



Original article

Potential impact of harvesting on the population dynamics of two epiphytic bromeliads



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ABSTRACT

Large numbers of epiphytes are extracted from cloud forests for ornamental use and illegal trade in Latin America. We examined the potential effects of different harvesting regimes on the population dynamics of the epiphytic bromeliads *Tillandsia multicaulis* and *Tillandsia punctulata*. The population dynamics of these species were studied over a 2-year period in a tropical montane cloud forest in Veracruz, Mexico. Prospective and retrospective analyses were used to identify which demographic processes and life-cycle stages make the largest relative contribution to variation in population growth rate (λ). The effect of simulated harvesting levels on population growth rates was analysed for both species. λ of both populations was highly influenced by survival (stasis), to a lesser extent by growth, and only slightly by fecundity. Vegetative growth played a central role in the population dynamics of these organisms. The λ value of the studied populations did not differ significantly from unity: *T. multicaulis* λ (95% confidence interval) = 0.982 (0.897–1.060) and *T. punctulata* λ = 0.967 (0.815–1.051), suggesting population stability. However, numerical simulation of different levels of extraction showed that λ would drop substantially even under very low (2%) harvesting levels. Matrix analysis revealed that *T. multicaulis* and *T. punctulata* populations are likely to decline and therefore commercial harvesting would be unsustainable. Based on these findings, management recommendations are outlined.

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1. Introduction

Epiphytes are extremely vulnerable to forest disturbance, fragmentation (Holbrook, 1991; Zhu et al., 2004; Wolf, 2005) and climate change, due to total dependence on established vegetation in order to complete their life cycle and a high sensitivity to microclimate (Benzing, 1998; Nadkarni and Solano, 2002). These plants are important elements of the diversity and physiognomy of tropical montane cloud forest (TMCF), one of the most threatened ecosystems worldwide (Scatena et al., 2010). Epiphyte populations in small forest remnants face high extinction risks since they are particularly vulnerable to environmental, demographic and genetic stochasticity (Menges, 1998; Young et al., 1996; Turner et al., 1994; Sodhi et al., 2008). In addition to the detrimental effect of forest disturbance and deforestation on epiphyte populations, over-

exploitation is also an important factor affecting remnant epiphyte populations (Turner et al., 1994; Wolf, 2005; Haeckel, 2009; Mondragón et al., in press).

The use of epiphytic bromeliads for ceremonial and ornamental purposes is widespread in Mexico and Guatemala (Hietz et al., 2002; Flores-Palacios and Valencia-Díaz, 2007). In the construction of just three ceremonial floral arches, 2438 inflorescences of *Tillandsia multicaulis* and 109 of *Tillandsia punctulata* were recorded (Flores-Palacios and Valencia-Díaz, 2007). In just four municipalities of the Mexican state of Veracruz, more than 70 floral arches are constructed every year to celebrate religious festivities (Haeckel, 2008). Moreover, the illegal collection of epiphytes for commercial purposes is commonplace in this region: each collector is expected to gather between 2000 and 6000 rosettes of *Tillandsia kirchhoffiana* per day (Toledo-Aceves, unpublished data). During this process, targeted trees are stripped bare of epiphytes, including orchids, ferns and mosses. This type of harvesting technique is extremely destructive and completely disregards the recovery capacity of the resources involved.

Demand for epiphytic bromeliads has increased in recent years in southern Mexico (Toledo-Aceves and Wolf, 2008; Haeckel,

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2008), adding to the already significant loss of TMCF in this region (Toledo-Aceves et al., 2011). As a result, various bromeliad species have now become locally rare and are listed as threatened (Flores-Palacios and Valencia-Díaz, 2007; Toledo-Aceves and Wolf, 2008; Haeckel, 2009). Implementation of carefully designed extraction systems in areas with robust populations has been proposed as a viable alternative to contribute to epiphyte conservation (Verhoeven and Beckers, 1999; Wolf and Konings, 2001). However, in order to develop appropriate management guidelines for sustainable harvesting systems, prior demographic analysis of the target population is required.

The canopy is a very restrictive environment from an ecological perspective (Benzing, 1990) and therefore many epiphytes present low individual growth rates, reach maturity relatively late in life and suffer high mortality rates (Hietz et al., 2002; Schmidt and Zotz, 2002; Mondragón et al., 2014). Previous studies evaluating the population dynamics of epiphytic bromeliads report that many populations display λ values below unity, indicating that they are likely in decline. Such is the case with *Tillandsia brachycaulis* (Mondragón et al., 2004), *Catopsis sessiflora*, *T. deppeana*, *T. multicaulis*, *T. punctulata* (Winkler et al., 2007), *T. flexulosa* (Wester and Zotz, 2010), *T. violacea* and *T. macdougallii* (Mondragón-Chaparro and Ticktin, 2011). Conversely, Zotz (2005) report average λ values above unity for *Werauhia sanguinolenta* and Valverde and Bernal (2010) for *T. recurvata*.

The study of population dynamics is a key tool with which to evaluate the likelihood of population growth or decline (Olmsted and Álvarez-Buylla, 1995; Ticktin et al., 2002). However, various demographic processes and life cycle routes can be responsible for such numerical trends in each population (Mandujano et al., 2007). Prospective analyses (i.e. traditional sensitivity and elasticity matrices) allow us to estimate how potential changes in matrix entries may affect λ . On the other hand, retrospective analyses (also called life table response experiments) allow us to examine the relative contribution of the observed variation in each vital rate to the recorded variation in λ , either overtime or between populations (Caswell, 1989; Martínez-Ballesté et al., 2005). The combined use of these two analyses has proved to be a powerful tool for assessing harvest sustainability in non-timber forest products (Zuidema et al., 2007; Schmidt et al., 2011). In the present study, we carried out a traditional demographic analysis of undisturbed populations of the epiphytic bromeliads *T. multicaulis* and *T. punctulata* over a 2-year period in a TMCF in the Mexican state of Veracruz. We then used both prospective and retrospective analysis to identify which vital rates, life-cycle stages and demographic processes make the largest contributions to the population dynamics of the species. To contribute to the design of appropriate management strategies, we used the demographic data to carry out numerical simulations assessing the potential impact of different harvesting regimes (including a non-harvesting scenario) on the population dynamics of these species. To support our management recommendations, we also used the approach proposed by Zuidema et al. (2007) to identify the vital rates that could be crucial in determining long-term population trends (i.e. those with high elasticities and high LTRE contributions).

2. Methods

2.1. Study area

The study was carried out in the tropical montane cloud forest of the municipality of San Andrés Tlalnelhuayocan, located in the centre of the Mexican state of Veracruz (19°31'03"N, 97°00'25"W; elevation: 1660 m; mean annual temperature: 18 °C). Total annual precipitation reported for the region in 2010 and 2011 was 1567

and 1757 mm, respectively (National Water Commission; <http://www.conagua.gob.mx/>). Three main seasons occur annually in this area: a cool and relatively dry season from November to March; a warm, dry season from April to May; and a warm, rainy season from June to October (Williams-Linera, 1997). The forest in the study area is highly fragmented, and features fragments of ca. 1–100 ha immersed within a matrix of pasturelands, crops (mainly maize) and abandoned pastures occupied by early successional forest; the fragments predominantly consist of secondary forests. Mean tree diameter at 1.3 m height (dbh) = 27.4 cm (only trees ≥ 10 cm dbh were included; Toledo-Aceves et al., 2014). The dominant tree species in this forest are *Quercus delgadoana* S. Valencia, Nixon & M.L. Kelly, *Liquidambar styraciflua* L. and *Q. lancifolia* Schldt. & Cham. (Toledo-Aceves et al., 2014).

2.2. Study species

The two studied epiphytic bromeliad species share several biological features. Both produce rosettes that reach 40 cm in height (Espejo-Serna et al., 2005). Individuals (genets) are sympodial, composed of a succession of rosettes, shoots, or modules that show determinate growth. The leading rosette dies after fruiting, but module production continues, thus the genets are polycarpic. This vegetative growth (i.e., production of new rosettes) can be observed even in relatively small plants (infants and juveniles). A single genet therefore simultaneously present several reproductive shoots that die after fruiting, and the genet regress to a smaller size category from one year to the next. Individual rosettes also decrease in size due to herbivory, leaf senescence, and/or desiccation. Vegetatively produced rosettes were never observed to detach from parent rosettes.

Both studied species feature a C₃ photosynthetic metabolism and are distributed mainly in TMCF in Mexico and Central America. *T. multicaulis* is generally found at altitudes of 1150–1900 m, and *T. punctulata* at altitudes between 1400 and 1800 m. Both inhabit TMCF but can occupy relatively more temperate forests, and *T. punctulata* colonize more tropical ecosystems, such as tropical rain forest, and tropical dry forest (Espejo-Serna et al., 2005; Toledo-Aceves et al., 2012a). Seeds of both species are plumose, ca. 3 mm long with a ca. 2-cm long appendix. Fruits mature in about 11 mo and seeds are wind-dispersed during the dry season (October to May; Toledo-Aceves et al., 2012b).

Rosettes of *T. multicaulis* have tank morphology. They produce one to five red inflorescences per rosette. A fertile rosette produces approximately 1129 ± 102 seeds (mean \pm s.e, $N = 7$; Toledo-Aceves et al., 2012b) and a genet comprise up to 14 rosettes; a single rosette produces as many as eight new rosettes per year.

The morphology of *T. punctulata* is intermediate between tank and atmospheric. Each fertile rosette bears only one red inflorescence that produce approximately 571 ± 89 seeds ($N = 11$; Toledo-Aceves et al., 2012b). A genet comprises up to 36 rosettes; a single rosette produces as many as 14 new rosettes per year. Single rosette abundance per tree in the forest is: 342.6 ± 58.4 in *T. multicaulis* and 299.6 ± 101.7 in *T. punctulata* (Toledo-Aceves et al., 2014).

In this study, we analysed the population dynamics of *T. multicaulis* and *T. punctulata* based on the identification and monitoring of genets. Previous studies on epiphytic bromeliads have used stage classes defined by the size of single rosettes (Hietz et al., 2002; Zotz et al., 2005; Winkler et al., 2007). Others have considered the size of the whole plant (genet), or its number of shoots, in order to subdivide the population into size categories (Valverde and Bernal, 2010; Mondragón-Chaparro and Ticktin, 2011). The latter categorizations based on genet size recognize that genets of differing sizes show differential growth, survival and reproductive rates (Clark-Tapia et al., 2005; Mondragón-Chaparro

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