



Assessing the importance of multiple threats to an endangered globose cactus in Mexico: Cattle grazing, looting and climate change



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ABSTRACT

Cacti are a priority for conservation because their slow recovery rates and high habitat specificity make their populations particularly susceptible to looters who raid their populations, anthropogenic disturbance and climate change (CC). Identifying the most damaging threat is critical to the direction and efficiency of conservation efforts. We analyzed the impacts of looting, disturbance and CC on the geographically rare globose cactus *Coryphantha werdermannii* in Coahuila, Northern Mexico. We collected evidence on looting and estimated the impacts of seed and adult plant extraction through demographic models. We compared 10 sites differing in disturbance intensity and analyzed the effect on plant density, size structure and reproduction. The potential distribution of *C. werdermannii* under current conditions and future CC was assessed through ecological niche modeling. We found that looting is mostly confined to seeds, which have little impact on population growth and therefore not responsible for population decline. As in many globose cacti, the density of *C. werdermannii* populations increased with disturbance, likely because cattle grazing increases recruitment rates. Contrastingly, even the most optimistic CC scenarios suggest a 90% reduction in the potential distribution area by 2050, indicating that *C. werdermannii* is an endangered species most threatened by CC. We suggest that relocation programs and the maintenance of livestock levels appropriate for this species (moderate-high) may effectively counteract or delay the effects of CC. Our results suggest that current efforts are devoted to relatively minor threats, while CC is neglected, and highlight the importance of formal assessments of multiple threats.

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1. Introduction

Cacti are considered a priority for conservation. They are the 13th most at risk flowering-plant family, with more species classified as endangered or critically endangered on the IUCN's Red List (IUCN, 2010), and the second with more taxa listed as threatened by the Mexican government (SEMARNAT, 2002). The whole family is included on Appendix II of CITES (CITES, 2010). Three anthropic factors have been considered to underlie this high degree of threat: anthropogenic disturbance, climate change and looting (Anderson et al., 1994; Bárcenas-Luna, 2003; Godínez-Álvarez et al., 2003; Hernández and Godínez-Álvarez, 1994; Martorell and Peters, 2005; Oldfield, 1997; Téllez-Valdés and Dávila-Aranda, 2003; Ureta et al., 2012).

Cacti are thought to be highly vulnerable to anthropogenic disturbance. Low growth rates and rare recruitment events suggest

that the replacement of individuals killed by disturbance may be extremely slow (Godínez-Álvarez et al., 2003; Hernández and Godínez-Álvarez, 1994). They also depend on nurse plants during establishment (Flores and Jurado, 2003; Franco and Nobel, 1989; Valiente-Banuet et al., 1991; Valiente-Banuet and Ezcurra, 1991), making vegetation clearing a threat to their survival. Many cacti are endemic to extremely small areas, so land use change may wipe out whole species (Godínez-Álvarez et al., 2003; Hernández and Godínez-Álvarez, 1994; Oldfield, 1997).

Little is known about the potential impacts of climate change (CC) on cacti. In the only assessment available, Téllez-Valdés and Dávila-Aranda (2003) suggest that CC might threaten several species by reducing their potential distribution area (PDA). Furthermore, the Chihuahuan desert, home to the largest cactus diversity in the world (Hernández and Bárcenas, 1995; Hernández and Gómez-Hinostrosa, 2011), is expected to be one of the regions most affected by CC worldwide (Solomon et al., 2007).

Looting is frequently singled out as the most important threat to some cacti (Godínez-Álvarez et al., 2003; Martínez-Peralta and Mandujano, 2009; Muro-Pérez et al., 2011; Oldfield, 1997;

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Robbins, 2003). This is especially important for the rarest species that are the most prized items in a collection. We lack robust data on the magnitude of the problem due to weak surveillance and opacity of the government agencies in charge of cactus protection. However, some 2000 individual plants from approximately 300 different species of Chihuahuan desert cacti are seized from looters each year (Bárcenas-Luna, 2003; Martínez-Peralta and Mandujano, 2009).

Thus far, we lack data on the relative importance of anthropogenic disturbance, CC and looting as determinants of the conservation status of cacti. Determining which factors are the greatest threats is critical for establishing appropriate policies (e.g., establishing cattle-free reserves, translocation of populations to climatically appropriate areas or enforcing laws against looting). Furthermore, because most cacti occur in developing countries with limited resources, conservation efforts need to be prioritized.

In this paper, we assess the effects of anthropogenic disturbance, CC and looting on the globose species *Coryphantha werdermannii*. This species is endemic to a relatively small area in the Chihuahuan desert, and is representative of Mexican cacti in terms of threats and legal status. Our specific aims are to (1) assess the current conservation status of *C. werdermannii* and its biological vulnerability, (2) determine the effects of chronic anthropogenic disturbance on *C. werdermannii* populations, (3) analyze the impact of CC on the potential distribution of *C. werdermannii* and (4) estimate the magnitude of looting and its effects on the viability of this species.

2. Methods

2.1. Study site and species

C. werdermannii is a solitary, globose cactus reaching 8–15 cm tall and 6–8 cm in diameter; seedling size is about 2 mm. Areoles surrounding the apex produce four dark spines once the reproductive stage is reached (Fig. 1). Flowering and fruiting occurs mostly in May and June, although further reproduction may be observed as late as September. *C. werdermannii* is endemic to the Cuatro Ciénegas region (Coahuila, Mexico), one of the most biodiverse cactus hotspots worldwide (Bravo-Holís, 1978; Hernández and Bárcenas, 1995). *C. werdermannii* is listed as endangered by Mexican law (SEMARNAT, 2002) and on Appendix I of CITES (CITES, 2010) because it is thought to experience intense looting (Lüthy, 2001), but has not yet been assessed for the IUCN Red List.

C. werdermannii grows in topographically complex regions, with steep sierras and wide bajadas. The climate has extreme temperatures and precipitation that vary with season and elevation. At the

lowest elevation (740–1200 m a.s.l.) the mean temperature is 21.2 °C, with a maximum in June of 34.8 °C and a minimum in January of 4.8 °C (mean of daily). The total annual precipitation is 252.5 mm, with a minimum in March of 5.5 mm and a maximum in September of 38.8 mm.

C. werdermannii grows in a microphyllous-succulent scrub. Naturally occurring vegetation provides food to livestock, which is the most important source of anthropogenic disturbance in the region: the county of Cuatro Ciénegas raises cattle on 92% of its land, and only 6% of the land has relatively intact plant cover (INEGI 2001, 2002). In addition, the extraction of candelilla (*Euphorbia antisiphilitica*) wax is common in the area, meaning a continuous movement of people, mules and trucks, as well as the removal of plant biomass (Martínez-Ballesté and Mandujano, 2013). Events of livestock grazing and candelilla harvest are of relatively low intensity, but are frequent and recurring, classifying them as chronic anthropogenic disturbances (CAD). However, CAD does not cause sudden land use change but rather a gradual degradation (Martorell and Peters, 2005; Singh, 1998). A mosaic of patches in different phases of deterioration occurs in the region, but the most affected areas have nearly no vegetation.

2.2. Conservation status

To assess the conservation status of *C. werdermannii* we used IUCN (2001) criteria, which require data on species distribution, number of populations and population sizes. Thus, in June 2005 we explored a large region looking for extant populations. We located 10 *C. werdermannii* populations in the area, which were delimited by a polygon joining the most distant plants found (see Martorell and Peters, 2009 for details). To estimate plant density, we randomly placed between 3 and 15 (depending on the population's area) 50 × 6 m transects in each site. Because large individuals (>5 cm) are relatively scarce and thus were unlikely to be properly represented in the sample if only a few transects were chosen, in small (<1 ha) populations we included all individuals >5 cm in a census. However, this method was inaccurate for counting small (1–5 cm) individuals. For this reason we still used transects that were thoroughly revised to sample such plants. In large (>1 ha) sites, we relied completely on transect data, which in this case included all individuals with diameters >1 cm. Plants <1 cm in diameter are difficult to find and their numbers cannot be estimated without considerable error, and were therefore excluded from the analyses. We also recorded the number of reproductive structures (flowers, buds and fruits) and the sizes of all individuals. Population sizes were obtained by extrapolation of transect data to the whole polygon area. In small populations,

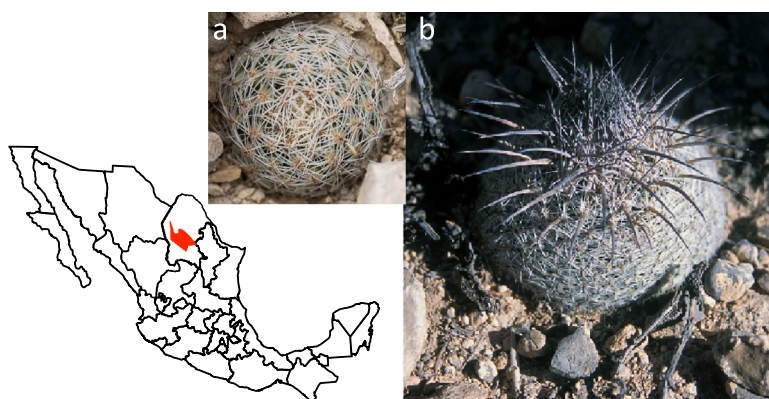


Fig. 1. Potential distribution area of *Coryphantha werdermannii* with (a) a juvenile ca. 3 cm in diameter and (b) adult plant with dark, central spines near the apex. The spot in the map corresponds to the distribution area of *C. werdermannii*.

these numbers were added to those obtained in the census of large plants. Density data for two additional 1 ha sites were taken from Portilla-Alonso (2010). Both sites are a non-random (high density) subsample from a large population discovered in December 2008. These data were only used for the application of IUCN criteria regarding total population numbers.

The IUCN criteria also require generation times and geographic range. The size of the latter was estimated by the mean propinquity method (Rapoport, 1982). We estimated the generation time using Cochran and Ellner's (1992) method, which estimates the mean age of the parents of all offspring produced at the population's stable size structure. For this calculation, we used the average of the projection matrices for three sites published by Portilla-Alonso and Martorell (2011).

2.3. Effects of disturbance

We measured CAD in each site through the Martorell and Peters' index (2009; 2005). This index uses 14 individual metrics to estimate the intensity of three disturbance agents: human activities (e.g., plant extraction or fuelwood harvesting), livestock raising and land degradation. The sum of these three indicators provides a measure for total disturbance. We then performed a disturbance response analysis (Martorell and Peters, 2009) based on two regressions. One relates density to total disturbance or disturbance agents, and provides estimates of the average CAD experienced by a species (pressure), the CAD intensity at which the species achieves its greatest density (ruderality) and the estimated reduction or growth in numbers expected if CAD is intensified (susceptibility – values above one indicate that a reduction in population size is expected if CAD increases, while the opposite would occur for susceptibilities below one). Based on a second regression of density on disturbance agents, the analysis also identifies agents responsible for changes in population size (sensitivity to human activities, livestock raising and land degradation – positive sensitivities correspond to agents that increase density, while negative sensitivities cause population decline). To identify the functions that better describe the relationship between density and total disturbance or disturbance agents, several models (linear, exponential, potential, and Michaelis–Menten functions, trying Poisson, negative binomial, normal and gamma error distributions) were initially fit, and the one with the lowest Akaike information criterion (AIC) was chosen. At this phase, all the explanatory variables were included in each model. For the regression involving total disturbance, the selected model used the reciprocal of the disturbance index as the explanatory variable and a gamma error distribution with a reciprocal link function. For disturbance agents, untransformed explanatory variables and a normal error with a log link was best. Significance of the explanatory variables was then assessed using the two selected models. The analyses were performed in R Development Core Team (2009).

To estimate the effect of CAD on reproduction, the logarithm of the mean number of reproductive structures produced per adult was regressed on the disturbance index and the indices for each disturbance agent with the assumption of normal error. The same was done with the fraction of small individuals (<4 cm in diameter) by means of a logistic regression.

CAD may have a negative effect on cacti if it removes the nurse plants on which they depend for recruitment. To assess whether *C. werdermannii* is associated to nurse plants, we randomly selected 60 points over three 50 m transects (20 points per transect) in each population. At each point, we recorded whether a plant growing there would be considered to be nursed by a shrub (i.e., it would be under a shrub's canopy). Because many globose cacti have been reported to be associated to nurse rocks (Lopez et al., 2009; Nobel and Zutta, 2007; Peters et al., 2008; Sánchez-Soto et al., 2010), we

also recorded if each random point occurred in a position where a cactus would be considered to be associated with a rock (i.e., <2 cm from a rock fixed to the substrate with a >15 cm maximum diameter). We recorded the microenvironment (shrub, rock or bare ground) of each individual sampled following the same criteria. Under a random distribution, the occurrence of cacti in each kind of microenvironment should be proportional to its availability. Thus, the number of individuals e_{ij} expected to occur in microenvironment i at site j was calculated as $e_{ij} = n_j \times p_{ij}$ where n_j is the number of individuals sampled in site j , and p_{ij} is the proportion of random points recorded in microenvironment i at the same site. The expected and observed frequencies were then summed over all sites and a χ^2 test was performed (Martorell et al., 2012). The standardized residuals were then analyzed through z tests to assess in which microenvironment the number of observed plants was significantly different from the expectation (Sheskin, 2000).

2.4. Changes in geographic distribution due to climate change

Ecological niche modeling helps to create an environmental characterization of a species niche through georeferenced occurrences and geographically explicit environmental data or “layers” (Peterson et al., 2011). The potential distribution area (PDA) of a specific species can be produced for current, future or past conditions if environmental layers are available (Martínez-Meyer et al., 2004; Pearman et al., 2010; Peterson et al., 2002; Thomas et al., 2004). Consequently, it is possible to evaluate the difference between PDA under current and future scenarios. Although *C. werdermannii* is associated with very specific habitat requirements (such as soil), in order to evaluate the possible climate change impacts on its distribution we thought it might be more useful to isolate the effect of bioclimatic variables that may change in the future.

Climatic data for current and future scenarios were obtained from the climatology regionalized scenarios produced by Conde et al. (2008b). The general circulation models used for this regionalization were: ECHAM5/MPI, UKHADGEM1, and GDFL CM 2.0 for the A1B, A2, B1 and B2 emission scenarios (Nakicenovic et al., 2001). Emission scenarios (SRES) cover demographic, economic and technological trends that are related to greenhouse gases emissions (IPCC, 2007; Nakicenovic et al., 2001). Although there are new scenarios (rcp2.6, rcp4.5, rcp6.0 and RCP8.5) (IPCC, 2014), they have not been downscaled for Mexico to a suitable scale for biodiversity studies. Consequently, we decided to work with the emission scenarios that have been downscaled to a 10 km² resolution: A2 (high emissions), A1B (mid-high emissions), B2 (mid-low emissions) and B1 (low emissions). Scenarios A1B, B2 and B1 might be used as stabilizing emission scenarios (with 750 ppm, 650 ppm and 550 ppm of CO₂ in the atmosphere, respectively) due to their similar trajectories. The A2 emission scenario is the worst-case emission scenario (“business as usual”) and its trajectory differs from any stabilizing emission scenario (Conde et al., 2008a; Parry et al., 2007).

These models were performed for two time periods, 2030 and 2050 (Conde et al., 2008b), using 19 bioclimatic variables (annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximal temperature of warmest month, minimal temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter) (WorldClim, 2014). The current climatic scenario is a subset of WorldClim (interpolation of weather stations from 1950–2000)

(Hijmans et al., 2005), while climate change scenarios were regionalized for Mexico by the Centro de Ciencias de la Atmósfera (CCA, 2014; Conde and Gay, 2008). Both current and future conditions were constructed in raster format with a grid size of 0.09° ($\sim 10 \text{ km}^2$). For comparability, resolution of current and future climatic scenarios was maintained.

To account for the uncertainty in ecological niche algorithms and climate projections, we used all of the general circulation models regionalized for Mexico and five niche algorithms to calculate a consensus or “ensemble forecast” (Araújo and New, 2007). The niche algorithms used were: BIOCLIM (Nix, 1986), Genetic Algorithm for Rule-set Production (GARP) with the selection of the best models “best subset” (Anderson et al., 2003; Stockwell and Peters, 1999), Envelope Score (Nix, 1986; Piñeiro et al., 2007), Environmental Distance (Carpenter et al., 1993), Maxent (Phillips et al., 2006) and Support Vector Machine (Schölkopf et al., 2001). Thus, we obtained 150 models (3 general circulation models \times 4 scenarios \times 6 algorithms \times 2 dates [for future PDAs] + 6 algorithms [for current PDAs]). The ensemble allowed us to find the areas where most models agree that *C. werdermannii* would be distributed (WorldClim n/d). To do so, maps that resulted from each niche algorithm were added to a binary map (presence-absence) using as a criterion that four out of the six algorithms agreed in their projections. We also performed an ensemble of the three general circulation models, but this time using as a criterion two out of the three models coinciding. This was repeated independently for each emission scenario to produce nine PDAs: 2030 A1B, 2030 A2, 2030 B1, 2030 B2, 2050 A1B, 2050 A2, 2050 B1, 2050 B2 and the current scenario. The PDAs were validated through the area under the curve (AUC) of the receiver operating characteristic (ROC) (Fielding and Bell 1997). The ROC plots were calculated for each algorithm separately, using 80% of the points as training data (random selection) and accepting a maximum omission rate of 15%. To validate our ensemble forecast we carried out a χ^2 test.

2.5. Looting

To assess whether looting occurs and estimate its coarse intensity we performed a review of published data by searching combinations of the terms “*C. werdermannii*” or “*Escobaria werdermannii*” and “sale” or “price” on the Internet for data on commerce. The first 500 results in each of the four possible combinations were checked for data on whether plants or seeds were offered, and for evidence on whether the plants were produced from seed or collected in the field. Data on the provenance of the seeds used were also recorded. The search was conducted in June 2012.

To assess the effect that the extraction of seeds or adult plants may have on the population growth rate, we used the demographic projection models published by Portilla-Alonso and Martorell (2011). We averaged the transition matrices for the three sites reported in that study. We then estimated the population growth rate (λ) after reducing fecundity entries by different fractions ranging from 0 to 0.5, corresponding to different amounts of seeds extracted from the population. To assess the effect of large-plant looting on λ , we reduced the growth and stasis entries of adults. A λ value > 1 indicates that the population would be viable despite the simulated harvest (Caswell, 2001).

3. Results

3.1. Conservation status

We found 17 populations of *C. werdermannii* after searching the area where it had been reported plus a belt around it of $\sim 40 \text{ km}$. Given that four of them are close together ($< 3 \text{ km}$), making genetic

flow likely, this number may be reduced to 13. The total area of the 10 populations sampled, plus those in Portilla-Alonso and Martorell (2011), was 27.6 ha with total of 6847 individuals (Table 1). Nevertheless, there are vast areas that were not accessible but seem prone to occupation by this cactus, making these figures conservative. According to IUCN criteria B2a, C and D this species would be considered of lesser concern because there are more than 10 populations, and likely more than 10,000 mature individuals in the wild (our sample comprises only a small fraction of the large population reported by Portilla-Alonso, 2010).

The extent of occupation was smaller than 5000 km^2 (3563 km^2 from the mean propinquity method, whereas a minimal convex polygon provides an estimate of 2163 km^2), which would correspond to EN (endangered) according to criterion B1, but only if there is evidence of decline. The two remaining criteria, A and E, are based on population reduction or extinction probabilities over (usually) three generations. The estimated generation time was 29.5 yr.

3.2. Effects of anthropogenic disturbance

Livestock raising and human activities were widespread, whereas land degradation was unusual (Table 1). Thus, the latter agent was excluded from the analyses with individual agents.

The density of *C. werdermannii* increased with total disturbance ($F = 9.96$, $P = 0.013$). Livestock raising was responsible for this effect ($F = 115.73$, $P < 0.001$), whereas human activities had no impact on density ($F = 1.20$, $P = 0.310$). However, the high density observed at site 10 seemed largely responsible for these trends (Fig. 2a and b), and therefore the analyses were repeated excluding this site. Results indicated no effect of total disturbance on density after its removal ($F = 0.65$, $P = 0.447$), but the positive influence of livestock remained significant ($F = 6.94$, $P = 0.003$).

The number of reproductive structures produced per adult was strongly diminished by total disturbance ($F = 10.26$, $P < 0.013$, Fig. 2c). In this case, human activities were attributed to this pattern ($F = 6.74$, $P < 0.036$) while livestock had no impact ($F = 0.84$, $P = 0.389$, Fig. 2d). The proportion of small plants increased with total disturbance ($\chi^2 = 35.09$, $P < 0.001$) as a result of positive effects of both livestock ($\chi^2 = 18.81$, $P < 0.001$) and human activities ($\chi^2 = 11.77$, $P = 0.036$). As before, the values from site 10 appeared to highly influence the results (Fig. 2e–f), and therefore the analyses were repeated without this point. In this case, total

Table 1

Descriptors of the 10 populations sampled plus two reported by Portilla-Alonso (2010; PA1 and PA2). Disturbance indices were calculated following Martorell and Peters (2005, 2009). Population area is in reported in ha, and density in individuals ha^{-1} . Population size is the total number of individuals occurring in the population, with the exception of PA1 and PA2, which are fragments of a much larger population. Fecundity is the average number of flowers, fruits and buds per adult plant. L.R.: Livestock raising, H.A.: Human activities, L.D.: Land degradation, S.P.: Fraction of individuals with a diameter $< 4 \text{ cm}$ in the population.

Site	Disturbance					Population attributes			
	Total	L.R.	H.A.	L.D.	Area	Density	Size	Fecundity	S.P.
1	10.9	5.1	5.7	0.0	2.34	105.5	247.2	1.94	0.11
2	11.2	8.5	2.7	0.0	4.87	141.7	690.5	2.36	0.21
3	12.1	2.2	10.0	0.0	0.10	273.1	28.2	1.33	0.26
4	12.8	7.5	4.3	1.0	2.68	76.7	205.7	2.28	0.07
5	13.1	1.3	3.2	8.5	3.29	73.0	240.5	2.05	0.05
6	15.3	11.1	4.2	0.0	1.58	650.0	1027.4	1.11	0.33
7	16.0	4.2	11.1	0.7	0.90	99.0	88.9	1.97	0.18
8	16.6	7.5	9.1	0.0	9.19	203.7	1871.5	0.93	0.13
9	20.1	0.0	20.9	0.0	0.32	218.2	70.6	1.03	0.16
10	22.9	16.4	6.4	0.0	0.34	1633.3	549.8	0.85	0.57
PA1					1.00	421.0	421.0		
PA2					1.00	1406.0	1406.0		

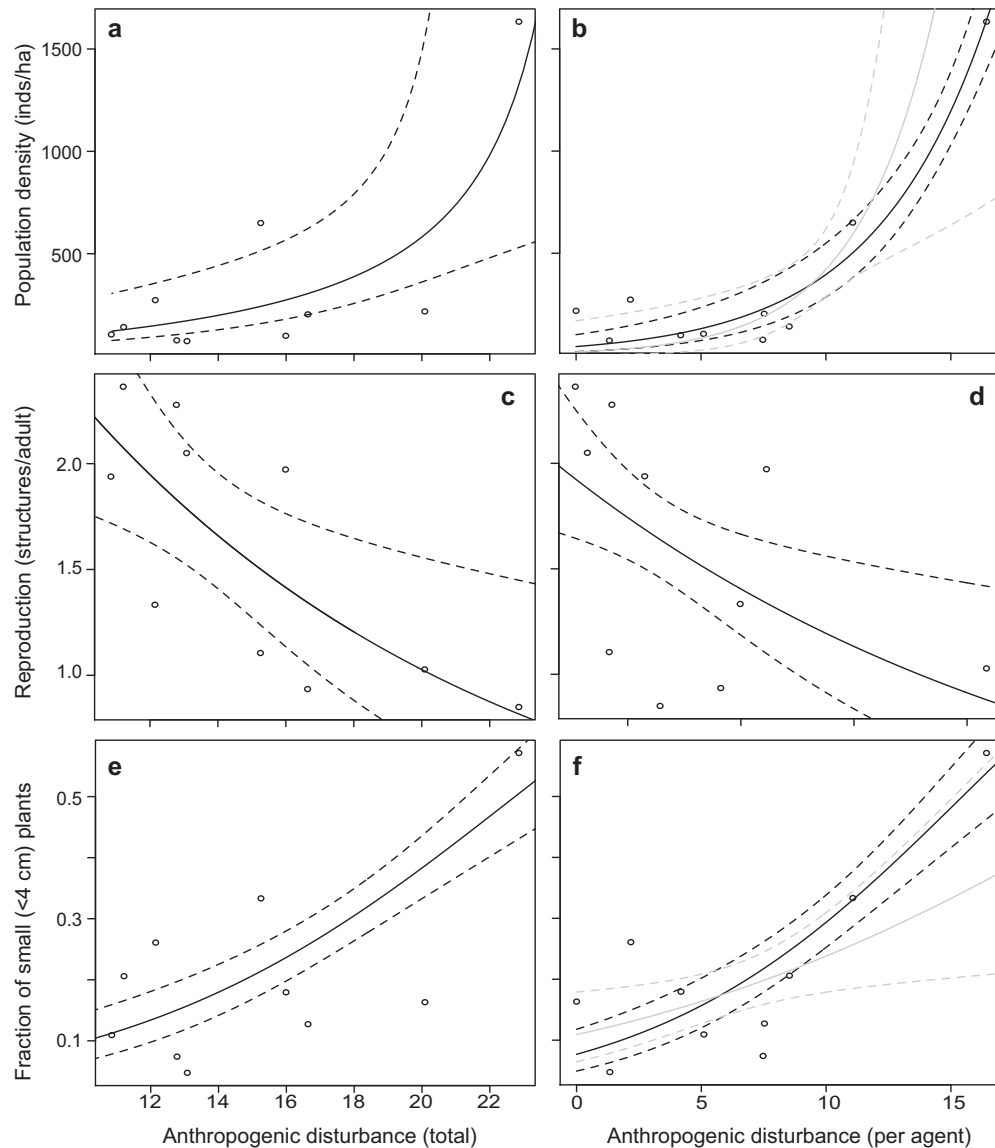


Fig. 2. Effects of disturbance on density, reproduction and fraction of small individuals of *Coryphantha werdermannii*. The responses to the individual disturbance agents (b,f: livestock raising, d: human activities) responsible for these effects are shown in the right column. Black lines: regression models including the most disturbed site. Grey lines: the same models excluding that site. This second regression was only performed for the analysis of density and fraction of small plants, and was not significant for total anthropogenic disturbance (not shown).

disturbance and human activities became insignificant ($\chi^2 = 0.58$, $P = 0.472$ and $\chi^2 = 3.08$, $P = 0.079$, respectively), while livestock raising remained significant ($\chi^2 = 6.36$, $P < 0.016$).

The disturbance pressure for this species was 15.1, a relatively low value compared to that estimated for southern Mexican deserts where this figure is usually three times larger. Using the regression on total disturbance, ruderality was estimated as 22.9 (the maximum disturbance observed). This number is well above the pressure value, suggesting that the disturbance that *C. werdermannii* requires to attain its maximum density has not yet been reached. Average susceptibility was 0.95, indicating that populations are expected to grow $\sim 1\%$ annually assuming that disturbance increases one point every twenty years. The sensitivity to livestock raising was positive (3.07), indicating a positive effect of livestock on this cactus, while human activities had no effect. There were not enough data to estimate the sensitivity to land degradation.

The distribution of *C. werdermannii* in the different microenvironments was non-random ($\chi^2 = 77.07$, d.f. = 2, $P < 0.001$). This cactus was positively associated with bare soil ($z = 5.58$,

$P < 0.001$), but negatively with nurse plants ($z = -6.45$, $P < 0.001$). Rocks had no significant effect on the distribution of this species.

3.3. Climate change

Our ecological niche algorithms independently yielded good performance with an average area under the ROC curve of 0.949 (Table 2). Similarly, the ensemble also presented a good

Table 2

Ecological distribution modeling validation. A ROC test AUC value near one means that the error rates are low. The values reported are the means of all models that fit.

Algorithm	ROC test AUC value
Bioclim	0.874
Envelope score	0.998
Environmental distance	0.999
GARP (best subsets)	0.999
Maxent	0.832
Support vector machines	0.992
Mean	0.949

performance ($\chi^2 = 403.77$, $P < 0.001$). Strong reductions in PDA are expected for 2030 and 2050 (Fig. 3). For 2030, worst-case emission scenarios, A1B and A2, project reductions in PDA of 75% and 67%, respectively. For 2050, both scenarios predict the complete disappearance of suitable habitat. Best-case emission scenarios, B1 and B2, had slightly worse mid-term projections but more optimistic long-term forecasts: for 2030, reductions of 72% and 77% were expected for B1 and B2, respectively, and in 2050, reductions reached 91% and 99%, respectively.

3.4. Looting

There are very few published reports on looting for *C. werdermannii*. In 1990, 41 probably illegally collected individuals were exported from Mexico (Lüthy, 2001), and 20 more specimens were seized from looters between 1996 and 2000 (Bárcenas-Luna, 2003).

After controlling for sellers that advertise at more than one website, we found 17 individuals or nurseries that sold *C. werdermannii* in June 2012. Established plants were sold in 12 of these sites. With the exception of one seller, who provided no explicit

data, most of the individuals offered were quite small (<3 cm in diameter) as would be expected for plants produced from seed. In the case of sites that published photographs, plants had the typical appearance of cultivated cacti. Nevertheless, there were no explicit mentions on the provenance of the seeds or their legality. The remaining five sellers dealt with packets containing 10–500 seeds. The origin of the seeds was either unspecified (two cases) or reported to be from wild populations in Mexico. No mention was made about any permit for seed collection. However, according to The CITES Trade Database, all the exports during the last 10 years originated in the US, Czech Republic or Malta from plants artificially propagated for commercial purposes, with none in Mexico (CITES trade statistics derived from the CITES Trade Database, UNEP World Conservation Monitoring Centre, Cambridge, UK). The lack of CITES records for some of the countries where the sellers seem to be based, and the cryptic pseudonyms chosen by some of the vendors in websites such as E-bay, casts serious distrust upon the lawfulness of much of the seed trade.

According to the demographic model, *C. werdermannii* can withstand seed extraction rates as high as 50% without experiencing

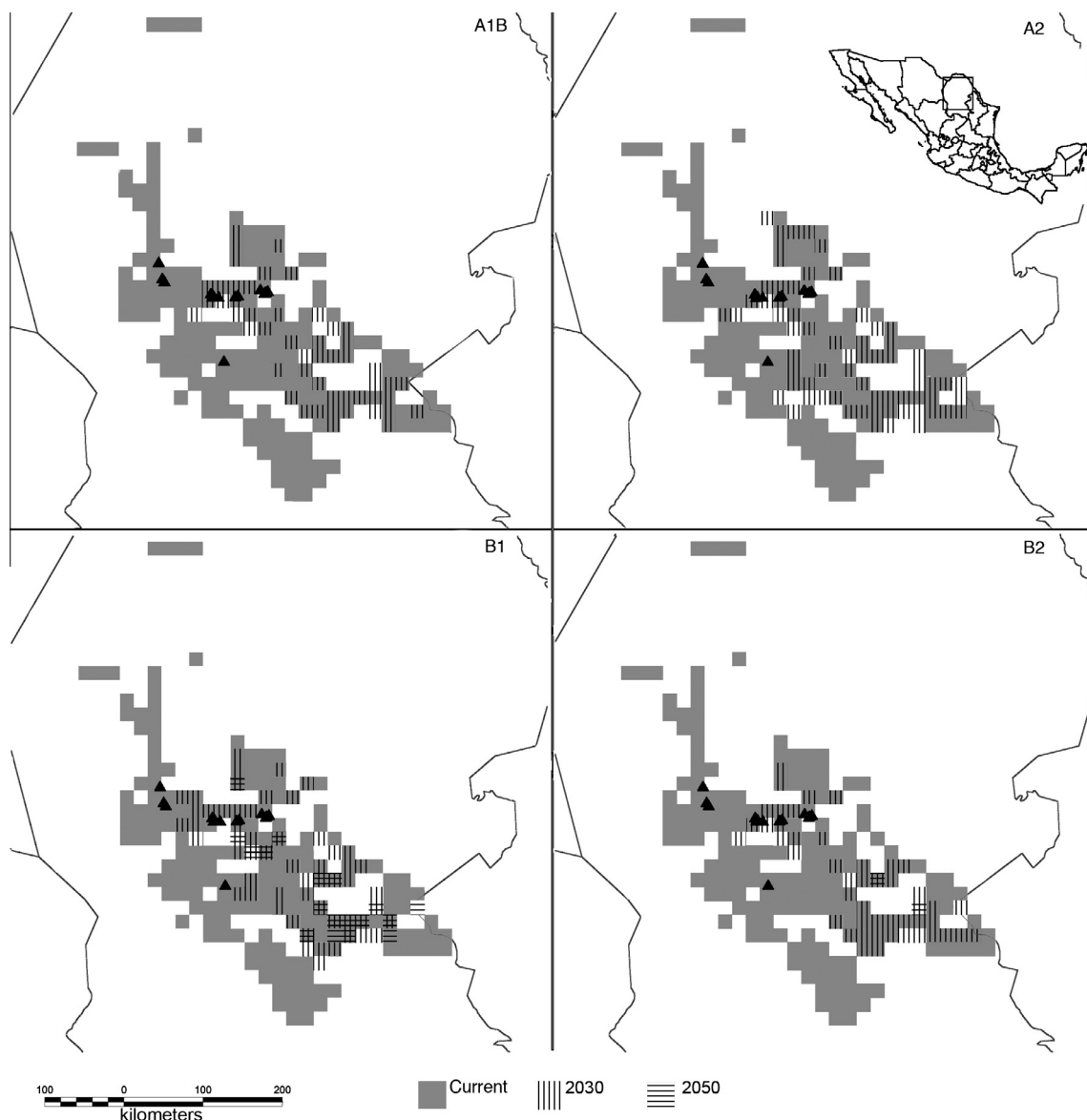


Fig. 3. Current and projected potential distribution areas (PDA) for four climate change scenarios: the worst case A1B and A2, and the best case B1 and B2: grey: current PDA, vertical lines: PDA in 2030, horizontal lines: PDA in 2050, triangles: known populations. Boundary lines correspond to Mexican state boundaries.

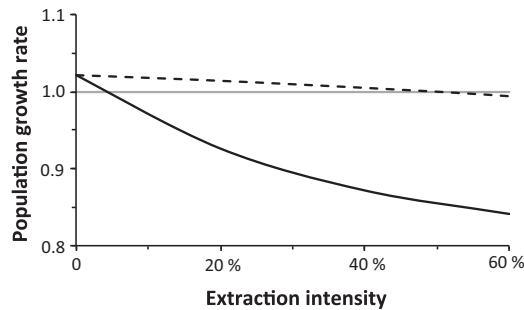


Fig. 4. Effects of the extraction of adults (continuous line) and seeds (dashed line) on the finite population growth rate (λ). The grey, horizontal line shows the population equilibrium ($\lambda = 1$).

any reduction in their population sizes. On the other hand, adult extraction rates as low as 3% sufficed to halt population growth, and greater removal rates would lead to extinction (Fig. 4).

4. Discussion

Our results show that the three purported threats had very contrasting effects on *C. werdermannii*. Whereas chronic anthropogenic disturbance (CAD) had a positive effect, looting seemed unimportant and climate change (CC) was expected to have a tremendously negative impact. The biology of the species explains these differences: the traits expected to make cacti vulnerable to CAD were lacking, and looting seemed restricted to seeds, on which species persistence does not depend. Adult extraction may, however, compromise the viability of the species if it becomes too intense. In contrast, it seems that the high habitat specificity typical of cacti makes *C. werdermannii* very susceptible to CC.

4.1. Effects of disturbance

As it happens in other globose cacti (Martorell et al., 2012; Martorell and Peters, 2009; Ureta and Martorell, 2009), *C. werdermannii* was favored by disturbance, probably because cattle substitute for wild herbivores. Human activities, in contrast, affected the production of reproductive structures negatively, as might be expected from a form of disturbance that has no evolutionary precedents. We measured fecundity at a single point in time, and thus it does not reflect total annual reproduction. However, reproduction events are remarkably synchronous (even populations 70 km away flower on exactly the same days, RM Portilla-Alonso, pers. comm), indicating that our data reflect the differences in fecundity across populations accurately.

Cactus seedlings are considered to be most susceptible to disturbance (Hernández and Godínez-Álvarez, 1994). Nevertheless, a pattern is emerging that increased reproduction is related to ruderality in globose cacti. Despite the fact that CAD reduced the reproductive output of adults, greater numbers of seedlings and small plants were found in disturbed sites, suggesting that increased germination and establishment probabilities exceedingly compensate the reduced fecundity. As other ruderal cacti (Martorell et al., 2012; Martorell and Peters, 2009; Peters et al., 2008; Saraiva and Souza, 2012), *C. werdermannii* did not require nurse plants for successful recruitment but preferred bare ground. Thus, shrub removal by cattle may explain the large numbers of seedlings in disturbed sites.

Probably as a result of such increased recruitment, *C. werdermannii* density increased with CAD. All populations were expected to grow with increasing CAD (susceptibility < 1). This is in line with demographic data for this cactus: through sowing experiments,

Portilla-Alonso and Martorell (2011) found that recruitment increased with disturbance, and that this sufficed to maintain population growth even in the most disturbed sites.

4.2. Effects of climate change

Climate change is expected to be one of the most important threats to *C. werdermannii*'s populations. Environmental conditions required for its persistence are expected to disappear rapidly in the future. Potential distribution areas (PDAs) of other species of cacti are also expected to diminish or shift (Téllez-Valdés and Dávila-Aranda, 2003). This highlights the great importance that national politics and international laws dealing with CC have on species conservation.

Cacti may be highly vulnerable to CC because they are highly specialized in terms of their environmental requirements. This is especially true for globose species, many of which occur in extremely small areas (Aguilar-Morales et al., 2011; Bravo-Holís, 1978; Hernández and Bárcenas, 1995; Hernández and Gómez-Hinostrosa, 2011). Ureta et al. (2012) found that a widespread cactus is able to cope with changing climate through increased homeostasis of population growth rates, whereas a microendemic cactus is expected to undergo strong reductions in population growth. Thus, it seems that *C. werdermannii* is sensitive to a changing environment because it is also restricted to a narrow set of climatic conditions.

Although our input occurrence data are of good quality, there is still uncertainty around the general circulation models and the ecological niche algorithms. Consequently, we used an ensemble forecast. We think that uncertainty around the models indicate that we must be conservative with conclusions, but our results definitely provide insight on how the environmental conditions where *C. werdermannii* is established will change in the mid- and long-term. The precautionary principle calls for immediate action.

4.3. Effects of looting

The scarce available data indicates that *C. werdermannii* trade is focused on seeds or seed-propagated plants. Extraction of adults does occur, as official statistics show, but its intensity is impossible to assess. Adult-plant looting is small relative to the number of plants we predict live in the very large (and mostly inaccessible) PDA of the species.

In most cacti, sexual reproduction makes only a minor contribution to population growth rates, which depend mostly on adult plant survival (Godínez-Álvarez et al., 2003). Thus, *C. werdermannii* could potentially withstand very large seed extraction rates because stasis of adults has the largest elasticity values in matrix projection models (Portilla-Alonso and Martorell, 2011). As a result, even a relatively small adult extraction rate would threaten a population. In absolute numbers and at the species level, such a rate may represent a very large number of plants annually, probably a far larger figure than the market's demand. Looting could nevertheless be intense in some areas. Considering the typically small number of plants that occur in a given site (Table 1), illegal trade could endanger some populations. This may threaten the evolutionary potential of species with populations that have distinctive genetic structures, as is the case with many cacti (Mandujano et al., 2010).

4.4. Status and conservation of *C. werdermannii*

Considering multiple threats to species success is critical for properly assessing its conservation status. As stated in the results section, only criteria A or B1 may be applied to *C. werdermannii*. Criterion B1 requires either fragmentation or extreme population

size fluctuations, for which there was no evidence. However, reductions in population size due to CC are expected and criterion A may apply. Accurate estimates of population decline cannot be obtained from PDAs, but our results suggest that *C. werdermannii* may be classified as CR (critically endangered) because a 90% reduction in suitable areas is expected within three generations (90 yr). If only looting or CAD were considered, *C. werdermannii* would not meet any of the IUCN criteria. It is interesting to note the amount of invested effort in understanding the effects of these two threats on cacti (e.g., Oldfield, 1997; Bárcenas-Luna, 2003; Martorell and Peters, 2009) and the lack of attention to CC.

Conservation biologists acknowledge that different threats act simultaneously on populations, each having specific effects on its own or in combination with the others (Bolten et al., 2010; Isaac and Cowlshaw, 2004; Martorell, 2007). Our results provide some clue as to how our three threats may interact. *C. werdermannii* is ruderal, indicating that appropriate levels of CAD may suffice to maintain viable populations despite CC as is the case with other microendemic cacti (Ureta et al., 2012). Thus, suitable livestock management may minimize the effects of a changing climate, allowing for *in situ* conservation. On the other hand, the population growth rate of this species in disturbed sites depends more strongly on recruitment compared with pristine environments (Portilla-Alonso and Martorell, 2011). This could result in a greater vulnerability from seed extraction if disturbance increases, or to the negative effects of human activities (primarily due to candelilla wax extraction) on the production of reproductive structures.

In addition to the appropriate management of livestock in extant populations, translocation may be a proactive action of “assisted adaptation” to preserve this particular cactus. Following the principles of Hunter (2007), *C. werdermannii* is a good translocation candidate because it is at high risk of extinction under climate change, has a low dispersal capability and has a non-keystone ecological role. To these characteristics, we could add that *C. werdermannii*'s biology is well known and understood.

Therefore, an important start to the conservation of *C. werdermannii* is to evaluate which translocation areas might be the best option in the forthcoming decades. Current uncertainty about future climate precludes the identification of appropriate sites because there is very little overlap in the areas projected using different models or emission scenarios. Translocation to several sites may be required to insure successful conservation. Targeting sites with high levels of livestock raising may also increase success rates. As long as we lack a further understanding of how human activities depress reproduction, candelilla harvest should be stopped to promote a copious establishment of plantlets. Translocation should be mainly focused on adult plants, which contribute the most to the population growth rate (Portilla-Alonso and Martorell, 2011). Finally, *ex situ* conservation is less risky than translocation and may be used in complement.

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