Ecology and conservation of peyote in Texas, USA: Comparative survey of *Lophophora williamsii* populations in Tamaulipan Thornscrub and Chihuahuan Desert.

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Abstract

Wild-harvested plants are a globally valuable source of food and medicines and provide livelihoods for millions of people. *Lophophora williamsii* (peyote) is a small psychoactive cactus native to Mexico and Texas, USA, with considerable cultural, religious and medicinal significance to many indigenous peoples of North America. Peyote, like many plant species globally, is facing multiple threats and is in decline due to legal and illegal harvesting pressure as well as habitat conversion to grazing, agriculture and other economic land uses. Most published studies on peyote have focused on the plant's anthropological, chemical and medical aspects. Surprisingly little is known about the ecology of this species, despite it being currently listed as Vulnerable on the IUCN Red List. Our study addresses this gap by providing the first detailed comparison of peyote populations growing in two distinct ecosystems in the USA: South Texas (Tamaulipan thornscrub) and West Texas (Chihuahuan desert). We highlight regional differences, whereby in West Texas plants at the surveyed sites plants were larger and densities were higher than in South Texas and note significant variability both within and between study sites. We also find significant effects of temperature and precipitation on plant size. Meaningful data about population size and structure across the range of habitats is the first necessary step in order to address a major conservation challenge of sustainable management of an overexploited resource. We conclude that urgent conservation and restoration efforts involving Native Americans and local landowners are needed to secure long-term survival of this vulnerable cactus.

Keywords

Cactaceae, *Lophophora williamsii,* plant conservation, population ecology, sustainable harvesting, ethnobotany.

Introduction

Global demand for wild-harvested resources is increasing, while natural habitat for such resources is being lost to a variety of anthropogenic disturbances [1–3]. More than 28,000 plants are used for medicinal purposes worldwide, many more have cultural and/or religious significance [4]. International Union for Conservation of Nature (IUCN) estimates that at least 15,000 of these are at risk of extinction from a combination of over-harvesting, habitat destruction and climate change [5]. Sustainable harvesting of wild species is a major global conservation challenge, yet the first necessary step for this is understanding distribution and population structure of species in question. Poor knowledge of ecology and population dynamics of plant species greatly limits conservation actions and can result in inappropriate decisions and policies that do not ensure long-term survival, as well as a waste of limited resources allocated to conservation [6]. Baseline population data across the whole distribution range of species are crucial for developing and testing conservation interventions, long-term monitoring and species responses to climate change [7]. This is especially important for plants that have been traditionally harvested from the wild to be traded and used during religious and cultural ceremonies or for their medicinal value. A challenge when studying or monitoring populations of threatened plants located on uneven terrain, amidst dense brush, with patchy occurrences and access restrictions, is being able to generate meaningful data about population size and structure. We undertook a study to establish a practical means of doing this in the field using best known statistical practices, providing a valuable case study.

Species introduction

Our subject species was the cactus *Lophophora williamsii* (Lem. Ex Salm-Dyck) J.M. Coulter (Cactaceae), commonly known as peyote. It is a small, grey-green, spineless, globular cactus native to central and northern Mexico and close to the Rio Grande river in Texas, USA (Fig 1). Its preferred habitats are calcareous desert and shrubland. It is a slow-growing species, taking up to 10 years to

59 mature from seed to harvestable size [8], which is not uncommon for cacti [9]. or other medicinal
60 plants, e.g. ginseng, cohosh, goldenseal [10,11]. Such slow growth is a well-known risk factor for
61 survival of these populations.

Fig 1 Distribution of 5 species of the genus *Lophophora*. Distribution map from [12] based on the recently confirmed locations. Question-marks represent uncertainty about the current presence of peyote and mark it range from older publications (e.g.[8]).

History of use and cultural significance

62 Archaeological evidence shows that peyote has been used for medicinal and religious purposes by
63 the indigenous peoples of North America for at least 6,000 years [13,14]. Members of the Native
64 American Church (NAC) consume peyote as a sacrament [8,15,16]. in the form of fresh or dried
65 "buttons" ("buttons" refer to the crowns of the peyote cactus see [17]. or as a tea. It is an integral
66 part of the religious practice of the 250,000–500,000 members of the NAC [18,19].

International and national listing

67 In 1970, mescaline, the main alkaloid responsible for peyote's distinctive psychoactive effects, and
68 the peyote cactus itself were listed as Schedule 1 drugs under the Controlled Substances Act in the
69 USA [20]. Native Americans are exempt on religious freedom grounds and can legally purchase and
70 consume peyote [21]. Internationally, mescaline, but not peyote, was listed by the 1971 United
71 Nations Convention on Narcotic Drugs [22]. This is the key feature distinguishing peyote from most
72 other wild-harvested plants which are managed as an open-access resource [23,24]. In contrast,
73 consumption as well as the location and number of people engaged in harvesting peyote is
74 restricted, and the effects (whether positive or negative) that this has on the populations are poorly
75 documented.

76 The IUCN Red List status of peyote is Vulnerable [25]. Peyote and other cacti are listed in Convention
77 on International Trade in Endangered Species (CITES), Appendix II [26]. Peyote is legally protected

in Mexico by the national list of species at risk of extinction, NOM-059-SEMARNAT-2010, where it is listed under the category "subject to special protection" [27]. It is not listed under Endangered Species Act in the USA.

Peyote conservation, ecology and threats

Despite the ethnobotanical and cultural importance of peyote, few studies have been undertaken on its ecology and biology; notable exceptions include work by Terry et al. and the Cactus Conservation Institute in the USA [14,17,28–30]. Reports dating back 35 years already noted declining populations resulting in shortages of supply for the NAC [31]. The main threats to peyote in the USA are habitat loss (for 'improved pastures', agriculture, urban development and energy infrastructures), over-harvesting through legal trade for the NAC, and poaching (see Fig 2) [8,32]. Their impacts have never been quantified. Experimental studies investigating the effects of harvesting on the survival and re-growth of peyote have shown that it takes at least 6-8 years for these cacti to regenerate after harvesting, even when the harvesting has been done with the best possible techniques [14,17,28,29]. Over-harvesting leads to populations with low densities, and reduced sexual reproduction, which in turn leads to loss of genetic diversity [33].

Fig 2. *Lophophora* williamsii (peyote) and its threats. Peyote cactus a) in flower; b) with fruit, c) growing in multi-crown cluster, d) harvested peyote drying on the rack of a licensed distributor, e) habitat loss through clearing of the native thorn-scrub, f) challenges of dealing with private landowners. a, b, c, d, e - Photos by the author; e – creative commons license.

Our study

The geographical scope of the present study is South Texas (STx), where most of the commercial harvesting of peyote occurs, and Trans-Pecos or West Texas (WTx, area of Texas west of Pecos river), where no commercial harvesting occurs because peyote is much harder to find [34]. There are no published data on the population densities and/or structures for *Lophophora williamsii* across its native range.

Aims and objectives

This is the first study assessing peyote populations in STx, in the areas close to where commercial harvesting is active and comparing them with populations from WTx with no commercial harvesting. Our study will serve as the baseline assessment for a longitudinal monitoring of these populations, enabling greater understanding of their dynamics, structure, and spatial interactions.

Therefore, our project will not only provide novel data on peyote ecology and population structures but will also contribute to the long-term conservation of this vulnerable cactus.

Our research addresses the following questions:

- What are the densities and size structures of peyote populations in the USA?
- Are these different between STx and WTx?
- How do environmental variables affect peyote populations?

Methods

Study areas

Study sites were selected with the aim to sample the entire range of peyote populations in Texas. All sites are in private ownership (Table 1). Verbal consent was obtained from the landowners prior to study site access. To protect the cacti from poaching, and at the request of some of the landowners, the exact locations of the study sites are not disclosed. Study sites 1-3 are located in STx (Tamaulipan Thornscrub), and sites 4-6 in WTx (Chihuahuan Desert) (Table 1, Fig 3).

Fig 3 Location of the study sites and population structures of *L. williamsii*. Map shows location of 6 study sites included in this study from Chihuahuan desert ecoregion (West Texas: 4, 5, 6) and Tamaulipan thornscrub (South Texas: 1, 2, 3). Distributions of the two population structure variables, plant volume and crown number are presented by site and region. Both regions have similar crown number, usually one or two, indicating that no recent harvesting has been happening on any of our sites. In the field, a good proxy for plant size is the number of ribs, with 5 common for juvenile plants, and 13 for the large, mature plants. Size structures are very different

in two regions: there were considerably more mature 13-ribbed plants in West Texas. In West Texas populations consisted mostly of the smaller, 5-8 ribbed plants.

Table 1 Details of the study regions and sites.

Site	Region	Ecoregion	County	Private property type	Property area (ha)	Suitable habitat (ha)	Peyote number	Transects surveyed	Transects with peyote
1	South Texas	Tamaulipan thornscrub	Starr	Ranch	197.93	118.15	71	27	4
2	South Texas	Tamaulipan thornscrub	Jim Hogg	Conservation	243.08	75.79	73	31	3
3	South Texas	Tamaulipan thornscrub	Starr	Conservation	183.02	73.66	53	26	1
4	West Texas	Chihuahuan desert	Val Verde	Ranch	74.96	74.96	25	14	1
5	West Texas	Chihuahuan desert	Terrell	Ranch	64.37	52.06	26	18	1
6	West Texas	Chihuahuan desert	Presidio	Conservation	725.26	375.35	46	5	4

Site	Surveyed area (ha)	Density (n/ha)	Crown number	Plant volume (cm^3)	Slope (°)	Aspect	Elevation (m)	Precipitation (mm)	Temperature max (C)	Temperature min (C)
1	0.27	262.96	1.11	15.89	1.60	S (3%), W (97%)	88.80	505.81	30.23	17.07

2	0.31	235.48	1.88	33.89	5.42	E (98%), S (1%), W (1%)	231.59	544.49	28.79	16.11
3	0.26	203.85	1.21	13.06	1.67	E (100%)	86.48	504.10	30.15	17.07
4	0.14	178.57	1.36	43.41	14.42	S (100%)	490.71	385.65	27.41	13.27
5	0.18	144.44	1.65	81.92	12.92	W (100%)	532.61	361.22	27.28	12.89
6	0.05	920.00	1.63	133.59	13.79	S (83%), W (17%)	1258.80	338.34	26.51	10.21

Additional information about study sites can be found in supplementary material S1 Text, S1 Fig, S1 Table.

Understanding regional differences helps to interpret study results. In Texas there is a strong regional variation in climate and elevation, indicating that it will be difficult to disentangle effects of environment variation independent of location. On average the climate of the Chihuahuan Desert is colder and dryer than that of the Tamaulipan Thornscrub. Though both regions get similarly hot during the day, nights and winters in the Chihuahuan desert are much colder. In WTx peyote starts to appear at higher elevation, on steeper slopes, and on South and Southwest facing slopes – to the exclusion of North-facing slopes. A detailed description of the two ecoregions can be found in S1 text, and environmental variation in S2 Fig.

Survey procedures and sampling universe

Fieldwork was conducted in May-July 2019. Our survey methodology was chosen to avoid bias, and to optimise the trade-offs between statistical rigour and sample size. We pre-determined 'suitable habitat', which, combined with accessibility criteria, established the sampling universe. The sampling universe included land that:

- had never been root-ploughed or converted to agriculture;
- had not been developed (i.e., roads, buildings, drains, pipelines, wind turbines);

- had suitable soil and terrain type (escarpment, limestone, grey/white but not red soils);
- was not near streams or other areas with very thick vegetation or excessive soil moisture;
- was accessible (within 200m of the road/trail, no further than 1-2km from the car);
- was not on very steep slopes.

The open-source Geographic Information System (GIS, in QGIS v. 3.8.2) was used to generate transects within the polygons delineated by the property boundaries and suitable habitat [35]. For ease of the layout process and to avoid biasing the study with the previously known locations, we used transects running North-South on major longitudinal lines of the Universal Transverse Mercator (UTM) coordinate system. UTM zone 13 North was used in the 2 most western study sites, and zone 14 North for the other 4. The World Geodetic System 84 (WGS 1984 or EPSG:4326) a current standard datum for GPS, was used throughout the study.

Transects were 25m long and 4m wide. Parallel transects that did not share the same longitude were at least 250m apart. A set of possible transects was generated in advance, and a random subset was selected to be surveyed at each site (S1 Fig). The pre-determined origin and terminus of each North-South transect were found in the field with Garmin s64 handheld GPS navigator, with 3-5m accuracy [36].

Data collection

Data were collected at both the transect and plant level (see S3 Fig for an example of our data sheets). At the transect level we recorded presence/absence of peyote, what other cacti were found within it (S1 Table), and general notes on the transect. For each individual plant we recorded number of crowns, number of ribs, shortest and longest diameters. Crowns were assumed to be from the same plant if touching. If the crowns were not touching, they were considered to be different plants.

Data sources and geospatial analysis

149 Publicly available spatially-referenced environmental data were obtained from Unites States
150 Geological Survey (USGS) for Digital Elevation Model (DEM), which provided elevation, slope, and
151 aspect; and also geological maps; Texas Natural Resources Information System (TNRIS) for land
152 parcel data – used to determine property boundaries; and the Parameter-elevation Regressions on
153 Independent Slopes Model (PRISM) Climate Database for 30-year average climate variables [37–39].
154 Soil data came from United States Department of Agriculture (USDA) National Resources
155 Conservation Service Web Soil Survey [40]. Peyote harvesting and sales data was obtained from the
156 Texas Department of Public Safety (TxDPS) [41] .

157 Geospatial analysis was performed with QGIS v. 3.8.2 [35], and layers were projected into the same
158 geographic coordinate system (WGS84) for final analysis.

Variables of interest

159 Total above-ground volume was calculated from the diameter of each crown by assuming that each
160 crown was a hemisphere: Vcrown= ⅔ π(diameter/2)3. Often peyote cacti have a single crown, but
161 some grow in caespitose clumps (Fig 2). In such a case the estimated volumes of all its crowns were
162 summed to obtain the total above-ground volume for the plant.

163 Another measure of population structure was the number of crowns per plant. Multiple crowns
164 often grow as a result of previous harvesting (which usually involves removing the apical meristem
165 along with the crown of the cactus) or other injury to the apical meristem.

166 Population density was measured as the number of plants per hectare of the habitat surveyed and
167 then extrapolated to the whole suitable habitat area. Summary of the study variables can be found
168 in S2 Table.

Statistical analysis

169 Statistical analyses were performed in SAS v9.4 and SPSS v25 [42,43].

170 Distributions of population structure variables between STx and WTx were compared using Mann-
171 Whitney tests.

172 General linear models (GLM) were developed to investigate relationships between response and
173 predictor variables (S2 Table). Spatial variation in plant volume was explored with the GLM ordinary
174 least squares means, and standard errors and probabilities were calculated using the Type I SS for
175 transect by site as an error term. We used this model because this is a hierarchical ('nested') analysis.
176 Assumption of the GLM is that residuals are normally distributed, which was the case ($W = 0.944269$,
177 $P < 0.0001$). SAS GLM (general linear model) procedure was used for these analyses.

178 To identify primary habitat characteristics and their effects on plant volume we repeated the model
179 with environment variables as covariates. The analyses were repeated with each of the
180 environmental variables individually, and significance level was adjusted using Bonferroni
181 correction for multiple comparisons, to $P < 0.0085$. It was necessary to separate the two regions to
182 statistically test the effect of aspect on plant size, due to the unbalanced design that combining the
183 analyses of aspect in the two regions would create.

184 For crown numbers and presence/absence of plants on the transect we used logistic regressions, a
185 type of generalised linear model. Logit link function with binomial distribution was used for
186 presences/absences, and negative binomial distribution for crown numbers. The SAS GLIMMIX
187 (generalised linear mixed models) procedure was used for these analyses. The relationships
188 between presence/absence and environmental variables were investigated as well and adjusted for
189 multiple comparisons as above.

Results

Densities and population structures

The 6 different study sites (Fig 3) had a total area of 1489 ha, 770 of which were suitable peyote habitat. We surveyed 121 transects, covering an area of 1.21 ha, recording and measuring 294 plants. Together these areas cover a wide range of altitudes (80-1300m above sea level), rainfall (average annual precipitation 330-545mm), and temperatures (average annual temperatures, max 26-30°C and min 10-18°C) (illustrated in S3 Fig).

We compared the distributions of population structure variables in two regions (Fig 3). The distributions of plant volumes differed significantly (Mann–Whitney U = 2771, STx = 197 WTx = 97, $P < 0.0001$). The distributions of crown numbers in the two regions did not differ significantly (Mann–Whitney U = 9252, STx = 197 WTx = 97, $P < 0.547$).

The plants on average were significantly larger in WTx, compared to STx (21.80 cm3 vs. 95.01 cm3, $t(292) = -10.598$, $p<0.0001$, t-test performed on log(volume)), but in both regions plants mostly had one or two crowns.

Densities were slightly higher in WTx, but this was largely driven by one study site which had no known history of harvesting (Table 1).

In terms of presences/absences, in STx 90% of transects did not have any peyote, while in WTx only 84% were empty. However, Fisher's exact test confirms that this difference is not significant ($P = 0.3565$).

Modelling spatial variation

First, we wanted to understand how variation in population structure is distributed at a spatial scale. For plant volume we find: a) regions are significantly different from each other, $F(1,4) = 13.38$, $P = 0.0216$; b) sites are not significantly different from each other within a location, $F(4,8) = 3.19$, $P = 0.0764$; c) transects are significantly different from each other within a site, $F(8,280) = 3.11$, $P =$

0.0022. Mean standard errors were quite large, which implies important variation between plants within a transect (R2 = 41%).

For crown numbers, as expected, site selection had a significant effect (F(4, 288) = 4.41, P =0.0018), but not region (F(1,288) = 1.37, P = 0.2436).

We have also run the models for presence/absence data per transect. Region was not significant (F(1, 115)=2.00, p=0.1600), but site had an effect (F(4, 115)=2.76, p=0.0308).

Modelling the effect of environmental variables

Second, we investigated the effect of environmental variables on plant volume (Fig 4). We find significant effects of precipitation (F(1,13)= 18.48, P=0.0036), max temperature (F(1,13)= 13.64, P=0.0077) and min temperature (F(1,13)= 14.71, P=0.0064), but not slope (F(1,13)= 0.31 P=0.5954), elevation (F(1,13)= 0.51, P=0.4993) nor aspect (F(1,188) = 0.37, P = 0.5441 for STx; F(1,90) = 0.11, P = 0.7448 for WTx).

Fig 4 Relationship between plant volume and environment variables. Elevation, aspect and slope are presented at the plant level, while climate variables are available at transect scale. 14 transects with plants are presented here. Note that plant volume has been transformed into log(volume).

Third, we modelled the effect of environmental variables on the presence/absence data. None of the environmental variables were significant.

Model results are summarised in tables S3, S4 and S5.

Discussion

There is a considerable knowledge gap around peyote conservation and ecology, and this study addresses this by developing and implementing a methodology for surveying peyote populations in Texas, USA. Applications of this work include: a) providing an important baseline for longitudinal studies estimating population dynamics; b) discovery of new plant populations; c) evaluating

229 harvesting impacts; d) identifying suitable habitat for restoration and preservation; e) improved
230 protection and management of populations and their habitat; and, ultimately, f) species
231 reintroduction. This study, despite its regionality and species specificity, is also relevant for other
232 sacramentally or medicinally harvested plants important for indigenous people.
233 We collected data from 294 plants and surveyed 1.21ha of land in the Tamaulipan thorn-scrub and
234 the Chihuahuan Desert – two ecoregions of Texas where peyote thrives.
235 Sites differed significantly in peyote densities, i.e., numbers of plants per unit area of suitable
236 habitat. One site in WTx had exceptionally high densities of 900 individuals/hectare – and this was
237 the site where, as far as we know, there has never been any form of harvesting. Sites in STx had
238 about 230 individuals/ha, and other sites in WTx had lower numbers.
239 Demand for peyote has been estimated at 5 - 10 million buttons per year (Anderson 1996). Data on
240 peyote sales from licensed distributors, collected by the TxDPS up until 2016, indicates that about
241 1,500,000 peyote buttons are sold annually (S5 Fig). A typical NAC ceremony requires about 300
242 buttons (Feeney 2017), and the membership of the NAC, is estimated at about 250,000 – 600,000
243 members (Prue 2014). Legal supply is struggling to satisfy demand, to an extent that in 1995 NAC
244 leaders declared a 'peyote crisis' [44]. In the last 25 years the situation has only grown worse.
245 Four registered peyote dealers operate in Texas, employing 1 to 11 peyoteros each [41]. Daily each
246 dealer receives about 500-1500 buttons. If our density estimations for STx are applied, this means
247 peyoteros need to explore 4.4 ha of suitable habitat per day, which amounts to about 550m^2 per
248 person. Given their expert local knowledge on where to find peyote, this seems reasonable,
249 although questionably sustainable in light of reduction in availability of suitable habitat and
250 restricted access to private properties. In fact, there are reports of rampant poaching (which in STx
251 is colloquially known as 'fence jumping'). Anecdotal evidence links these 'fence jumpers' to licensed
252 distributors, and there has been at least one case when a distributor's license has been suspended

253 when an employee has been caught trespassing on private property to collect peyote. The lines
254 between legal and illegal are blurred, as once peyote arrives at the drying racks of a legal peyote
255 distributor, the origin is impossible to determine. Future research, using a combination of fieldwork
256 and remote sensing should be conducted to estimate the rate of habitat loss and current extent of
257 suitable habitat. Another, overlooked avenue of research is investigating the extent of illegal trade
258 in peyote. Few studies investigate illegal wildlife trade in plants, a case of 'plant blindness' recently
259 highlighted by [45]. Yet cacti (and orchids) are among the plant groups most threatened with
260 extinction and are clearly impacted by the illegal trade [46,47].

261 We developed our methodology with the goal of being unbiased and statistically rigorous, and have
262 produced repeatable, unbiased definitions of the sampling universe and established transects
263 according to criteria independent of the previously known locations of populations. This resulted
264 in low peyote occurrence directly within sampled plots at 10% in STx and 16% in WTx.

265 Another question we explored was the influence of environmental variables on plant size using plant
266 volume as a measure of size. We found a strong regional effect on size of the plants: cacti were
267 significantly larger in WTx (86 cm^3) compared to STx (21cm^3), but it is important to note that there
268 was a lot of individual variability within sites/transects. Independent of the regional effects, plant
269 volume increased with precipitation and decreased with the increase in average temperatures. The
270 first one intuitively makes sense, in the dry season cacti shrink in size as moisture is lost [33].
271 Temperature effects are harder to interpret, and it might be related to the effects of shade and
272 nurse plants. Contrary to our expectations, we found no effects of elevation, slope or aspect. One
273 explanation could be that in STx these really are not particularly important, as the elevations are
274 much lower than those in WTx, and my sample size was not large enough to detect the effect for
275 WTx alone. From personal observation, in WTx peyote is most commonly found on South or South-
276 West-facing slopes and tops of the mountains, but never on North-facing slopes. Further research,

with a larger sample size, is needed to verify this observation. It would be even more informative for elucidating relationships between plant distribution and environmental variables to compare areas where plants are present or absent. However, none of the environmental variables turned out to be significant in my analysis.

Our analysis used 6 environmental variables plus soil and geology for the pre-selection of suitable habitat. Suitable habitat is composed of many features. One approach would be to investigate vegetation cover or collect other, more precise, field-based measurements. There is an informative dataset of shrubland cover from the National Landcover Database [48], unfortunately it is only currently available for the Western USA and could not be applied to three of the study sites.

The main finding of our study is that there are regional differences between South and West Texas. One implication for future conservation efforts is these regions need to be considered separately, rather than as one average habitat. Management interventions need to be site specific and driven by knowledge of the responses of the plants in those areas. It is important to develop and maintain site specific monitoring to detect changes which can influence the successful survival of this species.

Peyote can survive in different habitats. It would be interesting to know why these differences occur. One possibility is that these differences are genetic adaptations to different environments, but no studies so far have tested how closely genetically-related are the STx and WTx populations. Another possibility is that the effects that we see are the lingering after-effects of harvesting. Future studies should compare, and contrast harvested and unharvested populations to answer this question.

In the past it is likely that WTx and STx populations formed a continuous, much larger population, similar to peyote in Mexico, where populations in Tamaulipan Thornscrub and Chihuahuan Desert are still contiguous.

300 Most peyote populations in Texas grow on private land, therefore it was necessary to obtain
301 permissions and consent from the landowners to conduct the research. Conservation work on
302 private lands is a relatively new and promising field [49,50], which is especially relevant to the
303 context of Texas, where 96% of land is privately owned [51]. Nevertheless, it takes time to gain trust
304 from the local landowners, especially when it comes to discussing sensitive and controversial topics
305 such as peyote conservation.

306 Peyote is situated in a peculiar position because of its listing as a Schedule 1 drug in the USA. The
307 TxDPS and the federal DEA have extensive regulations regarding who can harvest, and where, yet
308 there are no regulations or even guidelines on how or what plants to harvest, as is usually the case
309 with other heavily harvested plant species, such as ginseng [11,24,52], frankincense [53], hoodia
310 [54], cork oak [55,56].

311 The current state of knowledge about peyote populations does not yet allow quantification of what
312 level of harvesting would be 'sustainable'. Sustainability has three key components, each of which
313 needs to be in place for the long-term conservation and security of the species [57]. For peyote,
314 sustainability can be measured as:

315 • Biological sustainability – understanding peyote population structures and dynamics can
316 inform what rate of harvesting is not damaging for the long-term survival of cacti in their natural
317 habitat.

318 • Social sustainability – maintaining a delicate balance between religious and conservation
319 needs, whereby there is guaranteed supply of the medicine for the NAC ceremonies, and Native
320 Americans are actively involved in any conservation decisions and actions.

321 • Financial sustainability – financial incentives for landowners to conserve peyote on their
322 property, for example through conservation easements; or tax breaks for landowners who work
323 with DEA licenced distributors or official NAC chapters.

324 To achieve this, it is necessary to bring together landowners, peyote distributors and NAC members,
325 collaborating towards conserving peyote for future generations. Private landowners, distributors
326 and the NAC are the key stakeholders without whose active participation and collaboration peyote
327 conservation would not be possible. A very close example to peyote is the situation with hoodia
328 (*Hoodia gordonii*). Many lessons can be drawn from studying the regulation of trade and harvesting
329 of this plant, and recognizing the importance of relationship building and active engagement with
330 indigenous people as partners [58].
331 Of course, an obvious solution to the 'peyote crisis' would be cultivation. Unfortunately, in the USA
332 there are serious regulatory hurdles to cultivation due to peyote being a Schedule 1 drug, which
333 entails restrictions on cultivation at the federal level, plus complete prohibition of cultivation in
334 certain states, including Texas, at the state level [30]. It is also important to challenge assumptions
335 held by some NAC chapters that medicine from the wild is better than from cultivated sources.
336 Fortunately, many Native Americans don't hold these beliefs, and would be willing to use the
337 cultivated plants [59]. Another impediment to cultivation is the lack of protocols and methods for
338 growing. Only two peer-reviewed studies have so far described peyote production [60,61] –
339 although there is a lot of information in the grey literature and from private growers that should be
340 analysed. Cultivating peyote could solve the shortages of supply for the NAC, and also contribute to
341 *ex situ* conservation by producing larger and earlier-flowering plants and generating seed or
342 seedlings for re-introduction into native habitats.

343 Conclusion

344 The evident unsustainability of the current legal system of peyote harvesting and distribution, does
345 not bode well for the future of peyote. The unknown but increasing population of peyote consumers,
346 with only minimal efforts to implement greenhouse cultivation to replace the peyote being steadily
347 consumed, suggest a steadily declining supply of peyote for the future generations if there is no

348 change in the current situation. In fact, one of the known peyote populations, from the Big Bend
349 National Park, disappeared almost in front of our eyes, likely harvested into oblivion [62] and this is
350 not the first time this has been documented [63].

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Supporting information

S1 Fig. Example of typical habitat, transect and tagged plant. a) Tamaulipan Thornscrub, transect flagged in pink, peyote flagged in green; b) Chihuahuan Desert, transect flagged in pink; c) example of completed and marked transect from one of the sites; d) tagged peyote partially shaded by its nurse plant. Photographs by the author. Tamaulipan Thornscrub, transect flagged in pink, peyote flagged in green; Chihuahuan desert, transect flagged in pink; example of completed and marked transects from one of the sites; tagged peyote partially shaded by its nurse plant. Photographs by the author.

S2 Fig. Environmental variation in the USA. Maps are from PRISMA (2019).

S3 Fig. Data sheets for transects and individual plants within one transect. D – diameter, L-R - left or right, harvested – whether there were obvious signs of harvesting

S4 Fig. Site differences in elevation, aspect, slope, precipitation and temperature. West Texas is generally colder, dryer and has higher elevations compared to South Texas. In West Texas, where peyote mostly grows on the mountain slopes, aspect is much more important – plants are commonly found on the South-West facing slopes, which in Northern hemisphere receive most sunshine. Note that here aspect is presented as counts of the 4 categories. Climatic data is only available at a coarse scale. For this reason confidence intervals are only present on the variables that are available at the plant level (slope, elevation and plant volume).

S5 Fig. Legal peyote trade data. Annual peyote sales data from 1986 to 2016 (when TDPS stopped collecting these data). Key market indicators from the regulated trade, the prices are rising, and the supply is dwindling. Data from TxDPS, 2019.

S1 Text. Study area descriptions.

S1Table. Additional site information: including number of cacti species, suitable soil and geology.

S2 Table. **Summary information on the variables used in our study.**

S3 Table. Results from the general linear model for log (plant volume).

S4 Table. Results from the generalised linear model for crown numbers.

S5 Table. Results from the generalised linear model for presence/absence data.

a)
b)
c)
d)
e)
CATERPILLAR
f)
SEARCHING
FOR
LAND LEASES
FOR
PEYOTE
Buy or Sale
CALL
844·0365
PRIVATE PROPERTY
DO NOT ENTER
If the dogs
don't get you,
I will!

Fig 2

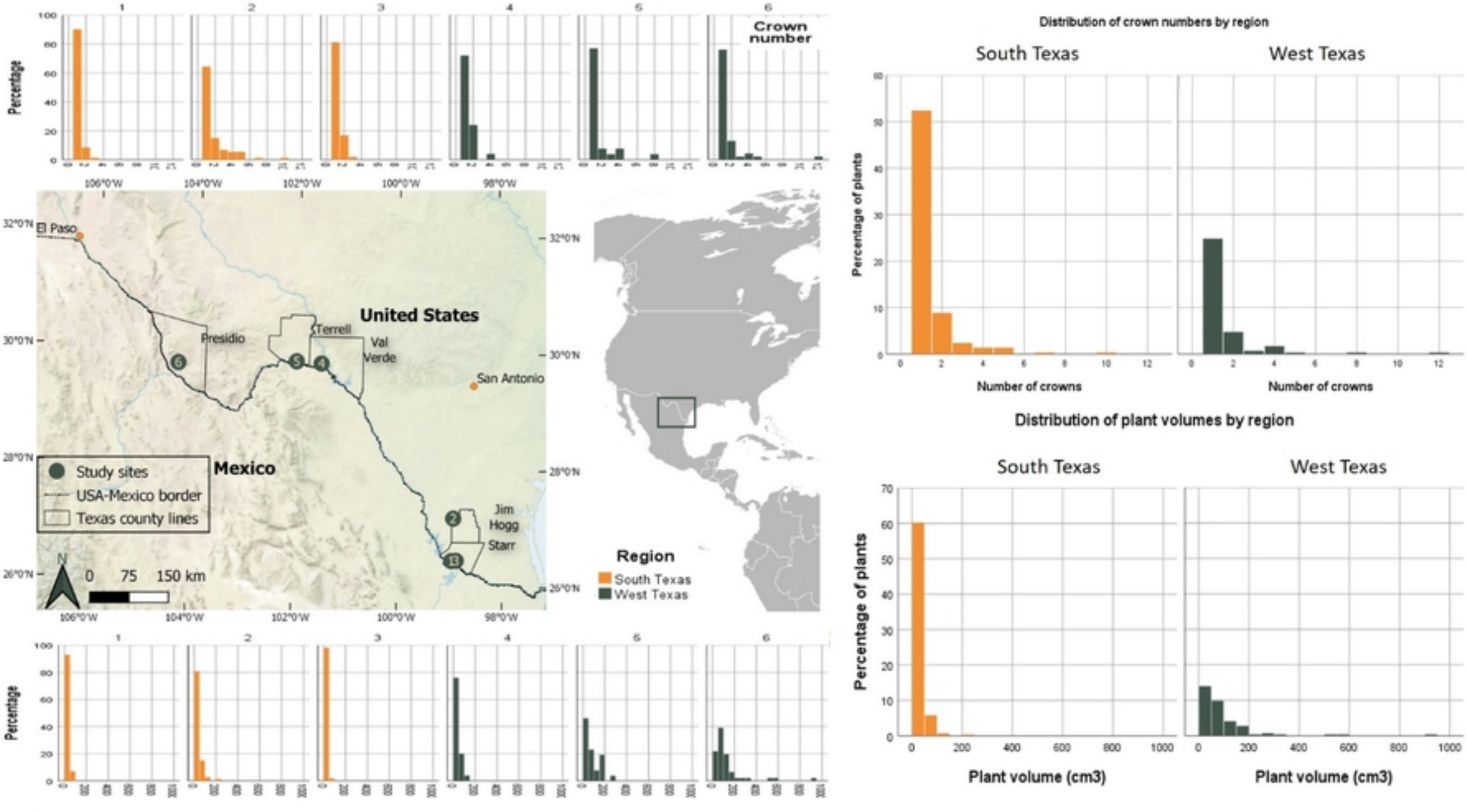
Crown number
Percentage
Distribution of crown numbers by region
South Texas
West Texas
Percentage of plants
Number of crowns
Distribution of plant volumes by region
Plant volume (cm3)
El Paso
United States
Presidio
Terrell
Val Verde
San Antonio
Mexico
Jim Hogg
Starr
Study sites
USA-Mexico border
Texas county lines
0 75 150 km
Region
South Texas
West Texas

Fig 3

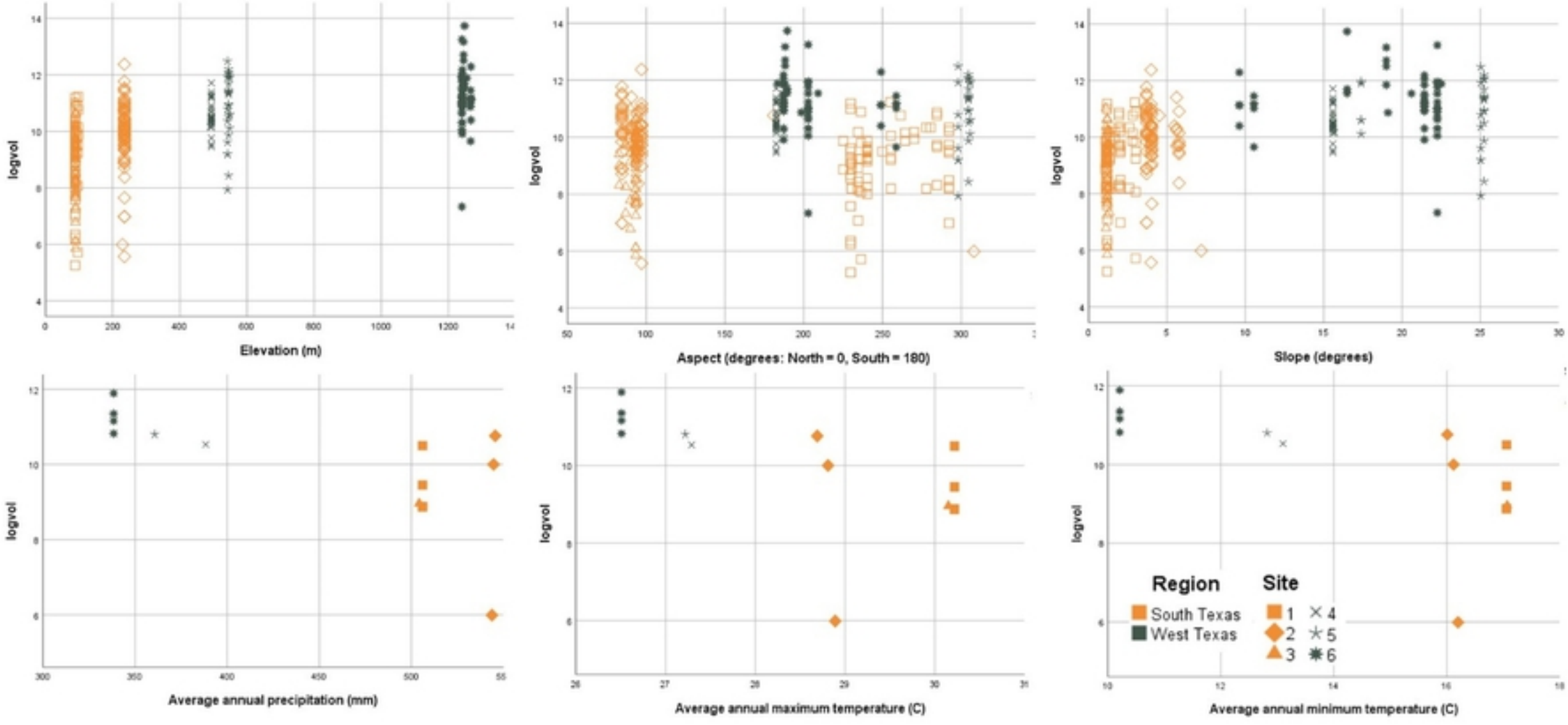
logvol
Elevation (m)
Aspect (degrees: North = 0, South = 180)
Slope (degrees)
Average annual precipitation (mm)
Average annual maximum temperature (C)
Average annual minimum temperature (C)
Region
South Texas
West Texas
Site
1
2
3
4
5
6

Fig 4

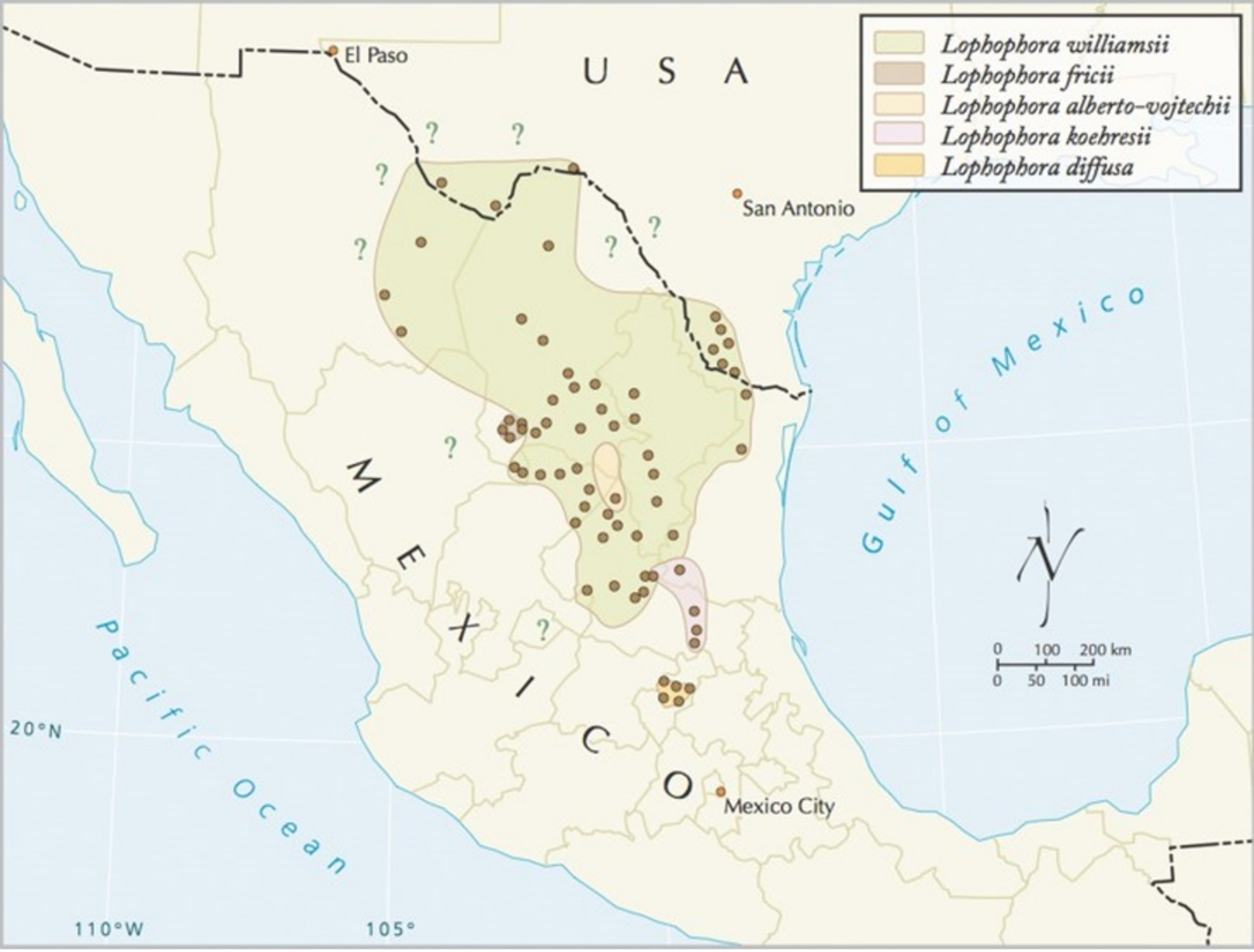
Lophophora williamsii
Lophophora fricii
Lophophora alberto-vojtechii
Lophophora koehresii
Lophophora diffusa
El Paso
U S A
San Antonio
M E X I C O
Mexico City
Gulf of Mexico
Pacific Ocean
N
0 100 200 km
0 50 100 mi
20°N
110°W
105°

Fig 1