

Original Article

# First steps to study the demography of vascular epiphytes in cities

Primeiros passos para estudar a demografia de epífitas vasculares em cidades

D. Mondragón<sup>a</sup>  and M. P. Mora-Flores<sup>a</sup> 

<sup>a</sup>Instituto Politécnico Nacional, Centro Interdisciplinario de Investigación para El Desarrollo Integral Regional – CIIDIR, Oaxaca, México

## Abstract

Urban ecosystems could jeopardize the existence of vascular epiphytes (VE) given that their occurrence is linked to phorophyte availability and particular climatic conditions. Despite reports of VE in cities, nothing is known about their demography. A first step in this direction is to describe their population structures (PS). We established the PS of VE present in urban parks in Oaxaca City (Mexico), addressing the following questions: 1) what is their demographic status? and 2) are there differences in the structure of populations growing in native versus exotic phorophytes? During 2021, we censused all the trees in six urban parks, recording their origin (native or exotic), the epiphytic species found on them and the development stages present in each VE population. Overall, five VE species were documented: *Tillandsia ionantha*, *T. makoyana*, *T. sp.*, *T. schiedeana* and *T. recurvata* (Bromeliaceae); the first three with only one individual and the latter two with 95 and 5,694, respectively. A MANOVA test indicated significant differences in PS between *T. recurvata* (type I structure, suggesting a growing population) and *T. schiedeana* (type III structure, suggesting a senile population) (Wilkes'  $\lambda=0.821$ , F-Ratio= 11.96  $P<0.001$ ). PS showed no differences related to tree origin. Our results indicate that it is necessary to conduct demographic studies to have a more accurate idea of the current condition of vascular epiphytes in cities. For instance, even though we found five VE species, only one of them seems to have viable populations in Oaxaca city.

**Keywords:** host effect, population structure, public parks, *Tillandsia*.

## Resumo

Ecosistemas urbanos podem comprometer a existência de epífitas vasculares (EV), dado que sua ocorrência está ligada à disponibilidade de forófitos e condições climáticas particulares. Apesar dos relatos de EV nas cidades, nada se sabe sobre sua demografia. Um primeiro passo nessa direção é descrever suas estruturas populacionais (PS). Estabelecemos o PS dos EV presentes nos parques urbanos da cidade de Oaxaca (México), abordando as seguintes questões: 1) qual é a sua situação demográfica? e 2) existem diferenças na estrutura das populações crescendo em forófitos nativos versus exóticos? Durante o ano de 2021, realizamos o censo de todas as árvores em seis parques urbanos, registrando sua origem (nativa ou exótica), as espécies epífitas encontradas nelas e os estágios de desenvolvimento presentes em cada população de EV. Ao todo, cinco espécies de EV foram documentadas: *Tillandsia ionantha*, *T. makoyana*, *T. sp.*, *T. recurvata* e *T. schiedeana*; as três primeiras com apenas um indivíduo e as duas últimas com 5.694 e 95, respectivamente. Um teste MANOVA indicou diferenças significativas no PS entre *T. recurvata* (estrutura tipo I, sugerindo uma população crescente) e *T. schiedeana* (estrutura tipo III, sugerindo uma população senil) (Wilkes'  $\lambda=0,821$ , F-Radio= 11,96 e  $P < 0,001$ ). PS não apresentou diferenças relacionadas à origem da árvore. Os resultados do presente trabalho indicam a necessidade de se realizar estudos demográficos para se ter uma ideia mais precisa da condição atual das epífitas vasculares nas cidades. Embora tenhamos encontrado cinco espécies de VE, apenas uma delas parece ter populações viáveis na cidade de Oaxaca.

**Palavras-chave:** efeito hospedeiro, estrutura populacional, parques públicos, *Tillandsia*.

## 1. Introduction

Vascular epiphytes are plants that rely on a phorophyte, usually a tree or a bush, without feeding directly from it, as parasitic plants do (Benzing, 1990). These plants represent 9% of vascular flora (Zotz, 2013) and play important roles in ecosystem functions, participating in hydrological and nutrient cycles (Gotsch et al., 2016; Hargis et al., 2019; Mendieta-Leiva et al., 2020; Pereira et al., 2022). Furthermore, vascular epiphytes increase the biodiversity of tropical

ecosystem (Gentry and Dodson, 1987; Catchpole and Kirkpatrick, 2011). They also provide shelter, food and water for numerous organisms ranging from bacteria to mammals (Mondragon and Cruz-Ruiz, 2008; Mondragon et al., 2015; Godoy-Güinao et al., 2018), to the extent that some, especially trash-basket epiphytes, have been considered secondary foundation species because they facilitate the establishment of other species (Ortega-Solis et al., 2021).

\*e-mail: dmondragon@ipn.mx

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Not all trees are suitable phorophytes for vascular epiphytes. Their potential as phorophytes depends on morphological (bark type, branch angle, deciduousness, etc.) and physicochemical (pH, water holding capacity of the bark, stem nutrient content and throughfall, etc.) features, which altogether create different micro niches for vascular epiphytes (Callaway et al., 2002; Einzmann et al., 2014; Ticktin et al., 2016; Zarate-García et al., 2020). Even though most epiphytes are generalists, they frequently show preference for certain phorophytes (Vergara-Torres et al., 2010; Wagner et al., 2021). Consequently, their presence and abundance are linked to the availability of their preferred phorophytes.

Other factors that strongly regulate the occurrence of vascular epiphytes are humidity and temperature (Benzing, 1990; Zotz, 2016). Their reliance on atmospheric sources of water due to their lack of a water reservoir (such as soil for terrestrial plants), make vascular epiphytes very susceptible to water stress (Benzing, 1990; Laube and Zotz, 2003; Zotz, 2016). In epiphytes with CAM photosynthesis, high temperatures, high evaporative demands and excessive exposition to solar radiation, tend to promote CAM-idling, a metabolic variation where the CO<sub>2</sub> produced by mitochondrial respiration becomes the only carbon source for photosynthesis. When vascular epiphytes go into CAM-idling, only survival, but not growth, is possible (Benzing, 1998). This explains why the presence of vascular epiphytes is quite restricted in human disturbed habitats and when present, their diversity is mostly limited to drought tolerant species (Williams-Linera et al., 1995; Köster et al., 2009; Parra-Sanchez and Banks-Leite, 2020).

Typically, in cities, most native vegetation has been displaced and any remains are usually confined to few vegetation fragments, limiting the availability of phorophytes for vascular epiphytes to the bushes and trees present on those fragments, in public parks, in private gardens or along roadsides. Besides the low availability of trees, in cities most native species have been replaced by exotic ones (Nielsen et al., 2014; Morgenroth et al., 2016; Chang et al., 2021) that are not necessarily adequate phorophytes for vascular epiphytes. Additionally, the trees growing in urban settings, particularly along streets, suffer border effects including increased temperature and exposition to solar radiation (Murcia, 1995), which have been demonstrated to have a strong negative impact on vascular epiphyte communities (Bianchi and Kersten, 2014; Parra-Sanchez and Banks-Leite, 2020). Additionally, air temperature in cities tends to be 1 to 3 °C higher than in surrounding rural and pristine vegetation areas, as a result of the heat island effect (Oke, 1982; Yang et al., 2019). Moreover, increased exposure to short-wave (Dahlhausen et al., 2018) and thermal radiation from buildings, asphalt, car tops, and concrete (Bassuk and Whitlow, 1985), could also strongly limit the presence of epiphytes in urban settings.

Despite all the unfavorable factors mentioned, vascular epiphytes have been reported in cities (Dislich and Mantovani, 1998; Bhatt et al., 2015; Jiménez-Orozco et al., 2019; Alvim et al., 2021; Alex et al., 2021; Figueiredo et al., 2021). This leads to our central question for this study: are urban epiphytes only declining remnants

of preexisting populations or perhaps isolated results of fortuitous dispersal events which don't necessarily represent established populations which will persist in the future? As Einzmann et al. (2014) mentioned, in order to understand how vascular epiphytes are dealing with urban environments it is necessary to develop demographic studies of their populations.

A first step in this direction involves examining the structure of these urban populations of epiphytes by looking at the proportion of individuals corresponding to each of the life stages recognized for these plants. This provides a quick and general notion of the demographic status of a population (Oostermeijer et al., 1994; Landi and Angiolini, 2011; Ramírez-Martínez et al., 2018). Landi and Angiolini (2011) developed the following classification to describe populations based on their demographic structure:

- Type I or dynamic population: the structure is dominated by a high proportion of individuals in the early life stages, suggesting recruitment and, in general terms, indicating the population is growing.
- Type II or stable population: characterized by a higher proportion of intermediate-stage individuals and adults, suggesting that the population is stable.
- Type III or senescent population: this structure is dominated by adult individuals, with few or no individuals in early life stages, suggesting a poor recruitment rate and hence, a declining population.

To contribute with baseline data to understand how epiphytes are behaving in urban environments, we determined the population structure of the species found in six public parks of Oaxaca city (México). By doing this we aimed to address the following questions: 1) what is the demographic status of these vascular epiphytes? and, 2) are there differences between the structure of populations growing in native *versus* exotic phorophytes? Due to the harsh conditions that urban environments represent for many epiphyte species, we expected to find mostly senescent populations with the exception of drought tolerant species for which we expected to find stable or dynamic populations (Williams-Linera et al., 1995; Köster et al., 2009; Parra-Sanchez and Banks-Leite, 2020). We also expected to find a higher proportion of dynamic populations growing on native trees than on exotic species. This prediction is based on results by Ramírez-Martínez et al. (2018) who found that epiphytes presented stable or dynamic population structures on their preferred phorophytes.

## 2. Methods

### 2.1. Study area

The city of Oaxaca de Juárez is the capital of the state of Oaxaca, Mexico, and has an extension of 85.48 km<sup>2</sup>. It is located in the Valles Centrales region between coordinates 17°01' and 17°10' N and 96°40' and 96°47' W, at an average altitude of 1555 m.a.s.l. According to Köppen's classification, different climates occur in the city, with 40% of its surface showing a semi-dry semi-humid climate (BS1h), an average

annual temperature of 22.2 °C and average rainfall of 727.2 mm (INEGI, 2021).

To establish the population structure of vascular epiphytes found in Oaxaca city, we chose six of its largest public parks: El Llano (12 natives and 15 exotics phorophyte species), Jardín Conzatti (13 and 17), La Alameda (9 and 9), El Zócalo (7 and 3), Jardín Labastida (5 and 9) and Madero Park (4 and 12) (Figure 1).

In each park we conducted a census of all the trees present recording the number, size, and species of all epiphytic individuals growing in each phorophyte. We considered any group of individuals belonging to the same epiphytic species growing in a tree, as a population (Valverde and Bernal, 2010). Additionally, we documented the species and type of origin of each phorophyte (native or exotic). We defined a species as native if its natural distribution includes Oaxaca state.

Even though we found five vascular epiphyte species in our park census, three species were represented by only one individual (*Tillandsia ionantha* Planch, *T. makoyana* Baker, *T. sp*). Therefore, our analyses of population structure were restricted to *T. recurvata* (Gaudich.) Barker and *T. schiedeana* Steud., based on 5,694 and 95 individuals, respectively.

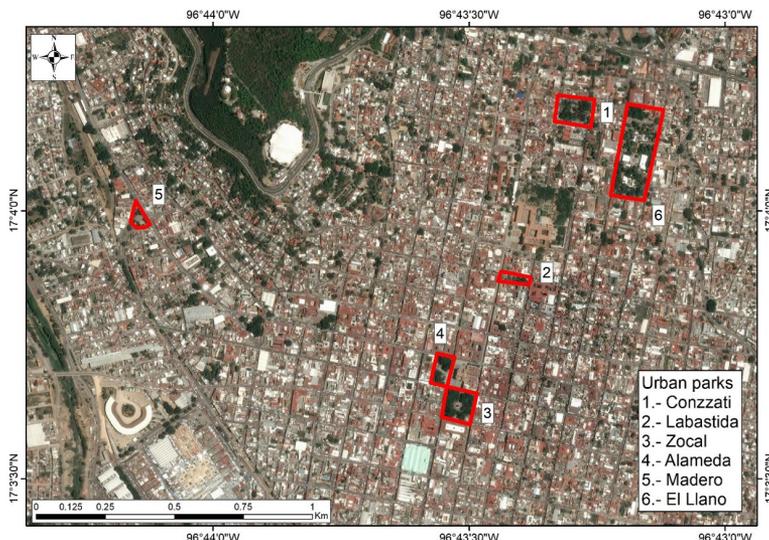
Since both species analyzed have a semi spherical shape, we decided to use diameter as a size measure combined with the presence of reproductive structures to establish life cycle stages, assuming that individuals belonging to the same stage present similar demographic behavior (Lefkovitch, 1965; Caswell, 2000; Mondragón et al., 2004; Valverde and Bernal, 2010). We established four size stages for each species: seedling (s), infant (i), juvenile (j), and adult (a). For *T. recurvata*: s = individuals with diameter < 1cm and leaves disposed as a fan; i = individuals with diameter < 2 cm and j = 2-5 cm in diameter, a = diameter > 5cm. For *T. schiedeana*: s = individuals with diameter < 1cm and leaves disposed as a fan, i = individuals with diameter < 2 cm, j = 2-9 cm in diameter, a = diameter > 9 cm.

After the census, we calculated the proportion of individuals belonging to each stage for each population. Subsequently, the resulting structures were classified according to the proposal by Landi and Angiolini (2011). To compare population structures between the two epiphytic species, and between the two phorophyte origins (native vs. exotic), we conducted a two-way multivariate analysis of variance (MANOVA) to detect any overall differences in the proportion represented by each life stage (response variable). When the MANOVA rendered significant differences, we then ran a univariate ANOVA (Zar, 2014).

### 3. Results

We sampled a total of 475 trees (188 natives, 285 exotics and two dead ones). The five species of vascular epiphytes we found belong to the *Tillandsia* genus in the Bromeliaceae family; and all are drought resistant species. *T. recurvata* presented in all sample parks has a type I populations structures dominated by individuals of non-reproductive classes, suggesting they are growing populations, whereas *T. schiedeana* presented on the Jardín Conzatti and Llano, has a type III structures dominated by individuals of adult classes with evidence of poor recruitment, suggesting they are senile populations in decline (Figure 2). The MANOVA analysis indicated statistically significant differences between the two species in the proportion of individuals in each life-stage (Wilkes'  $\lambda = 0.821$ , F-Ratio= 11.96 P<0.001), while the ANOVA revealed differences only regarding the infantile (F= 23.20, P= < 0.001) and adult stages (F= 44.79, P= < 0.001) with a higher proportion of infantile individuals in *T. recurvata*, and a higher proportion of adults in *T. schiedeana*.

Since we found no statistically significant interaction between the *Tillandsia* species and phorophyte origin (Wilkes'  $\lambda = 0.920$ , F-Ratio= 4.79, P<0.001), we decided to



**Figure 1.** Parks in Oaxaca city sampled during 2021 in search of vascular epiphytes.

perform a MANOVA per bromeliad species to evaluate the effect of phorophyte origin on the population structures of each species. We found no statistical differences in the structure of epiphytic populations of either species growing in native vs. exotic phorophytes (*T. recurvata* Wilkes'  $\lambda = 0.969$ , F-Ratio= 1.63, P=0.168; *T. schiedeana* Wilkes'  $\lambda = 0.688$ , F-Ratio= 1.59, P=0.233) (Figure 3).

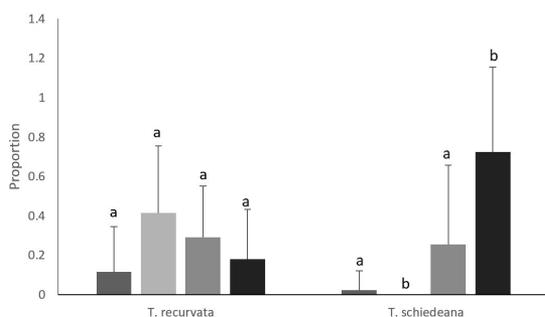
#### 4. Discussion

Our results shown that the demography status of vascular epiphytes in cities, depended of the species evaluated. On one hand, we have species capable to success in urban environments like *Tillandsia recurvata*. This species possesses one of the broadest distribution ranges of all the bromeliads, ranging from Florida to Argentina, with presence in almost every ecosystem, even in semi-desert environments (Smith and Downs, 1977). Different adaptations allow this species to thrive in the driest environments (e.g., CAM photosynthetic metabolism; presence of trichomes on both sides of the leaves that protect stomas preventing water loss (Loeschgen et al.,

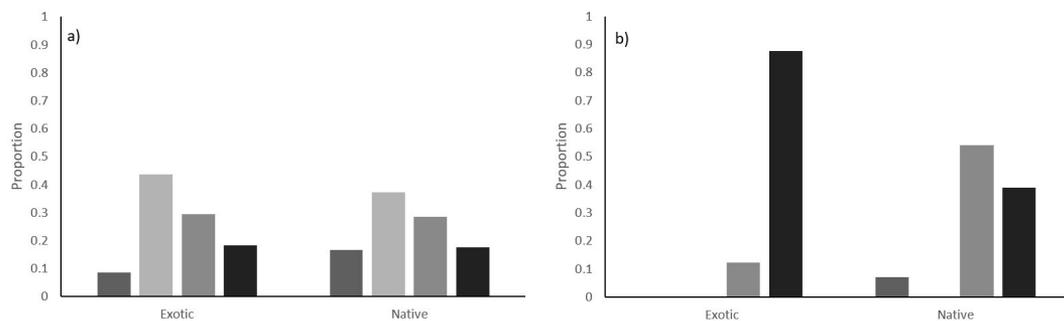
1993; Piazzetta et al., 2019) explaining why the species is considered the most xerophytic species among all epiphytes (McWilliams, 1992; Chaves and Rossatto, 2021). For instance, Pérez-Noyola et al. (2020) reported 100% vivipary in *T. recurvata* seeds evaluated in the Chihuahuan desert. Vivipary is germination inside the fruits and has been associated with thermoregulation, parental care, conspecific nursing and rapid seedling establishment, constituting an adaptation to harsh environments (Cota-Sánchez and Abreu, 2007; Pérez-Noyola et al., 2020). So, the presence of this trait could improve the establishment of *T. recurvata* in the harsh environment represented by Oaxaca city. However, to confirm this idea it is necessary to test the presence of vivipary in Oaxaca city, because Pérez-Noyola et al. (2020) found that the trait is not widespread in all *T. recurvata* populations. Another adaptation that could explain the dynamic population structure of this species in Oaxacan parks, is its ability to accumulate and filter air pollutants in cities without any decrement in its development (Graciano et al., 2003; Castañeda Miranda et al., 2016; Piazzetta et al., 2019).

Additionally, *T. recurvata* is one of the few vascular epiphytes classified as a weed (Claver et al., 1983), partly due to its huge reproductive capacity, both sexually (self-compatible, large number of fruits and seeds, relatively short periods for fruit ripening and size to first reproductive event) and asexually via vegetative propagation (Fernández et al., 1989; Orozco-Ibarrola et al., 2015; Chaves et al., 2021). This was reflected in the population structures recorded in Oaxaca city, with large proportions of seedlings and infants, evidencing good recruitment of new individuals. Such reproductive capacity together with the high abundance of *T. recurvata* already present in Oaxaca city, act synergistically to increase its abundance, producing heavy seed rain. According to different authors, epiphytic communities are reflections of the abundance and composition of propagule rain (Yeaton and Gladstone, 1982; Cascante-Marín et al., 2009; Zotz, 2016).

In addition, there are species that could not support the environmental conditions of cities like *T. schiedeana*, that despite its abundance of 95 individuals, the observed structures indicate a senescent or declining populations, with little evidence of recruitment. Even



**Figure 2.** Population structure of the two most abundant epiphytic species (*Tillandsia recurvata* and *Tillandsia schiedeana*) found in public parks in Oaxaca city during 2021. Columns represent development stages, from left to right: seedling, infantile, juvenile and adult. Bars marked with a “b” indicate a significant difference between species for that stage.



**Figure 3.** Population structures of (a) *Tillandsia recurvata* and (b) *Tillandsia schiedeana* on native or exotic phorophytes, in Oaxaca de Juarez during 2021. Columns represent development stages, from left to right: seedling, infantile, juvenile and adults. We found no statistical differences in the proportion of individuals in each development stage depending on phorophyte origin.

when the species has adaptations to deal with dry environments (e.g., CAM metabolism, peltate trichomes, CO<sub>2</sub> recycling (Loeschen et al., 1993), *T. schiedeana* has a smaller distribution range than *T. recurvata* and has lower abundances when growing simpatrically (Orozco-Ibarrola et al., 2015). This could result from the synergetic effect of: a) *T. recurvata* inhibiting the germination of other *Tillandsia* species, including *T. schiedeana* (Claver et al., 1983; Valencia-Díaz et al., 2012) and b) *T. schiedeana* producing less fruit and with longer ripening periods than *T. recurvata*. In our study site, *T. recurvata* could be limiting the germination of *T. schiedeana*, since almost all trees had individuals of *T. recurvata*, and we observed that *T. schiedeana* required a year from fruit production to seed dispersal, while *T. recurvata* only required six months (pers. obs.). But more studies are necessary to understand why the populations of *T. schiedeana* shows a type III structure.

On the other side, there are species as *T. ionantha* (Zocalo), *T. makoyana* (Madero Park) and *T. sp* (Conzatti). While only one individual, that could be the result of fortuitous long-distance dispersal events of the forest near the Oaxaca City, where those species has been documented (Rojas-Zárte and Mondragón, 2016). This dispersal event, could result in the establishment of new populations of these species or not. As many other epiphytic species *T. ionantha* and *T. makoyana* have mixed breeding systems that allow a single individual to produce viable seeds which can develop into adult individuals (Mondragon et al., 2015). However, these isolated dispersal events could result in populations which do not prosper, as in the case of *T. schiedeana*.

The lack of differences found in the structures of populations growing on native vs. exotic trees for both *Tillandsia* species, may be related to the fact that, within each host category, there was a mix of tree species with different morphological, physiological and chemical characteristics, which can impact the demographic behavior of epiphytic individuals (Einzmann et al., 2014; Martins et al., 2020; González and Ceballos, 2021; Ramírez-Martínez et al., 2022). This agree with results by Martins et al. (2020) showing a lack of preference between exotic and native hosts by vascular epiphytes in a Brazilian urban area. This lack of an effect of tree origin on associated species agrees with results by Berthon et al. (2021) who examined the relationship between native plants and animal biodiversity in urban areas. The authors found that the resources provided by the plants were more important predictors than their origin, but when in doubt, nativeness was a good surrogate of whether a plant would provide food for local animals. In our case, even when our result suggests that there are no differences in population structures related to tree origin, we recommend taking those results in consideration and developing an experiment to assess the effect of the origin of phorophytes over the demography of vascular epiphytes.

## 5. Conclusions

Our results showed that in order to have a real idea of the presence of epiphytes in cities, it is necessary not

only to consider richness or diversity, but also to develop studies of the state of their populations (Einzmann et al., 2014). Although in Oaxaca city we found five species of vascular epiphytes, in demographic terms we could say there is only one species, *T. recurvata*. Since population structure is a static picture of the state of a population, we strongly recommend developing long-term demographic studies in order to have a more accurate knowledge of the demographic status of the vascular epiphytes and the biotic and abiotic factors that are shaping their demographic behavior in urban ecosystems.

Through our study and the literature review conducted as part of it, we observed that the overabundance of *T. recurvata* in cities can jeopardize the survival of urban trees, since it can cause leaf abscission, branch death and ultimately the death of the phorophyte (Fernández et al., 1989; Claver et al., 1983; Pérez-Noyola et al., 2021). *T. recurvata* can also limit the presence of other epiphytes by producing substances that inhibit the germination of other epiphyte species (Valencia-Díaz et al., 2012). Consequently, we suggest conducting studies for their control without exterminating them; since these same plants are capable of capturing pollutants from the air (Graciano et al., 2003; Castañeda Miranda et al., 2016; Piazzetta et al., 2019); and increasing the biodiversity and functions of urban ecosystems by providing shelter for birds (Brush, 1999; Werner et al., 2015) and arthropods (Frank et al., 2004; Luna-Cozar et al., 2020). As Luna-Cozar et al. (2020) say “*T. recurvata* augments the quantity and/or quality of habitat in tropical dry forests that might increase arthropod survival and enhance resilience to disturbances and local extinctions, among other benefits”, this could apply for urban ecosystem, especially in cities with strong seasonality like Oaxaca de Juárez.

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