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Chronic Disturbance Affects the Demography and Population Structure of *Beaucarnea inermis*, a Threatened Species Endemic to Mexico

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Abstract

Beaucarnea inermis is a threatened plant of the seasonally dry tropical forests of the northeastern Sierra Madre Oriental mountains. It has been affected by habitat loss and fragmentation, mainly from changes in land use and poaching. The number of *B. inermis* plants, sexual proportion, and structural parameters were recorded in natural populations inside the Sierra del Abra Tanchipa Biosphere Reserve and unprotected sites. Effects of chronic disturbance on demography parameters and asymmetry coefficient were estimated. Average population density is 280 ind*ha^{-1} inside the protected area and 186 ind*ha^{-1} in unprotected sites. Life tables indicate a high seedling to juvenile mortality rate, but life expectancy increases in juveniles, suggesting a survival type III curve. Population size distribution skewness indicates differences associated with disturbance. Sex ratio was 0.93:1 (m:f) inside the protected area and 0.76:1 (m:f) in unprotected sites. Anthropogenic disturbance affects life expectancy and the survival and mortality rates mainly in early life classes; however, once the adult stage is reached, mortality rate is reduced and survival rate increases. The natural protected area represents a refuge for the species from the effects of anthropogenic disturbance and illegal poaching. Additional studies are needed to evaluate the genetic diversity in *B. inermis* in protected and unprotected sites, and how it is affected by disturbance. Also, it is important to highlight other species inside the protected area such as *Dioon edule, Zamia fischeri,* and *Stanhopea tigrina*, which are considered as endangered or threatened.

Keywords

seasonally dry tropical forest, in situ conservation, Sierra Madre Oriental, endangered plants, asymmetry coefficient

Introduction

Beaucarnea inermis (S.Watson) Rose (Asparagaceae) is an endemic plant of the Sierra Madre Oriental (SMOr), occurring in the states of San Luis Potosí and Tamaulipas in Mexico. It is listed as a threatened species (A) under Official Mexican Standard NOM-059-SEMARNAT-2010 (SEMARNAT, 2010) and is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora with other species that are not necessarily threatened with extinction now but may become endangered if trade is not tightly controlled. Locally, it is known as *soyate* and *cuhuich* from ancient languages. Along with other *Beaucarnea* species, *B. inermis* is known in the market as *pata de elefante*, elephant's

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foot palm, bottle palm, and the ponytail palm (Figure 1). All the species in the genus are used as living ornamentals, and some cultures use the flowers and leaves as food, or to elaborate handicrafts and ceremonial ornaments (Hernández-Sandoval et al., 2012). Owing to the demand for these species for ornamental use—mainly in the United States and Europe where prices are high—illegal poaching has affected the demography and structure of its natural populations (Hernández-Sandoval, 1993; Osorio-Rosales & Mata-Rosas, 2005). In addition, changes in land use, extensive livestock production, and the lack of planned forest harvesting strongly impact these species and their viability in future.

B. inermis inhabits the seasonally dry tropical forests (SDTF) of the SMOr, and its best conserved populations are in the Sierra del Abra Tanchipa Biosphere Reserve (SATBR) in San Luis Potosí (SEMARNAT-CONANP, 2014). The SATBR was declared a protected natural area in 1994 as the direct result of petitions signed by citizens and landowners who were concerned about the loss of biodiversity in the region. As part of the SMOr, the SATBR is an important connectivity link for threatened and endangered species in the region's ecological corridors.

The conservation of biodiversity requires an extensive understanding of how its different components are affected by current threats. Habitat destruction and fragmentation are considered the primary causes of species extinction, accelerating when anthropogenic disturbance is regular or chronic. This reduces the size of populations, affecting their demography and dynamics, and decreases their genetic diversity (Hernández-Oria, Chávez, & Sánchez, 2006; Lande, 1988; Rai, 2006; Ribeiro et al., 2016; Valencia-Díaz, Flores-Palacios, & Castillo-Campos, 2012).

Here, we present new information about the population structure of *B. inermis* in the SMOr for populations inside the SATBR protected area and in unprotected sites with different levels of anthropogenic disturbance. We describe the demography and population structure, and the ecological importance of the species, as well as the relationship of these variables to chronic disturbance.

Methods

Study Area and Sampling

We studied natural populations of *B. inermis* occurring in the SDTF of the SMOr with different levels of deciduousness. The climate in the region type Aw1(x′) is of subhumid warm, with a dry season from December to May. The main population of *B. inermis* is found in the SATBR, a protected natural area covering 21,464 ha, located between 22°05′00″ and 22°24′22″ N lat. and 98°52′46″ and 99°01′00″ W long. in the municipalities of Ciudad Valles and Tamuín in the state of San Luis Potosí. The other populations included in this study are in the municipalities of Ciudad Mante and Ocampo in Tamaulipas, and Tamasopo and Ciudad Valles in San Luis Potosí. We used thirteen 100×10 m plots (0.1 ha); seven plots were set up inside the SATBR, separated by 500 m, along an elevation gradient from 338 to 473 m a.s.l., and six plots were set up outside of the SATBR (Figure 2).

Structural, Morphological, and Demographic Parameters

On each plot, we recorded the number of *B. inermis* plants and estimated their density as individuals per hectarea (ind*ha^{-1}; number of individuals in each plot of 0.1 ha*10). To describe the population structure, morphometric and nonmorphometric traits were measured in each plant: (a) trunk base diameter, (b) neck diameter (where the base is narrowed), (c) total height of the plant, and (d) sex ratio in the flowering season. Plants were categorized according to life classes: (a) seedlings were plants that had germinated in the last reproductive event prior to sampling, without a developed base; (b) juveniles were nonreproductive plants with a developed base and only one rosette or a few, but not from flowering events; and (c) adults were plants with at least one branching and rosettes from flowering events.

Individual frequencies in life classes were used to construct static life tables at different disturbance levels (Martorell & Peters, 2005) in the analyzed plots (see Disturbance Index section), representing specific mortality and survival for each class (Odum, 1972; Smith & Smith, 2007). Static life tables are generated with different attributes describing a population based on temporal demographic traits: l_x, the proportion of surviving individuals entering class x, with respect to the initial number of individuals; q_x, mortality rate as the proportion of dead individuals during the time interval from class x to x+1, with respect to the original number of individuals; E_x, life expectancy as the expected life time of an individual of class x; R_0, net reproductive rate of each generation (Table 1). The intrinsic population growth rate was calculated as $\lambda = e^r$, where $e =$ Avogadro's constant of 2.71828 and $r =$ population growth rate per capita (Table 1). When $\lambda = 1$, population size is constant; $\lambda > 1$ indicates increase in population size per generation, while $\lambda < 1$ indicates decrease (Caswell, 2001; Castillo-Lara, Octavio-Aguilar, & De-Nova, 2017).

Seed frequencies were estimated from the literature and personal observations made during the study, taking the average number of seeds produced per panicle as ca. 2,000 based on Hernández-Sandoval et al. (2012), and counting the number of panicles on the plants sampled in each plot. The number of seedlings was

Figure 1. *B. inermis* in its habitat. (a) Adult plant, (b) male panicle, (c) fruit, (d) male flowers, (e) female flower, (f) seedlings, (g) juveniles, and (h) young adults.

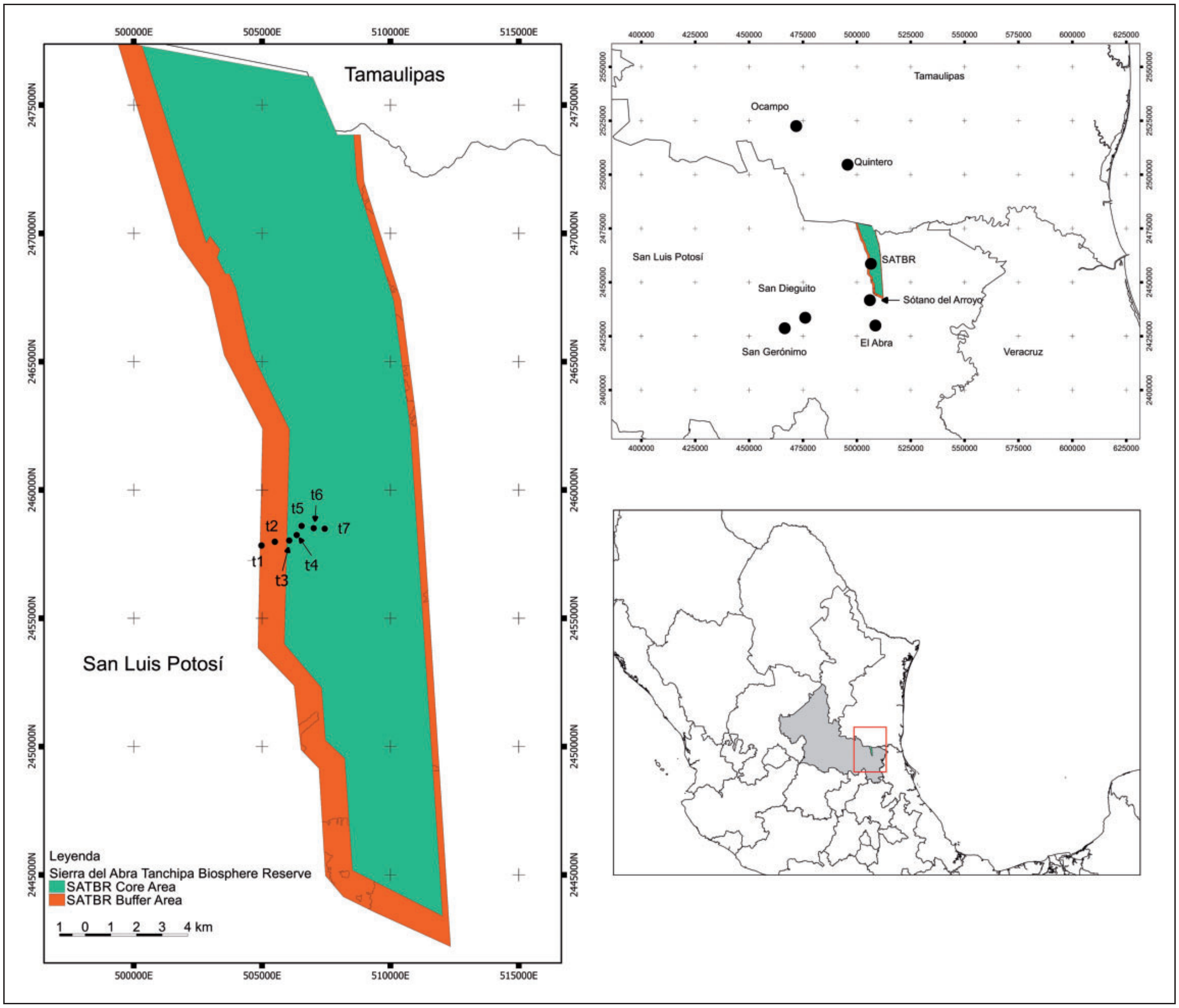

Figure 2. Study area, showing the location of the sample plots.

fixed at the highest number of seedlings found in all the plots sampled because the real frequency of the seedling class is very difficult to record in all seasons owing to the high mortality that occurs in the first months after germination.

Asymmetry Coefficient

To evaluate the inequality of size classes as an additional component of population structure, we estimate the Gini coefficient (*g1*) for each plot following Bendel, Higgins, Teberg, and Pyke (1989). We used (a) base diameter and (b) neck diameter for each *B. inermis* plant because they are more suitable than height to describe size in this genus. The *g1* index was calculated after Palacios-Wassenaar, Castillo-Campos, and Vázquez-Torres (2016) as follows: $\boldsymbol{g}_1 = \frac{\boldsymbol{n}\sum_i (x_1 - \boldsymbol{x})^3}{(\boldsymbol{n}-1)(\boldsymbol{n}-2)\boldsymbol{s}^3}$, where n is the number of plants, x_i is the logarithm of the diameter of base or neck for each plant i, $\boldsymbol{x}$ is the average of x, and s is the standard deviation of x_i.

Disturbance Index

We followed the method proposed by Martorell and Peters (2005) that combines 14 parameters clustered in three disturbance categories (livestock raising, human activities, and land degradation) to calculate a chronic disturbance index (CDI; Appendix 1, Supporting information), recorded for each plot in our study. Data were standardized and merged using a principal components analysis (PCA), discarding those with no variation for the sites as recommended in previous studies (e.g., Hernández-Oria et al., 2006; Martorell & Peters, 2005; Ribeiro et al., 2016). We constructed a frequency table

Table 1. Static Life Table Components From Valverde, Cano-Santana, Meave, and Carabias (2005).

Parameter	Represents	Formula
l_x	Proportion of surviving individuals entering class x, with respect to the initial number of individuals	$\frac{n_x}{n_0}$
d_x	Proportion of dead individuals during the time interval from class x to x+1, with respect to the initial number of individuals. When calculated from *n*, d_x represents the number of dead organisms between x and x+1	$l_x - l_{x+1}$ or $n_x - n_{x+1}$
q_x	Mortality rate as the proportion of dead individuals during the time interval from class x to x+1, with respect to the original number of individuals	$\frac{n_x}{n_{x+1}}$
P_x	Proportion of surviving individuals with respect to the total number of individuals entering class x	$1 - q_x$
m_x	Fecundity as the average number of descendants per individual (female) in each age class	$\frac{F_x}{n_x}$
F_x	Total number of descendants from class x	From field observations
E_x	Life expectancy as the expected life time of an individual of class x	$\frac{T_x}{n_x}$ $T_x = \sum L_x$ $L_x = \frac{n_x + n_{x+1}}{2}$
R_0	Net reproductive rate of each generation	$\sum l_x m_x$
T_G	Generation time. Average time between the birth of an individual and the birth of its descendants	$\frac{\sum x l_x m_x}{R_0}$
r	Population growth rate per capita	$\frac{\ln R_0}{T_G}$
λ	Intrinsic population growth rate	e^r

for CDI values for each studied plot using Sturges' rule to detect disturbance levels for the analyzed populations. We conduct a chi-squared test of independence to investigate the response of life stage frequencies to the disturbance level. Linear regressions were conducted to estimate the correlation of CDI with *lx*, *Ex*, *qx*, *λ*, R_0, density in each life class, morphological traits (total height and base and neck diameter), and the asymmetry coefficient *g1*¸ to evaluate the effects of the identified disturbance levels on the population demography and morphology of *B. inermis*. Statistical analyses were conducted in GNU PSPP v.0.10.4-g50f7b7 (Free Software Foundation, 2017).

Table 2. Adult and Juvenile Density of *B. inermis* Inside and Outside[a] of the SATBR.

Plot	ind^*plot^{-1}	ind^*ha^{-1}	Adults ind^*plot^{-1}	Adults ind^*ha^{-1}	Juveniles ind^*plot^{-1}	Juveniles ind^*ha^{-1}
t1	14	140	5	50	9	90
t2	8	80	8	80	0	0
t3	22	220	22	220	0	0
t4	9	90	8	80	1	10
t5	45	450	45	450	0	0
t6	43	430	43	430	0	0
t7	55	550	53	530	2	20
t8[a]	20	200	19	190	1	10
t9[a]	4	40	2	20	2	20
t10[a]	23	230	12	120	11	110
t11[a]	10	100	8	80	2	20
t12[a]	32	320	29	290	3	30
t13[a]	23	230	23	230	0	0

Note. SATBR = Sierra del Abra Tanchipa Biosphere Reserve.
[a]Plots outside of the SATBR.

Results

Structural and Demographic Parameters

A total of 405 plants were recorded in the 13 plots sampled, with an average density of 236.9 ind^*ha^{-1}; $SD = 158.76$ for juveniles and adults. Average density inside the SATBR was 280 ind^*ha^{-1}; $SD = 193.04$, with adults dominating (Table 2). Plots t5, t6, and t7 were the sites with the greatest density (476.66 ind^*ha^{-1}; $SD = 64.29$) and are located in the core area of the SATBR from 420 to 470 m a.s.l., in the less deciduous variant of SDTF. Outside of the protected area, the average density was 186.66 ind^*ha^{-1}; $SD = 100.73$; the plot t12 (El Abra) had the greatest density at 320 ind^*ha^{-1}. The dominant life class was adults both inside and outside of the natural protected area, and inside the SATBR, juveniles were only recorded in three plots (t1, t4, and t7).

The average height inside the SATBR was 7.65 m ($SD = 3.60$), and the maximum height recorded was 17 m for a plant in the core area in plot t2. The maximum base diameter recorded was 3.09 m, and the average base diameter was 1.35 m ($SD = 0.67$; Table 3). Outside of the protected area, the average height was 6.87 m ($SD = 3.57$), and the average base diameter was 1.20 m ($SD = 0.68$; Table 3). The average neck diameter inside SATBR was 0.48 m ($SD = 0.31$) and outside was 0.50 m ($SD = 0.35$; Table 3).

Table 3. Morphometric Traits and Skewness Coefficient for *B. inermis* Inside and Outside of the SATBR.

				Skewness coefficient	
Plot	Height	Base diameter	Neck diameter	Base diameter	Neck diameter
t1	3.636	0.741	0.228	0.489	1.039
t2	8.713	1.594	0.587	−0.568	−0.145
t3	8.453	1.490	0.579	0.295	1.05
t4	8.424	1.549	0.703	−1.175	−0.804
t5	8.497	1.450	0.480	−0.508	0.302
t6	5.681	1.910	0.605	−0.307	−0.796
t7	5.359	0.897	0.358	−2.501	−1.163
t8[a]	8.860	1.420	0.720	−0.498	−0.444
t9[a]	6.750	1.350	0.610	1.386	2.453
t10[a]	4.430	0.830	0.290	−0.081	0.362
t11[a]	6.070	1.380	0.590	−1.447	−1.604
t12[a]	7.020	1.180	0.440	−3.927	−2.096
t13[a]	7.450	1.310	0.520	0.037	−0.221

Note. SATBR = Sierra del Abra Tanchipa Biosphere Reserve.
aPlots outside of the SATBR.

Adults had the highest mean survival rate (l_x) (5.39×10^{-5}; $SE = 1.73 \times 10^{-5}$; Figure 3), and seedlings had the lowest (3.54×10^{-5}; $SE = 3.71 \times 10^{-6}$; Figure 3), as expected for a type III curve according to the criteria of Deevey (1947). Mean mortality rate (q_x) was high in the transition from seed to seedling (−0.471; $SE = 1.265$; Table 4) for all disturbance levels, but in the medium and high levels of disturbance, mortality also was detected in the transition from seedling to juvenile (−8.89; $SE = 3.89$; Table 3). The net reproductive rate (R_0) was <1 in the whole disturbance levels as expected in a declining population; however, the life expectancy (Ex) was higher in the classes juvenile and seedling (15.84; $SE = 6.73$ and 65.8; $SE = 2.19$, respectively) inside the SATBR where the lowest CDI value was registered (Table 4). Chi-squared test of independence rejects the null hypothesis that the frequencies of life stages are independent of the disturbance level ($p < 2.2e\text{-}16$).

Asymmetry Coefficient

The distribution of size classes analyzed with $g1$ shows differences between the plots (Table 3) ranging from −3.92 to 1.38 when base diameter is used and −2.09 to 2.45 with the neck diameter. Average $g1$ inside the

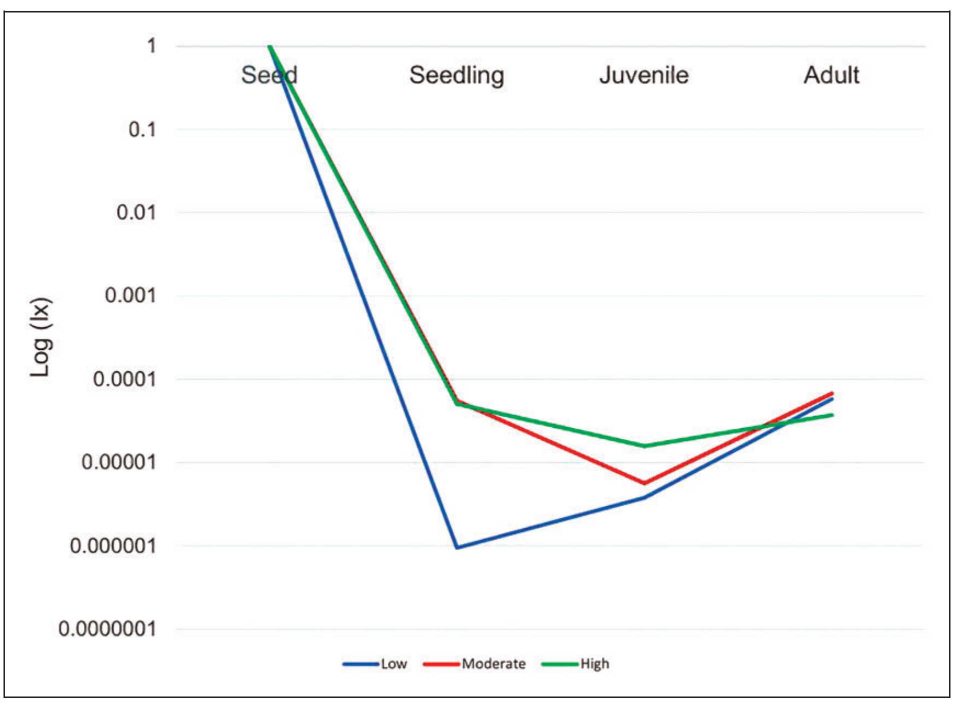

Figure 3. Survival curve for *B. inermis* for each CDI level.
CDI = chronic disturbance index.

Table 4. Life Table for *B. inermis* for Each of the Estimated CDI Levels.

Life stage	CDI level	*lx*	*qx*	*Ex*
Seedling	Low	9.40E-07	−3	65.83
	Moderate	5.48E-05	0.89	1.82
	High	5.04E-05	0.68	1.54
	M; *SE*	3.54E-05; 1.73E-05	−0.47; 1.265	23.06; 21.38
Juvenile	Low	3.76E-06	−14.33	15.83
	Moderate	5.60E-06	−11	12.5
	High	1.56E-05	−1.35	2.85
	M; *SE*	8.35E-06; 3.71E−06	−8.89; 3.89	10.39; 3.89
Adult	Low	5.76E-05	1	0.5
	Moderate	6.72E-05	1	0.5
	High	3.69E-05	1	0.5
	M; *SE*	5.39E-05; 8.93E-06	–	–
R_0	Low	3.06E-04		
	Moderate	2.11E-02		
	High	1.10E-02		
	M; *SE*	3.19E-02; 1.43E-02		
λ	Low	0.66		
	Moderate	0.82		
	High	0.79		
	M; *SE*	0.83; 2.31E-02		

Note. CDI = chronic disturbance index.

SATBR was −0.61 (base diameter) and −0.07 (neck diameter), and outside it was −0.75 (base diameter) and −0.25 (neck diameter), indicating the predominance of bigger plants (adults).

Sex Proportions

Both inside and outside of the SATBR the proportion of reproductive plants was close to 50%. The sex ratio for the population inside the SATBR was 0.93:1 m:f, and outside it was 0.76:1 m:f (Figure 4).

Disturbance Index

According to the analyses, the disturbance parameters with the greatest effect on the sample plots were the proportion of plants damaged by cutting, proximity to human populations and to areas of human activity, with human activity the main threat to *B. inermis*. Plots with the highest CDI were in San Gerónimo (t8), San Dieguito (t9), and Ocampo (t10), all outside of the SATBR.

For the PCA, we discarded goat droppings frequency (GOAT), soil compaction (COMP), land (LUSE), presence of soil islands (ISLA), and totally modified surfaces (TOMS) because they showed no variation for the plots analyzed (Table 5). Axis 1 explained 75.54% of the variation of all parameters analyzed in decreasing order with cattle droppings frequency (CATT), browsing (BROW), fuelwood extraction (FUEL), human trails surface (TRAS), evidence of wildfires (FIRE), human trails density (TRAN), settlement proximity (PROX), and contiguity to activity cores (CORE) ($p < .05$; Appendix 2, Supporting information). A high degree of positive correlation was found among most parameters (Appendix 2, Supporting information). Some negative coefficients were obtained between Erosion (EROS) and CATT, and BROW and livestock trail density (LTRA). Significant correlation was found between variables from human activities (CORE, FUEL, FIRE, PROX, and TRAS) and livestock raising (BROW, CATT, and LTRA). Values of Axis 1 were rescaled from 0 to 100, from the least to the most disturbed site, to generate a custom CDI for our sites. The Sturges' rule identified three different disturbance levels that we called low (CDI = 0.23–0.39) inside SATBR; moderate (CDI = 0.698–0.733) plots t11, t12, and t13; and high (CDI = 1.36–1.37) in plots t8, t9, and t10.

Variable Correlations

The custom CDI reveals a high degree of correlation with demographic parameters (Table 6) but not for

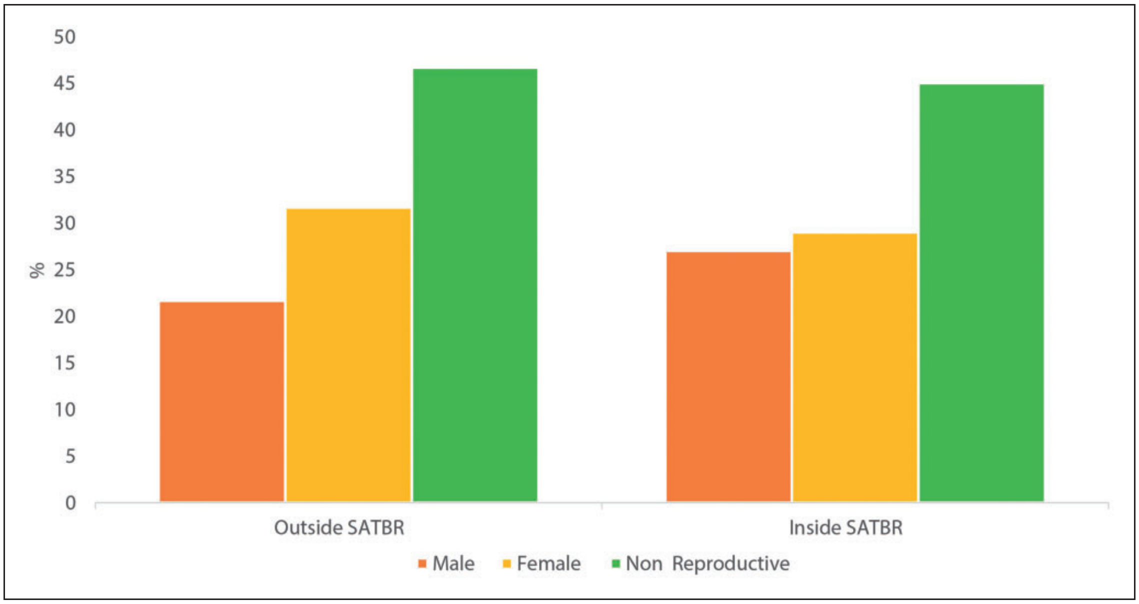

Figure 4. Proportions of reproductive (male and female) and nonreproductive *B. inermis* plants inside and outside of the SATBR. SATBR = Sierra del Abra Tanchipa Biosphere Reserve.

Table 5. Chronic Disturbance Index Values for the Sites Analyzed Inside and Outside[a] of the SATBR.

Plot	CATT	BROW	LTRA	FUEL	FIRE	TRAS	PROX	CORE	EROS	Total disturbance
t1	0	0	0	0	0	0	0.38	0.33	0	0.39
t2	0	0	0	0	0	0	0.38	0.33	0	0.39
t3	0	0	0	0	0	0	0.38	0.33	0	0.39
t4	0	0	0	0	0	0	0.25	0	0	0.23
t5	0	0	0	0	0	0	0.25	0	0	0.23
t6	0	0	0	0	0	0	0.25	0	0	0.23
t7	0	0	0	0	0	0	0.25	0	0	0.23
t8[a]	0	0	0	0.13	1	0.01	0.56	1	0.1	0.70
t9[a]	0	0	0	0.02	0	0	0.56	1	0	0.69
t10[a]	0	0	0	0.5	0	0.015	0.56	1	0	0.73
t11[a]	0	0	0	0.06	0	0.01	0.56	1	0.1	1.33
t12[a]	0.2	0.1	0	0.19	1	0	0.56	1	0	1.36
t13[a]	0.2	0.1	0.18	0.16	1	0.01	0.56	1	0	1.37

Note. CATT = cattle droppings frequency; BROW= browsing; LTRA = livestock trail density; FUEL = fuelwood extraction; FIRE = evidence of wildfires; TRAS = human trails surface; PROX = settlement proximity; CORE = contiguity to activity cores; EROS = Erosion; SATBR = Sierra del Abra Tanchipa Biosphere Reserve.
[a]Plots outside of the SATBR.

morphological traits such as height, and neck and base diameter (Table 6). The survival rate (lx) results positively correlated with CDI in all life stages (Table 6). Life expectancy (*Ex*) results are positively correlated with CDI only in the seedling ($R^2 = .73$, $F = 29.11$, $p = 2.18 \times 10^{-4}$) and juvenile stages ($R^2 = .96$, $F = 283.99$, $p = 3.32 \times 10^{-9}$). The mortality rate is also positively correlated with CDI in the seedling ($R^2 = .69$, $F = 24.49$, $p = 4.36 \times 10^{-4}$) and juvenile stages ($R^2 = .96$, $F = 283.99$, $p = 3.32 \times 10^{-9}$). Density and asymmetry coefficient show no correlation with CDI (Table 6). Total height and the base and neck diameter are not correlated with CDI (Table 6).

Discussion

The density estimated for *B. inermis* in the present study is one of the highest recorded for the genus. Maximum

Table 6. Correlations Between the CDI and the Demographic and Structural Parameters for *B. inermis* Inside and Outside of the SATBR.

Parameter	Life class	Statistics	Coefficient (*SE*)	Explained variance (%)
lx	Seedling	$F(1,11)=22.04^{**}$	4.914E-05 (1.038E-05)	67
	Juvenile	$F(1,11)=132.9^{**}$	9.389E-07 (11.5285)	92
	Adult	$F(1,11)=11.36^{**}$	−1.763E-05 (5.229E-06)	51
Ex	Seedling	$F(1,11)=29.11^{**}$	−63.31 (11.73)	73
	Juvenile	$F(1,11)=283.99^{**}$	−11.90 (0.706)	96
	Adult			
qx	Seedling	$F(1,11)=24.49^{**}$	3.65 (0.738)	69
	Juvenile	$F(1,11)=283.99^{**}$	11.90 (0.706)	96
	Adult			
R_0	Total	$F(1,11)=9.067$	0.00455 (0.015)	45
λ	Total	$F(1,11)=12.354$	−0.013 (0.0039	52
Density	Juvenile	$F(1,11)=1.563$	2.794 (2.235)	12.40
	Adult	$F(1,11)=2.99$	−17.27 (9.99)	21.30
	Total	$F(1,11)=2.203$	−14.483 (9.756)	16.60
Height	Adult	$F(1,11)=0.08$	−0.0224 (0.0775)	0.76
Base diameter	Adult	$F(1,11)=0.446$	−0.268 (0.401)	3.90
Neck diameter	Adult	$F(1,11)=0.146$	0.338 (0.883)	1.13
g1	Neck diameter	$F(1,11)=1.041$	0.803 (0.787)	0.086
	Base diameter	$F(1,11)=0.872$	0.826 (0.884)	0.073

Note. CDI = chronic disturbance index; SATBR = Sierra del Abra Tanchipa Biosphere Reserve.
$^{*}p<.05$. $^{**}p<.01$.

values for the species were recorded inside the SATBR core area and range from 280 to 550 ind*ha^{-1}, being higher in subdeciduous SDTF. Demographic studies for other species report lower values; for example, *B. recurvata* Lem. (130 ind*ha^{-1}) and *B. gracilis* Lem. (16.9 ind*ha). Only *B. sanctomariana* L.Hern. (301 ind*ha^{-1}) and *B. goldmanii* Rose (460 ind*ha^{-1}) had a higher average value (Hernández-Sandoval et al., 2012; Pérez-Farrera et al., 2012). Inside the SATBR *B. inermis* is the most dominant species, where it reaches sizes large enough to compete with or even displace abundant species like *Croton niveus*. Also, *B. inermis* can establish in the common rocky outcrops inside the SATBR, where few species can compete.

According to the survival curve, the population of *B. inermis* has a high mortality rate in the first stages of establishment (seed and seedlings), resulting in a high density of adults as previously reported in other studies (Cardel, Rico-Gray, García-Franco, & Thien, 1997; Hernández-Sandoval et al., 2012; Pérez-Farrera et al., 2012). Under lab conditions, more than 90% of the seeds germinate and become seedlings. In the wild, it is possible to have a high germination rate too, but seed predation by ants (personal observation) and of seedlings by herbivores (Cardel et al., 1997), as well as unfavorable conditions, increase mortality in these early stages, making the transition from seed to seedling ephemeral and difficult to record in the field. Mortality from seedling to juvenile was detected in the plots outside SATBR, and this could be associated some kind of disturbance like land use change, ranching, or poaching.

Additional studies of germination in the field are required to better estimate the population dynamics of *B. inermis*; however, the survival curve in our study represents a first attempt at understanding recruitment in the species. The curve coincides with a *k* strategy (Odum, 1972; Smith & Smith, 2007), with very low seed recruitment but great longevity in surviving plants. This is characteristic in plant species from SDTF that depend on canopy openings to establish and require more light, as occurs in pioneer species (Palacios-Wassenaar et al., 2016). In general, we found more juvenile plants in the unprotected sites outside of the SATBR, in accordance with the findings of Palacios-Wassenaar et al. (2016) who indicate that the high density of juveniles is related to the decrease in the number of adult plants in *Resinanthus aromaticus* (Cast.-Campos & Lorence) Borhidi. These individuals are more vulnerable to deforestation, trampling of cattle, or extraction, so they could not reach the adult stage, compared with those within the reserve that ensure their permanence in the population due to the protection offered by the SATBR.

The population of *B. inermis* inside the SATBR is dominated by adults (asymmetry coefficient $g1 < 0$), and only one plot (t1) located at the border of the protected area results dominated by juveniles. The coefficient $g1$ is not correlated with estimated chronic disturbance levels, although the plots that are outside the SATBR show an increasing density of small plants (mainly juvenile). This increasing density in earlier life classes could be associated to absence of adult individuals to compete with, in sites with higher levels of disturbance. It has been previously reported in large, sessile, passively dispersed plant species that small individuals (seedlings and juveniles) are likely to be shaded by large individuals, so they have less energy to devote to survival and reproduction (Harcombe, 1987). The consequence is higher mortality rates of shaded young individuals (Enright & Ogden, 1979; Hartshorn, 1975; Highsmith, Riggs, & D'Antonio, 1980; Hughes, 1984; Jackson, 1977; Lefkovitch, 1965; Werner & Caswell, 1977). Light-demanding species are relatively rare as seedlings because they are ephemeral, either dying quickly if shaded, or growing rapidly into large size classes if light levels remain high (Wright, Muller-Landau, Condit, & Hubbell, 2003). In the less disturbed sites, populations of *B. inermis* seem to reach stability with adults that are large in size, mainly on rocky outcrops, making it difficult for juveniles compete for space.

Flowering in *B. inermis* is not annual, and its periodicity has not been described with any accuracy. Our estimates indicate that *B. inermis* has a good balance of reproductive and nonreproductive plants (44%), and in the proportion of the sexes (27% male, 29% female), suggesting an equilibrium with no major competition among males, and thus a low reproductive cost (Cipollini & Stiles, 1991). However, the number of plants for which sex was recorded as indeterminate could change the proportion in future years because these plants could be young reproductive adults that are flowering less constantly than older adults.

The disturbance parameters analyzed in our study were used to generate an index of chronic disturbance for quantifying the effect of disturbance on the demography of *B. inermis*. The following were the parameters that had a major effect on total disturbance: CATT, BROW, CORE, EROS, FUEL, FIRE, LTRA, PROX, and TRAN. This highlights the significant impact of human activities on habitat degradation. The plots inside the SATBR show the lowest CDI levels, due to the almost null anthropogenic activity. However, the plots outside SATBR showed two different levels of disturbance according to its location. Medium disturbance is associated to livestock raising parameters (BROW, CATT, and LTRA). High disturbance is associated to human activities (CORE, FIRE, PROX, and TRAN), the parameters with the largest loadings for the CDI. Low intensity disturbance like livestock raising may actually benefit the establishment of some plant species (Martorell & Peters, 2008) and improve their recruitment, as in *B. inermis* where the sites with a medium disturbance have acceptable demographic parameters. The disturbance is as important for conservation as the direct management of the species (e.g., prescribed fire); however, when it comes to anthropogenic disturbance, its complete elimination is frequently the only management practice, and human influence may also be disguised in the shape of natural disturbance to minimize its impact (Hansen, Spies, Swanson, & Ohmann, 1991; Martorell & Peters, 2008; Niemelä, 1999).

The demographic parameters most affected by disturbance are life expectancy, and the survival and mortality rates. The most vulnerable stages are from seedling to juvenile because the pressures of disturbance mainly affect the recruitment. Newly emerged seedlings no longer have the ability to withstand the adverse conditions tolerated by the ungerminated seed because they do not yet have the physical robustness it will acquire with age (Kitajima & Fenner, 2000). The mortality in these early stages is affected for a wide range of biotic and abiotic factors, which vary spatially and temporally (Mack & Pyke, 1984). The high mortality in *B. inermis* at the seedling stage may act as a strong selective filter on seed traits and seedling traits like in other plant species (Kitajima & Fenner, 2000), where traits can be interpreted as "gap-detection mechanisms" in seeds restrict germination in time and space, enhancing the likelihood of seedling survival and growth. Also, many abiotic stress factors, such as shade, excess light, heat, water stress, and flooding, may not kill seedlings immediately but may lower their tolerance to biotic mortality agents, such as herbivores and pathogens (Augspurger, 1984; Augspurger & Kelly, 1984; Kitajima & Fenner, 2000). However, once the adult stage is reached in *B. inermis*, the population seems to be stabilized and the mortality rate and life expectancy remain constant, but the survival rate increases. This may be related to the size that individuals reach, which allows them to tolerate disturbances, likewise, it makes them less vulnerable to poaching.

Implications for Conservation

According to our results, it is correct to include *B. inermis* as a threatened species (A) under the Norma Oficial Mexicana NOM-059-SEMARNAT-2010 (SEMARNAT, 2010), and in Appendix II of the Convention on International Trade in Endangered

Species of Wild Fauna and Flora because unprotected populations are still subjected to illegal poaching of seedlings and juveniles, and the low survival and high mortality rates specially in early stages. The SATBR represents an effective refuge for *B. inermis*, protecting it from anthropogenic disturbance such as changes in land use and the illegal poaching of mainly seedlings and juveniles. Additional studies are needed to evaluate the genetic diversity of populations of *B. inermis*, genetic flow, and how it is affected by disturbance. Also, it is important to highlight other key species inside the protected area such as *Dioon edule* Lindl., *Zamia fischeri* Miq. ex Lem., and *Stanhopea tigrina* Bentam ex Lindl., which are considered as endangered or threatened according to the Official Mexican Standard NOM-059-SEMARNAT-2010 (SEMARNAT, 2010).

Supporting Information

Metrics that were recorded in plots (Appendix 1) and PCA results (Appendix 2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than the absence of material) should be directed to the corresponding author.

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