COMPARATIVE SURVEY OF *LOPHOPHORA WILLIAMSII* POPULATIONS IN THE USA AND PEYOTE HARVESTING GUIDELINES

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DECLARATION OF OWN WORK

I declare that this thesis, “Comparative survey of *Lophophora williamsii* populations in the USA and peyote Harvesting Guidelines”, is entirely my own work, and that where material could be construed as the work of others, it is fully cited and referenced, and/or with appropriate acknowledgement given.

Signature

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WORD COUNT

Word Count: 5985 (excluding abstract in Spanish).

LIST OF ACRONYMS

CCI – Cactus Conservation Institute

CSA – Controlled Substances Act

DEM – Digital elevation model

GIS – Geographic information system

GLIMMIX – Generalized linear mixed models

GLM – General Linear Model

GPS – Global positioning system

ICL: Imperial College London

IUCN – International Union for Conservation of Nature

NAC - Native American Church

NGO – Non-Governmental Organisation

NLCD – National Landcover Database

PRISM – Parameter-elevation Regressions on Independent Slopes Model

PRISMA - Preferred reporting items for systematic review and meta-analysis

SAS – Statistical Analysis System

SSURGO – Soil Survey Geographic Database

spp. – species

STx – South Texas

TNC – The Nature Conservancy

TDPS – Texas Department of Public Safety

TNRIS – Texas Natural Resources Information System

UN – United Nations

USDA – United States Department of Agriculture

USGS – United States Geological Survey

UTM - Universal Transverse Mercator

USA – United States of America

WTx – West Texas

WGS – World Geodetic System

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COMPARATIVE SURVEY OF *LOPHOPHORA WILLIAMSII* POPULATIONS IN THE USA AND PEYOTE HARVESTING GUIDELINES

Abstract

Lophophora williamsii (peyote) is a small psychoactive cactus native to Mexico and Texas, USA. It has considerable cultural, religious and medicinal significance to many indigenous peoples of North America. Peyote populations are rapidly declining due to harvesting pressure, increasing threats from habitat conversion to grazing and agriculture, other changes in landscape for economic purposes, as well as poaching. Most published studies on peyote have focused on the anthropological, chemical, cultural, and medical aspects, and surprisingly little is known about the ecology of this species, despite it being currently listed as Vulnerable on the IUCN Red List. My study addresses this gap by providing the first detailed comparison of peyote populations growing in two distinct ecosystems in the USA. I surveyed peyote populations and compared population densities and structures in South Texas (Tamaulipan thornscrub) and Trans-Pecos Texas (Chihuahuan desert) and identified primary habitat characteristics in these two ecological regions. My second objective was to create Sustainable Harvesting Guidelines, based on available literature on peyote, to be applied in the practice of legal harvesting. Peyote, like many other species, is facing multiple threats and is in decline. Therefore, it is essential that there be understanding and collaboration among all stakeholders - private landowners, distributors, peyoteros and Native American Church members - to ensure the survival of this species in the wild.

Resumen

Lophophora williamsii (peyote) es un pequeño cactus psicoactivo que se encuentra creciendo naturalmente en México y Texas, E.U. Tiene mucha significación culturál, religiosa, y medicinál para muchos pueblos indígenos norteamericanos. Las poblaciones de peyote se están disminuyendo rapidamente, debido a la presión de la sobrecosecha legal continua, amenazas crecientes en forma de la conversión de habitat a usos agrícolas, otros cambios en el uso de la tierra para propuestos económicos, y la amenaza constante de la sobrecosecha illegal - o sea el robo - de peyote en su habitat.

La mayoría de los estudios publicados hasta el presente han sido enfocados en los aspectos antropológicos, químicos, culturales y médicos, y se sabe relativamente poco sobre la ecología de esta especie, a pesar del hecho de que *L. williamsii* aparece en la lista de especies "Vulnerables" en la Lista Roja de la UICN. Nuestro estudio enfrenta este resquicio por proveer la primera omparación detallada de poblaciones de peyote creciendo en dos ecosistemas distintos en los EEUU. Nosotros examinamos poblaciones de peyote, y comparamos las densidades y estructuras de las poblaciones en el Sur de Texas [Tamaulipan thornscrub] y en el Oeste de Texas [el Trans-Pecos], e identificamos las características primarias de habitat en estas dos regiones. Nuestra segunda meta era crear una guia para la cosecha sustentable de peyote, basada en la literatura, para ser aplicada en la práctica de la cosecha legal de peyote. Peyote, comos otras especias, se enfrenta con amenazas múltiples, y por eso es importante que haya entendimiento y colaboración entra todos los grupos envolucrados - dueños de tierras,

peyoteros, distribuidores, y miembros del la Iglesia Norteamericana (NAC) - para asegurar que esta especie sobreviva en su habitat natural.

Impact Statement

Dissemination and implementation of Sustainable Harvesting Guidelines will help to ensure protection and conservation of peyote, stemming its decline in the wild.

Keywords

Lophophora williamsii, harvesting, sustainability, peyote, population ecology.

Introduction

Lophophora williamsii (Lem. Ex Salm-Dyck) J.M. Coulter (Cactaceae), commonly known as peyote, 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 habitat is shrubland desert. It is a very slow-growing species, taking up to 10 years for the plant to mature from seed (Anderson 1996).

Peyote has been used for medicinal and religious purposes by the indigenous people of North America for at least 6000 years (El-Seedi et al. 2005; Terry et al. 2006), and to this day is an integral part of indigenous heritage, especially in Mexico, e.g. among Huichol, Tahahumara, Cora tribes (Myerhoff 1976; Schaefer & Furst 1996; Labate & Cavnar 2016) where its use originated. Indigenous people of the USA and Canada have adopted peyote more recently, at the end of the 19th century (La Barre 1975; Schultes & Hofmann 1980; Stewart 1987; Dyck 2016). Peyote is consumed by members of the Native American Church (NAC) as a sacrament in the form of fresh or dried buttons or tea. It is an integral part of the religious practice of 250,000–500,000 members of this religious tradition in North America (Feeney 2016).

The main chemical compound responsible for peyote's distinctive psychoactive effects is an alkaloid called mescaline. Although its psychopharmacological properties and indigenous use have been researched extensively since the 1880s (Jay 2019) peyote remained relatively unknown to the general public until the advent of the counterculture movement of the late 1950's and 1960's. Backlash from the authorities resulted in listing not only mescaline, but also peyote cactus itself, as a Schedule 1 drug under the Controlled Substances Act of 1970 in the

USA (CSA, "The Controlled Substances Act", DEA 2019). Internationally, mescaline, but not peyote, is listed by the 1971 UN Convention on Narcotic Drugs ("United Nations Treaty Collection" 2019). Native Americans have been exempted on religious freedom grounds from the harsh penalties of the CSA and can legally purchase and consume peyote (Labate & Cavnar 2014).

Despite the great ethnobotanical and cultural importance of peyote, few studies have been conducted on its ecology and biology (notable exceptions are work by Terry et al. and the CCI in the USA)(Rojas-Aréchiga & Flores 2016). The latest IUCN Red List assessment, completed in 2009, lists this cactus as Vulnerable ("IUCN" 2019), however reports dating back as far as 35 years already note declining populations resulting in shortages of supply for the NAC (Morgan & Stewart 1984). The main threats to peyote in the USA are habitat loss (for 'improved pastures', agriculture, urban development and energy infrastructures), overharvesting through legal trade for the NAC, and poaching. 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 cacti to regenerate after harvesting, even when the harvesting has been done with the best possible techniques (Terry & Williams 2014; Terry & Mauseth 2006; Terry et al. 2011, 2012). Over-harvesting leads to populations with low densities, which result in reduced sexual reproduction, which in turn leads to a loss of genetic diversity (Rojas-Aréchiga & Flores 2016).

The geographical scope of the present study is South Texas (STx), where peyote populations have been declining rapidly and where most of the commercial harvesting of peyote takes place (Feeney 2017) and West Texas (WTx), where peyote is much harder to find, and there is no commercial harvesting. Although these threats are well-known, the extent to which each of them contributes to peyote population decline is not known. To this end I propose to assess peyote populations in STx, in the areas close to where commercial harvesting is happening and to compare them with populations from WTx. My study will be the baseline assessment for a longitudinal monitoring of these populations, enabling greater understanding of their dynamics, structure, and spatial interactions.

The outcome of this project, combined with the previous research data collected by Terry et al. and other relevant literature will result in the publication and dissemination of Sustainable Harvesting Guidelines, that will ideally be adopted by the commercial harvesters of peyote.

Therefore, my 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.

My research addresses the following questions:

- What are the densities and size structures of peyote populations in the USA?
- Are they different between South and West Texas?
- What are the primary habitat characteristics for peyote?
- What are threats, conservation priorities, gaps in knowledge, and research needs?
- What are the key messages to include into the first Sustainable Harvesting Guidelines?

Fig.1. Distribution of 5 species of genus *Lophophora* and main threats to the existing peyote populations in the USA. Distribution map from Terry et al.(2008)**.** Question-marks represent uncertainty about the presence of peyote, and older maps usually portray the range of *L. williamsii* as being more extensive. Photographs show peyote and its threats: cactus in flower, and with fruit, growing in multi-crown cluster, harvested peyote drying on the rack of a licensed distributor, habitat loss through clearing of the native thorn-scrub and challenges of dealing with private landowners. Photos by the author.

Methods

Ethics

This study was conducted in compliance with the Data Protection Act 2018, General Data Protection Regulations (Europe), Imperial College London and other regulatory requirements as appropriate.

Study areas

Study sites were selected with the aim to cover the entire range of peyote populations in Texas. All sites are in private ownership, so no federal permits were necessary (Tab.1). Verbal consent was obtained from the landowners prior to study site access. To protect the cacti at these sites from poaching, and at the request from some of the landowners, the exact locations of my study sites are not disclosed. Fieldwork was conducted in May-July 2019. Study sites 1-3 are located in STx (Tamaulipan thornscrub), and sites 4-6 in WTx (Chihuahuan desert) (Tab. 1).

Survey procedures and sampling universe

My 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, based on the following criteria:

- Land never root-ploughed or converted to agriculture;
- No development (i.e., roads, buildings, drains, pipelines, wind turbines);
- Suitable soil and terrain type (escarpment, limestone, grey/white but not red soils);
- Not near streams or other areas with very thick vegetation or excessive soil moisture;

- Accessible locations (within 200m of the road/trail, no further than 1-2km from the car);
- Not on very steep slopes.

A free and open-source Geographic Information System (GIS) (QGIS v. 3.8.2) was used to generate transects within the polygons delineated by the property boundaries and suitable habitat (QGIS Development Team 2019). For ease of the layout process and to avoid biasing the study with the previously known locations I have used transects running North-South on major longitudes of the Universal Transverse Mercator (UTM) coordinate system. UTM 13N was used in the 2 most western study sites, and 14N for the other 4. The World Geodetic System 84 (WGS 1984,) a current standard datum for GPS, was used throughout my study.

Transects were 25m long and 4m wide. There were at least 250m between transects along latitude lines. GPS coordinates for the origin and terminus of each north-south transect were recorded for the study and exported to a handheld device (Garmin s64) to facilitate finding the transect locations in the field. A set of possible transects was generated in advance, and a random subset was selected to be surveyed at each site (S.Fig.1).

Data collection

Each transect where I found peyote, I marked permanently with 11” nails every 2 metres, so that it would be easier to find on subsequent visits. I measured each peyote plant within the transect and marked it with a round, numbered aluminium tag (S.Fig. 1). I recorded its location with a GPS device and photographed it. Data was collected at both transect and plant levels (S.Fig.2). I placed an aluminium nail on the north side of the plant to aid its localisation in the subsequent surveys. Aluminium nails were chosen because calcareous soils are short in iron and zinc, and therefore runoff from standard nails could impact the plant. I tagged each individual plant because this work forms the baseline for a longitudinal study that will track population dynamics, such as seedling recruitment and survival over time.

Data sources and geospatial analysis

Publicly available spatially-referenced environmental data were obtained from Unites States Geological Survey (USGS, Digital Elevation Model, DEM which provided elevation, slope, and aspect; and also geological maps), Texas Natural Resources Information System (TNRIS; land parcel data - used to determine property boundaries), and the Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Database (30-year average climate variables)("PRISM" 2019; "TNRIS" 2019; USGS 2019). Soil data came from United States Department of Agriculture (USDA) National Resources Conservation Service (NRCS) Web Soil Survey (“Web Soil Survey" 2019). We obtained peyote harvesting and sales data from the Texas Department of Public Safety (“TDPS” 2019).

Geospatial analysis was performed with QGIS v. 3.8.2 (QGIS Development Team 2019), and layers were projected into the same geographic coordinate system (EPSG:4326) for final analysis.

Variables of interest

The main measure of plant size was total above-ground volume. It was calculated from the diameter by assuming that each crown was a hemisphere: $V_{crown} = \frac{2}{3}\pi(\text{diameter}/2)^3$. Some plants had multiple crowns. In such a case the estimated volumes of all its crowns were summed to obtain the total above-ground volume for the plant.

Another measure of population structure was the number of crowns per plant. Often peyote cacti have a single crown, but some grow in clumps with multiple crowns (Fig. 1). Multiple crowns often grow as a result of previous harvesting (which usually involves removing the apical meristem along with the crown of the cactus) or other injury to the apical meristem.

Population density was measured as the number of plants per hectare of the habitat surveyed and then extrapolated to the whole suitable habitat area.

Statistical analysis

Statistical analyses were performed in SAS v9.4 and SPSS v25 ("IBM SPSS Software" 2019; "SAS Studio" 2019).

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

General Linear Models (GLM) were developed to investigate relationships between response and predictor variables (S.Tab.2). Spatial variation in plant volume was explored with the GLM ordinary least squares means, and standard errors and probabilities were calculated using the Type I SS for transectid(siteid) as an error term. I used this model because this is a hierarchical ('nested') analysis. Assumption of the GLM is that residuals are normally distributed, which was the case ($W = 0.944269$, $P < 0.0001$). SAS GLM (general linear model) procedure was used for these analyses.

To identify primary habitat characteristics and their effects on plant volume I repeated the model with environment variables as covariates. It was impossible to include all the predictor variables at once, because I run out of degrees of freedom. Therefore, the analyses were repeated with each of the individual environmental variables, and significance level was adjusted using Bonferroni correction for multiple comparisons, to $P < 0.0085$. It was necessary to separate the two regions to statistically test the effect of aspect on plant size, due to the missing cells and unbalanced design that combining the analyses of aspect in the two regions would create.

For crown numbers and presence/absence data I used logistic regressions, a type of generalised linear model. Logit link function with binomial distribution was used for presences/absences, and negative binomial distribution for crown numbers. The SAS GLIMMIX (generalised linear mixed models) procedure was used for these analyses. The relationships between presence/absence and environmental variables were investigated as well and adjusted for multiple comparisons as above.

Literature search and selection of studies

I conducted systematic literature searches following guidelines from PRISMA (Moher et al. 2010). Scopus, Web of Science and PubMed databases were searched using terms ("*Lophophora williamsii*" OR "peyote") in the title, abstract or keywords. I searched all peer-reviewed publications up to August 2019, published in English or Spanish. I carefully reviewed all abstracts to identify relevant publications that met my inclusion criteria.

The inclusion criteria were that the main species is *Lophophora williamsii*, and the subject relates to peyote's biology, ecology, conservation, cultivation, harvesting, resource management or sustainable use. Complete articles published in peer-reviewed scientific journals, conference papers, book chapters and dissertations were included.

Table 1. Information about the study sites.

Site	Region	Ecoregion	County	Private property type	Property area (ha)	Suitable habitat (ha)	N peyote	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 (cm3)	Slope (°)	Aspect	Elevation (m)	Ppt.	T. max	T. min
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

Results

Densities and population structures

I studied peyote populations in 2 different regions – STx and WTx at 6 different study sites (Fig.2) with the total area of 1489 ha, 770 of which were suitable peyote habitat. We surveyed 121 transects, covering the 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). Densities were slightly higher in WTx, but this was largely driven by one of my study sites which had no known history of harvesting (Tab.1 and S.Tab.2).

I compared the distributions of my main population structure variables in two regions (Fig.2). The distributions of plant volumes differed significantly (Mann–Whitney $U = 2771$, $n_1 = 197$ $n_2 = 97$, $P < 0.0001$). The distributions of crown numbers in the two regions did not differ significantly (Mann–Whitney $U = 9252$, $n_1 = 197$ $n_2 = 97$, $P < 0.547$).

The plants on average were significantly larger in WTx, compared to STx (21.80 cm^3 vs. 95.01 cm^3, $t(292) = -10.598$, $p<0.0001$, t-test performed on log(volume)), but in both regions plants had mostly only one or two crowns.

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 ($P = 0.3565$).

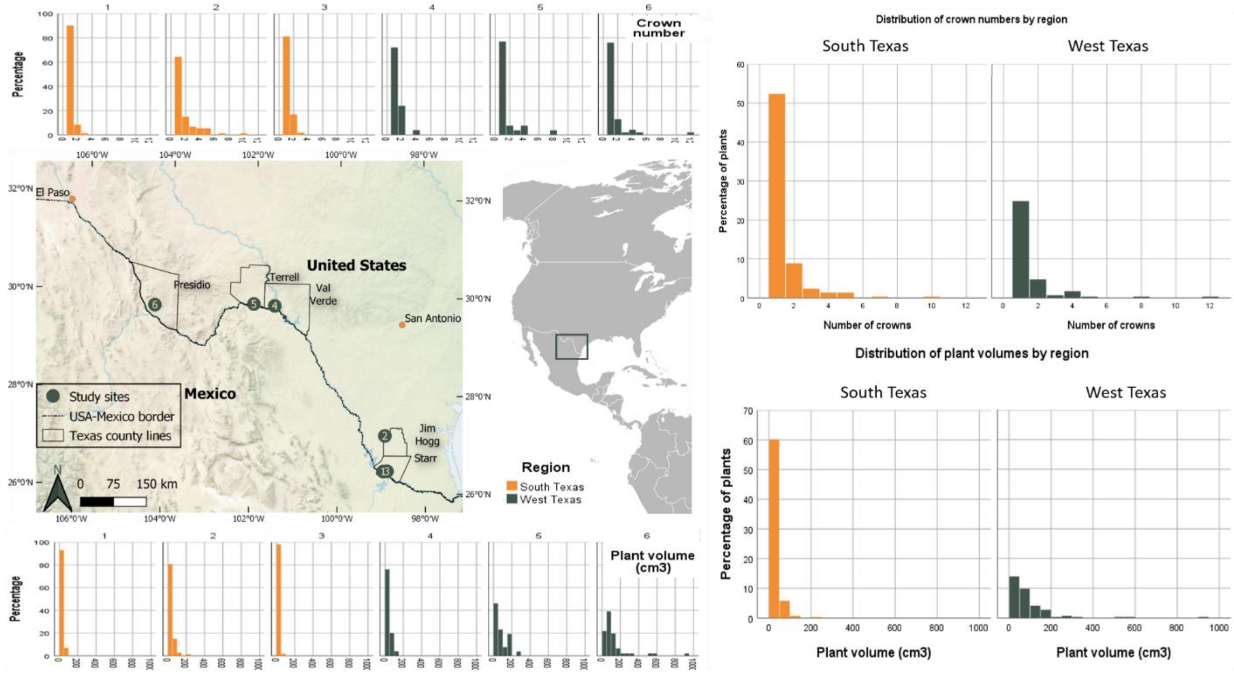

Fig. 2. Location of the study sites and population structures of *L. williamsii*. Map shows location of 6 study sites included in this study from Chihuahuan desert ecoregion (West Texas: 4, 5, 6) and Tamaulipan thornscrub (South Texas: 1, 2, 3). Distributions of the two population structure variables, 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. However, size structures are very different in two regions: there were considerably more mature, often 13-ribbed plants in West Texas. In West Texas populations consisted mostly of the juvenile and small, 5-8 ribbed plants.

Environmental variables

Understanding the regional differences helps to interpret model results (Fig. 3, 4 and S.Fig 2). In Texas there is a strong regional variation in climate and elevation, indicating that it will be difficult to disentangle effects of environment variable independent of location. On average the climate is colder and dryer in the Chihuahuan desert compared to Tamaulipan thornscrub. Though both regions get similarly hot during the day, nights in the Chihuahuan desert are much colder. In WTx peyote starts to grow at higher elevation, on steeper slopes, and aspect becomes more important – it is usually found on South and South-West-facing slopes.

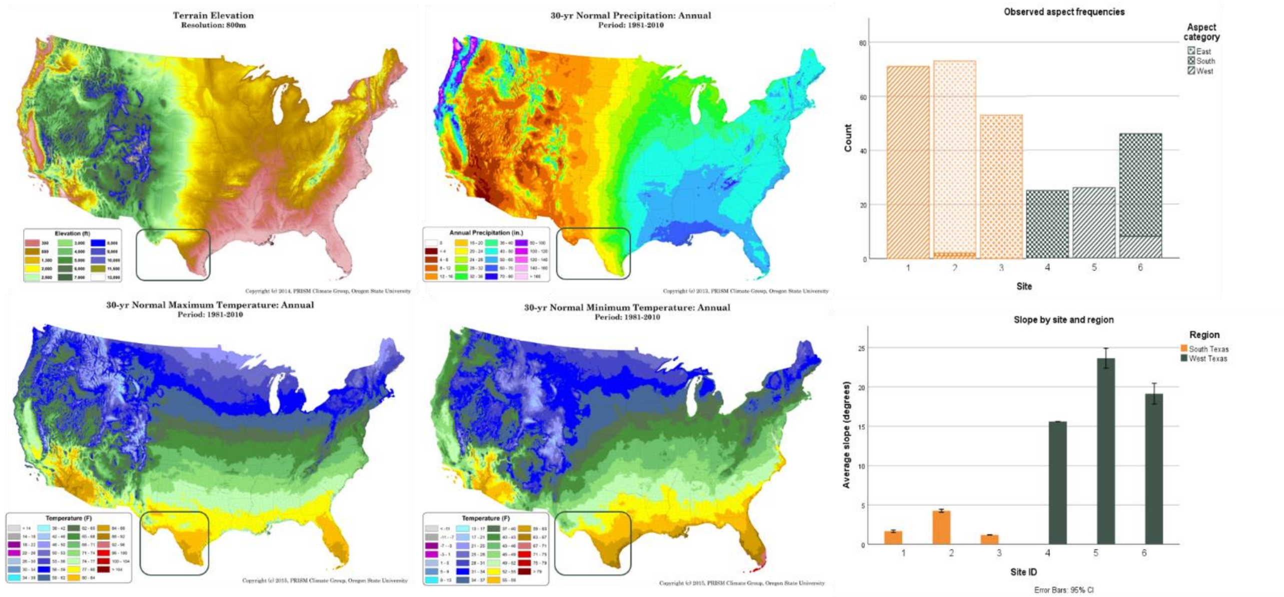

Fig. 3. Environmental variables at the study sites. West Texas is generally colder, dryer and has higher elevations compared to South Texas. In West Texas, where peyote mostly grows on the mountain tops and slopes, aspect is much more important – plants are commonly found on the South-West facing slopes, which in Northern hemisphere receive most sunshine. Maps are from PRISMA (2019).

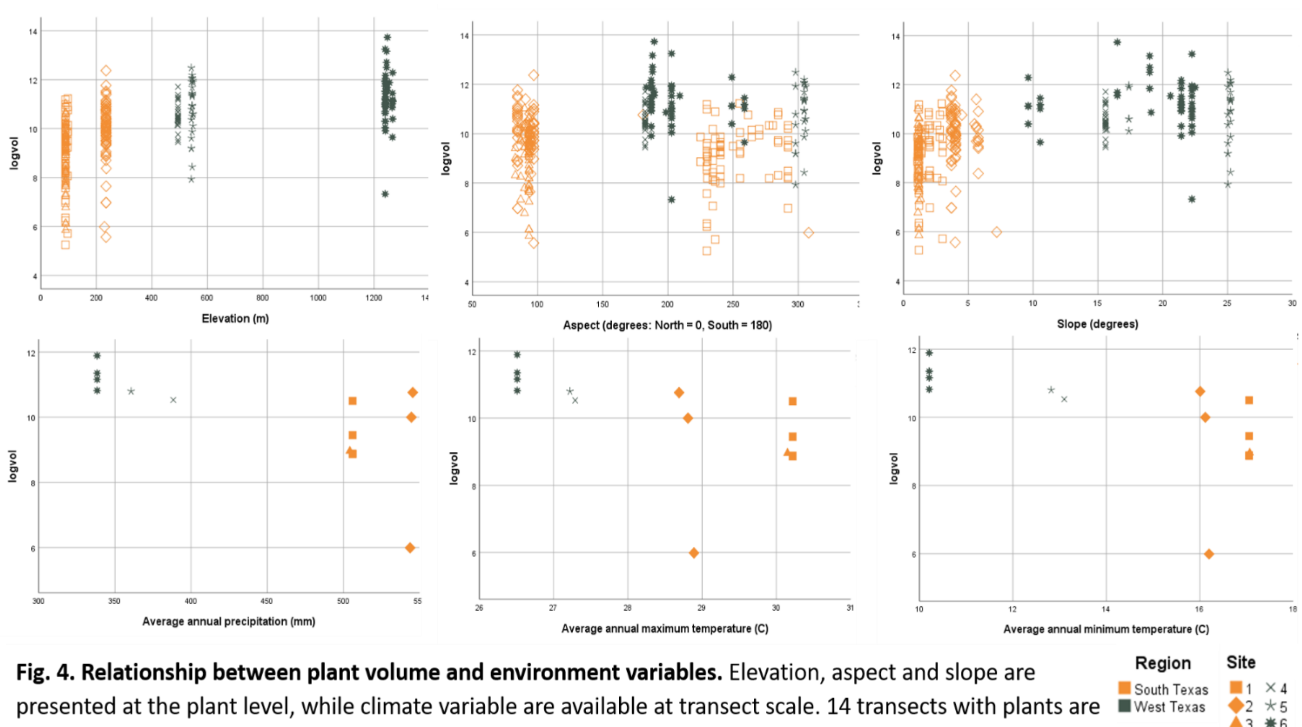

Fig. 4. Relationship between plant volume and environment variables. Elevation, aspect and slope are presented at the plant level, while climate variable are available at transect scale. 14 transects with plants are presented here. Note that plant volume has been transformed into log(volume).

Models

First, I wanted to understand how variation in population structure is distributed at a spatial scale. For plant volume I find: a) locations 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 had a significant effect ($F(4, 288) = 4.41$, $P = 0.0018$), but not region ($F(1,288) = 1.37$, $P = 0.2436$).

Second, I investigated the effect of environmental variables on plant volume (Fig.4). I 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 ($F(1,13)= 0.51$, $P=0.4993$) or aspect ($F(1,188) = 0.37$, $P = 0.5441$ for STx; $F(1,90) = 0.11$, $P = 0.7448$ for WTx).

Third, I examined presence/absence data. Region was not significant ($F(1, 115)=2.00$, $p=0.1600$), but site had an effect ($F(4, 115)=2.76$, $p=0.0308$). None of the environmental variables were significant (S.Tab.5).

Literature review

Initial search has resulted in 589 publications (including research articles, reviews, commentaries, book chapters). After screening, removing duplicates, retrieving full-text and identifying additional material in the references, the final count of the included publications was 27 (Fig. 6).

Literature review confirmed that there is a serious lack of up-to-date information on peyote's biology, ecology and propagation. Detailed analysis and review of the retrieved literature is beyond the scope of this paper, as my main aim was to collate all the available data and distill it to simple and easy-to-follow principles which form the basis of these first harvesting guidelines for peyote.

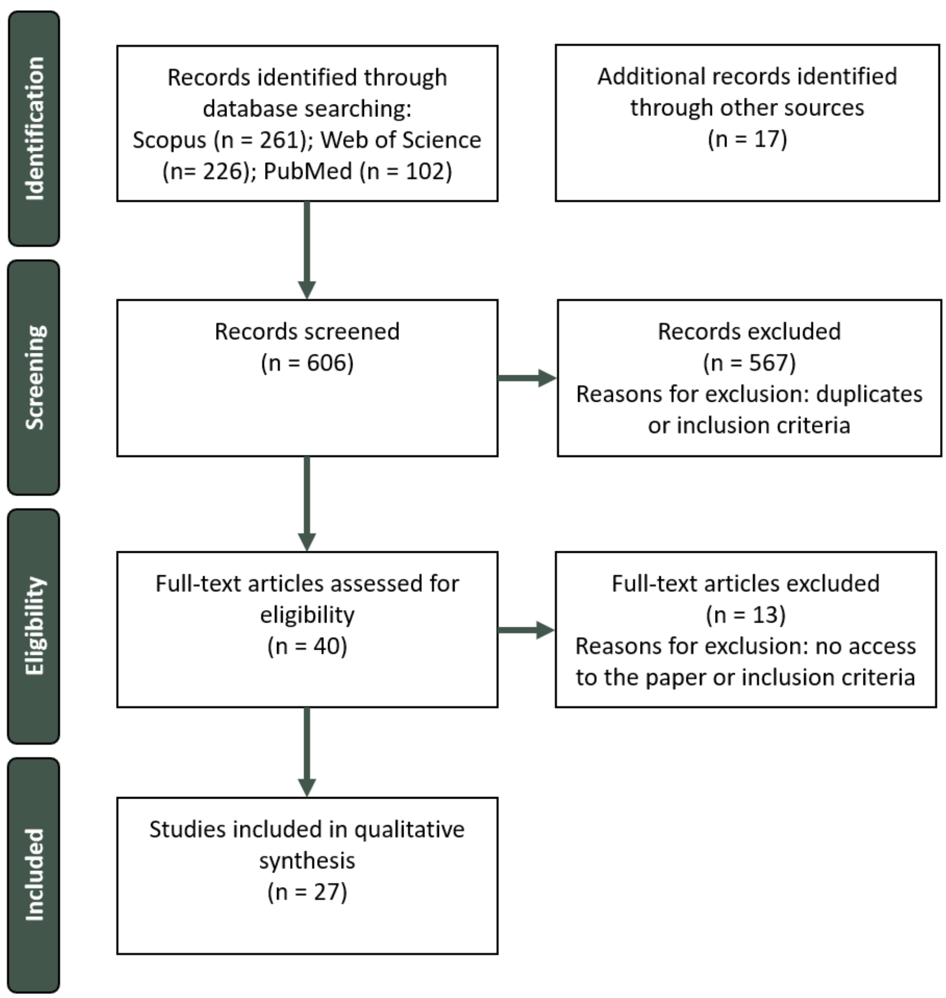

Fig. 5. Diagram for literature selection. Adopted from PRISMA Flow diagram (Moher et al., 2009)

Sustainable Harvesting Guidelines

1. Cut the green part of the plant, leaving subterranean stem and root intact

Correct harvesting technique has been described by (Terry & Mauseth 2006) (S.Fig.3). Many harvested individual plants normally regrow after a mass harvesting event in a population, but some do not. Failure of some plants to regrow after harvesting is in some cases attributable to a loss of areoles in the subterranean stem, due to "deep cutting". There really is no reason to harvest the whole plant because the average mescaline concentration in the stem is an order of magnitude lower than that in crown, and the mescaline concentration in root is two orders of magnitude lower than that in crown (Klein et al. 2015).

2. Rotate the gathering sites and re-harvest every 8 years

Relationship between harvest frequency and plant resilience has been investigated in one longitudinal study (Terry & Williams 2014; Terry et al. 2011, 2012). Although harvesting, if done correctly, does not kill peyote, removing the photosynthesizing part weakens it. Consequently, the re-growth is smaller and more susceptible to outside stressors, such as pathogens or extreme weather conditions. If harvesting is too frequent, it also depletes the reserves of the underground stem. The published data from the 6-year period of the longitudinal study demonstrates that 6 years is not enough for the plants to re-generate. 8- and 10-year results are currently being analysed.

3. Harvest only mature plants, with 8 or more ribs

Number of ribs correlates with age and size of the plant and is a metric that is easy to apply in the field. Small seedlings are usually 5-ribbed, and very old large 'grandfather' plants have 13 ribs.

4. Leave some larger plants for the future

Mescaline content increases with size but it is the largest plants that usually produce the most seed, so removing them from the populations can substantially decrease seed availability.

5. Look after the plants

If young seedlings are disturbed while harvesting larger plants or if cacti are found uprooted by feral hogs, plant them back.

6. Harvest during open season

Limiting harvesting to certain times of the year, e.g., after the seeds are produced might increase the resilience of populations. Currently in the USA peyote is harvested all year round. Seasonal variations in mescaline concentrations are unknown.

7. Leave the seeds

If there are seeds on the harvested plants, take them out and be sure to leave the seeds at the harvesting site.

8. Long-term solution to 'peyote crisis'

An ideal solution to overharvesting peyote from the wild is cultivation (Terry & Trout 2013). Although it is currently challenging in the USA, it is possible in other countries, and more research should be aimed at developing growth and propagation protocols.

Discussion

There is a considerable knowledge gap when it comes to peyote conservation and ecology. Books and hundreds of publications have been written about peyote over the 500 years of its written history (and archaeological evidence shows that it's been used as early as 6000 years ago, (El-Seedi et al. 2005). Peyote has been portrayed as a medicine, sacrament, the devil (e.g. some early Spanish writings (Dawson 2016), psychotomimetic agent, trade commodity, drug, ethnographic curiosity – but considerably little has been written about it as a cactus, a vulnerable species in need of protection in its native habitat.

This study is filling in this gap by developing and implementing methodology for surveying peyote populations in Texas, USA, establishing baselines for different ecoregions and understanding the primary habitat characteristics.

I have collected data from 294 plants and surveyed 1.21ha of land in the Tamaulipan thorn-scrub and the Chihuahuan desert – two ecoregions of Texas where peyote grows. Finding peyote in the field is not an easy task, even narrowing it down to the sites with appropriate soils (gray-white sandy loam) and geology (limestone) and geography (escarpment). I have developed my methodology with the aim to be unbiased and statistically rigorous, and have produced repeatable, unbiased definitions of the sampling universe and established transects according to criteria independent of the previously known locations of populations. Most of the transects that I surveyed had no peyote plants on them – although occasionally plants were growing just a few metres off a transect. In fact, more than 90% of transects in STx and 84% in WTx were without peyote.

What about the transects with peyote? Sites differed significantly in peyote densities, i.e., numbers of plants per unit area of suitable habitat. One of the sites in WTx had exceptionally high densities of 900 individuals/hectare – and this was the site where, as far as I know – there has never been any harvesting, commercial or otherwise. Sites in STx had about 230 inds/ha, and other sites in WTx had even lower numbers.

How does this relate to the legal peyote trade? Demand for peyote has been estimated to be between 5 and 10 million buttons per year (Anderson 1996). Data on peyote sales from licensed distributors, collected by the Texas Department of Public Safety up until 2016, indicates that about 1,500,000 peyote buttons are sold annually ("TDPS" 2019)(S.Fig.4). A typical NAC ceremony requires about 300 buttons (Feeney 2017), and the membership of the NAC, although unknown precisely, is estimated at about 250,000 – 600,000 members (Prue 2014). Legal supply is struggling to satisfy demand, to an extent that in 1995 NAC leaders declared 'peyote crisis' ("For Indian Church, a Critical Shortage" 1995)). In the last 25 years the situation has only got worse.

Four registered peyote dealers operate in Texas, employing 1 to 11 peyoteros each ("TDPS" 2019). Daily each dealer receives about 500-1500 buttons. If my density estimations for STx are applied, this means peyoteros need to explore 4.4 ha of suitable habitat per day, which per person amounts to about 550m^2. Given their expert local knowledge on where to find peyote, this seems reasonable, although how sustainable this is in light of reduction in availability of suitable habitat and restricted access to private properties is another question. In fact, there are reports of rampant poaching (which in STx is colloquially known as 'fence jumping'). Anecdotal evidence links these 'fence jumpers' to licensed distributors, and there has been at least one case when a distributor's license has been suspended when an employee has been caught trespassing on private property to collect peyote. Here the lines between legal and illegal are blurred, as once peyote arrives to the drying racks of a legal peyote distributor, it is impossible to determine where it came from. Future research, using a combination of fieldwork and remote sensing should be conducted to estimate the rate of habitat loss and current extent of suitable habitat. Another, much overlooked avenue of research is to investigate the extent of illegal trade in peyote. Not many studies investigate illegal wildlife trade in plants, a case of 'plant blindness' recently pointed out by (Margulies et al. 2019). Yet cacti (and orchids) are among the plant groups most threatened with extinction and are clearly impacted by the illegal trade (Bárcenas Luna 2003; Goettsch et al. 2015).

Another question I explored was the influence of environmental variables on plant size (I used plant volume as a measure of size). I found a strong regional effect on size of the plants: cacti were significantly larger in WTx (86 cm^3) compared to STx (21cm^3), but it is important to note that there was a lot of individual variability within sites/transects. Independently of the regional effects, plant volume increased with precipitation and decreased with the increase in average temperatures. The first one intuitively makes sense, in dry season cacti shrink in size as the moisture goes out of them (Rojas-Aréchiga & Flores 2016). Temperature effect is harder to interpret, and it might have something to do with the effects of shade and nurse plants. Contrary to my expectations, I find no effects of elevation, slope or aspect. One explanation could be that in STx they really are not particularly important, as the elevations are much lower than those in WTx, and my sample size was not large enough to detect the effect for WTx alone. From personal observation, in WTx peyote is most commonly found on South or South-

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 if I compare areas where plants occur (presences) and where they don't (absences). However, none of the environmental variables turned out significant in my analysis.

I only used 6 environmental variables in my analysis (plus soil and geology for the pre-selection of suitable habitat). Suitable habitat is composed of many features. The obvious thing would be to investigate vegetation cover or collect other, more precise, field-based measurements. There is a great dataset of shrubland cover from the National Landcover Database (Xian et al. 2015), unfortunately as of now it is only available for the Western half of the USA, meaning it could not be applied to 3 of the study sites. Further work should zoom-in deeper into environment variables in order to pin-point the detailed features of peyote habitat.

My original idea has been to compare peyote populations that have never been harvested, that have been harvested legally, and some that have been illegally harvested. Once I arrived for my fieldwork in Texas, I realized that I had seriously overestimated what can be done in two months. Because most of peyote populations grow on private land, it was necessary to obtain permissions and consent from the landowners to do research. Conservation work on private lands is a relatively new and promising field (Drescher & Brenner 2018), which is especially relevant to the context of Texas, where 96% of land is privately owned ("Texas Land Trends" 2019). It takes much longer that a few weeks to gain trust from the local landowners, especially when it comes to discussing sensitive and controversial topics such as peyote conservation.

In practice, this meant that it would be impossible to study properly the effects of harvesting, as I could only get access to six sites, most of which had not been harvested in the previous few years, and some have possibly never been harvested – but there was no way to be certain about that. This is the major limitation of my study.

Peyote is situated in a very peculiar position because of its listing as a Schedule 1 in the USA. The Texas DPS and the federal DEA have extensive regulations regarding *who* can harvest, and *where,* yet there are no regulations on *how or what plants* to harvest, as is usually the case with other heavily harvested plant species, such as ginseng (McGraw et al. 2013; Schmidt et al. 2019), frankincense (Lemenih & Kassa 2011), hoodia (Wynberg 2010), cork oak (Gil & Varela 2008; Oliveira & Costa 2012) and many others.

In addition to scientific contributions, my study also has a very practical output: creating the first Harvesting Guidelines, where I present the essential components for sustainable peyote harvesting. They include rotating the harvesting sites and regulating harvesting intensity and frequency to allow these slow-growing cacti to recover. Minimizing stress and injury to plants by harvesting correctly and at specific times of a plant's life cycle is also crucial.

The current state of knowledge about peyote populations does not yet allow quantification of what level of harvesting would be 'sustainable'. What I collated and distilled from the published literature, and learned from doing fieldwork, are the necessary first steps, a set of common-sense rules that are easy to apply in harvesting practice. As our knowledge increases, these guidelines should be refined and modified accordingly.

Sustainability has three key components, each of which needs to be in place for conservation effects to be effective in the long-term. Biological sustainability means that harvesting does not compromise the integrity of biological systems. Social sustainability implies cultural compatibility, social support and institutions that can function long-term. Financial sustainability indicates that activity outcompetes unsustainable alternative in profit generation (Milner-Gulland & Rowcliffe 2007). For peyote, it can look like this:

- Biological sustainability – understanding peyote population structures and dynamics can inform what rate of harvesting is not damaging for the long-term survival of cacti in their natural habitat.
- Social sustainability – maintaining a delicate balance between religious and conservation needs, whereby there is guaranteed supply of the medicine for the NAC ceremonies, and Native Americans are actively involved in any conservation decisions and actions.
- Financial sustainability – financial incentives for landowners to conserve peyote on their property, for example through conservation easements; or tax breaks for landowners who work with peyoteros or NAC chapters.

I hope that these harvesting guidelines will be disseminated and shared widely, including raising awareness of the peyote crisis among the NAC members and helping to reconnect them with their sacred medicine growing in the wild in its natural habitat.

Implementing, monitoring and enforcing rules, regulations and suggestions is challenging, and it would be too optimistic to assume that knowledge of the guidelines would modify the current harvesting practices that have been in place for many decades. Moreover, even if there are existing regulation in place, they are often not complied with, as was observed with wild harvesting of ginseng (McGraw et al. 2010). Therefore, in the long-term it is essential to ensure that there are incentives for the peyoteros and distributors to comply with them. One way of achieving this is though consumer choice, whereby Native Americans would refuse to buy buttons that are too small and harvested with the roots. In practice, this is not easy for the people who have travelled across the USA to Texas to purchase their medicine to refuse buying it, but it is more feasible than to expect any other compliance and regulatory measures to be enforced. Another way to increase financial sustainability is to incentivize landowners to lease their land for peyote harvesting on the condition that harvesting takes place only at certain intervals. This can be done using conservation easements, with tax breaks, a system already in place for other conservation purposes in the USA (Cortés Capano et al. 2019).

Of course, an obvious solution to the 'peyote crisis' would be cultivation. Unfortunately, in the USA there are serious regulatory hurdles to cultivation due to peyote being a Schedule 1 drug, which entails restrictions on cultivation at the federal level, plus complete prohibition in certain states, including Texas, at the state level (Terry & Trout 2013). It is also important to challenge assumptions held by some churches that medicine from the wild is better than cultivated one. Fortunately, many NA don't hold these beliefs, and would be willing to use the cultivated plants (Prue 2016). Another barrier to cultivation is the lack of protocols and methods for growing. Only two studies so far described peyote production (Cortes-Olmos, 2017 and Ortiz-Montiel & Alcantara-Garcia, 1997) – although there is a lot of information in the grey literature and from private growers that should be analysed and verified. Yet, cultivating peyote could not only solve the shortages of supply for the Native American Church, but could also contribute to *ex* *situ* conservation by producing larger and earlier-flowering plants and generating seed or seedlings for re-introduction into native habitats.

In conclusion, the evident unsustainability of the current legal system of peyote harvesting and distribution, do not bode well for the future of peyote. The unknown but increasing population of peyote consumers (namely members of the NAC), with only minimal efforts to implement greenhouse cultivation to replace the peyote being steadily consumed, suggest a steadily declining supply of peyote for the future generation of NAC members if there is no change in the current situation. In fact, one of the known peyote populations, from the Big Bend National Park, disappeared almost in front of our eyes, likely harvested into oblivion (Trout, 2019, CCI blogpost) and this is not the first time this has been documented (Salas et al. 2011).

My study for the first time quantifies peyote population densities, presents population structures and Harvesting Guidelines. Application of this work include, but not limited to: a) providing an important baseline for longitudinal studies for estimation population dynamics; b) discovery of new plant populations; c) identification of suitable habitat for restoration and preservation; d) improved protection and management of all populations and their habitat; and hopefully e) establishment of reintroduced populations.

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Supporting information

Description of the two ecoregions (Appendix S1), methods clarification (Appendix S2), supplementary results (Appendix S3), legal trade data (Appendix S4) and model outputs (Appendix S5) are available online. The author is solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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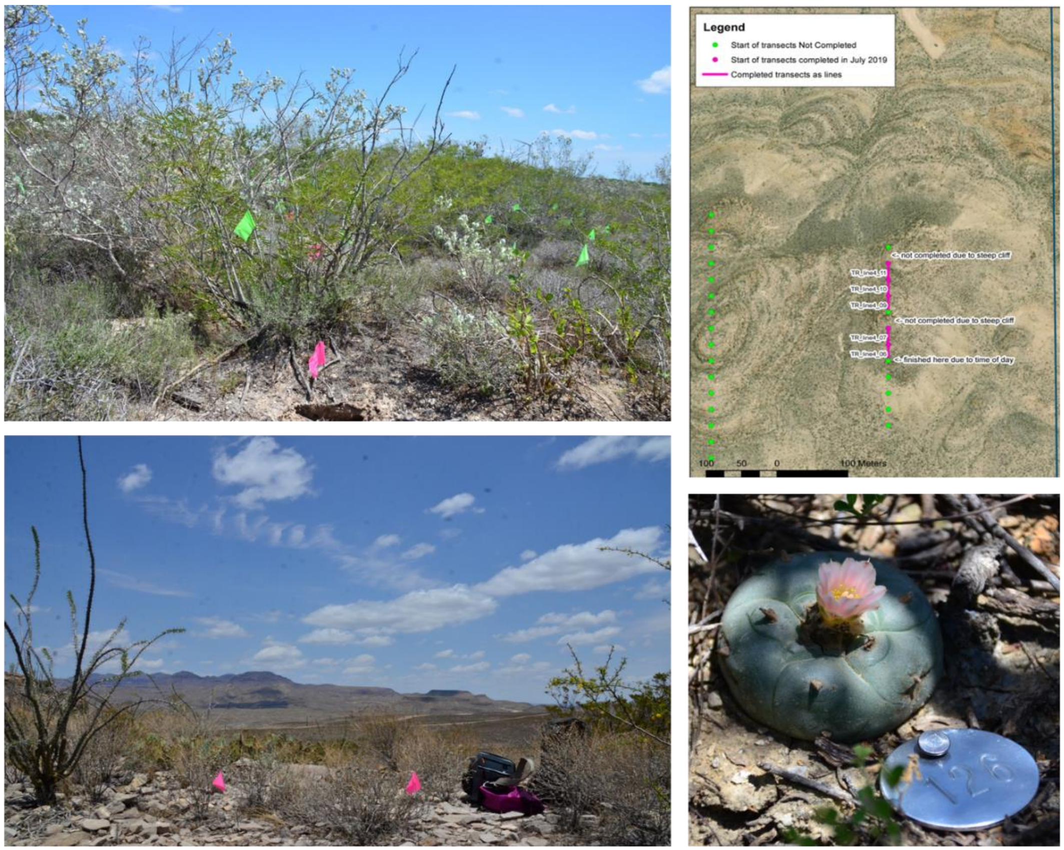
SUPPORTING INFORMATION

Appendix I: Regional descriptions

In South Texas, peyote populations are found in the Tamaulipan Thornscrub habitat. Typical habitat is shrublands of ridges and caliche plateaus with moderate shrub cover and sometimes a sparse and not very tall (less than 2m) overstory canopy. Shrublands are often dominated by species such as *Vachellia rigidula* (blackbrush), *Leucophyllum frutescens* (cenizo), and *Vachellia berlandieri* (guajillo) (S.Fig1).

In West Texas peyote is found in the Chihuahuan Desert thornscrub. Peyote typically occupies dry slopes with significant substrate of exposed rock (typically limestone) or gravel. Shrub species such as *Larrea tridentata* (creosotebush), *Parthenium incanum* (mariola), *Viguiera stenoloba* (skeleton-leaf golden eye or agarito), and *Forestiera angustifolia* (desert olive) may be present, but succulents such as *Yucca torreyi* (Torrey's yucca), *Dasylirion texanum* (Texas sotol), *Agave lechuguilla* (lechuguilla), *Fouquieria splendens* (ocotillo), *Dasylirion leiophyllum* (smooth sotol), *Euphorbia antisyphilitica* (candelilla), and *Opuntia spp*. (pricklypears) are also very common. Overall cover is generally low and bare rock or gravel is easily visible . Herbaceous cover is low, with grasses such as *Bouteloua eriopoda* (black grama), *Bouteloua ramosa* (chino grama), and *Bouteloua curtipendula* (sideoats grama) sometimes present. Ferns and fern allies, such as *Astrolepis spp.* (cloakferns), *Cheilanthes spp*. (lipferns) and *Selaginella lepidophylla* (resurrection plant) are often common (S.Fig1).



S.Fig. 1. Examples of typical habitat, transects and tagged plants. 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.

Appendix II: Methods

Date | Peyote Conservation Study | Site ID

NOTES ON THE TRANSECTS

Transect Number	Peyote (Y/N)	Peyote Tag #	Other Cacti	Notes on the transect (vegetation, soil, habitat suitability, etc.)

Date: | Peyote Conservation Study | Site ID:
Transect ID:

Italics indicate measurements required per crown! Please use one row per crown.

Plant ID (tag #)	Length from start of tr. (m)	Dist. from transect (m, L-R)	# of crowns	*# of ribs*	*D. long axis (mm)*	*D. short axis (mm)*	Harvested (Y/N)	Coordinates (S.Tx UTM 14N; W.Tx UTM 13N)	GPS Waypoint (# or Y/N)	Photo (Y/N)	Notes on location (e.g. landmarks, features etc.)	Notes on condition (e.g. flowers or seeds, chewed/damaged etc.)

S.Fig. 2. Data sheets for transects and individual plants within one transect.

Supplementary Table 1. Additional site information, including number of cacti species recorded on site, and suitable soil and geology.

Site	N spp.	Cactus species identified on site	Soil	Geology
1	17	*Ancistrocactus (Sclerocactus) scheeri, Astrophytum asterias, Coryphantha (Escobaria) emskoetteriana, Coryphantha macromeris var. runyonii, Cylindropuntia leptocaulis, Echinocereus enneacantthus, Echinocereus fitchii, Echinocereus pentalophus, Echinocereus poselgeri (wilcoxii), Hamatocactus hamatocanthus, Grusonia schottii, Lophophora williamsii, Mammillaria heyderi (likely ssp. heyderi), Mammillaria (Dolichothele) sphaerica, Opuntia engelmannii, Thelocactus bicolor, Thelocactus setispinus*	Fine sandy loam	Unconsolidated > Fine-detrital > Clay
2	11	*Ancistrocactus scheerii, Cylindropuntia leptocaulis, Echinocereus enneacanthus, Echinocereus fitchii, Echinocereus penthalophus, Escobaria emskoetteriana (or runyonii), Lophophora williamsii, Mammillaria heyderi, Mammilaria (Dolichothele) sphaerica, Opuntia engelmanii spp. lindheimeri, Thelocactus setispinus*	Loam	Sedimentary > Clastic > Sandstone Unconsolidated > Fine-detrital > Clay
3	14	*Astrophytum asterias, Coryphantha macromeris var ranyoni, Cylindropuntia leptocaulus, Echinocereus enneacanthus, Echinocereus fitchii, Echinocereus pentalophus, Homalocephala texensis, Grusonia schottii, Lophophora williamsii, Mammilaria heyderi, Mammilaria (Dolichothele) sphaerica, Opuntia engelmanii, Thelocactus setispinus, Sclerocactus scherii*	Clay and fine sandy loam	Unconsolidated > Fine-detrital > Clay
4	10	*Ariocarpus fussiratus, Cylindropuntia leptocaulis, Echinocactus horizonthalonius, Echinocereus coccineus, Echinocereus enneacanthus, Ferocactus hamatacanthus, Grusonia (Opuntia) schottii, Lophophora williamsii, Mammilaria heyderi, Opuntia engelmanii ssp. engelmannii*	Gravelly loam, channery clay loam and cobbly silt loam over limestone rock outcrop	Sedimentary, Carbonate > Limestone

5	27	*Ariocarpus fissuratus, Coryphantha albicolumnaria, Coryphantha echinus, Coryphantha ramillosa, Coryphantha tuberculosa, Cylindropuntia leptocaulis, Echinocactus horizonthalonius, Echinocereus coccineus, Echinocereus enneacanthus, Echinocereus pectinatus ssp. wenigeri, Echinocereus stramineus, Echinocereus reichenbachii, Epithelantha micromeris, Ferocactus hamatacanthus, Grusonia schottii, Homalocephala texensis, Lophophora williamsii, Mammillaria heyderi, Mammillaria lasiacantha, Opuntia atrispina, Opuntia engelmannii, Opuntia mackensii, Opuntia macrocentra, Opuntia phaeacanth, Opuntia rufida, Sclerocactus mariposensis, Sclerocactus uncinatus*	Very gravelly loam over limestone rock outcrop	Sedimentary > Carbonate > Limestone
6	17	*Ariocarpus fissuratus, Coryphantha echinus, Coryphantha pottsii, Coryphantha tuberculosa, Cylindropuntia leptocaulis, Echinocactus horizonthalonius, Echinocereus dasyacanthus, Echinocereus stramineus, Epithelantha bokei, Epithelantha micromeris, Ferocactus hamatacanthus, Lophophora williamsii, Mammillaria lasiacantha, Opuntia camanchica, Opuntia engelmanii, Opuntia rufida, Sclerocactus uncinatus*	Very gravelly loam over limestone rock outcrop	Sedimentary > Carbonate > Limestone

Supplementary Table 2. Summary information on the variables used in my study.

Variable name	Type	Values	Units	Dataset	Source	Resolution/level	Purpose
Region	Categorical	STx, WTx	NA	NA	Field data	-	Design variable
Site	Categorical	1, 2, 3, 4, 5, 6	NA	NA	Field data	-	Design variable
Transect	Categorical	1-121	NA	NA	Field data	-	Design variable
Total plant volume	Numerical	Range of continuous variables	cm3	NA	Field data	Plant	Response variable
Crown number	Numerical	0-12	Counts	NA	Field data	Plant	Response variable
Presence/absence	Categorical	Presence, absence	NA	NA	Field data	Transect	Response variable
Precipitation	Numerical	Range of continuous variables	mm	PRISMA 30-year average for 1980-2010	Oregon state university	Transect (800m)	Predictor variable
Max temperature	Numerical	Range of continuous variables	°C	PRISMA 30-year average for 1980-2010	Oregon state university	Transect (800m)	Predictor variable
Min temperature	Numerical	Range of continuous variables	°C	PRISMA 30-year average for 1980-2010	Oregon state university	Transect (800m)	Predictor variable

Elevation	Numerical	Range of continuous variables	m	Digital elevation model (DEM)	USGS	Plant (3m)	Predictor variable
Slope	Numerical	Range of continuous variables	°	Digital elevation model (DEM)	USGS	Plant (3m)	Predictor variable
Aspect	Categorical	Cardinal directions (N, E, W, S)	NA	Digital elevation model (DEM)	USGS	Plant (3m)	Predictor variable
Soil	Categorical	Soil classification categories	NA	Web soil survey	USDA	Site	Sampling universe selection
Geology	Categorical	Geo classification categories	NA	Texas geological map data	USGS	Site	Sampling universe selection

Values for elevation, slope and aspect were extracted from the DEM for the individual plant's coordinates. Aspect values, initially presented as degrees from 0 to 360, were re-coded into 4 equally-spaced categories (N, E, S, W).

Literature search terms

Scopus

(TITLE-ABS-KEY (lophophora AND williamsii) OR TITLE-ABS-KEY (peyote))

Web of Science Core Collection

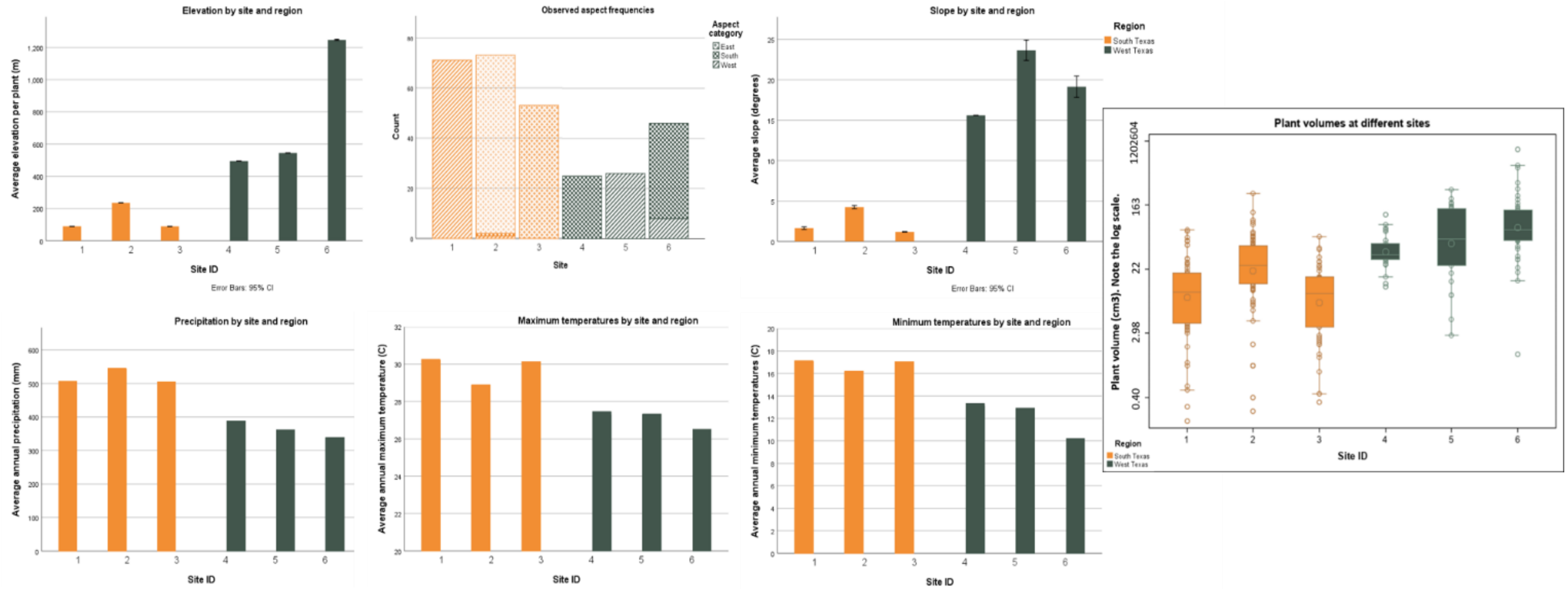
(Lophophora williamsii) OR TOPIC: (peyote)

Timespan: All years. Indexes: SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, ESCI.

PubMed

(Lophophora williamsii[Title/Abstract]) OR peyote[Title/Abstract]

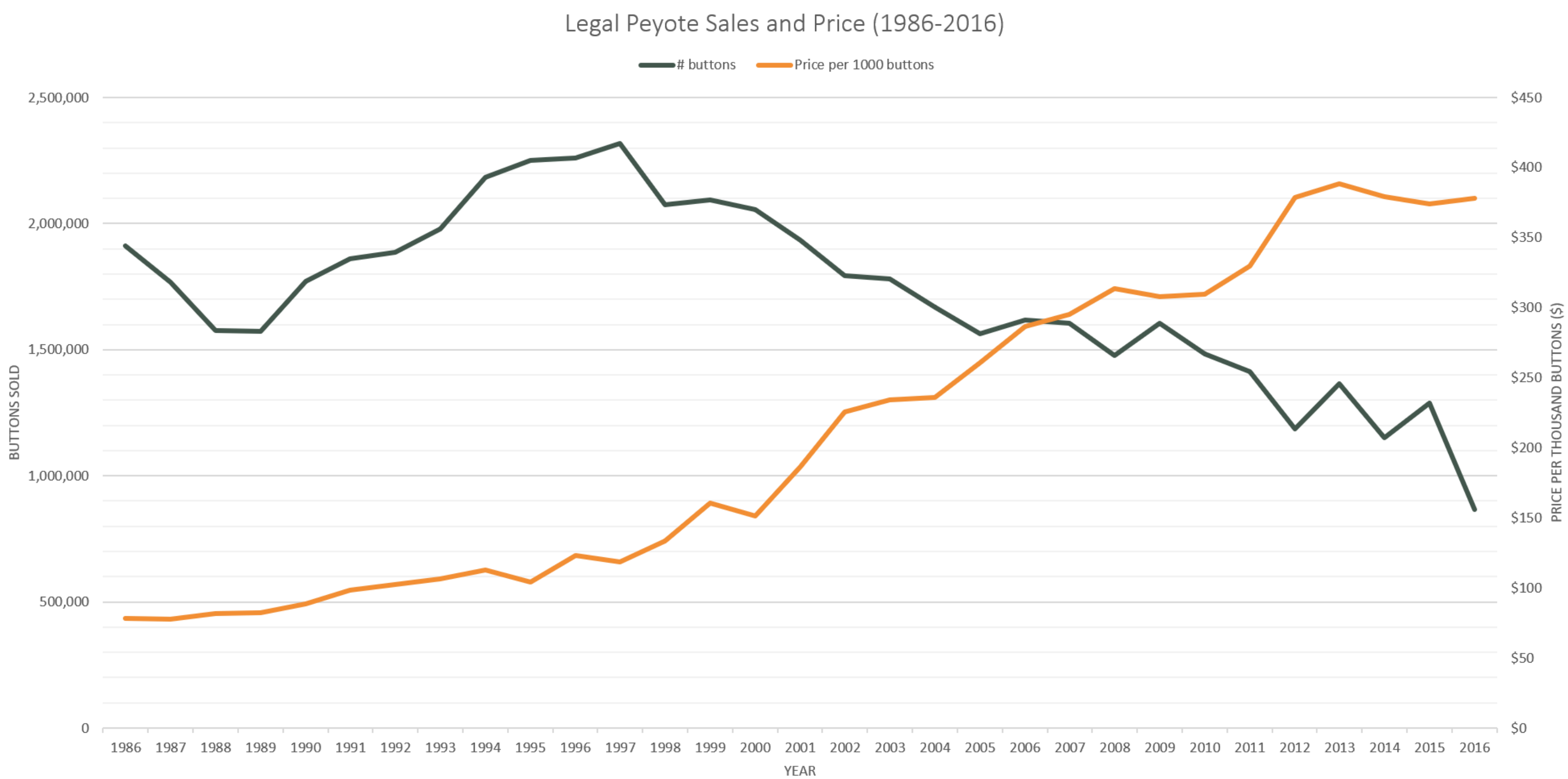
Appendix III: Results



S.Fig. 3. Environmental variables and plant volume at different sites. 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.

S.Fig. 4. Peyote harvesting and regeneration (from Terry et al., 2006). Plant is cut transversely at the base of the crown; Harvested crown (green tissue), subterranean stem (bark-covered tissue undernearth) capable of regenerating new crowns, tapering root; Two peyote ‘pups’ regenerating from the stem of the plant that has been harvested 7.5 months before. The plants can generate new stem branches only from areoles on the subterranean stem of the adult plant, and when harvesting is done by cutting the plant too deeply below ground level, there is no possibility of regrowth, as the subterranean areoles just below the base of the crown are removed along with the crown of the harvested plant.

Appendix IV: Legal trade



S.Fig. 5. Legal peyote trade data. Annual peyote sales data from 1986 to 2016 (when TDPS stopped collecting these data). The number of buttons sold annually has been steadily declining over the last 20 years. So does the size of the individual buttons, and it takes many more buttons to achieve the desired effect. Key market indicators from the regulated trade, the prices are rising, and the supply is dwindling. Data from TDPS, 2019.

Appendix V. Model analyses

Supplementary Table 3. Results from the general linear model for log (plant volume).*significance at P=0.0085 (Bonferroni corrected).

Predictor variable	N	Df	Type I sum of squares	Mean square	F value	Pr > F
Region*	2	1	162.1786287	162.1786287	13.38	0.0216
Site	6	4	48.46812419	12.11703105	3.19	0.0764
Transect*	121	8	30.41291477	3.80161435	3.11	0.0022
Precipitation*	14	1	11.25506945	11.25506945	18.48	0.0036
Max temperature*	14	1	10.25657296	10.25657296	13.64	0.0077
Min temperature *	14	1	10.51469738	10.51469738	14.71	0.0064
Elevation	14	1	1.04913121	1.04913121	0.51	0.4993
Slope	14	1	0.65694961	0.65694961	0.31	0.5954

Aspect STX	97	1	0.49410163	0.49410163	0.36	0.5531
Aspect WTx	97	1	0.10732464	0.10732464	0.11	0.7448

Supplementary Table 4. Results from the generalised linear model for crown numbers. *significance at P = 0.05.

Predictor variable	N	-2 log likelihood	AIC	Pearson chi-square / DF	Num DF	Den DF	F-value	Pr > f
Region	2	814.23	828.23	0.89	1	288	1.37	0.2436
Site*	6	814.23	828.23	0.89	4	288	4.41	0.0018

Supplementary Table 5. Results from the generalised linear model for presence/absence data.

Predictor variable	N	-2 log likelihood	AIC	Pearson chi-square / DF	Num DF	Den DF	F-value	Pr > f
Region	121	70.77	82.77	121.00	1	115	2.00	0.1600
Site					4	115	2.76	0.0308
Precipitation	121	68.60	82.60	1.08	1	114	1.73	0.1906
Max temperature	121	69.03	83.03	1.05	1	114	1.65	0.2011
Min temperature	121	68.65	82.65	1.01	1	114	2.04	0.1564
Elevation	121	69.67	83.67	1.00	1	114	0.96	0.3292
Slope	121	65.18	79.18	0.99	1	114	4.30	0.0403