

Research Article

Consequences of habitat fragmentation on the reproductive success of two *Tillandsia* species with contrasting life history strategies

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Abstract. Fragmentation of natural habitats generally has negative effects on the reproductive success of many plant species; however, little is known about epiphytic plants. We assessed the impact of forest fragmentation on plant–pollinator interactions and female reproductive success in two epiphytic *Tillandsia* species with contrasting life history strategies (polycarpic and monocarpic) in Chamela, Jalisco, Mexico, over three consecutive years. Hummingbirds were the major pollinators of both species and pollinator visitation rates were similar between habitat conditions. In contrast, the composition and frequency of floral visitors significantly varied between habitat conditions in polycarpic and self-incompatible *T. intermedia* but not in monocarpic self-compatible *T. makoyana*. There were no differences between continuous and fragmented habitats in fruit set in either species, but *T. makoyana* had a lower seed set in fragmented than in continuous forests. In contrast, *T. intermedia* had similar seed set in both forest conditions. These results indicate that pollinators were effective under both fragmented and continuous habitats, possibly because the major pollinators are hummingbird species capable of moving across open spaces and human-modified habitats. However, the lower seed set of *T. makoyana* under fragmented conditions suggests that the amount and quality of pollen deposited onto stigmas may differ between habitat conditions. Alternatively, changes in resource availability may also cause reductions in seed production in fragmented habitats. This study adds to the limited information on the effects of habitat fragmentation on the reproductive success of epiphytic plants, showing that even related congeneric species may exhibit different responses to human disturbance. Plant reproductive systems, along with changes in pollinator communities associated with habitat fragmentation, may have yet undocumented consequences on gene flow, levels of inbreeding and progeny quality of dry forest tillandsias.

Keywords: Bromeliaceae; fragmentation; hummingbird pollination; monocarpy; polycarpy; reproductive success.

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Introduction

Anthropogenic loss and fragmentation of natural habitats have profound consequences on the structure of biological communities and populations (Fahrig 2004). In plants, habitat fragmentation may impact the genetic and demographic structure of populations resulting in local or species-level extinctions, but more commonly, fragmentation has effects on plant growth and reproduction through changes in the biotic and abiotic environments (Honnay *et al.* 2005; Aguilar *et al.* 2008; Quesada *et al.* 2011). Thus, long-term persistence of plant populations in fragmented habitats ultimately depends on the effect habitat fragmentation has on abiotic factors like soil and microclimate, and on biotic processes, such as herbivory, pollination and seed dispersal (Bawa *et al.* 2003; Fuchs *et al.* 2003; Mix *et al.* 2006). A large number of studies have tested the impact of habitat fragmentation on pollination and plant reproductive success, many of them in tropical angiosperms; however, vascular epiphytes have received considerably less attention (Aguilar *et al.* 2006; Parra-Tabla *et al.* 2011).

Epiphytes are non-parasitic plants that grow on other plants (phorophytes) and they represent almost 10 % of vascular plant species (Benzing 1990; Zotz 2016). Vascular epiphytes are important elements of tropical forests due to their high taxonomic and functional diversity, and their role in supplying nutrients, water and shelter for other organisms (Zotz 2016). Moreover, epiphytes represent an important proportion of the total biomass in tropical forests, playing an essential role in forest nutrient fluxes and water retention (Hofstede *et al.* 1993; Zotz and Bader 2009). Epiphytes are considered particularly sensitive to habitat disturbance because they have low growth rates, delayed sexual maturity, limited seed dispersal and recruitment, and no seed bank (Turner *et al.* 1994; Martin *et al.* 2004; Cascante-Marín *et al.* 2009). In terms of habitat fragmentation, most studies on epiphytic plants show that the abundance, diversity, growth, dispersal and genetic parameters of epiphytes are negatively affected by fragmentation (González-Astorga *et al.* 2004; Flores-Palacios and García-Franco 2004; Werner and Gradstein 2008, 2009; Aguirre *et al.* 2010). This has been related to the dependence of epiphytes on their host trees, which makes epiphytes vulnerable to changes in the availability and traits of their phorophytes (Magrath *et al.* 2012; Sáyago *et al.* 2013). Surprisingly, the impact of habitat fragmentation on the pollination and reproductive success of vascular epiphytes is poorly known, except for a number of orchid species (e.g. Parra-Tabla *et al.* 2000, 2011; Murren 2002), and few species in the Cactaceae and the Bromeliaceae families (Aizen and Feinsinger 1994).

One aspect that deserves attention in studies of habitat fragmentation is related to the response of plants to habitat changes with respect to variation in plant life history strategies. In general terms, polycarpic or iteroparous species have more than one reproductive event during their lifetimes, whereas monocarpic or semelparous species have a single reproductive event, after which they die (Amasino 2009). Associated with each life history strategy is the number of offspring produced by reproductive event, which is generally higher in monocarpic than in polycarpic species (Cole 1954). Furthermore, monocarpic species often have breeding systems that allow them to reproduce in the absence of pollinators, such as autonomous self-pollination (Cole 1954; Brys *et al.* 2011). Monocarpism is generally associated to annual herbs, but it is also present across all plant life forms, including a reduced number of long-lived trees and epiphytic species (Benzing 2000; Poorter *et al.* 2005). While monocarpism is rare in epiphytes, it apparently evolved more than once in epiphytic bromeliads of the genus *Tillandsia* (Young and Augspurger 1991). Nonetheless, evidence is lacking for how long-lived monocarpic epiphytes respond to habitat fragmentation.

Bromeliads provide a relevant study system to assess the impact of habitat fragmentation on the reproduction of epiphytic plants as they are one of the most important components of vascular epiphyte communities in the Neotropics (Benzing 2000). In this study, we focused on two tropical dry forest *Tillandsia* species with contrasting life histories to determine the impact of habitat fragmentation on plant-pollinator interactions and the reproductive success of epiphytes with monocarpic and polycarpic life history strategies. To accomplish this, we compared pollinator assemblages, pollinator visitation rates, flower production, fruit set and seed set between fragmented and continuous habitats of a tropical dry forest across 3 years. We expected a greater reproductive display per individual in the monocarpic than in the polycarpic species associated with a greater pollinator visitation and therefore, little or no effect of habitat fragmentation on fruit and seed set. For the polycarpic species, we expected that lower pollinator visitation would lead to greater temporal variance in reproductive success and possibly a negative effect of fragmentation on reproduction.

Methods

Study site

The study was conducted in the region of Chamela, state of Jalisco, Mexico, in the northernmost natural protected

area of tropical dry forest in the Americas and surrounding areas (Fig. 1). Climate in this region is strongly seasonal with a wet season extending between July and October and a long dry season the rest of the year. Mean annual rainfall is 748 mm and mean annual temperature is 24.9 °C (García-Oliva et al. 2002). This location is one of the most species rich of all Neotropical dry forests including a number of species that are endemic to the Pacific coast of Mexico (Lott and Atkinson 2006). The most species-rich family is Fabaceae, followed by Euphorbiaceae and Convolvulaceae; the Bromeliaceae with 22 species occupies the sixth place in species richness in Chamela (Gentry 1995). Along the Pacific coast of Mexico, tropical dry forest habitats have been exposed to high levels anthropogenic disturbance (Trejo and

Dirzo 2000; Quesada and Stoner 2004). Cattle ranching and agriculture have fragmented most of the forest in the study region, except for the Chamela-Cuixmala Biosphere Reserve (13 142 ha; Sanchez-Azofeifa et al. 2008). Fragmentation of the continuous forest in this region was promoted in the 1950s under a government programme that advocated colonization of the Pacific coast of Mexico (Quesada et al. 2014).

Study species

The genus *Tillandsia* is the second most species-rich genus of the whole flora of Chamela. The study species: *Tillandsia intermedia* and *T. makoyana*, are both in the subgenus *Tillandsia*. These species were selected due to their contrasting reproductive strategies (monocarpic

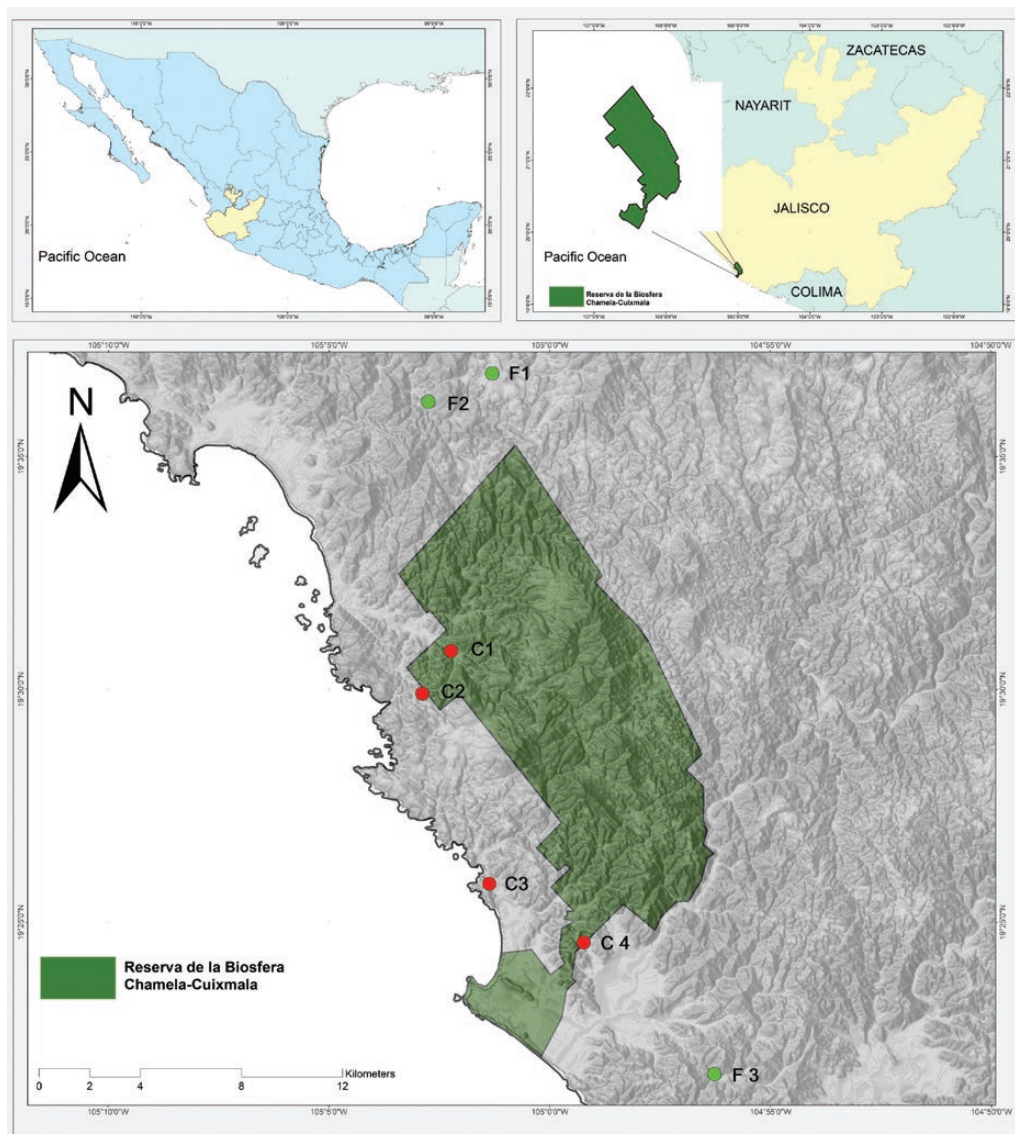


Figure 1. Map of the region of Chamela, Jalisco, Mexico, showing the continuous sites (C1–4) and fragmented sites (F1–3) where *Tillandsia intermedia* and *T. makoyana* were studied during 2008–10.

vs. polycarpic), shared pollinators (hummingbirds) and similar flowering seasons. Across the three study years, populations of both *Tillandsia* species flowered from April to early July each year, at all sites. Fruits develop and mature 1 year after flowering (Sáyago 2016).

Tillandsia intermedia is endemic to Mexico, mostly distributed along the central Pacific coast of the country (<https://www.gbif.org/species/2695234>). It is a polycarpic, clonal herb, characterized by hollow pseudobulbs that are formed by overlapping leaf bases; leaf blades are involute, and contorted (Fig. 2A). Inflorescences are spikes with pink tubular, perfect flowers that produce on average seven flowers (Sáyago 2016; Fig. 2B); anthesis lasts 1 day and flowers produce on average 0.7 μL of nectar (Arizmendi and Ornelas 1990; syn. *T. paucifolia*). This species has the potential for secondary dispersal by asexual means, when ramets (clones) detach.

Tillandsia makoyana is distributed from Mexico to Costa Rica. It is a monocarpic tank bromeliad with leaves

up to 70 cm long (Fig. 2C). Inflorescences are long compound spikes that produce on average 84 perfect flowers with light-purple tubular corollas (Fig. 2D); anthesis lasts 1 day and flowers produce, on average, 7 μL of nectar per day. *Tillandsia makoyana* is a single rosette and individuals may live several decades before their unique reproductive event. Plant senescence begins after flowering and most plants are dry by the time seeds are dispersed a year later (Sáyago 2016).

Sampling design

We sampled *T. makoyana* and *T. intermedia* at three continuous and three fragmented tropical dry forest sites for 3 years (2008–10). To determine areas with the highest density of adult individuals, we conducted a preliminary survey of all trails within the Chamela-Cuixmala Biosphere Reserve (CCBR) and forest fragments within a 30 km radius from the biological station. We found both *Tillandsia* species co-occurring at three fragmented sites

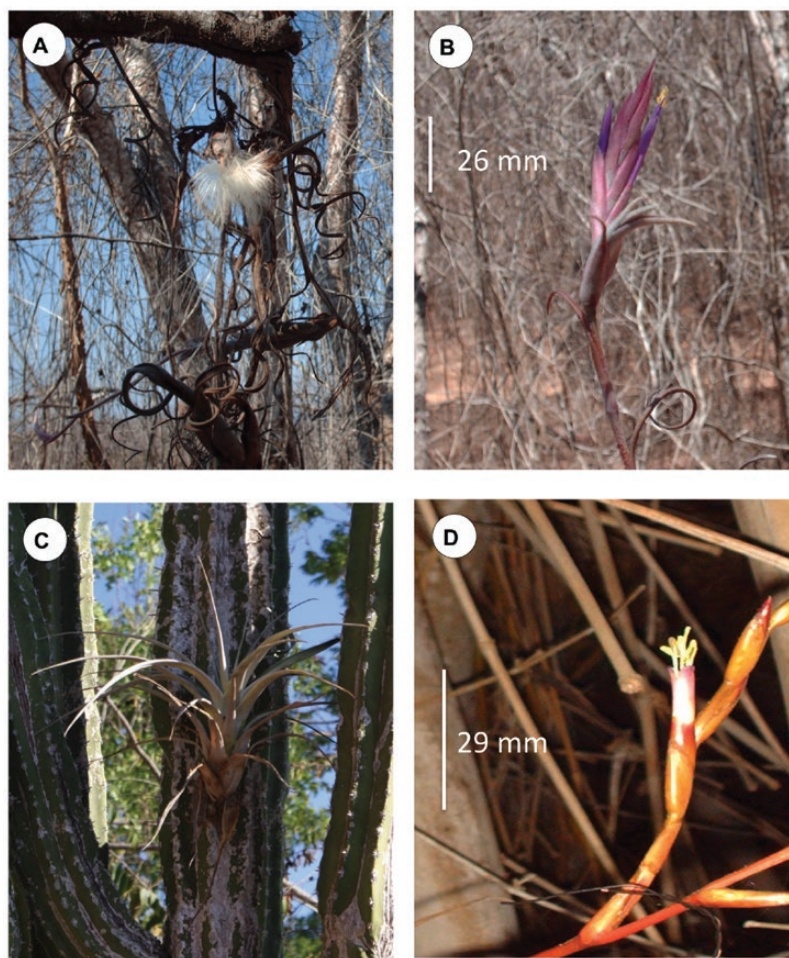


Figure 2. Plants and flowers of polycarpic *Tillandsia intermedia* and monocarpic *T. makoyana* from the region of Chamela, Jalisco, Mexico. Ramets of a single genet of *T. intermedia* dispersing seeds (A) and inflorescence showing one open flower (B); *T. makoyana* single ramet plant (C) and flower (D).

and at two continuous forest sites. Thus, we included two additional sites with a single species each within the continuous forest to have three replicate sites per species. The four study sites of continuous habitat were all within the large forested area that comprises the CCBR at least 200 m away from the forest edge (Fig. 1). Continuous forest sites shown near edges of the reserve are not actual forest edges, since the continuous forest extends beyond the official boundaries of the CCBR. The sites in closest proximity to each other were 2 km apart in a straight line, and the most distant ones were 13 km apart. The fragmented study sites were isolated remnants of old-growth forest trees including two to five adult phorophytes (400–700 m²), located within a matrix of human settlements, cultivated land, active cattle pastures and secondary growth; these sites were between 4 and 8 km away from the edges of the CCBR (Fig. 1).

Both *Tillandsia* species are generalist in terms of phorophyte use, occurring in at least 30 plant species distributed in 11–14 families; the most common phorophytes were *Apoplanesia paniculata* and *Cesalpinea eriostachys* for both species (Sáyago et al. 2013). At fragmented sites, reproductive individuals of the two *Tillandsia* species were selected from the few large trees that remained after forest clearance. These phorophyte species were a subsample of the phorophytes found within the continuous forest.

For both *Tillandsia* species, we selected reproductive individuals that could be accessed with ladders. Since *T. intermedia* is a clonal species, we chose individuals that were located on different branches of the tree that were clearly independent from other selected individuals. Reproductive individuals were identified by the presence of immature inflorescences.

Breeding system

At two sites in the continuous forest during the flowering season of 2011, we determined the capacity for autonomous self-pollination in 98 plants of *T. intermedia* (Site C2 in Fig. 1) and 28 plants of *T. makoyana* (Sites C1 and C2 in Fig. 1). We contrasted the fruit set of bagged inflorescences with the fruit set of open-pollinated inflorescences on different plants (since rosettes produce a single inflorescence during the season). We calculated the autofertility index (AFI) as the fruit set of bagged flowers divided by the fruit set of open-pollinated flowers (modified from Lloyd and Schoen 1992).

Pollinator visitation

We conducted pollinator observations during three consecutive years (2008–10). Overall, we observed 161 individuals of *T. intermedia* (59 in continuous forests and 102 in forest fragments) and 175 individuals of *T. makoyana*

(101 in continuous forests and 74 in forest fragments). This work was conducted on 73 different days for a total of 483 h for *T. intermedia* and 525 h for *T. makoyana* with a Sony Digital Handycam DCR-PC 100 for 3-h periods distributed throughout the day from 0700 to 1900 h. We recorded the identity of the visitor, the duration of the visit, and whether or not it contacted stigmas and anthers. The two *Tillandsia* species had exerted reproductive organs; therefore, contact with the pollinator's bill or body was always possible to determine from video recordings.

In 2008, we recorded visitation to flowers throughout day and night. However, no pollinator visits were recorded during night-time; therefore, the following years we only conducted observations during daytime. Pollinator visitation rates were estimated by dividing the total number of visits to an inflorescence by the number of hours observed; thus, we report number of visits per inflorescence per hour considering only daytime observations.

Female reproductive success

To test for differences in reproductive success between continuous and fragmented habitats, we tagged one inflorescence on each of 703 individuals of *T. intermedia* (329 in continuous and 374 in fragmented) and 226 individuals of *T. makoyana* (158 in continuous and 68 in fragmented) over 3 years (2009–11). We quantified the total number of flowers and mature fruits produced per inflorescence. The fruit set of each plant was calculated as the total number of fruits divided by the total number of flowers produced per inflorescence each year.

Seed production was quantified from fruits collected in 2011 from 64 individuals of *T. intermedia* (35 in continuous and 29 in fragmented) and 65 individuals of *T. makoyana* (38 in continuous and 27 in fragmented). Seeds were counted on 1–3 fruits per individual, depending on fruit availability. Seeds were considered viable if they had a fully developed endosperm and coma (filamentous structure that allows dispersal and attachment to substrate). Smaller wrinkled seeds were classified as aborted seeds. The sum of viable and aborted seeds was considered the total number of ovules produced per ovary.

Statistical analyses

Statistical analyses were conducted through generalized linear mixed models using PROC GLIMMIX in SAS (SAS Institute Inc. 2008). Since we were interested in understanding the temporal effect of habitat fragmentation on plant reproductive success, we included year (2008–10) and habitat condition (continuous vs. fragmented) as fixed factors. The interaction term between fixed

factors was eliminated from the model because it was not statistically significant for either *Tillandsia* species. Site was considered a random factor nested within habitat condition. Response variables included: number of flowers, number of fruits, and pollinator visitation rates (following a Poisson distribution with a log link function), ovule number (following a normal distribution), and fruit and seed set (following a binomial distribution with a logit link function). Back-transformed means were obtained using the *ilink* function. *P*-values for multiple comparisons were Tukey-adjusted. For number of ovules and seed set (number of viable seeds/number of ovules) a simple analysis of variance was performed to assess differences between continuous and fragmented conditions, since these variables were only measured for a subset of individuals during 2011.

Results

Breeding system

In *T. intermedia*, the mean fruit set (\pm SEM) of open-pollinated inflorescences was 32 % (\pm 12.1), and there was no fruit production in bagged inflorescences with pollinators excluded. In *T. makoyana*, the mean fruit set of open-pollinated inflorescences was 40 % (\pm 10.6), while the fruit set of bagged inflorescences was 19 % (\pm 4.8). The AFI, an estimate of the potential for autonomous self-pollination, was zero for *T. intermedia* and 0.47 for *T. makoyana*.

Pollinator assemblages and visitation rates

Pollinator observations revealed that flowers of *T. intermedia* and *T. makoyana* are visited by hummingbirds and bees, but hummingbirds are the predominant pollinators under both landscape conditions. Hummingbirds

generally visited flowers for 1–2 s and they contacted both stigmas and anthers on every visit, therefore, hummingbirds can be considered legitimate pollinators. Secondary pollinators included orchid bees (*Euglossini*) and stingless bees (*Meliponini*), the former being rare and present only in continuous forest sites. Stingless bees, the second most abundant group of floral visitors, contacted the reproductive structures 83 % of their visits and spent long periods of time on each flower (5.4 ± 2.8 minutes per visit). In all cases, bees moved to neighbouring flowers and plants on the same branch before moving out of sight.

Although pollinator functional groups did not differ between habitat conditions, the relative abundances of different visitors significantly changed with habitat fragmentation, particularly in the case of *T. intermedia* (Table 1). In this species, the frequency of visitation by stingless bees increased in forest fragments, as well as visitation by the broad-billed hummingbird *Cyanthus latirostris*, a species that was extremely rare at *Tillandsia* flowers in the continuous forest.

Visitation rates (visits per inflorescence per hour) were similar between continuous and fragmented forests for both species (*T. intermedia* $F_{1,4} = 3.7$, $P = 0.13$; *T. makoyana* $F_{1,4} = 0.03$, $P = 0.86$; Fig. 3A), although there was a trend for higher visitation in forest fragments, particularly evident in *T. intermedia*. There was temporal variation for both species, with visitation being higher in 2010 than in previous years (*T. intermedia* $F_{2,149} = 6.64$, $P < 0.005$; *T. makoyana* $F_{2,167} = 11.98$, $P < 0.0001$; Fig. 3B).

Female reproductive success

Tillandsia makoyana individuals produced 10 times as many flowers as *T. intermedia* plants in a single reproductive episode. Likewise, the number of fruits produced

Table 1. Pollinator assemblages of *Tillandsia intermedia* and *T. makoyana* recorded during 2008–10 in continuous and fragmented tropical dry forest sites in the region of Chamela, Jalisco, Mexico. Values indicate percent number of visits by each animal taxon that contacted the reproductive organs of flowers. *N* is the total number of legitimate visits to inflorescences observed in each habitat condition. Analyses of differences in pollinator composition between continuous and fragmented habitats are shown for each *Tillandsia* species (*** $P < 0.0001$).

Floral visitor	<i>T. intermedia</i>		<i>T. makoyana</i>	
	Continuous (N = 80)	Fragmented (N = 356)	Continuous (N = 1059)	Fragmented (N = 716)
<i>Amazilia rutila</i>	75	42	80	82
<i>Cyanthus latirostris</i>	0	21	1	2
<i>Heliomaster constantii</i>	0	2	0.5	4
<i>Euglossa</i> sp. (bee)	11	0	0.5	0
Meliponinae (bee)	14	35	18	12
Chi-square value	16.98***		0.02	

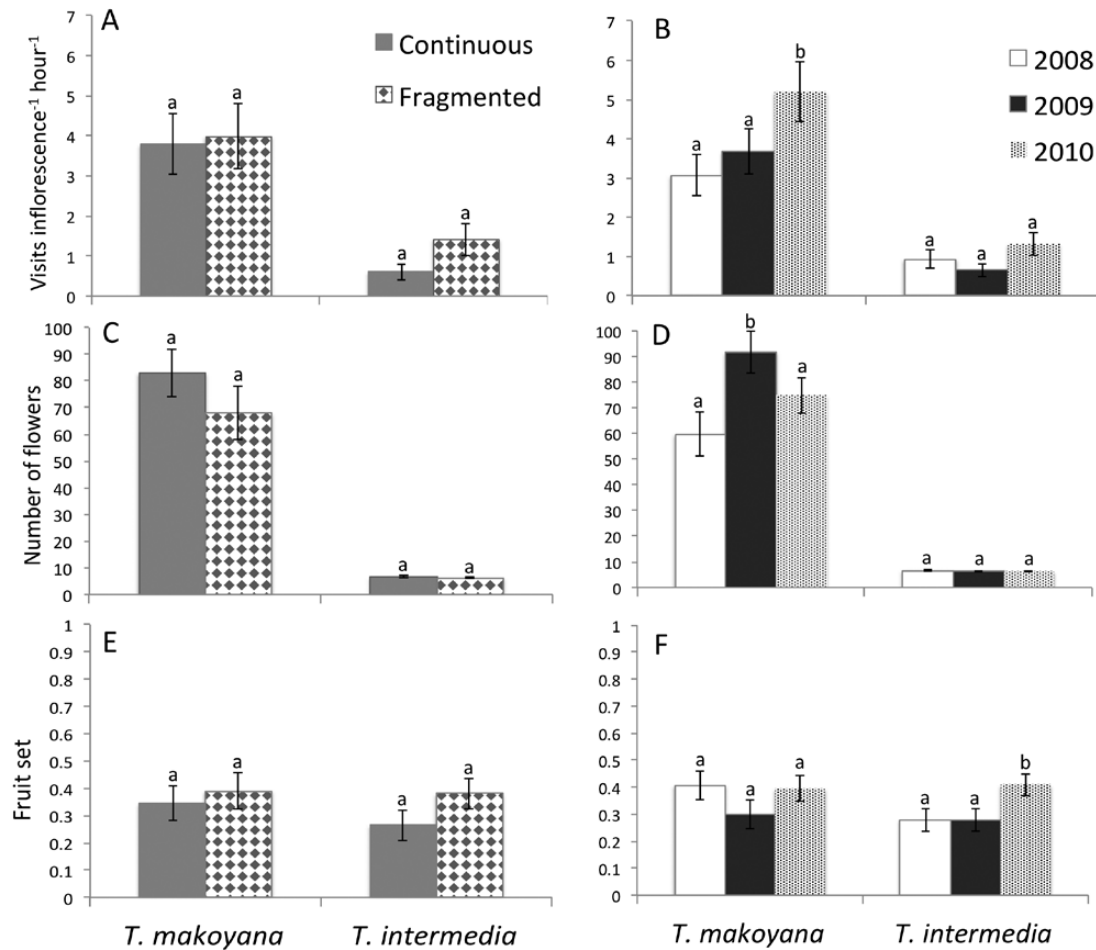


Figure 3. Pollinator visitation (visits per inflorescence per hour) (A and B), flower production per plant (B and C) and fruit production (E and F) of polycarpic *Tillandsia intermedia* and *T. makoyana* during 2008–10 at continuous and fragmented sites in the region of Chamela, Jalisco, Mexico.

by *T. makoyana* individuals 10-folded the fruit production of *T. intermedia* individuals. In absolute terms, *T. makoyana* individuals produced on average 3800 seeds per ramet per reproductive episode, 14 times more seeds than *T. intermedia* individuals, which produced on average 260 seeds per ramet.

When comparing flower production per individual between habitat conditions, both species produced a similar number of flowers in continuous and fragmented forests (*T. intermedia* $F_{1,4} = 1.3, P = 0.32$; *T. makoyana* $F_{1,4} = 0.3, P = 0.60$; Fig. 3C). The temporal analysis indicated that flower production was similar across time for *T. intermedia* ($F_{2,695} = 2.0, P = 0.13$; Fig. 3D), but differed between years for *T. makoyana*, with greater flower production in 2009 ($F_{2,220} = 8.1, P < 0.0005$; Fig. 3D).

The number of fruits produced per inflorescence by *T. intermedia* was similar in continuous and fragmented forests ($F_{1,4} = 1.0, P = 0.37$; Table 2), but it was higher in 2010 than in the previous 2 years ($F_{2,695} = 11.6,$

Table 2. Mean number of ovules, proportion of viable seeds \pm SE (%) produced during 2011 by *Tillandsia intermedia* and *T. makoyana* under continuous and fragmented conditions in the tropical dry forest of Chamela-Cuixmala, Mexico. Numbers in bold indicate significantly different means at $P > 0.05$.

	<i>T. intermedia</i>		<i>T. makoyana</i>	
	Continuous	Fragmented	Continuous	Fragmented
Ovules	173 \pm 5.7	164 \pm 6.1	171 \pm 8.9	181 \pm 9.9
Seed set	78 \pm 2.8	79 \pm 2.7	86 \pm 2.4	77 \pm 4.1

$P < 0.0001$). The proportion of flowers becoming fruits (fruit set) did not differ between continuous and fragmented forests for *T. intermedia* ($F_{1,4} = 2.2, P = 0.22$; Fig. 3E), but fruit set was higher in 2010 than in previous years ($F_{2,695} = 17.7, P < 0.0001$; Fig. 3F). The mean number of ovules did not differ between continuous and fragmented forests ($F_{1,58} = 1.22, P = 0.273$; Table 2), nor did seed set ($F_{1,58} = 0.14, P = 0.714$; Table 2).

In *T. makoyana* individuals, the mean number of fruits produced per inflorescence was similar between habitat conditions ($F_{1,4} = 0.02$, $P = 0.893$; Table 2), and years ($F_{2,220} = 0.3$, $P = 0.76$). Fruit set did not differ between habitat conditions ($F_{1,4} = 0.25$, $P = 0.64$; Fig. 3E), but differed between years ($F_{2,220} = 4.6$, $P = 0.01$; Fig. 3F). Ovule number did not differ between conditions either ($F_{1,60} = 0.55$, $P = 0.460$; Table 2); however, seed set was higher in continuous than in fragmented forest ($F_{1,60} = 4.3$, $P < 0.05$; Table 2).

Discussion

Habitat fragmentation generally has negative consequences on the reproductive success of plants; however, some species show positive or no responses to fragmentation (Aguilar et al. 2006, 2008). The few studies that include vascular epiphytes, all of them polycarpic species, have found contrasting results: some species are negatively affected by fragmentation (*Rhipsalis lumbricoides*, *Tillandsia ixioides*, Aizen and Feinsinger 1994; *Myrmecophila christinae*, *Oncidium ascendens*, Parra-Tabla et al. 2000, 2011), while other species show temporal variation ranging from negative to positive effects across years (*Catasetum viridiflavum*, Murren 2002). Adding to this diversity of effects, this study showed that, despite differences in life history strategies, most reproductive variables in *T. intermedia* and *T. makoyana* did not differ between habitat conditions. The only variables that changed with fragmentation were the composition of pollinator assemblages in *T. intermedia*, and seed set in *T. makoyana*, which was lower in fragmented habitats. These results may be related to intrinsic plant traits such as breeding system and floral display, and to external factors such as the availability of resources or pollinators.

Plant reproductive systems are important to understand the impact of habitat fragmentation on plant fitness because they relate to the capacity of plants to set seed in the absence of conspecifics or pollinators (Aguilar et al. 2006, 2008). Epiphytism has been associated with self-compatible and autonomous breeding systems in various plant families (Bush and Beach 1995; Martín-Rodríguez et al. 2015); however, in the Bromeliaceae, both self-compatible and self-incompatible breeding systems have been documented (Matallana et al. 2010). Given that monocarpic species have a single opportunity to reproduce in a lifetime, self-pollination is expected to provide reproductive assurance in monocarpic epiphytes (Cole 1954). Consistent with this prediction, this study showed that only monocarpic *T. makoyana* is self-fertile, despite the fact that pollinator visitation rates were higher and floral displays

larger than they were in *T. intermedia* (Fig. 3). In contrast, polycarpic *T. intermedia* showed no capacity for autonomous self-pollination; therefore, it is dependent on pollinators for reproduction. A greater effect of habitat fragmentation on plant female reproductive success is expected in self-incompatible and other pollinator-dependent plants, which more often have seed production limited by pollinators or pollen (Cunningham 2000; Aguilar et al. 2006). Surprisingly, female reproductive success in *T. intermedia* was similar between fragmented and continuous habitats, indicating that, at least during the three study years, pollinators were equally good at effecting fruit and seed set under both habitat conditions. Nevertheless, given that *T. intermedia* is self-incompatible and clonal, it is vulnerable to pollen limitation, particularly in habitats where pollinator populations are low or where they fluctuate in time. For instance, hurricanes have hit the study area twice in the past 8 years (Tapia-Palacios et al. 2018), causing changes in vegetation structure and declines in natural populations of bromeliads (R. Sáyago et al., unpubl. data). Large storms could also cause temporal variation in pollinator visitation and increase pollen limitation in *T. intermedia*, but these questions require further study.

Results indicate that *T. intermedia* and *T. makoyana* are primarily pollinated by hummingbirds, as are many species in the family Bromeliaceae (Stiles 1975; Buzato et al. 2000; Kaehler et al. 2005). *Amazilia rutila*—the most common pollinator—has a bill length of 23 ± 1.3 mm (Arizmendi and Ornelas 1990); therefore, it is one of few species that can effectively access nectar from *T. intermedia* and *T. makoyana* flowers (mean \pm SEM: 26 ± 0.6 and 29 ± 0.8 mm long, respectively), along with the cinnamon hummingbird *C. latirostris*, a slightly smaller species. Both hummingbird species are permanent residents of Chamela and they are both territorial, but *A. rutila* dominates most territorial interactions (Arizmendi and Ornelas 1990). *Cyananthus latirostris* is a particularly common species in disturbed environments and cities across dry and arid regions of Mexico (Arizmendi and Ornelas 1990; Arizmendi and Berlanga 2014). Consistently, *C. latirostris* had a relatively high visitation frequency to flowers of *T. intermedia* in forest fragments. The relative abundances of other floral visitors to *T. intermedia* also varied between habitat conditions; for instance, stingless bees increased their frequency in forest fragments, whereas Euglossine bees showed the opposite trend (Table 1). This change in relative visitation frequencies among pollinator species—only observed for *T. intermedia*—may be the result of different factors: (i) the populations of certain groups of floral visitors, such as Euglossine bees, are often negatively impacted by habitat loss or fragmentation (e.g.

Storck-Tonon and Peres 2017); (ii) the movement of animal pollinators may be constrained by open spaces in fragmented habitats (Volpe et al. 2016); and (iii) pollinator behaviour may change along with vegetation structure and floral resources after fragmentation (Goverde et al. 2002; Hadley and Betts 2009). In this study, Euglossine bees did not visit *Tillandsia* flowers in forest fragments, and hummingbirds changed their frequencies according to habitat condition in *T. intermedia*. For instance, *C. latirostris* feeds from a variety of tree species whose flowers contain relatively high amounts of nectar in the continuous forest (Arizmendi and Ornelas 1990); however, in fragmented areas, this species uses lower rewarding *T. intermedia* flowers. A possible explanation for this result is that *T. intermedia* is clonal and occurs in high abundance on isolated trees in small forest fragments, flowering during the driest months of the year when other floral resources are scarce (Sáyago 2016). *Tillandsias* tend to occur in relatively high numbers on large- and medium-sized trees (Sáyago et al. 2013); therefore, the overall reward obtained by visiting multiple flowers on the same host tree possibly provides enough energy to hummingbird pollinators. This behaviour might cause limited pollen movement within forest fragments, high genetic structuring, and low gene flow between populations, a genetic pattern that has been observed in vertebrate-pollinated epiphytic bromeliads in fragmented habitats (González-Astorga et al. 2004; Paggi et al. 2015). Similarly, the foraging behaviour of stingless bees may promote self-pollination in forest fragments where these bees are more abundant; however, the genetic consequences associated with changes in pollinator composition and behaviour in fragmented landscapes are still unknown for Mexican dry forest *tillandsias*.

While the composition and frequency of pollinators of *T. intermedia* changed with forest fragmentation, overall pollinator visitation rates and fruit set were comparable among habitat conditions in both *Tillandsia* species. These results follow a general prediction previously stated in the literature that large-bodied pollinators (e.g. mainly vertebrates) are less affected by long distances between flower resources in remnant fragments than smaller pollinators (Ghazoul and Shaanker 2004). However, it has been demonstrated, particularly in rainforest environments, that some hummingbirds are exclusively forest species that are negatively affected by forest fragmentation, while others are capable of surviving and moving across anthropized landscapes or fragmented habitats (Stouffer and Bierregaard 1995; Hadley et al. 2018). The two hummingbird species that visited *Tillandsia* flowers in this study, *A. rutila* and *C. latirostris*, are altitudinal migrants and have broad geographic

distributions across dry continuous and open habitats (Ornelas and Arizmendi-Arriaga 1995; Arizmendi and Berlanga 2014); therefore, their presence in the fragmented habitats of the Chamela region is another indicator that these hummingbird species can act as effective pollen vectors in disturbed environments.

Changes in the visitation frequencies and behaviours of different pollinator species between habitats could influence the quantity or quality of pollen received by flowers, which would likely affect plant reproductive success and progeny quality (Quesada et al. 2001; Cascante et al. 2002). In self-compatible species like *T. makoyana*, autonomous self-pollination might provide reproductive assurance, but this benefit could be countered by the negative effects of inbreeding on the progeny produced via self-pollination (Herlihy and Eckert 2004). The lower seed set of *T. makoyana* under fragmented habitat conditions might potentially be the result of increased inbreeding depression, since the main pollinator, *A. rutila*, is a highly territorial species (Arizmendi and Ornelas 1990), and bees tend to move between neighbouring flowers within the same host trees; these behaviours might promote geitonogamous crosses and perhaps crosses between related individuals (e.g. Feinsinger 1978). The few studies available on epiphytic bromeliads indicate low genetic variation and low outcrossing rates, in addition to limited gene flow and restricted neighbourhoods, particularly in self-pollinating species (Soltis et al. 1987; Gonzalez-Astorga et al. 2004; Cascante-Marín et al. 2014); however, for *T. makoyana* these ideas remain elusive. Another potential explanation for the reduced seed set of *T. makoyana* in forest fragments is that greater attack by herbivores and pathogens in forest fragments would lower resources for reproduction or directly affect the developing seeds. However, a recent meta-analysis shows that fragmentation generally does not cause an increase in herbivory and there was no evidence of herbivory or seed predation in the study species (Rossetti et al. 2017). In addition, herbivory levels are generally relatively low in epiphytes (Zotz 2016). An alternative explanation is that, since epiphytes are often nutrient-limited (Boelter et al. 2014), low resources for reproduction might reduce seed production in disturbed habitats because large isolated trees in fragmented habitats are more exposed to wind, desiccation and nutrient leaching (Flores-Palacios and García-Franco 2004).

Despite observing similar female fruit set in continuous and fragmented habitat conditions, we should not infer that there are no fragmentation effects on demographic or genetic parameters of these *Tillandsia* species. It should be highlighted that the density of *T. makoyana* individuals is drastically reduced in fragmented and successional sites as a result of a reduction in the abundance

of appropriate phorophytes in comparison to the continuous forests; for example, at continuous forest sites, the mean number of *T. makoyana* individuals in a sample of 100 m² plots was 21 (SD = 26.1), while at successional/fragmented sites it was 0.2 (SD = 0.38) (Sáyago 2016). Likewise, disturbance has marked negative effects on the diversity and composition of the phorophyte community (Quesada et al. 2009; Munguía-Rosas and Montiel 2014), and in microclimatic conditions (Laurance 2004), which are critical for the survival of epiphytic species in dry forest habitats. Studies on epiphytic plants show contrasting results: some have found lower diversity but higher recruitment in secondary cloud forests (Cascante-Marín et al. 2006), or lower seedling establishment on isolated trees than in old-growth forests (Werner and Gradstein 2008), while other studies show that some rainforest epiphytes actually increase in abundance in human-modified environments (Einzmann and Zotz 2017). Nevertheless, for epiphytes that depend on trees with particular characteristics, such as dry forest *Tillandsia* species, the reduction in the abundance of appropriate phorophytes affects the recruitment of new plants and possibly the long-term viability of epiphyte populations (Sáyago et al. 2013). Under these conditions, the populations would not only experience greater environmental and demographic stochasticity, but they would also be vulnerable to reduction in genetic variation and increased inbreeding depression (Keller and Waller 2002).

In conclusion, this study demonstrates that pollinator communities significantly changed in species composition and relative abundances between habitat conditions in polycarpic *T. intermedia*, but they did not in monocarpic *T. makoyana*. In addition, habitat fragmentation was associated with a lower seed set in *T. makoyana* but not *T. intermedia*. However, fruit production was similar between habitat conditions for both *Tillandsia* species despite their different breeding systems and life history strategies. This result is possibly due to the fact that hummingbirds with wide geographic distributions and broad habitat use are the main pollinators of the study species. Future studies should address the consequences of habitat fragmentation and changes in pollinator communities and behaviour on genetic structuring, gene flow via pollen and seeds, levels of inbreeding and progeny quality.

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Contributions by the Authors

R.S. and M.Q. designed the study, performed fieldwork and data processing; R.A., M.L.-M. and L.A. contributed with fieldwork and data processing; S.M.-R. conducted statistical analyses and wrote the manuscript with contributions from all authors.

Conflict of Interest

None declared.

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