmean (when above 14 °C) in all phorophyte species. In *Q. martinezii*, SD was influenced by Tmin (when inferior or to 9.5 °C), in *Q. castanea* by canopy openness (CO; when inferior to 35%), and in *Q. rugosa* by Tmean (when inferior to 9.5 °C) (Supplement 2).

Tillandsia plumosa: IF was influenced mainly by Tmean (when above 14 °C) in *Q. martinezii* and *Q. castanea*, while in *Q. rugosa* was by Tmin (when inferior or to 9.5 °C). In *Q. martinezii*, primarily explained mostly by CO (when above 35%) and *Q. castanea* and *Q. rugosa* by Tmin (superior and inferior to 9.5°C, respectively). In *Q. martinezii*, FRU was primarily influenced by CO (when inferior to 33 %), Tmin in *Q. castanea* (when inferior or to 9.5 °C), and RH in *Q. rugosa* (when above 75 %). Any factor in any host tree showed a significant effect on SD (Supplement 3).

Alamania punicea: in both host tree species, IF and FLO were primarily influenced by Tmin. FRU was only related to canopy openness in *Q. rugosa* (when inferior to 35%), and in *Q. martinezii*, any of the variables showed a significant effect on this phenophase. In *Q. martinezii*, SD was only explained by CO (when above 35%) and in *Q. rugosa* by Tmin (when inferior to 9.5 °C) and HR (when inferior to 75%) (Supplement 4).

Oncidium brachyandrum: in *Q. rugosa*, IF and FLO were influenced for all variables, but in *Q. martinezii* only CO (when above 35%) and Tmin (when inferior or to 9.5 °C) were significant. FRU and SD in all phorophyte species were influenced by CO (when above 35%). Other variables were not important (Supplement 5).

Discussion

We can separate into two groups of factors: group one, where the effect of the host tree species was not detected (frequency)) and group two, where the host tree effect was seen (start date, peak date, duration, and seasonality). We will discuss each group separately.

a) Group one

We could not observe any effect of host tree species on the frequency since all phenophases were annuals, except for FRU that took more than 9 months. The annual frequency pattern is typical for vascular epiphytes (Ramírez-Martínez et al., 2021) growing in forests with a marked seasonality (Sakai, 2001) as our study site. Also, this pattern is usual across other lifeforms such as trees, herbs, and shrubs growing in this kind of ecosystem (Fenner, 2012; Freitas et al., 2013; Stevenson et al., 2008; Williams-Linera & Meave, 2002). For epiphytes, seasonality and annual frequency have been reported in Bromeliaceae (Canela & Sazima, 2003), Orchidaceae (Nunes et al., 2016; Texier et al., 2018), Cactaceae (Marques et al., 2004), Gesneriaceae (Buzato et al., 2000; Sazima et al., 1995) and Piperaceae families (Cascante-Marín et al., 2017).

Usually, the reproductive phenological events are restricted to specific periods where the resources needed for reproductive structures formation are available and/or when herbivores are not active or when the presence of pollinators can increase the fitness of plants (Ackerman, 1983). For example, in this study, inflorescence formation and flowering patterns differed for *T. prodigiosa* compared with the other three epiphyte species. The construction of reproductive structures for *T. prodigiosa* matches the rainy season, so they start to form inflorescences when water is available; this gives this species the possibility to assign resources to shoot production and inflorescences development. In the case of orchid species, probably their pseudobulbs which function as store water and nutrients, make it possible to form inflorescences and flowers during the dry season, while some resources obtained during the wet season are probably assigned to their vegetative growth, and the remaining are stored for the next reproductive season. *Tillandsia plumosa* inflorescence formation and flowering patterns resemble more orchid species than their more related *T. prodigiosa*. *Tillandsia plumosa* probably depends more on atmospheric resources of water and nutrients (as other atmospheric species; (Benzing, [1990]) and perhaps dew deposition is higher during the dry season, similar to reports from other seasonal forests (Cervantes et al., 2005). Flowering time differences across these epiphyte species also could be influenced 1) by biotic factors like competence for pollinators with other life forms (*e.g.*, herbaceous and trees) this may be the case for *T. prodigiosa* that hummingbirds probably pollinate; 2) matching the time of flowering with the time when most tree species are leafless, could benefit flower display to pollinators, and 3) matching flowering time with the presence of pollinators. For example, It has been reported that for some forests, hummingbird diversity is higher during the dry season, while insects (possible pollinators of orchid species) are more abundant during the rainy season (Ramírez-Martínez et al., 2021).

On the other hand, seed dispersal of all epiphyte species started at the end of the dry season, likely due to their anemochory seed dispersal mode. This has two advantages 1) seeds could disperse longer distances since most host tree species are leafless at that time and perhaps wind speed is faster, and 2) seeds may be ready before the rainy seasons starts (Augspurger, 1983; -García-Franco & Rico-Gray, 1991; Mondragon & Calvo-Irabien, 2006)

b) Group two

The beginning of a phenophases is determined by abiotic factors, as temperature, rainfall, and photoperiod, across others (Peñuelas et al., 2004; Polgar & Primack, 2011; Ramírez-Martínez et al., 2021), together with the nutritional status of the individuals and linked with the availability of nutrients of the site where they grow (Primak 1987, Fenner 1994). So, variations on those factors promote variations in the phenology of individuals (Williams-Linera & Meave 2002). In our study, we observed variation for the start date, the peak, the duration, and the seasonality of all phenophases, probably as a result of variation of the microclimatic conditions even when according to our measures in chapter II, there are no statistical differences. But for plants, maybe those differences are enough, together whit variation in the availability of nutrients present across the host tree species of our study (greater concentrations of phosphorus and potassium in *Q. martinezii* and *Q. rugosa* see chapter II).

We observed that most of the time, individuals growing on *Q. rugosa* started early all the phenophases. This could be the result of a combination of characteristics of *Q. rugosa*: as the nutrient content of its runoffs (higher concentrations), water retention capacity of its barks (higher capacity, for orchids whose root systems, are functional, this may be important), and opening of the canopy (smaller than in the other *Quercus* species, that even where not are statistical different present smaller values that the other species in period 1, across other traits that we don´t evaluate.

Even when we observed the general effects of the host trees on those AI parameters, it is important to notice that they don´t act the same way on different epiphyte species and phenophases. So, contrary to our expectation, it seemed that on *T. prodigiosa* and *T. plumosa*, there is the strongest effect of host tree identity. We were not expecting that since bromeliads depend most on wet and dry depositions because their roots are not functional. Instead, orchids are more dependent on host trees since their roots absorb water and nutrients diluted in host trees stemflows (Cardelús et al., 2009; Cardelus & Mack, 2010; Liu et al., 2002; Marler, 2018). Even when we can´t explain why bromeliad varies more than orchids, we can speculate that individuals that were growing on *Q. rugosa* start and peak early than individuals growing of *Q. martinezii* or *Q. castanea*, due to a variation in the nutrition status of the individuals, and even when *T. plumosa* don´t absorb the nutrient of foliar and cortical runoff by its roots, it absorbed the nutrients by its trichomes of those sources. At the same time, prodigiosa receive part of those runoffs in its tanks, and also receive the leaf litter of these species (that probably, possess more nutrients, but need to be tested).

In addition to the nutritional aspect, it was observed that the microclimatic factors have different effects on the phenology of epiphytes, and their impact vary over time. So, we observed that the host tree effect on phenophases and species showed interannual differences. That supports the idea that trees are dynamic entities with traits (e.g., tree architecture, phenology, bark features, etc.) that can vary in space and time. These changes modify the habitat conditions for epiphytic plants (Callaway et al., 2002; Wagner et al., 2015; Rasmussen & Rasmussen, 2018). While this effect has not been measured on phenology itself, it has been tested that different microhabitats cause variation in the growth, reproductive potential, and flower production of vascular epiphytes (Cervantes et al., 2005; de la Rosa-Manzano et al., 2014; Einzmann et al., 2015; Petter et al., 2016). For instance, Ticktin et al. (2016) showed that host tree effect on different demographic parameters (*e.g.*, growth and reproduction) of populations of atmospheric bromeliad *Tillandsia macdougalli* differed across years depending on the amount of rainfall since perennial host trees acted as buffers in dryer conditions contrary to deciduous trees. That demonstrates that variations in weather from year to year, changes in phorophyte traits, and pollinator abundance (not measured in Ticktin et al. 2016) may result in inconsistent selective pressures on phenophases, especially flowering times, favoring early, average or late individuals in different years, those variations of micro-niches could promote variations for start date and duration of the individuals, which is reflected in the variation of seasonality values of individuals growing on the different host trees, as was our case.

Talking specifically about the microclimatic variations between host tree species, our model indicated that the microenvironment could have different effects on epiphyte species and phenophases. It is known that an increase in solar radiation combined with a decrease in minimum temperature is environmental cues that have been demonstrated to affect the floral phenology of *Werauhia sintenisii* (Baker) J.R. Grant (an epiphytic bromeliad growing in a cloud forest,[Lasso & Ackerman, 2003]). In this study, possibly the same factors affect *T. prodigiosa* individuals growing on *Q. castanea* trees since canopy openness and Tmin significative effect on FLO. For *T. plumosa* Tmin (below 9.5 °C) had a significant impact on individuals growing in *Q. castanea* and *Q. rugosa*. A similar pattern was found for atmospheric bromeliad *Tillandsia usneoides,* where minimum temperatures under 5°C were reported to affect flowering (Barve et al., 2015). Fruiting for *T. prodigiosa* in all phorophyte species and *T. plumosa* on *Q. castanea* and *Q. martinezii* seem to depend less critically on RH, as reported by Barve et al. (2015).

The effect of environmental factors on the phenology of epiphytic orchid species has not been explored. But it is known that for terrestrial orchids, temperature triggers flowering. For example, the flowering of some species of *Phalaenopsis* Blume is favored by low ambient temperatures, generally below 26 ° C (Blanchard & Runkle, 2006); and it can be reversed if the ambient temperature rises. *Dendrobium* flowering activity is also favored by low ambient temperatures (Campos & Kerbauy, 2004). The flowering of *Miltoniopsis* and *Zygopetalum* are favored by temperatures of 11 to 14 ° C (Lopez & Runkle, 2006). For *Oncidium,* the change in ambient temperature improves or is neutral to its flowering activity (Wang et al., 2019). In our case temperature especially, minimum temperature was the variable that most influenced the behavior of the phenophases.

Conclusions

There is an effect of the host on the phenology of vascular epiphytes, and this differs across epiphytic species, and phenophases, and AI parameters. For bromeliad species, the inflorescence formation phenophase seems to be more sensitive to the host effect. Orchid species were less affected probably because the study only included two host tree species, so a bigger sample size is needed to make better conclusions. Microenvironmental conditions within host tree canopies showed a slight effect on epiphyte phenology. Although other biotic factors also could have an impact, more detailed experiments are needed.

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Miscellaneous papers

At the beginning of the project, one of our goals was to test the host tree effect on orchids, bromeliads, ferns, and one *Echeveria* species. However, the sample size for ferns and *Echeveria* was small, so we decided to exclude those species from all sections above. But with the few data collected, we write a scientific note for the *Echeveria* species because to date, there is little information about species of this genera.

Ramírez Martínez, A., & Mondragón Chaparro, D. Fenología y estado poblacional de *Echeveria nodulosa* en un bosque estacional en Oaxaca. *Contribución al Conocimiento Científico y Tecnológico de Oaxaca*, 5 (5), 40-49.

Additionally, to divulge information about epiphyte phenology, we write a popular science paper.

Ramírez Martínez, A., & Mondragón Chaparro, D. La fenología de bromelias y orquídeas epífitas en un bosque de encino estacional. *Desde el herbario CICY*, 12: 1-5.

We attached both papers below.

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Artículo

Fenología y estado poblacional de *Echeveria nodulosa* en un bosque estacional en Oaxaca

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Resumen

Conocer aspectos básicos de la ecología de una especie es fundamental para su conservación, por ello, evaluamos la fenología reproductiva y el estado de la población de *Echeveria nodulosa,* especie endémica de México y con valor ornamental, en un bosque de encino en Oaxaca. En enero de 2018, se marcaron siete individuos epífitos adultos y se monitorearon mensualmente hasta diciembre de 2020, las fenofases analizadas fueron formación de inflorescencia, floración, fructificación y liberación de semillas, se determinó fecha de inicio, fecha máxima actividad, frecuencia y duración. Para las estructuras poblacionales se marcaron los individuos presentes durante 2018 y 2019, los cuales se clasificaron en categorías de tamaño y se determinó el tipo de estructura. La formación de inflorescencias comenzó en julio, con un máximo de actividad en agosto; la floración en septiembre con un máximo de actividad en octubre, la formación y maduración de los frutos fue de diciembre a marzo y en este último mes también se comenzaron a liberar las primeras semillas con una máxima actividad en abril.

Todas las fenofases fueron anuales con duración intermedia. Durante 2018 se encontraron 23 individuos, que presentaron una estructura poblacional tipo I (principalmente plántulas e infantiles), en tanto que en 2019 se encontraron 10 individuos con una estructura tipo II (principalmente juveniles y adultos), al parecer como resultado de variación interanual de la precipitación. Si bien nuestro estudio amplió el conocimiento de la ecología de esta especie, es necesario realizar estudios para entender más profundamente, los mecanismos que regulan su fenología y demografía.

Palabra clave: Crassulaceae; ciclo de vida; epífita facultativa; planta suculenta

Abstract

Knowledge on the basic aspects of the ecology of a species is fundamental for its conservation. Therefore, we evaluated the reproductive phenology and the structure of a population of *Echeveria nodulosa,* an endemic to México species with ornamental value, in an oak forest in Oaxaca. In January 2018, we marked seven epiphytic adult individuals and monitored them monthly through December 2020. The phenophases we analyzed included inflorescence formation, flowering, fruiting and seed liberation. For each phase we recorded onset and maximum activity dates, frequency, and duration. To analyze population structure, we marked all individuals present during 2018 and 2019, classifying them by size and determining the populations' structure types, depending on the distribution of size-classes. Inflorescence formation began on July, with a maximum activity in August; flowering began on September with a maximum activity in October; fruit formation and maturation occurred from December to March; and the first dispersing seeds were observed in March with a maximum activity in April. All phenophases had annual cycles with intermediate durations. During 2018 we found 23 individuals conforming a type I population structure (dominated by premature phases: seedlings and infants), while in 2019 we only found 10 individuals corresponding to a type II structure (dominated by intermedium and late phases: juvenile and adults), possibly as a result of inter-annual variation in precipitation patterns. Although our study broadened our knowledge on the biology of this species, further research is needed for in-depth understanding of the mechanisms regulating the phenology and demography of *E. nodulosa*.

Key Words: Crassulaceae; facultative epiphyte; life cycle, succulent

Introducción

El género *Echeveria*, (Crassulaceae), es endémico de América y se distribuye desde Texas hasta Argentina. México es el centro de su diversidad con 127 especies, de las cuales el 83% son endémicas, en donde el estado de Oaxaca es el más diverso (47 spp.) (Reyes-Santiago et al., 2011). Este género se caracteriza por incluir plantas herbáceas, suculentas, acaules, con hojas dispuestas en forma de roseta, con inflorescencias laterales. Poco se sabe de su biología reproductiva, pero se ha reportado que ciertas especies son auto incompatibles (Rodríguez-Rojas et al., 2015), mientras que otras no lo son (Álvarez-Álvarez et al., 2021; Parra et al., 1993); en cuestión de polinizadores, si bien la entomofilia es común en la familia, en el género se ha reportado la polinización por colibríes (Parra et al., 1993); la propagación asexual es común en el género (Reyes-Santiago et al., 2011; Ult, 1992). Crecen mayormente como saxicolas, aunque también se reportan como terrestres o epífitas y se les puede encontrar en bosques de pino, encino, matorrales xerofitos y ocasionalmente en selvas bajas caducifolias (Reyes-Santiago et al., 2011).

Dada la belleza de su morfología, las especies de este género son altamente apreciadas por horticultores y coleccionistas (Ortiz-Oliveros et al., 2021; Reyes-Santiago et al., 2011), lo que ha provocado que individuos, principalmente en la fase adulta, sean extraídos ilegalmente de sus hábitats naturales para su venta (Reyes-Santiago et al., 2011), esto, aunado con la pérdida de su hábitat ha puesto en peligro a 7 especies y 7 variedades (Álvarez-Álvarez et al., 2021; Secretaria del Medio Ambiente y Recursos Naturales [SEMARNAT], 2010). Es por ello, que es importante desarrollar planes de manejo y conservación para estas especies, para lo cual se requiere conocer aspectos básicos de la biología de estas, como son aspectos de su fenología y su demografía. Desafortunadamente, existe muy poca información sobre estos aspectos, y en general sobre la biología de estas especies (Álvarez-Álvarez et al., 2021; Reyes-Santiago et al., 2011).

La fenología de plantas es el estudio de los eventos recurrentes (*e.g*. caída y brote de hojas, floración, fructificación y dehiscencia de frutos, etc.) dentro del ciclo de vida de estas y las causas de su ocurrencia, que pueden ser factores bióticos (*e.g.* interacción con polinizadores, dispersores, herbívoros, etc.), abióticos (*e.g*. variaciones en temperatura, precipitación, fotoperiodo, etc.) y filogenéticos (Lieth, 1974).

Conocer la fenología de las especies es importante para implementar estrategias de manejo y conservación de las especies, ya que con dicho conocimiento es posible, entre otras cosas, planear la conservación *ex situ* (como colectas de germoplasma), conocer la vulnerabilidad de las especies ante cambios climáticos y relacionarla con la presencia de competidores y depredadores, entre otros (Morellato et al., 2016; Peng et al. 2021).

Otro aspecto importante para comenzar a definir estrategias de conservación de una especie es el conocimiento del estado de sus poblaciones y poder reconocer los estadios más vulnerables dentro de su ciclo de vida; una forma rápida de obtener dicha información es a través de la determinación de sus estructuras poblacionales (Landi y Angiolini, 2011; Nurfadilan, 2020).

Las estructuras poblacionales son como una fotografía que muestran el estado actual de una población, a partir de la cual se pueden hacer inferencias de la magnitud de ciertos procesos demográficos, como la supervivencia, mortalidad y natalidad. Sin embargo, es importante considerar que si bien las estructuras brindan una idea bastante adecuada del estado actual de la población, este resultado es estático y brinda poca información del estado futuro de las mismas, por lo que es importante reforzarlas con estudios de dinámica poblacional a largo plazo.

El conocer el estado de las poblaciones, es crucial para aquellas especies en alguna categoría de riesgo o endémicas (Kienberg y Becker, 2017) o que están siendo aprovechadas, como es el caso de *Echeveria nodulosa* Baker Ed. Otto.

Esta especie es ampliamente utilizada como planta ornamental y se vende tanto en mercados nacionales como internacionales. A pesar de que su propagación por esquejes es fácil, individuos adultos de poblaciones silvestres son colectados para su venta, poniendo en riesgo sus poblaciones.

Por lo que, en este estudio exploramos la fenología y la estructura poblacional de *E. nodulosa*, una especie epífita facultativa (que puede crecer sobre otras plantas (epífita) o en el suelo (terrestre) en un bosque de encino estacional en la mixteca Oaxaqueña, con la finalidad de obtener información relevante que pueda ser utilizada en un futuro, para el desarrollo de planes para su conservación y aprovechamiento sostenible.

Materiales y Métodos

Sitio de estudio

El estudio se realizó en un bosque de encino con régimen de lluvias estacional, en la localidad de Santo Domingo, Yanhuitlán, Oaxaca (Figura 1). Este sitio se encuentra dentro del

Geoparque Global Mixteca alta, a 2577 m.s.n.m (Organización de las Naciones Unidas para la Educación, la Ciencia y la Cultura [UNESCO], 2017). La precipitación anual acumulada es de 804 mm con un promedio mensual de 67.02 ± 68.67 mm, con máximos en los meses de junio y septiembre; la temporada de sequía comprende de octubre a abril. La temperatura media es de 14.36 ± 1.34 ° C, el promedio de las máximas de 23.27 ± 1.75 ° C y el de mínimas de 7.02 ± 2.87° C (Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias [INIFAP], 2020).

La vegetación arbórea esta predominada *Quercus candicans* Neé, *Q. castanea* Neé, *Q. crasifolia* Humb. & Bonpl., *Q. rugosa* Neé, *Juniperus fláccida* Schltdl., *Arbutus xalapensis* Kunth y manchones de pinos (comúnmente introducidos por los programas de reforestación).

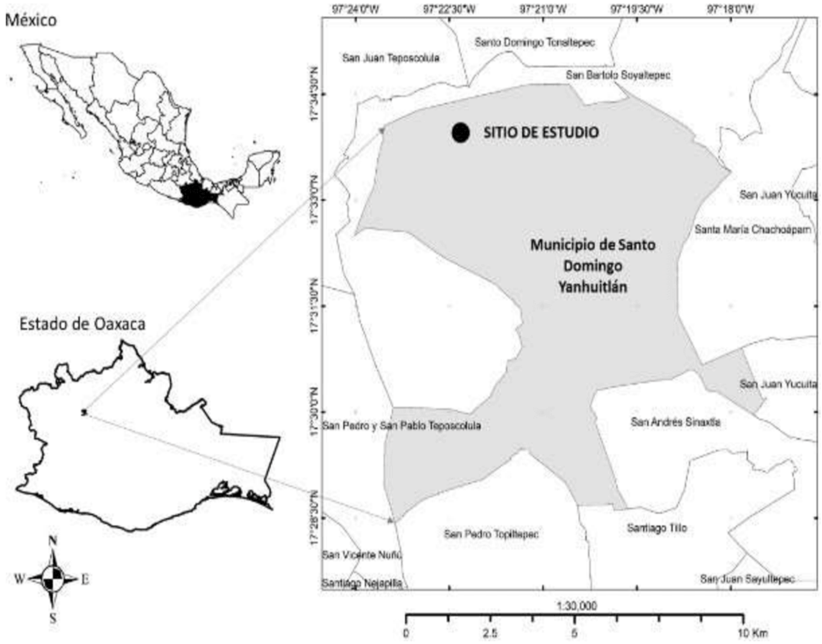


Figura 1. Localización del sitio dentro del municipio de Yanhuitlán, Oaxaca.

La flora epífita está representada por *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 & A.F.Tryon, *Polypodium martensii* Mett., *Oncidium brachyandrum* Lindl. y *Alamania punicea* Lex. in La Llave & Lex.

Especie de estudio

Echeveria nodulosa es una planta herbácea perenne con hojas verdes (en ocasiones con máculas rojas) suculentas, simples, enteras, obovadas-cuneadas y filotaxia espiralada. Su inflorescencia es lateral y axilar compuesta por un tallo floral o pedúnculo que sostiene a las flores y brácteas en forma de racimo. Las flores de color naranja se arreglan en espiral a lo largo del pedúnculo, cada una sobre el pedicelo que se encuentra en la axila de una bráctea.

Los pedicelos llevan dos bractéolas (Figura 2). Esta especie probablemente es polinizada por colibríes, ya que fueron observados visitando estas plantas (obs. per)

En el área de estudio se encuentra creciendo tanto como terrestre como de forma epífita. Para este estudio, que formó parte de un estudio mayor sobre el efecto de los árboles hospederos en la demografía y fenología de epífitas vasculares (Ramírez-Martínez, 2021), se utilizaron individuos epífitos de *E. nodulosa*. Cabe mencionar que del total de árboles hospederos muestreados en el proyecto antes mencionado (21 árboles de *Quercus martinezii* C.H. Muller, 17 de *Q. rugosa* Née y 47 de *Q. castanea* Née), *E. nodulosa* solamente se encontró creciendo sobre cuatro árboles de *Q. martinezii* y un árbol *Q. rugosa.*

Metodología

Para seguir la fenología reproductiva, que comprende las fenofases de floración, fructificación y liberación de semillas, se marcaron siete individuos adultos de *E. nodulosa* (todos los presentes en el área de estudio), con etiquetas de plástico y se monitorearon mensualmente de enero de 2018 a diciembre de 2020. Con los datos recabados se estimaron:

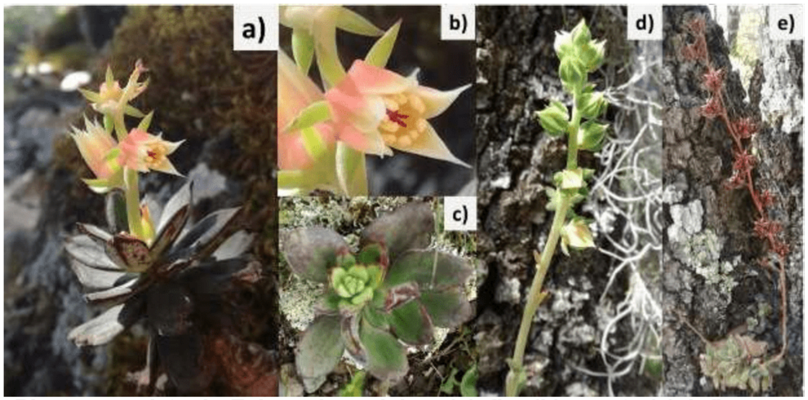


Figura 2. Planta completa de *Echeveria nodulosa* (a), flor (b), roseta (c), inflorescencia (d) y frutos abiertos (e).

- Tiempo de ocurrencia: esto incluye el mes de inicio y el mes de máxima actividad de cada fenofase.
- Frecuencia: se adaptó la propuesta de Newstrom et al. (1994) y cada evento fenológico se clasificó como continua (siempre reproductiva con ninguna o pocas interrupciones breves hasta 2 meses entre muchos episodios reproductivos), anual (solo un ciclo mayor por año, 1-9 meses de fase reproductiva), o subanual (más de un evento por año separados por intervalos de 2 meses o más entre episodios reproductivos).
- Duración: cuando una fenofase mostraba un patrón anual, se clasificó en breve (<1 mes), intermedia (2-5 meses) o prolongada (> 5 meses).

Para poder determinar la estructura poblacional de *E. nodulosa*, en 2018 se midieron todos los individuos, creciendo sobre los mismos árboles que los individuos adultos estudiados en la parte fenológica, a los que se les midió el ancho y alto de las rosetas, dicho procedimiento se repitió en 2019; posteriormente, se calculó el área de cada una de ellas con la fórmula de un círculo y se establecieron cuatro categorías de tamaño. Las plántulas (p) tenían rosetas de 0.03 a 0.3 cm^2, los infantiles (i) de 0.31 a 4 cm, juveniles (j) de 4.1 a 12.6 cm^2 y los adultos (a) de más de 12.6 cm^2. Finalmente, se clasificó la estructura poblacional de acuerdo con lo propuesto por Landi y Angiolini (2011):

- Estructuras tipo I o dinámicas: la estructura está dominada por una alta proporción de individuos en las etapas tempranas (plántulas e infantiles), y sugiere que las poblaciones están creciendo.
- Estructuras tipo II o estables: se observa una mayor proporción de individuos de etapas intermedias (juveniles) y tardías (adultos), lo que sugiere que las poblaciones están estables.
- Estructuras tipo III o senescentes: las cuales están dominadas por individuos adultos y no existe evidencia alguna de reclutamiento activo, lo que sugiere que la población está decreciendo.

Resultados

Fenología

La formación de inflorescencias comenzó en julio, con una máxima actividad en agosto, la frecuencia de esta fenofase fue clasificada como anual, con una duración intermedia (4 meses). La floración comenzó en septiembre, con una máxima actividad en octubre, tuvo una frecuencia anual y duración intermedia de 3 meses.

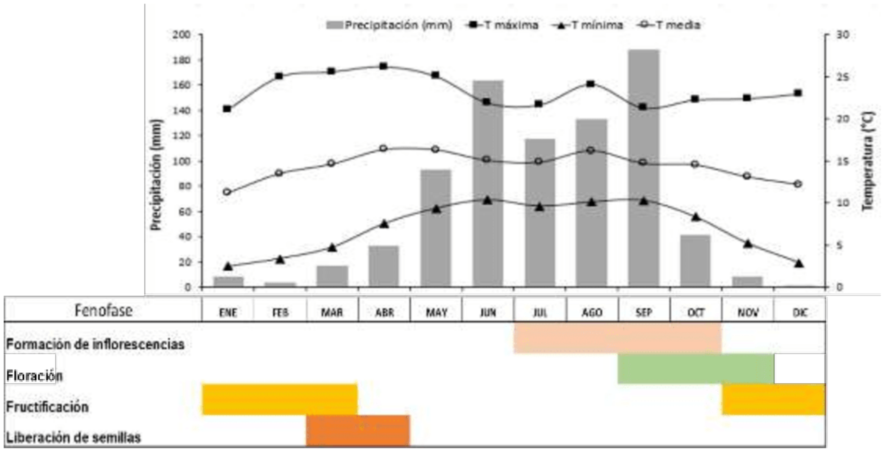
La formación y maduración de las cápsulas se dio de diciembre a marzo y en este último mes también se comenzaron a liberar las primeras semillas con una máxima actividad en abril, ambas fenofases fueron anuales con duración intermedia (Figura 3).

Estado poblacional

En 2018 se encontraron 23 individuos (8 p, 14 i, 1 j, 1 a), los cuales presentaron una estructura dominada por individuos de etapas tempranas, por lo que se clasificó como dinámica o tipo I (Figura 4); en tanto que en 2019 solamente se encontraron 10 individuos (0 p, 4 i, 4 j, 2 a), con una preponderancia de individuos en etapas intermedias y tardías, por lo que la estructura se clasificó como estable o tipo II.

Discusión

La formación de inflorescencias de *E. nodulosa* en este sitio coincide con la temporada de lluvias, posiblemente esto les permite a las plantas producir biomasa y al mismo tiempo asignar recursos (agua y nutrientes) para reproducción. La floración comenzó a finales de la temporada de lluvias a diferencia de otras especies de epífitas que lo hacen al inicio (Ramírez-Martínez y Mondragón, 2020) y otras herbáceas terrestres que florecen a mediados de la misma. Esto podría evitar que *E. Nodulosa* compita con estas especies, ya que algunas también son visitadas por colibríes (Ruíz-Contreras, 2019). La liberación de semillas de *E. nodulosa* es durante la estación seca, en esta temporada la baja humedad presente puede favorecer la deshidratación de sus frutos foliculares y la liberación de las semillas justo antes del inicio de la estación de lluvias (Cortés-Flores et al., 2017).



Fenofase	ENE	FEB	MAR	ABR	MAY	JUN	JUL	AGO	SEP	OCT	NOV	DIC
Formación de inflorescencias							■	■	■	■		
Floración									■	■	■	
Fructificación	■	■	■								■	■
Liberación de semillas			■	■								

Figura 3. Climograma de Santo Domingo Yanhuitlán Oaxaca, en la parte superior; y calendario fenológico de *Echeveria nodulosa*, en la parte inferior

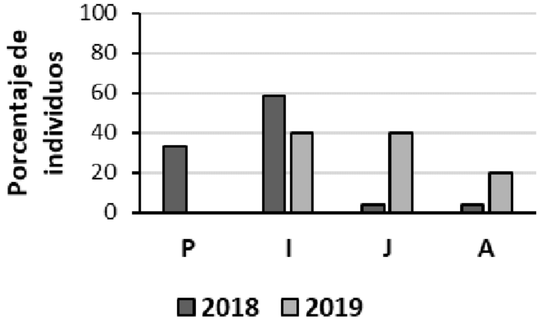


Figura 4. Estructura de una población de *Echeveria nodulosa* en Yanhuitlán, Oaxaca.

La interpretación del estado general de la población evaluada a través de las estructuras poblacionales de *E. nodulosa*, debe ser tomada con precaución. Primero, porque las estructuras muestran el estado de la población en un momento dado (como vimos en 2018 era tipo I y en 2019 tipo II) y debido al error asociado al bajo tamaño muestral (aunque eran todos los individuos epífitos presentes en la zona de estudio). Teniendo eso en consideración podemos decir que existe variación interanual en las estructuras poblacionales de *E. nodulosa*, resultado de que durante 2018 se encontró un número significativo de plántulas (8) e infantiles (14), cosa que en 2019 no. Esto pudiera ser el resultado de que durante 2017 se presentó una mayor precipitación, permitiendo la germinación de las semillas y la formación y sobrevivencia de plántulas, que fueron las que censamos en enero de 2018, ya que se sabe que la disponibilidad de agua es clave en estos estadios de vida de las epífitas (Mondragón et al., 2015).

Por otra parte 2018 fue uno de los años más secos reportados en la zona, lo que no permitió el reclutamiento y favoreció la mortalidad de individuos, ya que como se ha reportado para epífitas la falta de agua es una de las principales causas de muerte de los estadios prematuros (Mondragón et al., 2015). La presencia de años con alto reclutamiento de plántulas, resultado del incremento en la precipitación, ya ha sido reportado anteriormente para otras epífitas (Mondragón et al., 2004).

Conclusión

Nuestros resultados aportan información básica de la biología de *E. nodulosa*, especie muy poco estudiada, planteando la necesidad de realizar estudios más específicos para evaluar el efecto de la disponibilidad de agua y la competencia por polinizadores como modeladores de la fenología floral de esta especie, así como la necesidad de realizar estudios de dinámica poblacional a largo plazo, tanto de individuos epífitos como terrestres, para tener un mejor entendimiento del estado de la población, y de los factores bióticos y abióticos que lo regulan.

Agradecimientos

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La fenología de bromelias y orquídeas epífitas en un bosque de encino estacional

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La fenología de bromelias y orquídeas epífitas ha sido poco estudiada a pesar de las diferentes aplicaciones de esta disciplina. Aquí presentamos información sobre la fenología reproductiva de cuatro especies de epífitas vasculares, en un bosque de encino estacional en el estado de Oaxaca y enfatizamos que hay un campo extenso de estudio con potencial para futuras líneas de investigación.

Palabras clave: Dispersión de semillas, epífitas vasculares, floración, Oaxaca, México.

Las epífitas, plantas que crecen sobre otras plantas (Benzing 1990), representan cerca del 10 % de la flora vascular, con 27,614 especies, las cuales se encuentran distribuidas en una variedad de ecosistemas. Sus funciones ecológicas que van desde ser fuente de alimento, agua y refugio para vertebrados e invertebrados, hasta ser eslabones en el ciclo del agua y de los nutrientes (Zotz 2013).

Los estudios sobre la ecología de epífitas han sido enfocados, principal- mente, a estudiar su abundancia, su distribución y diferentes aspectos eco- fisiológicos, pero existen otros campos pocos explorados como su fenología. La fenología es el estudio de los eventos recurrentes (*e.g.* caída de hojas, floración, fructificación y dispersión) y las causas de su ocurrencia con respecto a factores abióticos (*e.g.* temperatura y precipitación) y bióticos (*e.g.* presencia de polinizadores y herbívoros; Lieth 1974).

El estudio de la fenología de plantas tiene diferentes aplicaciones de importancia para la conservación de las especies: fa- cilita el establecimiento de calendarios de colecta de germoplasma para la conser- vación *in situ* y *ex situ* de plantas; pro- porciona información sobre la producción de flores y frutos de especies en peligro de extinción, lo que permite realizar planes de conservación que consideran no sólo a las especies objetivo, sino también sus interacciones ecológicas (*e.g.* polini- zadores); provee información sobre los impactos del cambio climático sobre feno- logía, lo que ayuda a guiar acciones de mitigación e identificar grupos de plantas más vulnerables o resistentes a estos cambios, entre otras (Morellato *et al.* 2016).

Desafortunadamente, la fenología de epífitas vasculares ha sido pobremente estudiada (Morellato *et al.* 2010), incluso en la revisión más reciente de epífitas vasculares de Zotz (2016), no se incluye un capítulo sobre este tema. Actualmente solamente existen 35 estudios a nivel mundial que se enfocan específicamente a estudiar la fenología de diferentes especies epífitas, por lo que este campo presenta potencial para futuros estudios y líneas de inves- tigación.

Con el fin de contribuir al conocimiento de la fenología de este tipo de plantas, realizamos un estudio de dos orquídeas: *Oncidium brachyandrum* Lindl. y *Alamania punicea* Lex. y dos bromelias: *Tillandsia plumosa* Baker y *Tillandsia prodigiosa* (Lem.) Baker (Figura 1), en un bosque de encino a 2,145 m s.n.m. en la Mixteca oaxaqueña, que presenta una mar- cada estación seca (diciembre a abril). Para este estudio, marcamos individuos adultos de las cuatro especies y los revisamos mensualmente (enero a diciembre 2018), registrando floración y dispersión de semillas.

La floración de las dos especies de orquídeas duró dos meses y su tiempo de ocurrencia fue a finales de la estación seca en Abril y principios de la estación lluviosa en Mayo (Cuadro 1). El florecer durante dicho periodo confiere la ventaja de una mayor visibilidad de sus flores para los polinizadores, ya que los encinos pierden sus hojas. Los polinizadores de ambas especies son insectos, los cuales además alcanzan su mayor abundancia en secas (Zimermann *et al.* 1989).

En el caso de las dos especies de bromelias, solamente nos fue posible observar el inicio de la floración de *Tillandsia prodigiosa* que fue a finales de lluvias y principios de secas (Figura 2). A diferencia de las especies de orquídeas, esta especie es polinizada por colibríes, los cuales están presentes en el sitio durante todo el año (Ruíz-Contreras 2019). Florecer en la estación seca también le confiere una ventaja a *T. prodigiosa*, pues en esta estación no existe tanta competencia con hierbas que también son polinizadas por colibríes (Ramírez 2002). Además, *T. prodigiosa* es una bromelia tipo tanque que tiene la capacidad de almacenar agua y materia orgánica en su interior, por lo que tiene recursos de reserva para poder florecer incluso en la estación de mayor escasez de agua (Zotz 2016). La otra especie, *Tillandsia plumosa*, florece tanto en lluvias como en secas, y posiblemente por su naturaleza cleistógma (la flor no abre y se autopoliniza y autofecunda, Fran- kel y Galun 1977) su fenología de floración podría no estar limitada por la disponibilidad de polinizadores, sin embargo, esto tendría que probarse.

Las cuatro especies evaluadas dispersaron sus semillas a finales de secas y principios de lluvias. Para especies que se dispersan por viento, como las semillas tipo polvo de las orquídeas y las semillas tipo pluma de las bromelias (Benzing 1990), la estación seca es la óptima pues en esta época la mayoría de las especies de árboles hospederos pierden sus hojas y las semillas pueden moverse con mayor facilidad por el bosque. Por otro lado, dispersar antes de que

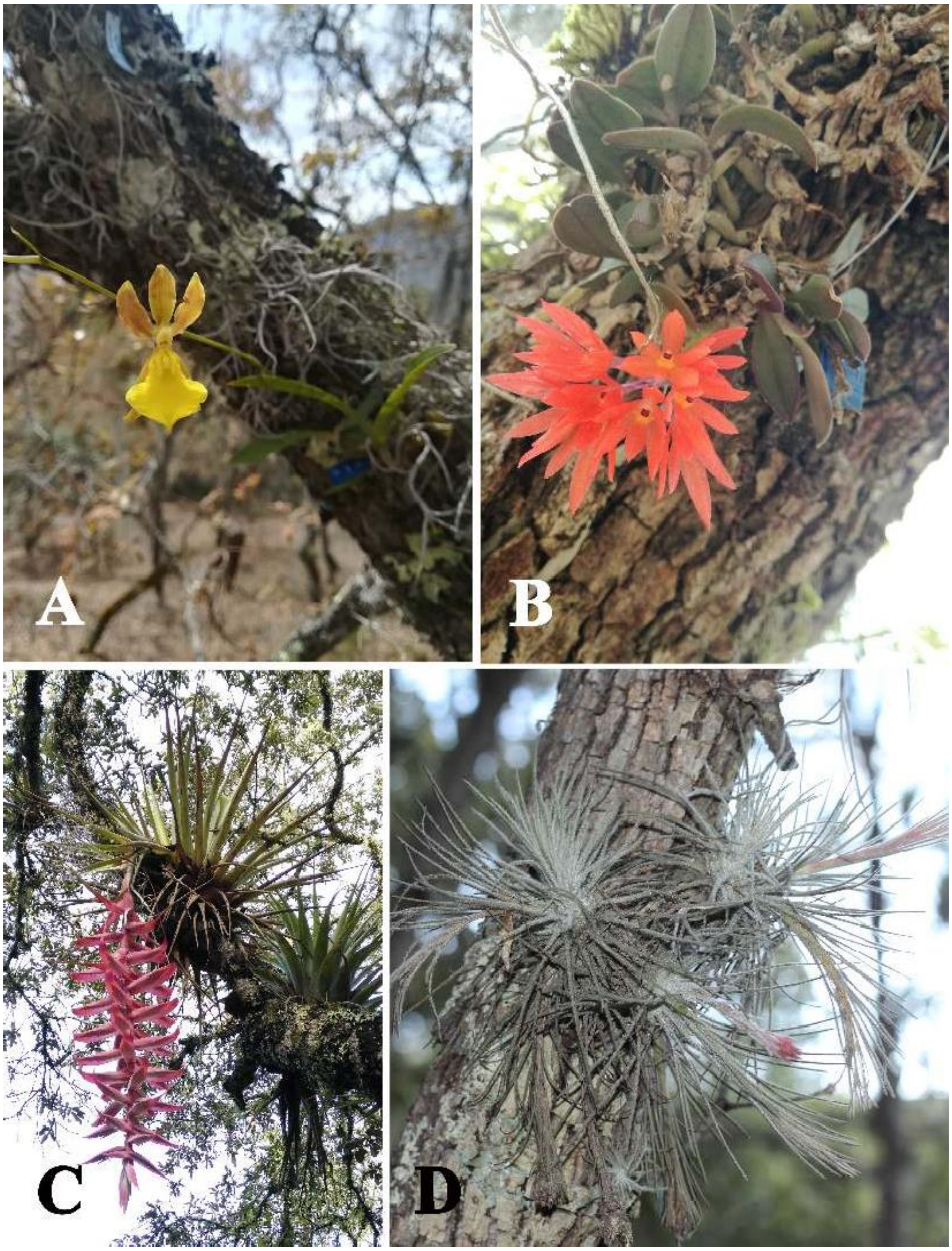
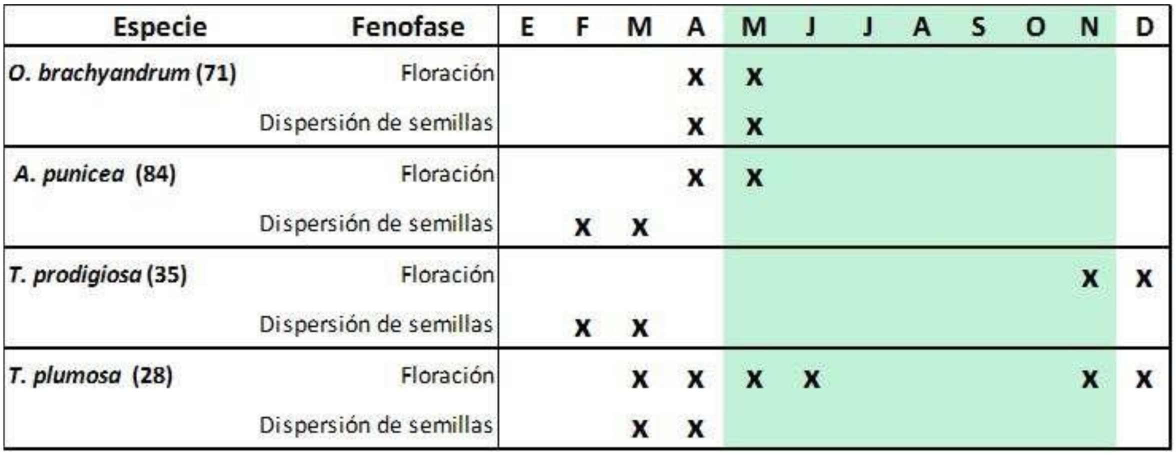


Figura 1. Especies de estudio. **A.** *Oncidiun bracyandrum*, **B.** *Alamania punicea*, **C.** *Tillandsia prodigiosa* y **D.** *Tillandsia plumosa* (Fotos: **A y B**. Adriana Ramírez- Martínez, **C y D**. Daniel Ruíz-Contreras).

Cuadro 1. Calendario fenológico de las cuatro especies de estudio. Entre paréntesis se encuentra en número de individuos monitoreados y la parte coloreada corresponde a la estación de lluvias.



Especie	Fenofase	E	F	M	A	M	J	J	A	S	O	N	D
O. brachyandrum (71)	Floración				X	X							
	Dispersión de semillas				X	X							
A. punicea (84)	Floración				X	X							
	Dispersión de semillas		X	X									
T. prodigiosa (35)	Floración											X	X
	Dispersión de semillas		X	X									
T. plumosa (28)	Floración			X	X	X	X					X	X
	Dispersión de semillas			X	X								

comiencen las lluvias intensas asegura que las semillas estén listas para recibir el agua y posteriormente comenzar su germinación (Mondragón *et al.* 2015).

Tanto la floración como la dispersión de semillas de las epífitas de un bosque de encino estacional de la Mixteca oaxaqueña están sincronizadas con la estación seca porque posiblemente existe una menor competencia por polinizadores, los vientos son más fuertes y la mayor parte de los árboles pierden sus hojas. Sin embargo, falta mucho por explorar para determinar los factores bióticos y abióticos relacionados con la fenología de estas y otras especies de epífitas. Los campos por explorar pueden incluir las similitudes o diferencias con otras formas de vida o entre especies de epífitas con diferentes historias de vida, el efecto de sus árboles hospederos, el efecto filogenético para ver si las especies emparentadas tienen fenologías similares, así como el papel de la fenología de epífitas en el ensamble de comunidades, entre otros aspectos.

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CHAPTER IV. HOST TREE EFFECT ON THE DEMOGRAPHY OF AN EPIPHYTIC BROMELIAD AND ORCHID SPECIES

Introduction

Vascular epiphytes comprise 10% of all global plant species (Zotz, 2013) and more than 25% of all tropical vascular plants (Nieder et al., 2001). They play important roles in the ecosystems since they increase the structural complexity of forests, change patterns of rainfall interception and atmospheric nutrient capture (Van Stan & Pypker, 2015; Hargis et al., 2019; Mendieta-Leiva et al., 2020); also they facilitate food, water, and shelter to several species of insects, birds, reptiles, mammals, across others (Boechat et al., 2019; Borst et al., 2019; Seidl et al., 2020).

Epiphytes have a tight relationship with their host trees. However, not all host tree species have the same traits (*e.g.,* bark type, growth form, the foliage density, size, etc.) and do not offer the same probabilities of seed capture, establishment, growth, and reproduction for epiphyte populations. Some traits related to epiphyte demographic rates are physical and chemical bark traits. For example, trees with rugose barks with high water absorption capacities and no secondary metabolites production could enhance fecundity and survival rates due those characteristics enhance epiphyte seed capture and germination and seedling survival (Callaway et al., 2002; López-Villalobos et al., 2008; Harshani et al., 2014). Also, trees with higher bark exfoliation and branch fall rates increase the mortality rate since they allow epiphyte dislodgment from host trees. Other traits, like the chemical composition of throughfalls and stemflows (primary nutrient sources for vascular epiphytes) and deciduousness intensity, could affect the growth and fecundity of the individuals (Benzing, 1990; Cervantes et al., 2005). So, tree features could have a direct effect on the demographic rates of vascular epiphytes and may influence long-term population growth rates (Ticktin et al., 2016).

Unfortunately, few studies have explored the effects of host trees on the complete demographic behavior of vascular epiphytes; the only research that has approached is Ticktin et al. (2016), who tested the demographic variation on individuals de *Tillandsia macdougallii* L. B. Sm growing on species of the genus of pines and oaks, they found differences in the demographic behavior of populations of growing on pines than those population over oaks. Although this study clearly showed that there was a host tree effect, it is known that host tree species belonging to the same genera could diffe in some traits, so we can expect that epiphyte populations growing on different species of the same genus present variations in itheir demographic behavior.

Since epiphyte are one of the most threatened groups due to 1) their dependence for other plants or “phorophytes” which make them especially vulnerable to forest deforestation and fragmentation, which represent and apparent loss of habitat (Mondragón et al., 2015); 2) reforestation practices with non-native tree species and implementation of monocultures which change the habitat quality for epiphytes species and promote, for most sensitive species, a richness decline (Boelter et al., 2011; Ceballos, 2020); 3) Over collecting of species with anthropogenic value(Toledo-Aceves et al., 2014, Mondragon et al. 2016, Emeterio-Lara et al., 2021); 4) climate change due: a) to their dependence for atmospheric sources of water and nutrients (Zotz, 2016), and b) to the possible change in the distribution ranges of their host plants (Jump & Peñuelas, 2005; Hsu et al., 2012; Köster et al., 2013); It is important to understand the factors that shape its population dynamics, in order to develop robust programs to maintain or restore their populations.

For those reasons, in this study, we test the effect of three *Quercus* species on the demography of a vascular epiphyte community in a seasonal oak forest in Yanhuitlán, Oaxaca. We address the following questions: 1) Do host species influence the demographic parameters on vascular epiphytes? 2) Do the host tree effects vary across years and epiphyte species?

Background

Demographic studies focus on analyzing population size and its fluctuations over time, which is the result of birth, growth, mortality, and migration rates (Begon et al., 2009). The study of plant demography began in the early 1970s with the work of Harper, from there the number of such studies has increased considerably, mainly for certain life forms such as herbs, shrubs, trees, and palm trees (Olmsted & Alvarez-Buylla, 1995; Shefferson et al., 2020; Silvertown et al., 1993), excluding other life forms like vascular epiphytes (Mondragón et al., 2015).

Demographic studies of vascular epiphytes have been carried out primarily on species of Orchidaceae and Bromeliaceae families (Mondragón et al. 2015) using matrix analyzes which are an important tool for modeling population dynamics in plant and animal species. Matrices allow estimating the intrinsic rate of population growth (λ), values of $\lambda > 1$ indicate that the population is growing, while values of λ <1 Indicate that the population is in decline, values equal to 1 indicate a numerical equilibrium of the population (Caswell, 2001). In addition, it can be calculated the stable structure of sizes (*w*), which represents the population structure when the population reaches the equilibrium, and the reproductive value (*v*), which represents the reproductive value of the individuals in different stages (Caswell, 2000; Groenendael et al., 1988).

a) Vascular epiphytes´ demography

The study of the demography of vascular epiphytes is scarce; in the review realized by Mondragón et al. (2015) about the demography of vascular epiphytes, the reported that only 20 studies reported demographic information of 30 species of epiphytic angiosperm and 38 populations. These studies were carried out over a period of 20 years. Of the 30 studies mentioned above, they followed the entire life cycle of the plants studied and applied population projection matrices for their analysis. We developed a search of new studies since 2015. We found that only 14 were added to the bibliographic base of knowledge (Scopus, google scholar, etc.), studying three species of bromeliad and 11 orchid species.

The following demographic patterns have been observed up to date:

Germination: the germination rate under natural conditions is low (Mondragón et al., 2004; Mondragon & Calvo-Irabien, 2006), and it is usually not due to the amount of non-viable seeds because, in laboratory experiments, some species may have up to 90% germination. Different causes could explain this discrepancy, such as desiccation, physical eviction, attack by pathogens, predation, and the lack of associations with mycorrhizae (Chilpa-Galván et al., 2017; Valencia-Díaz et al., 2010).

Growth and survival: individuals of the smallest stages, within the life cycle of epiphytes, are the most vulnerable. The growth of epiphytes is low, and it has been observed that in some populations, there is a "juvenile bank" showing that transit to adult sizes is difficult (Ramírez-Martínez et al., 2018). However, in other cases, the highest growth rates have been reported for infantile and juvenile individuals. Some species show vegetative reproduction (Mondragón et al., 2004). In general, the first reproduction of epiphytic species ranges from 9 to 20 years, except for twig epiphytes. The slow growth of epiphytes is attributed to a lack of nutrients and water and radiation in the epiphytic environment. Some of the causes of mortality of individuals in early stages are desiccation, the lack of mycorrhizal fungi that provide them with water and nutrients, the presence of allelopathic substances, and the instability of the substrate (Callaway et al., 2002; Mondragón et al., 2015; Zotz, 2016).

Reproduction: It has been suggested that epiphytes, due to the somewhat ephemeral nature of their substrate and their relatively small size (relative to terrestrial plants), together with their frequently low population densities, should exhibit high rates of inbreeding relative to terrestrial perennials (Bush & Beach, 1995; Hooper & Haufler, 1997). The available evidence partially confirms this expectation. Although most of the Bromeliaceae and members of other families such as Gesneriaceae or Melastomataceae are mostly self-compatible (Bush & Beach, 1995; Matallana et al., 2010), most orchids and ferns present obligate xenogamy. Many epiphytes propagate vegetatively through the emergence of new shoots or ramets. This implies the growth of modules in the form of new rosettes that can eventually become physiologically independent of the mother plant while being genetically identical (Mondragón et al., 2004; Mondragón and Ticktin, 2011).

Mortality: it has been reported to be higher in the early stages and the adult stage in the case of monocarpic species. Across the main causes are the desiccation and instability of the substrate; however, other reasons such as damage by pathogens cannot be discarded (Sarmento Cabral et al., 2015; Scheffknecht et al., 2010; Toledo-Aceves et al., 2014).

Some demographic patterns observed from the application of matrix analysis for the epiphyte population are:

The lowest value reported for the population growth rate (λ) is 0.398 in a population of *Erycina crista-galli* (Rchb.f.) N.H.Williams & M.W.Chase and the highest for *Laelia speciosa* (Kunth) Schltr. (λ=1.323). Fifty percent of the populations of bromeliads and 37% of those of orchids show values above unity. According to the Observed Population Structure Index (OPSI), orchid populations tended to have OPSI values close to unity, more than bromeliad populations, indicating that populations of orchid species are composed of a higher proportion of individuals in adult stages. This is generally due to the high mortality of individuals in the early stages. Regarding the elasticity values in epiphytic orchids, summarize this information for populations of 19 species of orchids commercialized in Mexico. In general, the permanence of adult individuals (reproductive individuals) or juveniles have the highest elasticity values and have a greater effect on the λ values. The lowest elasticity values were observed for fertility. These patterns have also been reported for other species of epiphytic bromeliads (Mondragón et al., 2015; Toledo-Aceves et al., 2014).

Mechanisms that act on the population dynamics of epiphytes have been focused on:

a) Identity of host trees: It has been shown that some characteristics such as architecture (*e.g.,* arrangement and thickness of branches), bark characteristics (physical and chemical, *e.g.* pH, water retention capacity, nutrient content of its runoffs), phenology, and the growth rate of the host tree influence the dynamics of epiphyte populations (Callaway et al., 2002; Chaves et al., 2016; Ticktin et al., 2016; Valencia-Díaz et al., 2010).

b) Size and age of host trees: larger and older trees have a greater number of microclimates and microniches (Woods et al., 2015), where epiphyte seeds have a greater probability of germination and establishment (Ramírez-Martínez et al., 2018; Valverde & Bernal, 2010).

Also, the population dynamics of vascular epiphytes have been linked to precipitation ,and most studies have found that the demographic patterns observed in different years are mainly due to the interannual variation of this environmental variable (Mondragón et al., 2004; Zotz, 1998). Likewise, given that the epiphytic environment is characterized by a lack of water and nutrients, it has been attributed that the leading cause of mortality in seedlings is desiccation (Callaway et al., 2002). However, the effect of other factors such as temperature and humidity variation in the canopy has not been analyzed.

b) Host tree effect

Even though there is a close relationship between epiphytes and their host tree, only Ticktin et al. (2016) have directly tested, on a long-standing study, the effect of host tree on population growth rates of an epiphytic species. They found that the projected long-term population growth rates (λ) of *Tillandsia macdougallii* (Bromeliaceae) on pines were higher than on oaks. These differences were attributed to variations in host trees' nutrient status and their deciduous behavior, although these variables were not directly measured to host trees.

From a decade ago, vascular epiphytic populations have been treated as metapopulations for some authors to understand their population dynamics (Valverde & Bernal, 2010; Winkler et al., 2009). Some conditions for metapopulations were specified by Hanski and Gaggiotti (2004). Epiphyte populations satisfy the following: (1) suitable habitats occur in discrete patches (=the individual tree) that may be occupied by local populations, (2) even large local populations have a measurable risk of extinction (branch or tree fall), (3) habitat patches are usually not too isolated to prevent recolonization following local extinctions, and (4) local populations do not have completely synchronous dynamics.

Aim, objectives, and hypotheses

Aim

Test the influence of different host tree species on the demography of three epiphytic species in an oak forest.

Objectives

- Evaluate the effect of the host tree on the vital rates (survival, growth, and reproduction) of populations of *Tillandsia prodigiosa*, *Alamania punicea,* and *Oncidium brachyandrum*, growing on *Quercus rugosa, Q. castanea,* and *Q. martinezii*

-Evaluate the host effect in the long-term population dynamics of populations of *T. prodigiosa*, *A. punicea,* and *O. brachyandrum*, growing on *Q. rugosa, Q. castanea,* and *Q. martinezii*

- Evaluate if temporal variation of the host tree effect has a significative effect on vital rates of *T. prodigiosa*, *A. punicea*, and *O. brachyandrum.*

Hypotheses

- Epiphyte vital rates will vary across host tree species since they offer different microhabitats since tree species with rugose barks and higher water holding capacities (Callaway et al. 2002) promote higher survival rates, and host tree species with the higher mineral content of throughfalls (Cardelús et al., 2009; Cardelús & Mack, 2010) will promote higher epiphyte growth rates and capsule production.

- There will be interannual variation in epiphyte population dynamics since host traits change over time, same as weather conditions which affect host tree performance and may affect epiphyte vital rates as reported by Ticktin et al. (2016).

Materials and methods

a) Demographic censuses

In December 2017, we tagged plants of bromeliad *Tillandsia prodigiosa* (growing on *Q. rugosa, Q. castanea,* and *Q. martinezii*); and individuals of orchids *Oncidium brachyandrum*, and *Alamania punicea* (growing on *Q. martinezii and Q. rugosa* [Table 9]). Each December from 2017 to 2020, we seek every epiphyte-tagged individual to determine survival, size, and fruiting status. In addition, we searched for new seedlings.

Table 9. Number of plant sample for three epiphyte species growing on three *Quercus* species in an oak forest at Tooxi, Yanhuitlán, Oaxaca.

Epiphyte species	*Quercus martinezii N=21*	*Quercus castanea N=42*	*Quercus rugosa N=17*	*Total*
Tillandsia prodigiosa	834	704	804	2342
Oncidium brachyandrum	278		96	374
Alamania punicea	351		374	725

On each census, we took different measurements to every epiphyte individual to later make analyses and find the best predictor of vital rates. For bromeliad, we measured the size of the longest leaf, which is one of the best predictors of biomass according to Schmidt & Zotz (2002). For orchids, we measured the largest pseudobulb height and width, the length of the longest leaf, and counted the number of alive pseudobulbs; these measurements have been reported as some predictors of vital rates (Mondragón, 2009; Winkler et al., 2009).

Summary of host traits and climatic data

Next, we present a summary of host tree traits to facilitate future interpretation and discussion of the data. This information is also described in Chapter III (Table 10).

Table 10. Host traits of three *Quercus* species in a seasonal oak forest in Yanhuitlán, Oaxaca, Mexico.

Trait	Hos tree species		
	Quercus martinezii	*Quercus castanea*	*Quercus rugosa*
Deciduousness	Deciduous Trees shed their leaves massively between February and March and new leaves emerge between April and May.		Semi-deciduous. Trees shed their leaves gradually throughout the year.
Diameter at breast height (DBH, cm) ± S.D.^{1}	36.10 ± 12.60^{ab} (n=21)	23.12 ± 9.10^{b} (n=42)	29.66 ± 15.51^{b} (n=17)
Height (m) ± S.D. ^{2}	9.69 ± 2.03 ^{a} (n=21)	7.74 ± 4.20^{b} (n=42)	8.60 ± 2.68^{ba} (n=17)
Bark rugosity (cm) ± S.D.^{3}	5.875 ± 1.24^{a} (n=10)	3.92 ± 0.80^{b} (n=10)	5.53 ± 1.90^{a} (n=10)
Throughfall phosphorus content (mg/l) ± S.D.^{4}	0.18±0.04^{a} (n=5)	0.12±0.01^{b} (n=6)	0.15±0.04^{ab} (n=6)
Throughfall potassium content (mg/l) ± S.D.^{5}	2.56±1.06^{a} (n=5)	0.87±0.41^{b} (n=6)	2.6±1.11^{a} (n=6)

[1] Significant differences among phorophytes ($F_{(2,77)}$= 3.574, p<0.05)
[2] Significant differences among phorophytes ($F_{(2,77)}$= 6.332, p<0.01)
[3] Significant differences among phorophytes ($F_{(2,29)}$= 5.606, p<0.01) (Hernandez-Álvarez, 2020)
[4] Significant differences among phorophytes ($F_{(2,14)}$= 4.013, p<0.05)
[5] Significant differences among phorophytes ($F_{(2,14)=}$10.068. p<0.01)

Macroclimatic data: Climatic data from Oaxaca state showed that year 2018 was drier than year 2019 and 2020. However, we did not find statistical difference across years (P>0.05, $F_{(2,33)}$= 0.0427, Table 11).

Table 11. Monthly rainfall across three years in Oaxaca, México.

Month	2018	2019	2020
January	25.0	14.9	29.5
February	13.6	4.7	17.0
March	20.5	9.6	2.8
April	49.3	8.5	25.9
May	73.2	96.9	63.5
June	231.7	155.8	148.6
July	86.2	145.2	169.1
August	208.4	162.7	303.2
September	178.6	227.3	238.2
October	257.9	209.9	66.0
November	44.1	47.7	51.7
December	28.6	6.3	10.1
Mean	101.43	90.79	93.80
Standard deviation	91.10	85.68	98.52

b) Data analyses

Demographic patterns

We tested differences in individual epiphytes level survival, growth, and reproduction on different *Quercus* species, using generalized linear mixed models (GLMMs). Initial size (initial log-transformed), host species (*Q. martinezii*, *Q. castanea*, and *Q. rugosa*), and year were fixed effects. Since we have several size measurements for orchid species, we run regression analyses with each of them to find the best predictor of growth, reproduction, and survival. Additionally, for *A. punicea*, we constructed an index (consisted of number of leaves times area of the longest leaf), and for *O. brachyandrum,* we calculated pseudobulb area. These two size approximations showed a better fit for models, so we used them in subsequent analyses.

For model selection, we used Akaike´s information criterion (AIC) to determine whether to drop or keep a given fixed-effect term, maintaining factors that 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 and reproduction for all epiphyte species. The probability of capsules production was modeled with negative binomial GLMMs for orchid species and lineal GLMM for bromeliad.

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 model the probability of reproduction with the minimum size observed for plant reproduction (sizes: *T. prodigiosa* ≥ 35 cm, *A. punicea* ≥ 1.44 cm^{2}, and *O. brachyandrum* ≥ 0.7854 cm^2). All analyses were carried out using the glmmTMB package in R version 1.1.2.3.

Population growth rates

We apply **integral projection models** (IPMs) to project the long-term population growth rates (λ values) of each epiphyte species growing on different *Quercus* species. Integral projection models are built from continuous functions that describe size-dependent growth, survivorship, and fecundity. This represents an improvement over traditional matrix models, where individuals need to be classified into size or stage-classes. The IPMs describe how the size distribution of individuals changes from one-time step to another (Easterling et al., 2000; Metcalf et al., 2015). The 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 all epiphyte 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 p (x,y) represents the production of new seedlings of size (x) produced from plants of size (y). This was calculated for *T. prodigiosa*, *A. punicea* and *O. brachyandrum* plants of reproductive size ($\geq$35 cm, $\geq$1.44 cm^2, and $\geq$ 0.79 cm^2, respectively). 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; p_E is the number of new seedlings 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 long-term asymptotic projected population growth rate **(λ)** for each IPM using the popbio 2.7 package in R (Stubben & Milligan, 2007).

To assess how variation in different vital rate functions contributed to the substantial differences in annual λ values across host species, we conducted a **Life table response experiments analysis** ([LTRE], Caswell, 2000) comparing the host species with the higher λ value versus other species. After the analysis, we obtained a graphic representation where darker colors represent life-history transitions that make greater contribution to higher λ values. Survival and growth occur along the diagonal and subdiagonal, and fecundity is captured in the top row. See the example four-stage projection model.

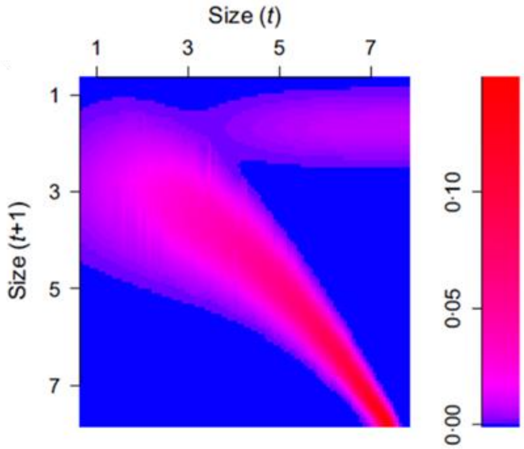

Figure 13. Graphic representation of Life Table Response Experiment (LTRE) analysis for Integral projection models (IPMs). Taken from Merow et al. (2014).

Results

a) Demographic patterns

1. Host tree effects on bromeliad species

Survival of *T. prodigiosa* increased with size and varied across host species, but effect of host species differed across years. Plants growing on *Q. castanea* had higher survival than those growing on the other host species in year 1 and 2; and higher survival than those on *Q. rugosa* in year 3 as well. In terms of variation across years, plants growing on all three hosts had lower survival in years 2 and 3, than in year 1, but the year 2 decrease in survival was much larger for plants growing on *Q. martinezii* and *Q. rugosa* than for plants on *Q. castanea*. In year 3, survival of plants growing on *Q. castanea* was lower than in year 2, while the reverse was true for plants growing on the other two host species. Growth did not differ between plants growing on *Q. castanea* and those on *Q. martinezii* in any year. Growth on *Q. rugosa* was significantly higher than the other host species in year 1. For all tree hosts, growth was lower in years 2 and 3 than in year 1, but the decline was greater for plants growing on *Q. rugosa* than on the other two hosts (Table 13, Fig. 14 y 15). Both the probability of reproduction (for individuals ≥ 35 cm) and the number of capsules produced per reproducing individual, increased significantly with size. There were no differences among host species or across years (Table 13).

Table 12. Estimated coefficients from mixed-effect models of the probability of survival, growth, reproduction, and probability of producing capsules for *Tillandsia prodigiosa* plants growing on three *Quercus* species.

Fixed effects	Estimate	SE	Z value	P value
Probability of surviving to *t*+1 †				
Intercept	2.0979	0.1928	10.880	< 2e-16
Size at start	0.2541	0.0354	7.178	7.06e-13
Year 2 (2018-2019)	-0.3662	0.1890	-1.937	0.052713
Year 3 (2019-2020)	-0.7074	0.1955	-3.619	0.000296
Host species (*Q. martinezii*)	-0.2684	0.2176	-1.233	0.217546
Host species (*Q. rugosa*)	-0.2582	0.2173	-1.188	0.234662
Year 2 × *Q. martinezii*	-0.9902	0.2386	-4.151	3.32e-05
Year 3 × *Q. martinezii*	-0.5680	0.2478	-2.292	0.021897
Year 2 × *Q. rugosa*	-0.5524	0.2428	-2.275	0.022908
Year 3 × *Q. rugosa*	0.2917	0.2557	1.141	0.253942
Size at *t* +1 of surviving individuals (growth) §				
Intercept	0.46413	0.02531	18.34	<2e-16
Size at start	0.87410	0.00397	220.19	< 2e-16
Year 2 (2018-2019)	-0.12904	0.01625	-7.94	2.00e-15
Year 3 (2019-2020)	-0.11270	0.01696	-6.65	3.01e-11
Host species (*Q. martinezii*)	-0.01295	0.03263	-0.40	0.691367
Host species (*Q. rugosa*)	0.10446	0.03074	3.40	0.000677
Year 2 × *Q. martinezii*	0.01241	0.02299	0.54	0.589277
Year 3 × *Q. martinezii*	0.01047	0.02452	0.43	0.669300
Year 2 × *Q. rugosa*	-0.14789	0.02265	-6.53	6.66e-11
Year 3 × *Q. rugosa*	-0.05905	0.02356	-2.51	0.012180
Probability of producing capsules at time *t* (for individuals ≥ 35 cm) †				
Intercept	-37.584	8.147	-4.613	3.96e-06
Size at start	9.274	2.061	4.500	6.80e-06
Capsules produce per reproductive plant at time *t* §				
Intercept	-4.4178	1.8563	-2.380	0.0173
Size at start	2.2489	0.4684	4.802	1.57e-06

† We used binomial (logit) GLMMs models
§ We used GLM normal

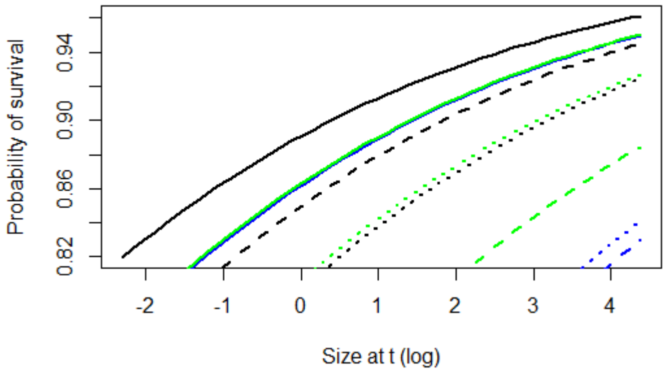

Figure 7. Survival as function of size, for *Tillandsia prodigiosa* plants growing on three oak species a) *Quercus martinezii* (blue lines), b) *Q. castanea* (black lines), and c) *Q. rugosa* (green lines). Solid lines indicate year 2017-2018, dashed lines year 2018-2019 and dotted line year 2019-2020.

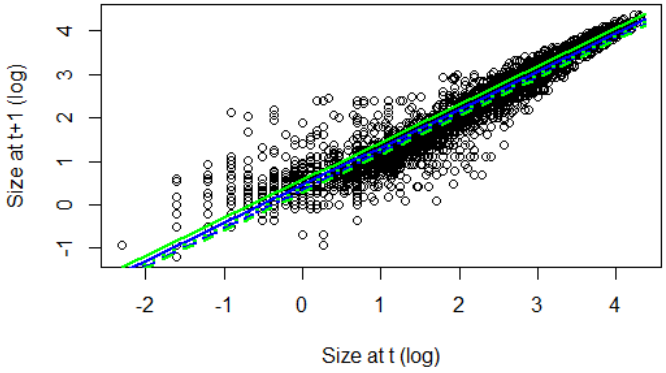

Figure 15. Growth as function of size, for *Tillandsia prodigiosa* plants growing on three oak species a) *Quercus martinezii* (blue lines), b) *Q. castanea* (black lines), and c) *Q. rugosa* (green lines). Solid lines indicate year 2017-2018, dashed lines year 2018-2019 and dotted line year 2019-2020.

2. Host tree effects on orchid species

Survival of *A. punicea* also increased with size but did not vary across host species. The best fit model included an interaction between host species and year, though it was not significant at $p< 0.05$. Survival was lower in years 2 and 3 than in year 1 on both host species but for plants growing on *Q. rugosa*, the decrease was less in year 2. For plants growing both host species, growth was lower in year 2 and higher in year 3, than in year 1. For those growing on *Q. rugosa,* the decrease in growth in year 2 was less than that for plants growing on *Q. martinezii* (Table 14, Fig. 16 y 17). The probability of reproduction and number of capsules produced by reproducing plants increased with size (Table 14).

Table 13. 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

† We used binomial (logit) GLMMs models
§ We used GLM normal
* We used negative binomial GLMM

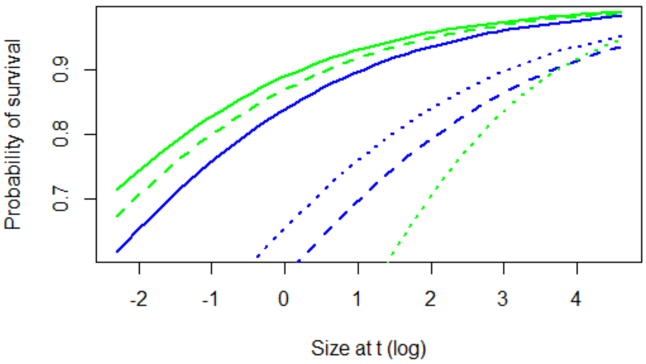

Figure 16. Survival as function of size, for *Alamania punicea* plants growing on two oak species *Quercus martinezii* (blue) and *Q. rugosa* (green) Solid lines indicate year 2017-2018, dashed lines year 2018-2019 and dotted lines year 2019-2020.

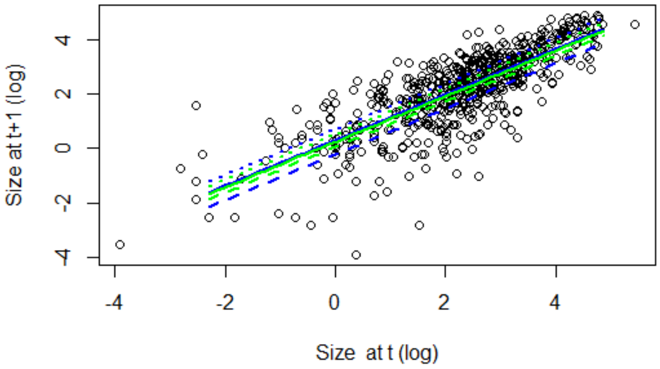

Figure 17. Growth as function of size, for *Alamania punicea* plants growing on two oak species *Quercus martinezii* (blue) and *Q. rugosa* (green) Solid lines indicate year 2017-2018, dashed lines year 2018-2019 and dotted lines year 2019-2020.

Survival on *O. brachyandrum* increased with plant size and was higher on year 1. For years 2 and 3, survival was higher for plants growing on *Q. rugosa* than on *Q. martinezii*. For plants growing on *Q. rugosa*, survival was higher in year 2 than year 1 and highest in year 3; in contrast, for plants growing on *Q. martinezii*, survival was lowest in year2, and similar in years 1 and 3. For plants growing on both host species, growth was higher in year 2 and 3 than in years 1, but the increases were greater for plants growing on *Q. rugosa* (Table 15, Fig. 18 y 19). Larger individuals have higher probabilities of capsule production and number of capsules produced per reproductive plants on *Q. martinezii* and *Q. rugosa* did not differ across host species or among years (Table 15, Fig. 20).

Table 15. 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				
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 ≥ 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

† We used binomial (logit) GLMMs models
§ We used GLM normal
* We used negative binomial GLMM

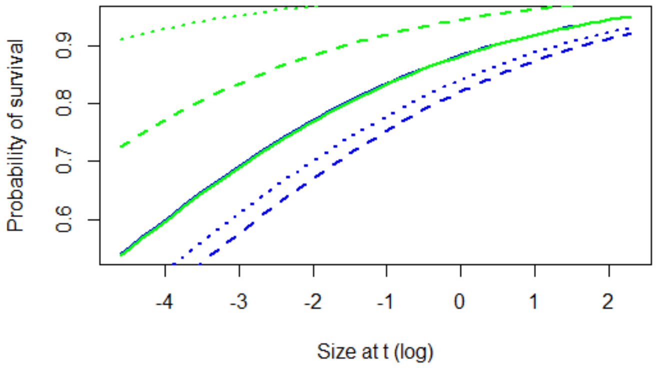

Figure 18. Survival as function of size, for *Oncidium brachyandrum* plants growing on two oak species a) *Quercus martinezii* (blue), and b) *Q. rugosa* (green). Solid lines indicate year 2017-2018, dashed lines year 2018-2019 and dotted line year 2019-2020.

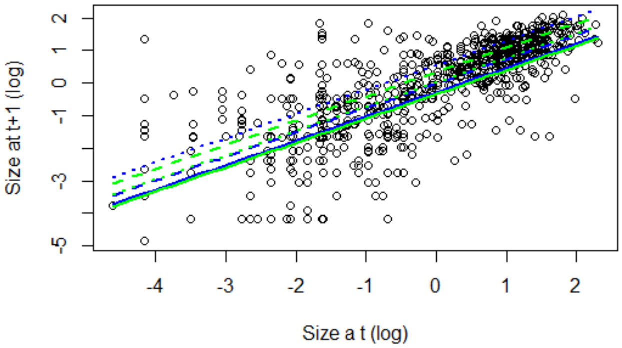

Figure 19. Growth as function of size, for Oncidium brachyandrum plants growing on two oak species a) *Quercus martinezii* (blue), and b) *Q. rugosa* (green). Solid lines indicate year 2017-2018, dashed lines year 2018-2019 and dotted line year 2019-2020.

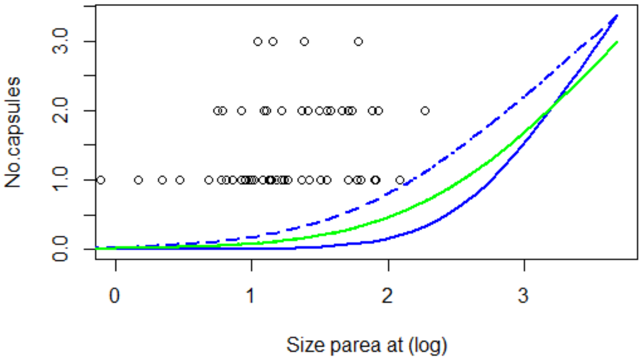

Figure 20. Reproduction function of size, for *Oncidium brachyandrum* plants growing on two oak species a) *Quercus martinezii* (blue), and b) *Q. rugosa* (green). Solid lines indicate year 2017-2018, dashed lines year 2018-2019 and dotted line year 2019-2020. Some lines overlap.

b) Population growth rates

Population growth rates for *Tillandsia prodigiosa* were lower on *Q. rugosa* than *Q. castanea* and *Q. martinezii* in year 1. *Quercus castanea* also showed the higher λ values in year 2 and in year 3 values were like *Q. rugosa*. *Quercus martinezii* showed the lowest values on years 2 and 3 (Fig. 21).

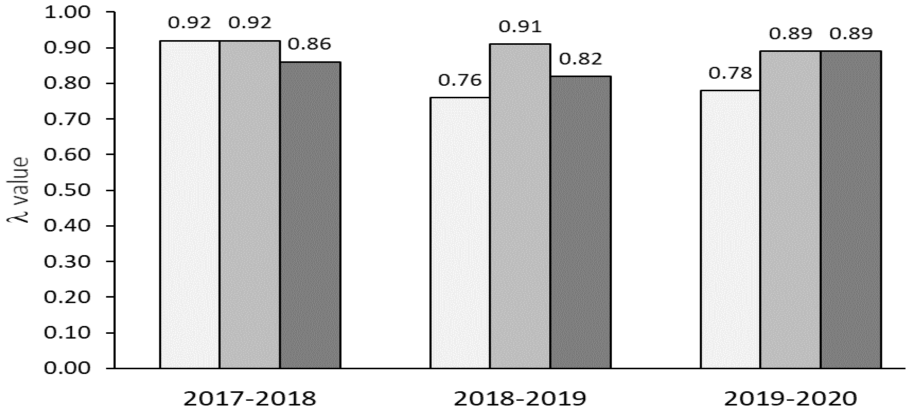

Figure 21. Lambda values for populations of *Tillandsia prodigiosa* growing on *Quercus martinezii* (white bars, *Q. castanea* (light gray bars) and *Q. rugosa* (dark gray bars).

Population growth rates *A. punicea* were similar for both host species on year one, while on year 2 *Q. rugosa s*howed the highest value. However, on year 3 exhibited the lowest. For *O. brachyandrum*, *Q. martinezii* had the highest value on year 1, while on years two and tree presented the lowest (Fig.22).

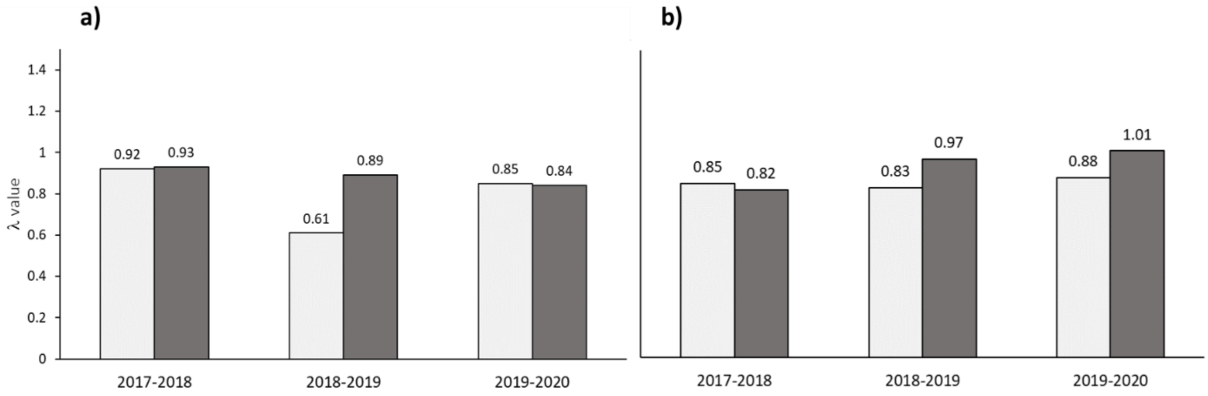

Figure 22. Lambda values for populations of **a)** *Alamania punicea* and **b)** *Oncidium brachyandrum* growing on *Quercus martinezii* (white bars) and *Q. rugosa* (dark gray bars).

a) LTREs analyses

For these analyses we compared the specie with the higher λ values versus other host specie with a lower value within years.

For *T. prodigiosa* between *Q. martinezii* and *Q. rugosa*, survival of adult individuals (longest leaf ≥ 35 cm), and in minor intensity fecundity contributed the most to higher λ values for population in both host comparisons, same pattern for *Q. castanea* versus *Q. rugosa* on year 1, and *Q. castanea* vs. *Q. martinezii* on year 2. Analysis for *Q. castanea* vs. *Q. rugosa* on year 2 showed that survival of adult individuals contributed most to higher λ values on *Q. castanea* and in less intensity growth. For year 3, *Q. rugosa* vs. *Q. martinezii* growth of adult individuals had an important influence, on the other side, when comparing *Q. castanea* and *Q. martinezii* growth of adult individual contributed the most (Fig. 23).

For *A. punicea Q. rugosa* vs. *Q. martinezii* showed that survival of juveniles had a significative contribution in year 1 and in minor intensity fecundity. While *Q. rugosa* vs. *Q. martinezii* survival of juveniles had a major effect in year 2. Finally, *Q. martinezii* vs. *Q. rugosa* the growth of adult individuals and in less intensity survival and fecundity contributed the most to the higher λ values for populations on *Q. martinezii* in year 3 (Fig. 24).

For *O. brachyandrum* growth and fecundity of juveniles contributed the most to the higher λ value of *Q. martinezii* when comparing versus *Q. rugosa* in year 1. The survival of adult individuals was more important and in less strength fecundity when contrasting *Q. rugosa* vs. *Q. martinezii* in year 2. The growth of juvenile individuals and in less strength, fecundity had the major impact on *Q. rugosa* vs. *Q. martinezii* (Fig. 25).

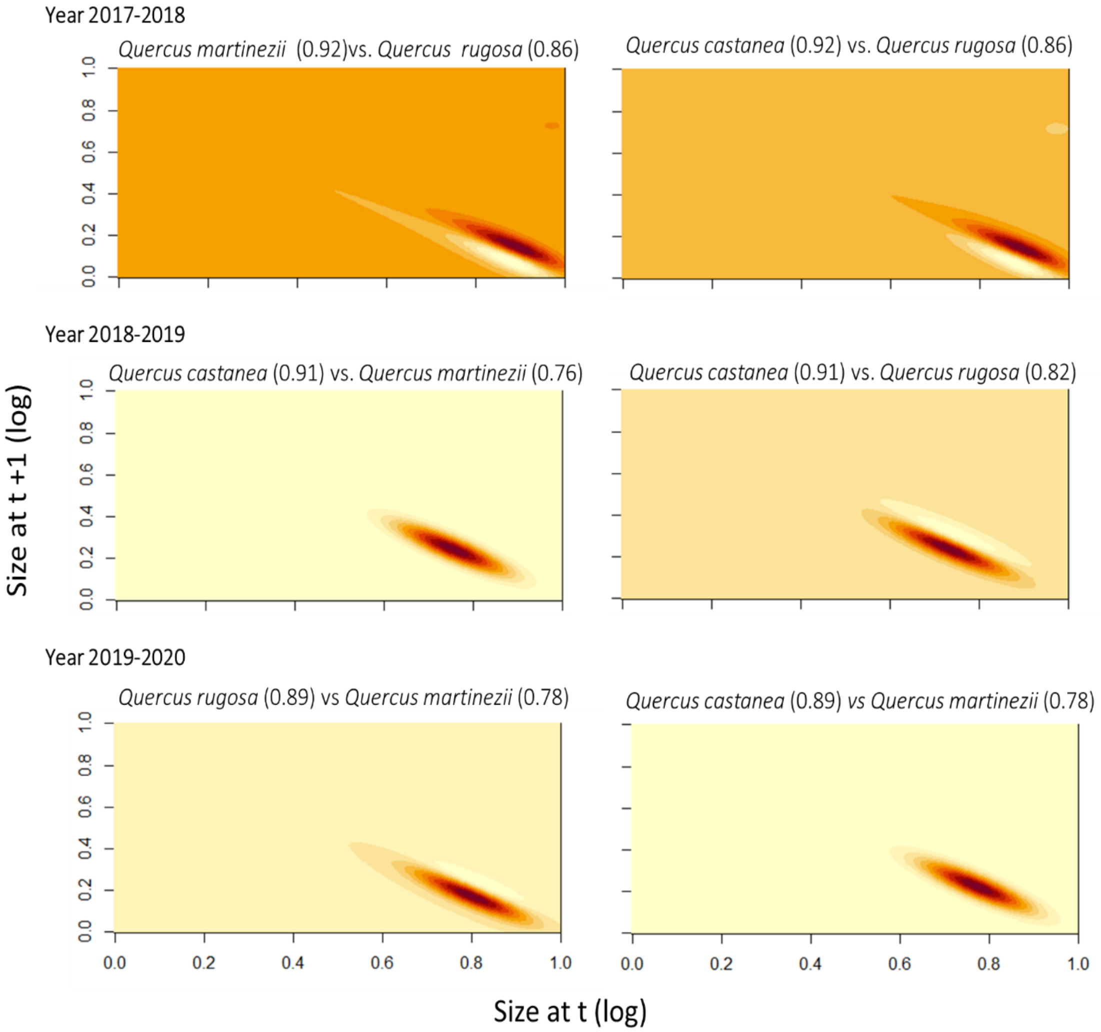

Figure 23. Life table response experiment contributions for *Tillandsia prodigiosa* plants growing on three *Quercus* species. After each host tree name are lambda values enclosed in parentheses. Darker colors represent life-history transitions that make greater contributions to higher λ values observed. 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.

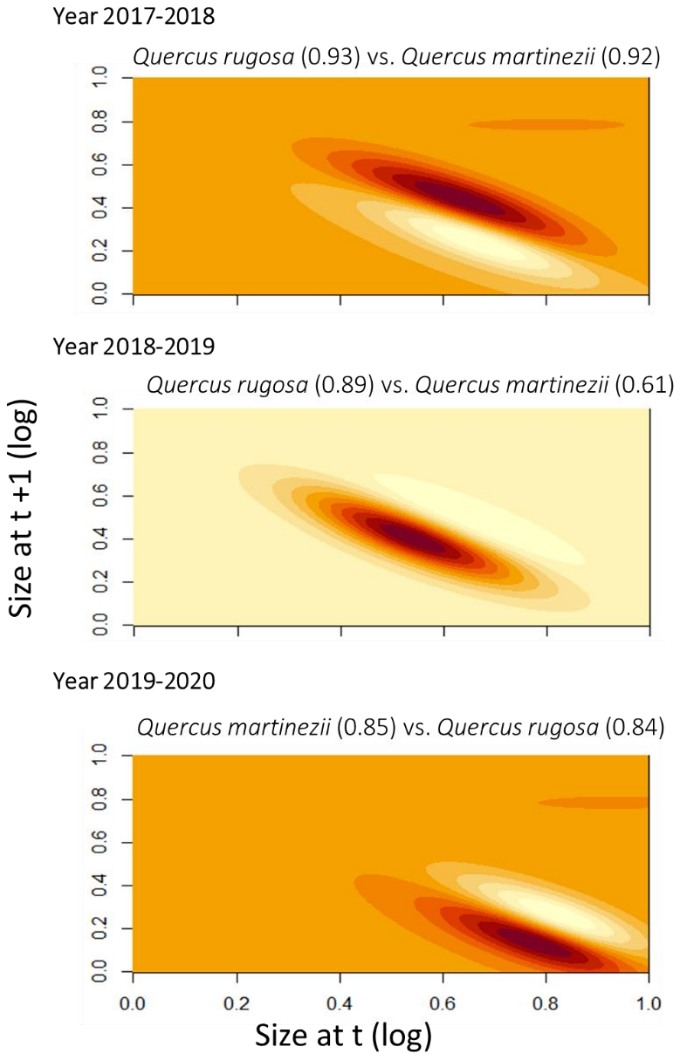

Figure 24. Life table response experiment contributions for *Alamania punicea* plants growing on two *Quercus* species. After each host tree name are lambda values enclosed in parentheses. Darker colors represent life-history transitions that make greater contributions to higher λ values observed. Values across the diagonal represent contributions from survival, and those below diagonal represent contributions from growth. Fecundity contributions are represented in the top right corner.

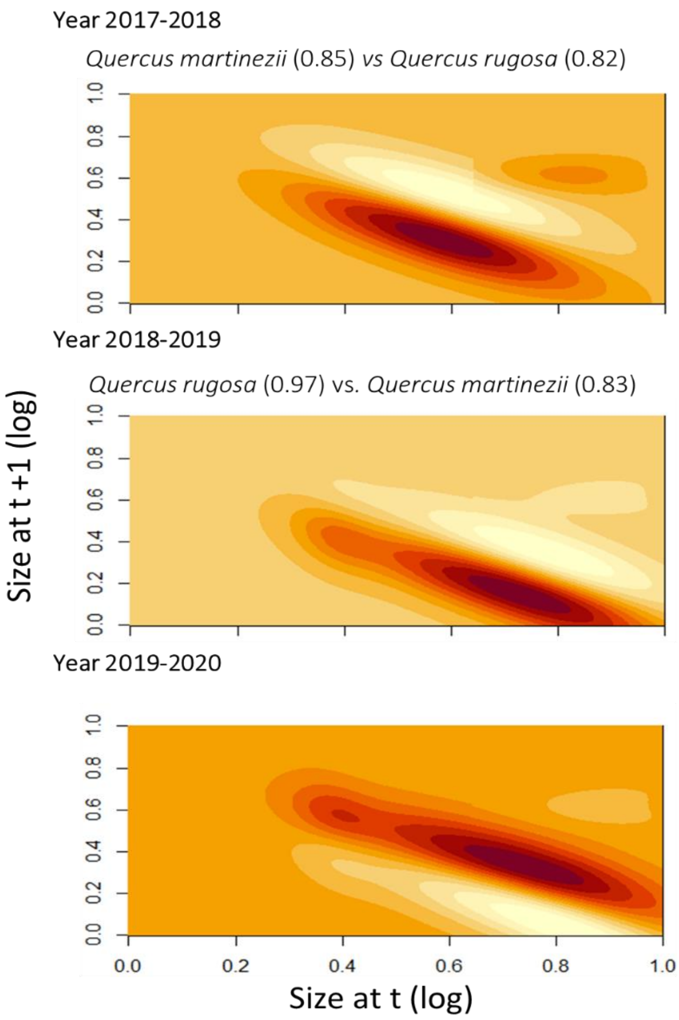

Figure 25. Life table response experiment contributions for *Oncidium brachyandrum* plants growing on two *Quercus* species. After each host tree name are lambda values enclosed in parentheses. Darker colors represent life-history transitions that make greater contributions to higher λ values observed. 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.

Discussion

Our results clearly showed that demographic rates for all epiphyte species vary considerably across host tree species and years. That information is important to understand population dynamics of vascular epiphytes in seasonal forests.

Some general patterns like higher survival on year 1 and for individuals of bigger sizes can be explained as follow. According to weather stations year 1 reported higher values of precipitation (approx.10 % greater) than year 2 and 3, since the epiphytic environment is characterized for low water availability (Benzing, 1990; Zotz, 2016)slight changes in precipitation could have negative effects on survival of individuals specially those of smaller stages (like seedlings and infants) which in fact have been reported as the more vulnerable to drier conditions (Mondragón et al., 2004; Toledo-Aceves et al., 2014; Valverde & Bernal, 2010).

Differences in vital rates across host tree species

There was a clear effect of host species on vital rates, and its effect varied across epiphytes species and years mostly linked with macroclimatic conditions which probably influence on host tree suitability.

Host tree effect on survival on populations of *Tillandsia prodigiosa* was evident. On *Q. castanea* individuals had a higher probability of survival. Even when Q. *castanea* is a deciduous species and exhibited higher values of maximum canopy openness in year 1, 2, and possibly on year 3 (data not available, Chapter III) than other phorophyte species, Q. *castanea* trees occupy a lower stratum than other phorophyte species, so *T. prodigiosa* individuals had higher access to light (due to the deciduous nature of *Q. martinezii*) but possibly do not suffer the level of stress due to insolation, than individuals growing on other species, since *Q. rugosa* leaves buffer and probably regulate microclimatic conditions within the forest during the dry season.

There was a lower survival on Q. *martinezii* and *Q. rugosa* (on year 1 and 2) this could be related with higher branch fall rates (pers. obs), especially for thinner branches, however this need to be test quantitatively. We observed that thinner branches were highly colonized by individuals of smaller stages (mainly infantile and juveniles), while individuals of bigger sizes were located on trunks, primary and secondary branches, so this could explain the higher rates of survival of individuals on *Q. rugosa* on year 3 which also were the remanent plants located on safer sites and with lower probabilities of falling. On the other side, host tree architecture changes on time (Rasmussen & Rasmussen, 2018) and possibly branches became more thicker and less susceptible to breakage avoiding epiphyte falling.

Host tree effect on *T. prodigiosa* growth also was evident since two host species seem enhance this bromeliad growth. These two oaks, *Q. martinezii* and *Q. rugosa,* share some traits like the amount of water holding retention of their barks, and similar quantities of potassium, and phosphorus of their throughfalls. This higher availability of water and nutrients possibly enhance growth of *T. prodigiosa* individuals specially those of bigger sizes. Zotz et al. (2001) support the idea that photosynthetic capacities of epiphytes increase from the smallest to the largest size plants, since they have higher area to absorb light, bigger tanks to store water, and higher trichome cover to absorb it.

Host tree effect on *T. prodigiosa* reproduction was not evident, since reports suggest that tank bromelias became self-sufficient to water and nutrients obtention, due to the different process that take place inside their tanks. This autonomy makes adult *T. prodigiosa* plants less dependent from host trees.

Host tree effect on both orchid species survival was evident. A combination of good microclimatic conditions and nutrients made *Q. rugosa* a good host. However, we did not observe its effect on reproduction that was like individuals on *Q. martinezii*. This could be related with similar stemflow nutritional status between these two oak species, although we did not evaluate it. It is known that stemflows are a main source of nutrients for orchid species who possess functional roots that can absorb mineral and water from them. Another trait that does not vary across these two oak species is water retention capacity of their barks, a trait that could enhance mycorrhizae fungi growth (Harshani et al., 2014; Rasmussen et al., 2015). Mycorrhizae provide epiphytes of minerals and water, and according to Hernández – Álvarez (2021) percentage of colonization of roots by mycorrhizal fungi of individuals of *A. punicea* and *O. brachyandrum* growing on *Q. martinezii* and *Q. rugosa* is similar.

Differences in population growth rates across host species

Our result suggest that host species can affect long-term population dynamics. And differences in λ values across host species are due to different contribution of growth and survival bigger individual like juveniles or adults. This pattern had already been observed for other bromeliad and orchid species (Mondragon et al. 2015; Ticktin et al. 2016). We also observed that patterns differed host species and years, and this supports the idea that host trees are dynamic entities, and the effect of their traits on epiphytes vital rates could vary depending on macro climatic conditions (Ramírez-Martínez et al., 2018; Wagner et al., 2015). While in some years traits could enhance some vital rates on others could have a negative effect on them as demonstrated by Ticktin et al. (2016) for a bromeliad specie. So, it is important to make long-term studies and apply new approaches to have a better understanding of the complex population dynamics of vascular epiphytes.

The low lambda values found (most <1) for this species and for other epiphytic bromeliad and orchis species reflect harsh environmental conditions faced by epiphytes, especially on drier years. Even though this λ values indicate a possible long-term population decline, these results should be taken with caution, since according to studies realized more than two decades ago that reported values under the unit for different populations of vascular epiphytes (Mondragón et al., 2015) by now those populations are not extinct.

Differences for population growth rates found in our study might indicate that there is demographic asynchrony across populations of epiphytes growing on different host species, a prerequisite for metapopulation functioning (Hanski & Gaggiotti, 2004). Possibly migration of seeds is common across host species and this process avoids local population extinctions. In addition, our results also indicate that the degree of asynchrony varies across epiphyte species, and it is influenced by the host specie they area living on.

Conclusions

There is an effect of the host over the demography of the vascular epiphytes and this effect differed across epiphytic species and years. For *T. prodigiosa* trees of *Q. castanea* seemed more stable hosts but their suitability has interannual variation. For orchid species, *Q. rugosa* individuals enhance survival but their effect changes over time possibly for the interaction with other micro and macroenvironmental conditions. Differences in population growth rates across host species usually is given by growth or survival of juvenile and reproductive adult individuals. Our study gives relevant information about population dynamics although interpretation on population growth rates should be taken with caution, since these population might behave as metapopulations.

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CHAPTER V. GENERAL CONCLUSIONS

1. There is a host tree effect on reproductive phenology of vascular epiphytes. This effect was more evident in bromeliad species and in the inflorescence formation phenophase. Activity index also evidence more differences in onset date for bromeliad than orchids than for other parameters. It seemed that microenvironmental conditions within host tree canopies showed a slight impact on epiphyte phenology.

2. There is host tree effect on demography of vascular epiphytes. Host tree affected survival, growth, and reproduction, but this effect depends on the vascular epiphyte studied, and across years. According to population growth rates trees of *Q. castanea* seemed more stable hosts for *T. prodigiosa*, but their suitability varied across years. For orchid species, *Q. rugosa* trees enhanced survival but their effect changed over time, possibly interacting with other micro and macroenvironmental factors. Differences in population growth rates across host species usually were given by the growth or survival of juvenile and reproductive adult individuals, and in some cases, by fecundity.

SUPPLEMENTS

Supplement 1. Results of Pearson correlation between relative humidity and maximum temperature. For three *Quercus* species in an oak forest in Yanhuitlán, Oaxaca.

	Q. martinezii	***Q. rugosa***	***Q. castanea***	***Q. martinezii***	***Q. rugosa***	***Q. castanea***
R values	Tmax1	Tmax2	Tmax3	Rh1	Rh2	Rh3
Tmax1	■	0.82178	0.7387	-0.89149	-0.8954	-0.9028
Tmax2		■	0.79348	-0.70395	-0.76602	-0.75193
Tmax3			■	-0.61632	-0.61206	-0.7156
Rh1				■	0.93825	0.98278
Rh2					■	0.9487
Rh3						■

P values	Tmax1	Tmax2	Tmax3	Rh1	Rh2	Rh3
Tmax1	■	8.49E-03	3.75E-01	5.08E-05	3.46E-05	1.60E-05
Tmax2		■	3.73E-02	0.00012372	1.28E-02	2.27E-01
Tmax3			■	0.0013414	0.0014795	8.45E-01
Rh1				■	1.29E-07	1.26E-13
Rh2					■	1.76E-08
Rh3						■

Tmax 1 and Rh1 maximum temperature and relative humidity in *Q. martinezii*, Tmax 2 and Rh2 maximum temperature and relative humidity in *Q. rugosa*, Tmax 3 and Rh3 maximum temperature and relative humidity in *Q. castanea.*

Supplement 2. Results of the GAMLSS model for the activity index of inflorescence formation, flowering, fruiting, and seed dispersal for *Tillandsia prodigiosa* growing on three *Quercus* species. In an oak forest in Yanhuitlán, Oaxaca.

Host tree species	Phenophase	Predictive Variable	Estimate	SE	t value	P	GD	AIC	SBC
Quercus martinezii	Inflorescence formation	Intercept	-20.087567	2.351338	-8.543	6.23e-08	516.6415	526.6415	532.5318
		CO	-0.013868	0.009092	-1.525	ns			
		Tmean	1.23352	0.185347	6.655	2.30e-06			
		Tmin	-0.17309	0.166944	-1.037	ns			
		RH	0.10209	0.015194	6.719	2.02e-06			
Quercus castanea	Inflorescence formation	Intercept	-15.68629	2.102	-7.463	4.63e-07	327.3491	337.3491	343.2394
		CO	-0.04758	0.01728	-2.754	0.012639			
		Tmean	0.78173	0.18803	4.158	0.000535			
		Tmin	-0.16157	0.20648	-0.782	0.443568			
		RH	0.13613	0.01867	7.29	6.48e-07			
Quercus rugosa	Inflorescence formation	Intercept	-8.56858	1.37174	-6.247	5.34e-06	316.0939	326.0939	331.9842
		CO	0.09078	0.01624	5.589	2.17e-05			
		Tmean	-0.09626	0.12131	-0.793	0.437			
		Tmin	-0.24801	0.16483	-1.505	0.149			
		RH	0.14732	0.01561	9.438	1.33e-08			
Quercus martinezii	Flowering	Intercept	55.66165	5.55607	10.018	5.11e-09	95.21903	105.219	111.1093
		CO	-0.75344	0.16261	-4.633	0.000181			
		Tmean	-3.67376	0.3641	-10.09	4.56e-09			
		Tmin	2.49944	0.30059	8.315	9.40e-08			
		RH	-0.07554	0.01516	-4.984	8.25e-05			
Quercus castanea	Flowering	Intercept	29.52773	3.99122	7.398	5.25e-07	193.8577	203.8577	209.7479
		CO	-0.84625	0.18614	-4.546	0.000221			
		Tmean	-0.43353	0.30589	-1.417	0.172589			
		Tmin	0.72877	0.29375	2.481	0.022630			
		RH	-0.05289	0.02835	-1.866	0.077609			
Quercus rugosa	Flowering	Intercept	-5.78528	3.85507	-1.501	0.149870	191.4658	201.4658	207.3561
		CO	-0.49357	0.08021	-6.153	6.5e-06			
		Tmean	1.32768	0.29339	4.525	0.000232			
		Tmin	-2.37949	0.49971	-4.762	0.000136			
		RH	0.33933	0.05979	5.676	1.8e-05			
Quercus martinezii	Fruiting	Intercept	0.636133	1.460444	0.436	0.66805	588.962	598.962	604.8523
		CO	-0.081685	0.010012	-8.158	1.25e-07			
		Tmean	0.401693	0.120414	3.336	0.00347			
		Tmin	-0.050656	0.12791	-0.396	0.69650			
		RH	-0.001576	0.011023	-0.143	0.88783			
Quercus castanea	Fruiting	Intercept	-4.43746	1.402302	-3.164	0.00511	454.0631	464.0631	469.9533
		CO	-0.061744	0.009341	-6.61	2.52e-06			
		Tmean	0.896756	0.11132	8.056	1.51e-07			
		Tmin	-0.690966	0.127012	-5.44	3.00e-05			
		RH	0.04063	0.012443	3.265	0.00407			
Quercus rugosa	Fruiting	Intercept	-5.762028	1.213394	-4.749	0.00014	548.3015	558.3015	564.1918
		CO	-0.024472	0.008793	-2.783	0.01185			
		Tmean	0.736175	0.094039	7.828	2.31e-07			
		Tmin	-0.548395	0.108261	-5.065	6.87e-05			
		RH	0.054404	0.009707	5.605	2.10e-05			
Quercus martinezii	Seed dispersal	Intercept	14.34268	4.23943	3.383	0.00312	152.0967	162.0967	167.987
		CO	-0.305	0.08078	-3.776	0.00128			
		Tmean	0.68085	0.25929	2.626	0.01664			
		Tmin	-1.004	0.28997	-3.462	0.00261			
		RH	-0.07943	0.04264	-1.863	0.07799			
Quercus castanea	Seed dispersal	Intercept	69.42487	12.86871	5.395	3.32e-05	88.74405	98.74405	104.6343
		CO	-4.17993	0.78561	-5.321	3.90e-05			
		Tmean	4.05523	0.64391	6.298	4.80e-06			
		Tmin	-1.60366	0.30468	-5.263	4.43e-05			
		RH	0.10786	0.04245	2.541	0.01990			
Quercus rugosa	Seed dispersal	Intercept	-22.3483	6.73864	-3.316	0.00363	60.85672	70.85672	76.74699
		CO	-0.26252	0.1082	-2.426	0.02537			
		Tmean	2.94424	0.53828	5.47	2.82e-05			
		Tmin	-3.92949	1.01704	-3.864	0.00105			
		RH	0.33253	0.09097	3.655	0.00168			

ns not significant = P > 0.05, GD global deviation, AIC Akaike information criterion, SBC Schwarz Bayesian criterion, Tmean mean temperature, Tmax maximum temperature, Tmin minimum temperature, CO canopy openness, RH relative humidity

Supplement 3. Results of the GAMLSS model for the activity index of inflorescence formation, flowering, fruiting, and seed dispersal for *Tillandsia plumosa* growing on three *Quercus* species. In an oak forest in Yanhuitlán, Oaxaca.

Host tree species	Phenophase	Predictive Variable	Estimate	SE	t value	P	GD	AIC	SBC
Quercus martinezii	Inflorescence formation	Intercept	-19.41603	3.48839	-5.566	2.28e-05	329.7593	339.7593	345.6496
		CO	0.09969	0.01066	9.351	1.53e-08			
		Tmean	1.66882	0.26663	6.259	5.21e-06			
		Tmin	-1.19775	0.2347	-5.103	6.32e-05			
		RH	0.07536	0.02192	3.438	0.00276			
Quercus castanea	Inflorescence formation	Intercept	23.410798	1.615305	14.493	1.01e-11	666.9875	676.9875	682.8778
		CO	0.041629	0.008483	4.907	9.78e-05			
		Tmean	-1.183728	0.150988	-7.84	2.26e-07			
		Tmin	0.568506	0.172361	3.298	0.00378			
		RH	-0.149908	0.015978	-9.382	1.45e-08			
Quercus rugosa	Inflorescence formation	Intercept	6.00056	1.57584	3.808	0.001188	283.924	293.924	299.8142
		CO	-0.05917	0.01707	-3.466	0.002586			
		Tmean	0.37484	0.12481	3.003	0.007309			
		Tmin	-0.70954	0.169	-4.198	0.000487			
		RH	-0.01153	0.01507	-0.765	0.453707			
Quercus martinezii	Flowering	Intercept	-8.68614	3.65286	-2.378	0.028064	426.6356	436.6356	442.5259
		CO	0.18187	0.02195	8.287	9.89e-08			
		Tmean	-0.33597	0.33158	-1.013	0.323671			
		Tmin	-0.20919	0.3881	-0.539	0.596130			
		RH	0.14293	0.0334	4.279	0.000405			
Quercus castanea	Flowering	Intercept	-16.18676	5.07243	-3.191	0.00481	193.4619	203.4619	209.3522
		CO	0.0926	0.01845	5.019	7.61e-05			
		Tmean	0.32317	0.40411	0.8	0.43376			
		Tmin	1.07067	0.39177	2.733	0.01322			
		RH	-0.02146	0.03649	-0.588	0.56347			
Quercus rugosa	Flowering	Intercept	36.71078	5.69754	6.443	3.55e-06	142.6982	152.6982	158.5885
		CO	0.113	0.01353	8.352	8.78e-08			
		Tmean	-3.00157	0.52202	-5.75	1.53e-05			
		Tmin	3.26762	0.60595	5.393	3.33e-05			
		RH	-0.38161	0.05429	-7.029	1.08e-06			
Quercus martinezii	Fruiting	Intercept	5.973478	1.180619	5.06	6.96e-05	269.8209	279.8209	285.7112
		CO	-0.205199	0.014682	-13.977	1.90e-11			
		Tmean	0.122882	0.103052	1.192	0.248			
		Tmin	0.101172	0.109809	0.921	0.368			
		RH	0.016449	0.009892	1.663	0.113			
Quercus castanea	Fruiting	Intercept	-3.23377	1.006949	-3.211	0.00459	465.8365	475.8365	481.7267
		CO	-0.083438	0.009032	-9.238	1.86e-08			
		Tmean	0.727313	0.087342	8.327	9.19e-08			
		Tmin	-0.732248	0.111712	-6.555	2.82e-06			
		RH	0.08216	0.010575	7.769	2.58e-07			
Quercus rugosa	Fruiting	Intercept	0.61628	1.22888	0.501	0.621784	249.305	259.305	265.1952
		CO	-0.04801	0.01359	-3.534	0.002219			
		Tmean	0.06317	0.10523	0.6	0.555411			
		Tmin	-0.07914	0.1295	-0.611	0.548376			
		RH	0.0488	0.01214	4.018	0.000735			
Quercus martinezii	Seed dispersal	Intercept	-44.19889	22.53646	-1.961	0.0647	24.84621	34.84621	40.73647
		CO	-0.04598	0.0815	-0.564	0.5792			
		Tmean	3.72409	1.81315	2.054	0.0540			
		Tmin	-1.0283	1.23498	-0.833	0.4154			
		RH	-0.036	0.11861	-0.304	0.7648			
Quercus castanea	Seed dispersal	Intercept	-455.717	5454.95	-0.084	0.934	13.93117	23.93117	29.82144
		CO	0.204	27.266	0.007	0.994			
		Tmean	28.061	536.067	0.052	0.959			
		Tmin	-15.116	498.593	-0.03	0.976			
		RH	2.139	35.88	0.06	0.953			
Quercus rugosa	Seed dispersal	Intercept	798.3665	6183.9774	0.129	0.899	14.28673	24.28673	30.17699
		CO	-0.5042	11.9254	-0.042	0.967			
		Tmean	61.4997	481.384	0.128	0.900			
		Tmin	-124.0605	975.9315	-0.127	0.900			
		RH	-10.058	78.5604	-0.128	0.899			

ns not significant = P > 0.05, GD global deviation, AIC Akaike information criterion, SBC Schwarz Bayesian criterion, Tmean mean temperature, Tmax maximum temperature, Tmin minimum temperature, CO canopy openness, RH relative humidity

Supplement 4. Results of the GAMLSS model for the activity index of inflorescence formation, flowering, fruiting, and seed dispersal for *Alamania punicea* growing on three *Quercus* species. In an oak forest in Yanhuitlán, Oaxaca.

Host tree species	Phenophase	Predictive Variable	Estimate	SE	t value	P	GD	AIC	SBC
Quercus martinezii	Inflorescence formation	Intercept	1.45841	3.77318	0.387	0.70341	174.9039	184.9039	190.7941
		CO	0.08762	0.01752	5.001	7.92e-05			
		Tmean	0.72195	0.29842	2.419	0.02575			
		Tmin	-1.04815	0.31009	-3.38	0.00314			
		RH	-0.05786	0.02713	-2.133	0.04618			
Quercus rugosa	Inflorescence formation	Intercept	19.55439	3.42567	5.708	1.68e-05	167.5219	177.5219	183.4122
		CO	0.07755	0.011	7.047	1.04e-06			
		Tmean	-0.89724	0.29216	-3.071	0.00629			
		Tmin	0.71231	0.33692	2.114	0.04794			
		RH	-0.20627	0.03073	-6.712	2.05e-06			
Quercus martinezii	Flowering	Intercept	6.33865	10.249	0.618	0.543613	48.18814	58.18814	64.07841
		CO	0.24815	0.04036	6.148	6.57e-06			
		Tmean	-2.97606	0.97588	-3.05	0.006594			
		Tmin	4.21897	1.01262	4.166	0.000524			
		RH	-0.21053	0.07077	-2.975	0.007784			
Quercus rugosa	Flowering	Intercept	5.60969	5.3809	1.043	0.310255	137.2147	147.2147	153.105
		CO	0.04409	0.02246	1.963	0.064429			
		Tmean	-1.62348	0.57297	-2.833	0.010620			
		Tmin	3.27776	0.7174	4.569	0.000210			
		RH	-0.20354	0.05188	-3.924	0.000912			
Quercus martinezii	Fruiting	Intercept	1.763493	3.258031	0.541	0.595	108.4756	118.4756	124.3659
		CO	0.008838	0.01886	0.469	0.645			
		Tmean	0.014332	0.284954	0.05	0.960			
		Tmin	-0.203345	0.307772	-0.661	0.517			
		RH	0.018049	0.025963	0.695	0.495			
Quercus rugosa	Fruiting	Intercept	3.04239	1.61696	1.882	0.0753	206.5164	216.5164	222.4066
		CO	-0.04432	0.01786	-2.482	0.0226			
		Tmean	-0.01559	0.13932	-0.112	0.9121			
		Tmin	-0.16549	0.1765	-0.938	0.3602			
		RH	0.03298	0.01627	2.027	0.0569			
Quercus martinezii	Seed dispersal	Intercept	0.43523	12.33349	0.035	0.972218	35.70544	45.70544	51.59571
		CO	0.19541	0.0423	4.62	0.000187			
		Tmean	0.21705	1.04135	0.208	0.837107			
		Tmin	-0.95443	1.07338	-0.889	0.385024			
		RH	-0.0329	0.09035	-0.364	0.719769			
Quercus rugosa	Seed dispersal	Intercept	13.35697	6.23275	2.143	0.0453	62.29572	72.29572	78.18599
		CO	0.0311	0.0335	0.928	0.3649			
		Tmean	0.59614	0.44993	1.325	0.2009			
		Tmin	-1.41821	0.65714	-2.158	0.0439			
		RH	-0.15797	0.05945	-2.657	0.0156			

ns not significant = P > 0.05, GD global deviation, AIC Akaike information criterion, SBC Schwarz Bayesian criterion, Tmean mean temperature, Tmax maximum temperature, Tmin minimum temperature, CO canopy openness, RH relative humidity

Supplement 5. Results of the GAMLSS model for the activity index of inflorescence formation, flowering, fruiting, and seed dispersal for *Oncidium brachyandrum* growing on three *Quercus* species. In an oak forest in Yanhuitlán, Oaxaca.

Host tree species	Phenophase	Predictive Variable	Estimate	SE	t value	P	GD	AIC	SBC
Quercus martinezii	Inflorescence formation	Intercept	-8.576251	8.832955	-0.971	0.34378	56.25503	66.25503	72.1453
		CO	0.155473	0.034028	4.569	0.00021			
		Tmean	1.283426	0.699896	1.834	0.08241			
		Tmin	-1.702585	0.7024	-2.424	0.02550			
		RH	0.005394	0.060033	0.09	0.92934			
Quercus rugosa	Inflorescence formation	Intercept	34.22855	6.48007	5.282	4.25e-05	109.0504	119.0504	124.9406
		CO	0.09846	0.01613	6.106	7.18e-06			
		Tmean	-2.50167	0.57663	-4.338	0.000354			
		Tmin	2.55691	0.6493	3.938	0.000883			
		RH	-0.35097	0.0604	-5.811	1.34e-05			
Quercus martinezii	Flowering	Intercept	-0.67422	19.21281	-0.035	0.97237	22.8578	32.8578	38.74807
		CO	0.34056	0.09101	3.742	0.00138			
		Tmean	-3.46465	1.95257	-1.774	0.09202			
		Tmin	5.17061	2.12574	2.432	0.02506			
		RH	-0.22111	0.1308	-1.69	0.10728			
Quercus rugosa	Flowering	Intercept	12.75287	8.66363	1.472	0.15739	78.12564	88.12564	94.01591
		CO	0.0812	0.03419	2.375	0.02824			
		Tmean	-2.64366	0.94835	-2.788	0.01174			
		Tmin	4.50636	1.21787	3.7	0.00152			
		RH	-0.29107	0.08838	-3.293	0.00382			
Quercus martinezii	Fruiting	Intercept	0.18282	2.90598	0.063	0.9505	105.8224	115.8224	121.7127
		CO	-0.04846	0.01968	-2.463	0.0235			
		Tmean	0.19689	0.25099	0.784	0.4424			
		Tmin	-0.17727	0.27271	-0.65	0.5235			
		RH	0.0296	0.02331	1.27	0.2194			
Quercus rugosa	Fruiting	Intercept	2.28841	1.58549	1.443	0.165	134.3606	144.3606	150.2509
		CO	-0.02379	0.01507	-1.579	0.131			
		Tmean	0.06694	0.13563	0.494	0.627			
		Tmin	-0.22453	0.1715	-1.309	0.206			
		RH	0.02596	0.0152	1.708	0.104			
Quercus martinezii	Seed dispersal	Intercept	5.36519	23.90497	0.224	0.82481	27.45676	37.45676	43.34703
		CO	0.26163	0.07281	3.593	0.00194			
		Tmean	-0.83616	1.91896	-0.436	0.66794			
		Tmin	0.50629	1.80425	0.281	0.78204			
		RH	-0.14177	0.1635	-0.867	0.39672			
Quercus rugosa	Seed dispersal	Intercept	3.23385	13.03576	0.248	0.80674	27.00718	37.00718	42.89745
		CO	0.1441	0.04282	3.365	0.00325			
		Tmean	-1.36923	1.26868	-1.079	0.29399			
		Tmin	2.54686	1.62916	1.563	0.13448			
		RH	-0.19849	0.12303	-1.613	0.12315			

ns not significant = P > 0.05, GD global deviation, AIC Akaike information criterion, SBC Schwarz Bayesian criterion, Tmean mean temperature, Tmax maximum temperature, Tmin minimum temperature, CO canopy openness, RH relative humidity