

First steps to study the demography of vascular epiphytes in cities

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Abstract

Urban ecosystems could jeopardize the existence of vascular epiphytes (VS), given that their occurrence is linked to phorophyte availability and particular climatic conditions. Despite reports of VS 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 VS present in urban parks in Oaxaca City, addressing the following questions: what is their demographic status? and 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 VS population. Overall, five VS species were documented: *Tillandsia ionantha*, *T. makoyana*, *T. sp.*, *T. recurvata* and *T. schiedeana*; the first three with only one individual and the latter two with 5,694 and 95, 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 VS species, only one of them seems to have viable populations in Oaxaca city.

Introduction

Vascular epiphytes are plants that rely on a host, 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 et al. 2011). They also provide shelter, food and water for numerous organisms ranging from bacteria to mammals (Mondragon et al. 2008, 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).

Not all trees are suitable phorophytes for vascular epiphytes. Their potential as hosts 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. 2015; 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 hosts.

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 CO₂ 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 perturbed 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; de Castro 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. (2015) 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. By doing this we aimed to address the following questions: what is the demographic status of these vascular epiphytes? and, 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 (William-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.

Methods

Study area

The city of Oaxaca de Juárez is the capital of the state of Oaxaca, Mexico, and has an extension of 85.48 km². 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 choose six of its largest public parks: El Llano, Jardín Conzatti, La Alameda, El Zócalo, Jardín Labastida and Madero Park (Fig. 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 < 1 cm and leaves disposed as a fan; i = individuals with diameter < 2 cm and j = 2–5 cm in diameter, a = diameter > 5 cm. For *T. schiedeana*: s = individuals with diameter < 1 cm 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).

Results

We sampled a total of 475 trees (188 native, 285 exotic trees 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 a type I populations structures dominated by individuals of non-reproductive classes, suggesting they are growing populations, whereas *T. schiedeana* presented a type III structures dominated by individuals of adult classes with evidence of poor recruitment, suggesting they are senile populations in decline (Fig. 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 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, $P = 0.233$) (Fig. 3).

Discussion

The five epiphytic species we found belong to the Bromeliaceae family, the second with most epiphytic members (1770 spp, Zotz 2016), and to the genus *Tillandsia*, the richest in epiphytic species (635 epiphytic species) among the Bromeliaceae (Zotz 2013). This over representation of bromeliad species, especially *Tillandsia* species in urban ecosystems has been already reported for America (Furtado and

Neto 2015; Santana et al. 2017; Alvim et al. 2021). It is probably owed to drought adaptations in *Tillandsia* species, together with the tolerance that some species of this genus have for air pollution (Benzing 2000; Graciano et al. 2003; Miranda et al. 2016; Piazzetta et al. 2019).

Furthermore, there is indication that cities and other human-altered ecosystems, have an over representation of xerophytic species that are tolerant to conditions related to human activity which cause microclimatic changes such as higher solar radiation, temperature and wind velocity, as well as lower humidity compared to undisturbed environments (Padmawathe et al. 2004; Wolf 2005; Cascante-Marín et al. 2006; Werner and Gradstein 2008).

The fact that only *T. recurvata* indicated viable populations structures could be linked to this species having 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 (Loeschen 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; Miranda et al. 2016; Piazzetta 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 the case of *T. schiedeana*, despite an abundance of 95 individuals, the observed structures indicate a senescent or declining populations, with little evidence of recruitment. Even when the species has

adaptations to deal with dry environments (e. g. CAM metabolism, peltate trichomes, CO₂ recycling (Loeche 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) *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 (per. Obs.). But more studies are necessary to understand why the populations of *T. schiedeana* shows a type III structure.

The presence of only one individual of *T. ionantha*, *T. makoyana* and *T. sp.* could be the result of fortuitous long distance dispersal events, that could result in the establishment of new populations of these species. 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. 2015; Martins et al. 2020; González and Ceballos 2021; Ramirez et al. in press). 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.

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 (Eizemman et al. 2015). 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 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; Miranda et al. 2016; Piazzetta 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 Juarez

Declarations

Ethics approval

We approve to comply the ethical standards.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Authors' contributions

D.M designed the study, did the fieldwork and wrote the manuscript.

MPM analyzed the data and prepared the figures.

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Availability of data and material

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Figures

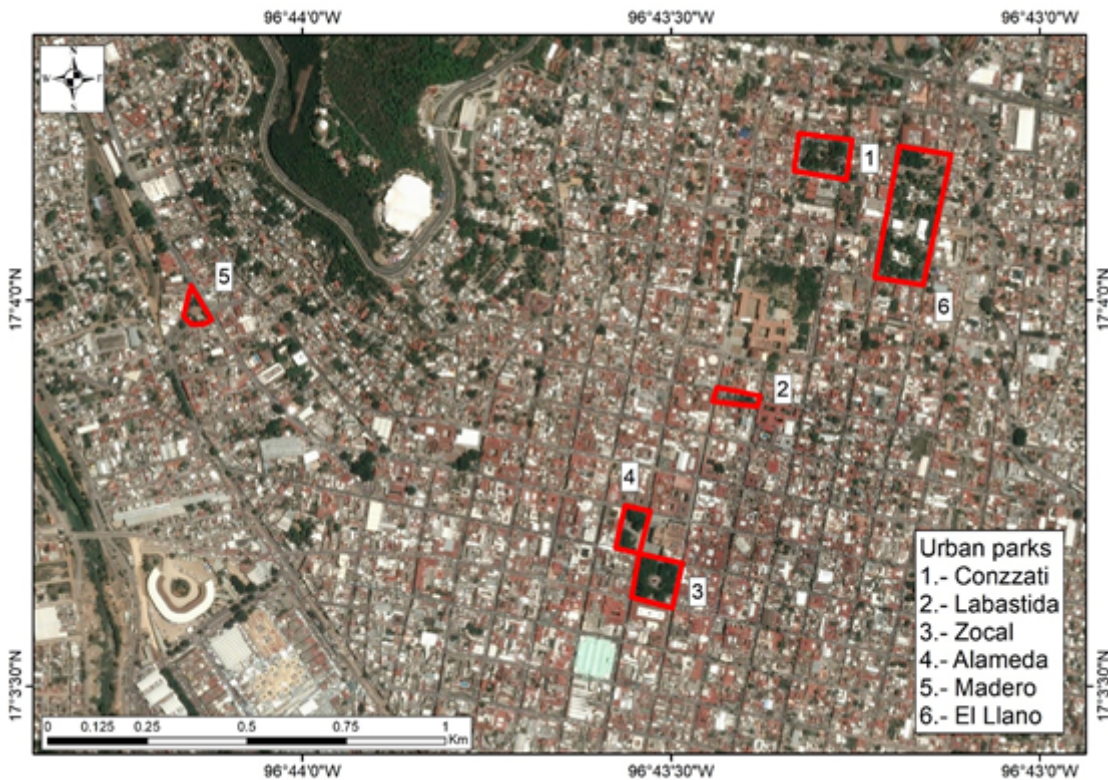


Figure 1

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

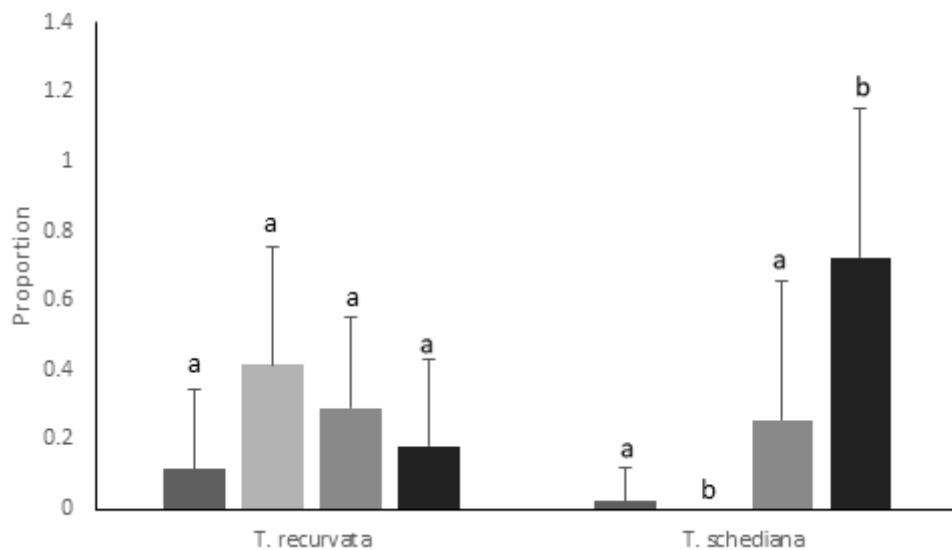


Figure 2

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.

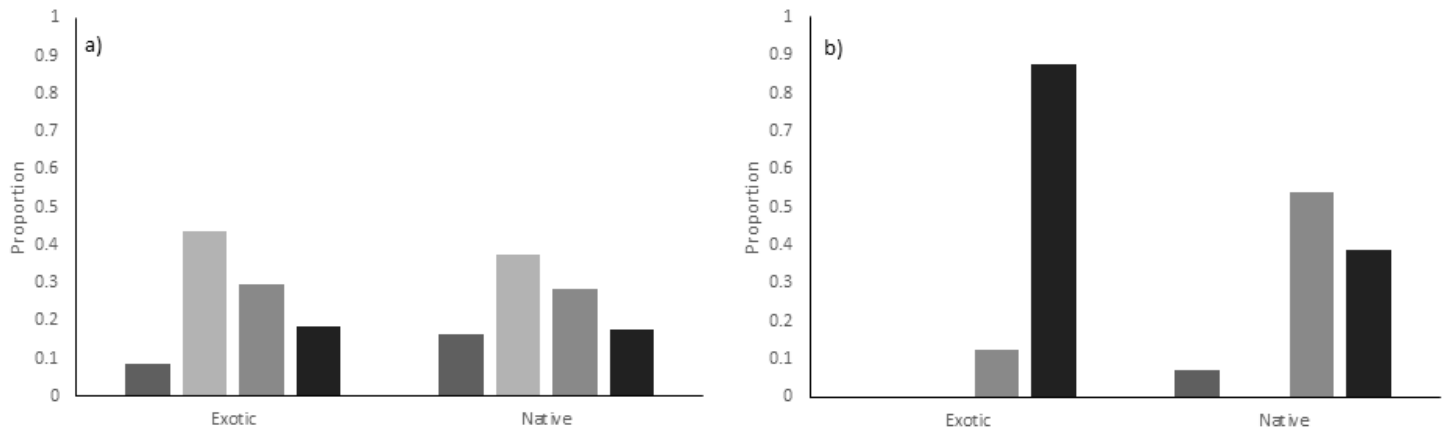


Figure 3

Population structures of a) *Tillandsia recurvata* and b) *Tillandsia schiedeana* 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.