

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

Anna Ermakova

CID: 01615602

August 2019

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
and the Diploma of Imperial College London

Formatted in the journal style of *Conservation Biology*.

Submitted for the MSc in 2019

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

Name of student: Anna Ermakova

Name of Supervisors: Colin Clubbe, Martin Terry

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

ACKNOWLEDGMENTS

Thank you, Martin Terry for being the most incredible teacher and mentor. Your knowledge about wildlife, sense of humour, patience, kindness and erudition has made my time in Texas unforgettably wonderful.

Thank you, Deirdre Terry, for sharing your stories – and organizing us when we most need it. Your strength and wisdom will continue to inspire me.

Thank you, Norma Fowler, for your support and help with study design and analysis. You have always come to my rescue when I needed most.

Thank you, Carolyn Whiting, for your invaluable help with data collection and sagely advice.

Thank you, Colin Clubbe for being amazing project supervisor and for your time, support and helpful comments.

Thank you, Trout Keeper from the Cactus Conservation Institute for your encyclopedic knowledge and willingness to share it.

Thank you, Bia Labate from Chacruna, for your very timely piece of advice, and amazing skills at bringing the right people together.

Thank you, Nimrod Gileadi, for being there, my partner, my love, for protecting me from the worst of horrors (programming, math and computational modelling, what else!) and cooking the best food in the world.

Big thank you to family, whose unconditional love and support has allowed me the freedom to explore different paths in life and nurtured the curiosity about the world.

Thank you, my lovely ConSci classmates for making this course most enjoyable, engaging and fun!

And last, but not least, thanks to Wade Davis, a brilliant anthropologist and ethnobotanist, for writing “One River”, the book that inspired me to change life direction and follow my heart.

TABLE OF CONTENTS

Abstract	1
Resumen	2
Impact Statement.....	3
Keywords.....	3
Introduction	4
Methods	8
Ethics	8
Study areas.....	8
Survey procedures and sampling universe	8
Data collection	9
Data sources and geospatial analysis	10
Variables of interest	10
Statistical analysis.....	11
Literature search and selection of studies	12
Results.....	14
Densities and population structures	14
Environmental variables	15
Models	17
Literature review.....	17
Sustainable Harvesting Guidelines	19
Discussion	21

Acknowledgements	28
Supplementary information description.....	30
Literature cited	31
Appendix I: Regional descriptions	35
Appendix II: Methods	37
Appendix III: Results	43
Appendix IV: Legal trade	45
Appendix V. Model analyses.....	46

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.

22 **Resumen**

23 *Lophophora williamsii* (peyote) es un pequeño cactus psicoactivo que se encuentra creciendo
24 naturalmente en México y Texas, E.U. Tiene mucha significación cultural, religiosa, y medicinal
25 para muchos pueblos indígenas norteamericanos. Las poblaciones de peyote se están
26 disminuyendo rapidamente, debido a la presión de la sobre cosecha legal continua, amenazas
27 crecientes en forma de la conversión de habitat a usos agrícolas, otros cambios en el uso de la
28 tierra para propuestos económicos, y la amenaza constante de la sobre cosecha ilegal - o sea el
29 robo - de peyote en su habitat.

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

52 Introduction

53 *Lophophora williamsii* (Lem. Ex Salm-Dyck) J.M. Coulter (Cactaceae), commonly known as
54 peyote, is a small, grey-green, spineless, globular cactus native to central and northern Mexico
55 and close to the Rio Grande river in Texas, USA (Fig.1). Its preferred habitat is shrubland desert.
56 It is a very slow-growing species, taking up to 10 years for the plant to mature from seed
57 (Anderson 1996).

58 Peyote has been used for medicinal and religious purposes by the indigenous people of North
59 America for at least 6000 years (El-Seedi et al. 2005; Terry et al. 2006), and to this day is an
60 integral part of indigenous heritage, especially in Mexico, e.g. among Huichol, Tahahumara,
61 Cora tribes (Myerhoff 1976; Schaefer & Furst 1996; Labate & Cavnar 2016) where its use
62 originated. Indigenous people of the USA and Canada have adopted peyote more recently, at
63 the end of the 19th century (La Barre 1975; Schultes & Hofmann 1980; Stewart 1987; Dyck
64 2016). Peyote is consumed by members of the Native American Church (NAC) as a sacrament in
65 the form of fresh or dried buttons or tea. It is an integral part of the religious practice of
66 250,000–500,000 members of this religious tradition in North America (Feeney 2016).

67 The main chemical compound responsible for peyote's distinctive psychoactive effects is an
68 alkaloid called mescaline. Although its psychopharmacological properties and indigenous use
69 have been researched extensively since the 1880s (Jay 2019) peyote remained relatively
70 unknown to the general public until the advent of the counterculture movement of the late
71 1950's and 1960's. Backlash from the authorities resulted in listing not only mescaline, but also
72 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). Overharvesting 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?

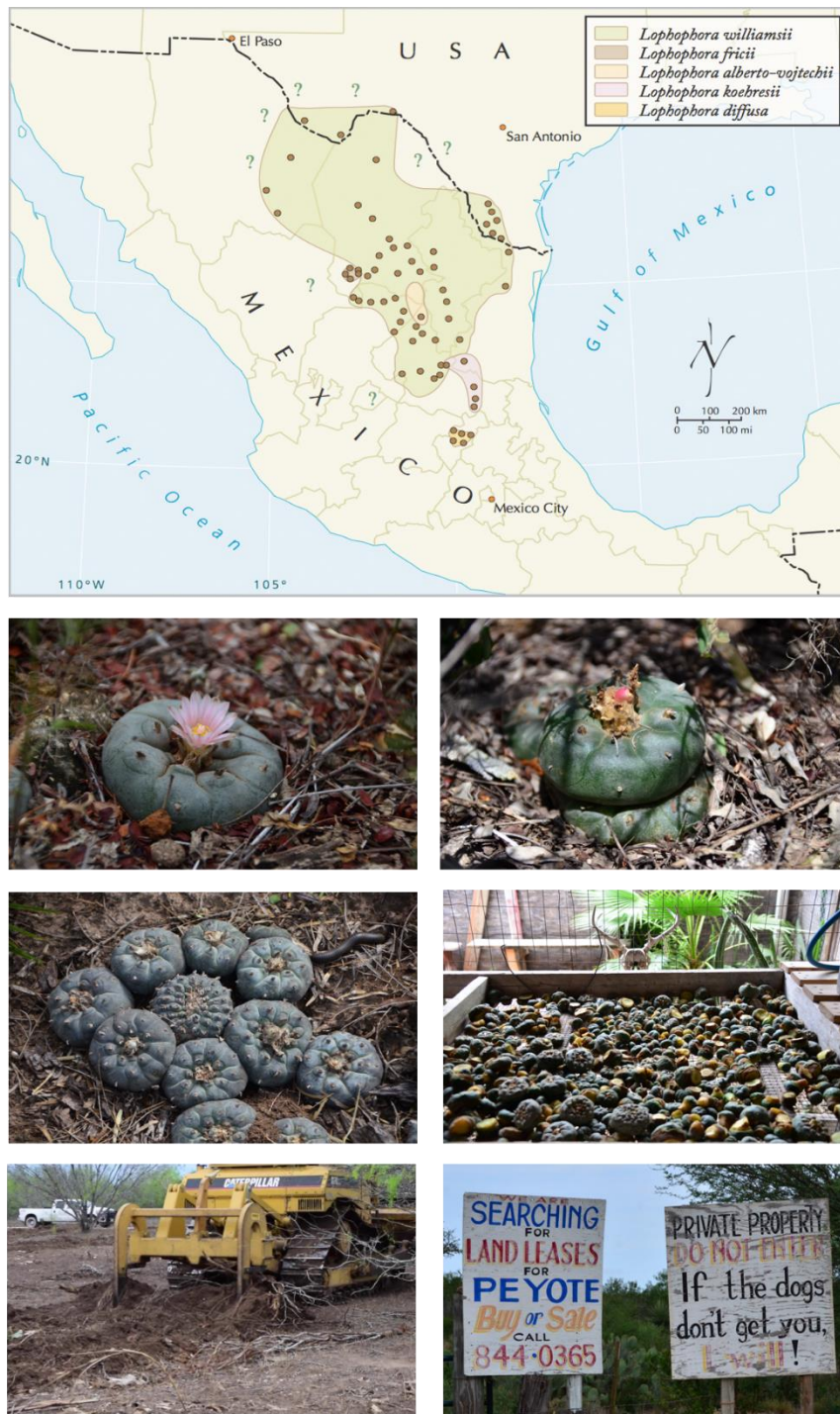


Fig.1. Distribution of 5 species of genus *Lophophora* and main threats to the existing peyote populations in the USA. Distribution map from Terry et al.(2008). Question-marks represent uncertainty about the presence of peyote, and older maps usually portray the range of *L. williamsii* as being more 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.

113 **Methods**

114 ***Ethics***

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

118 ***Study areas***

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

125 ***Survey procedures and sampling universe***

126 My survey methodology was chosen to avoid bias, and to optimise the trade-offs between
127 statistical rigour and sample size. We pre-determined 'suitable habitat', which, combined with
128 accessibility criteria, established the sampling universe, based on the following criteria:

- 129 - Land never root-ploughed or converted to agriculture;
- 130 - No development (i.e., roads, buildings, drains, pipelines, wind turbines);
- 131 - Suitable soil and terrain type (escarpment, limestone, grey/white but not red soils);
- 132 - 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 United 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: $V_{\text{crown}} = \frac{2}{3} \pi (\text{diameter}/2)^3$. 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.

217 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 (cm ³)	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

218

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 cm³ vs. 95.01 cm³, $t(292) = -10.598$, $p < 0.0001$, 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 ($P = 0.3565$).

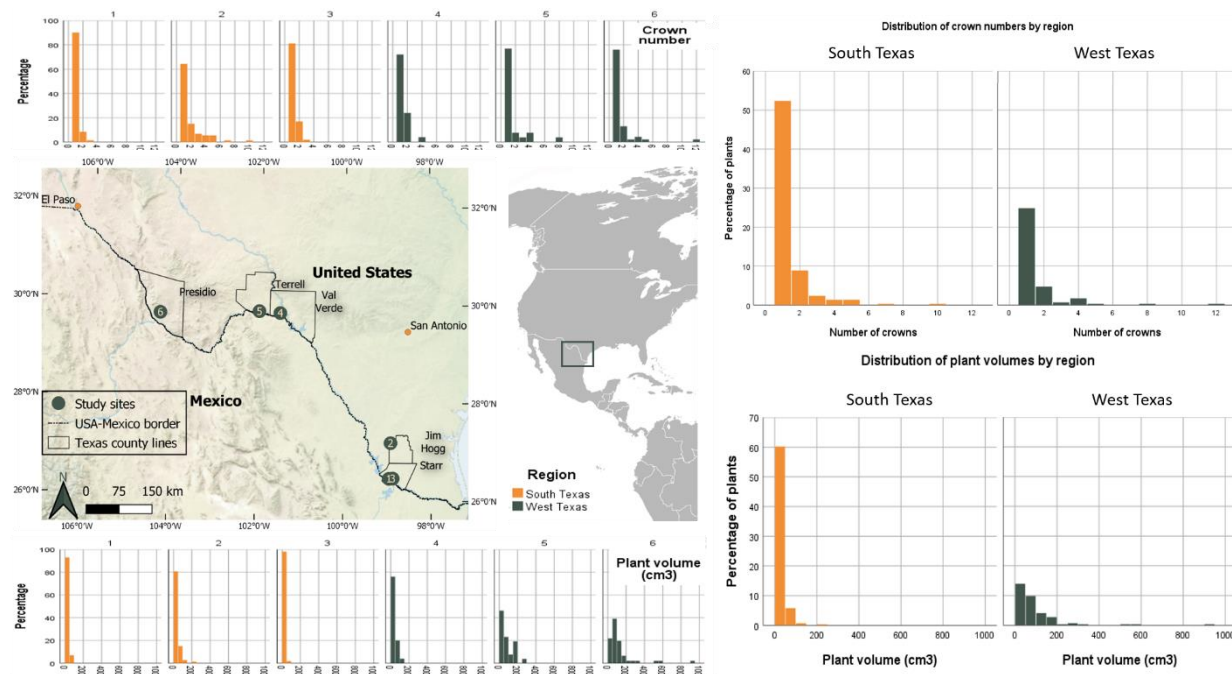


Fig. 2. Location of the study sites and population structures of *L. williamsii*. Map shows location of 6 study sites included in this study from Chihuahuan desert ecoregion (West Texas: 4, 5, 6) and Tamaulipan thornscrub (South Texas: 1, 2, 3). Distributions of the two population structure variables, 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.

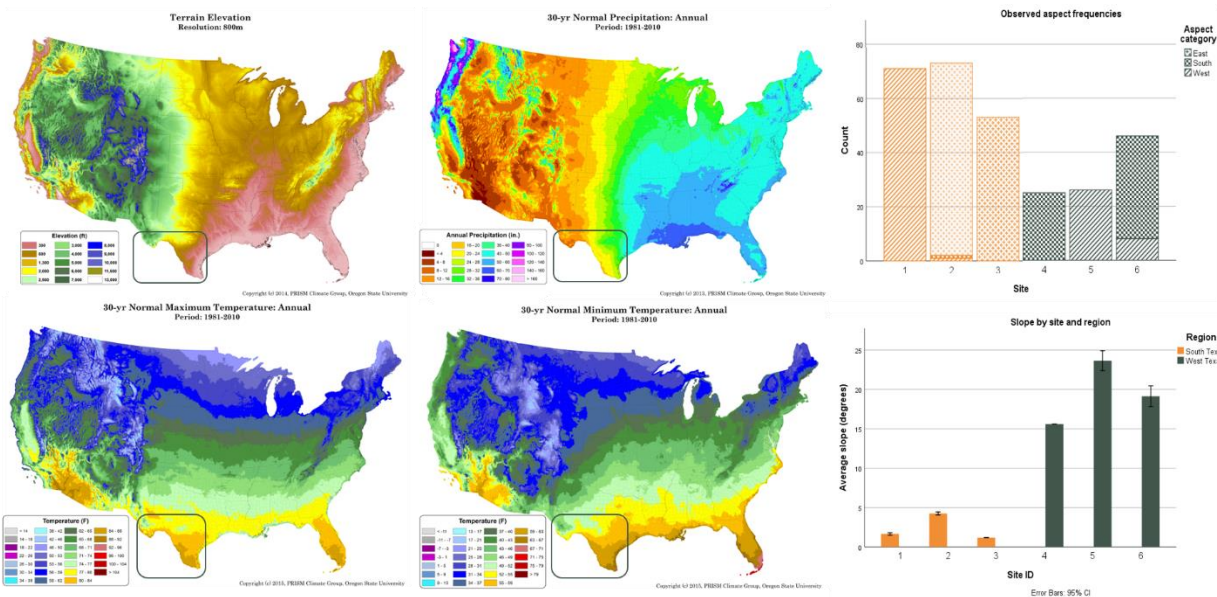


Fig. 3. Environmental variables at the study sites. West Texas is generally colder, dryer and has higher elevations compared to South Texas. In West Texas, where peyote mostly grows on the mountain tops and slopes, aspect is much more important – plants are commonly found on the South-West facing slopes,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

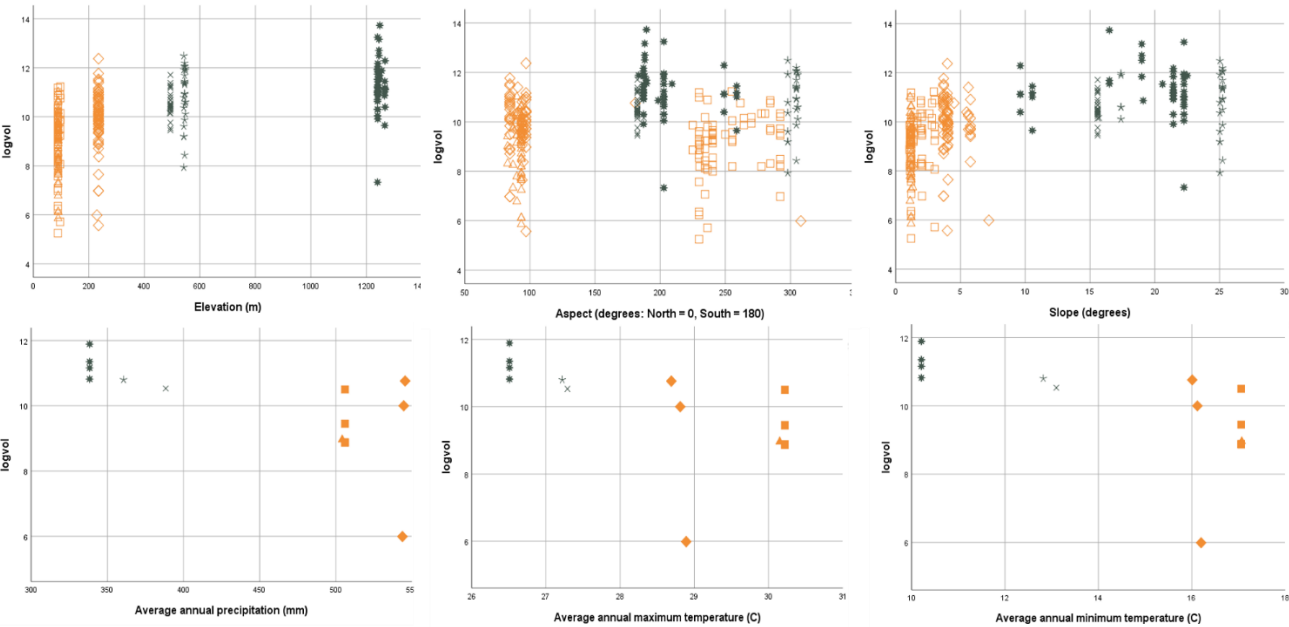


Fig. 4. Relationship between plant volume and environment variables. Elevation, aspect and slope are presented at the plant level, while climate variable are available at transect scale. 14 transects with plants are presented here. Note that plant volume has been transformed into log(volume).

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 ($R^2 = 41\%$).

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

270 identifying additional material in the references, the final count of the included publications

271 was 27 (Fig. 6).

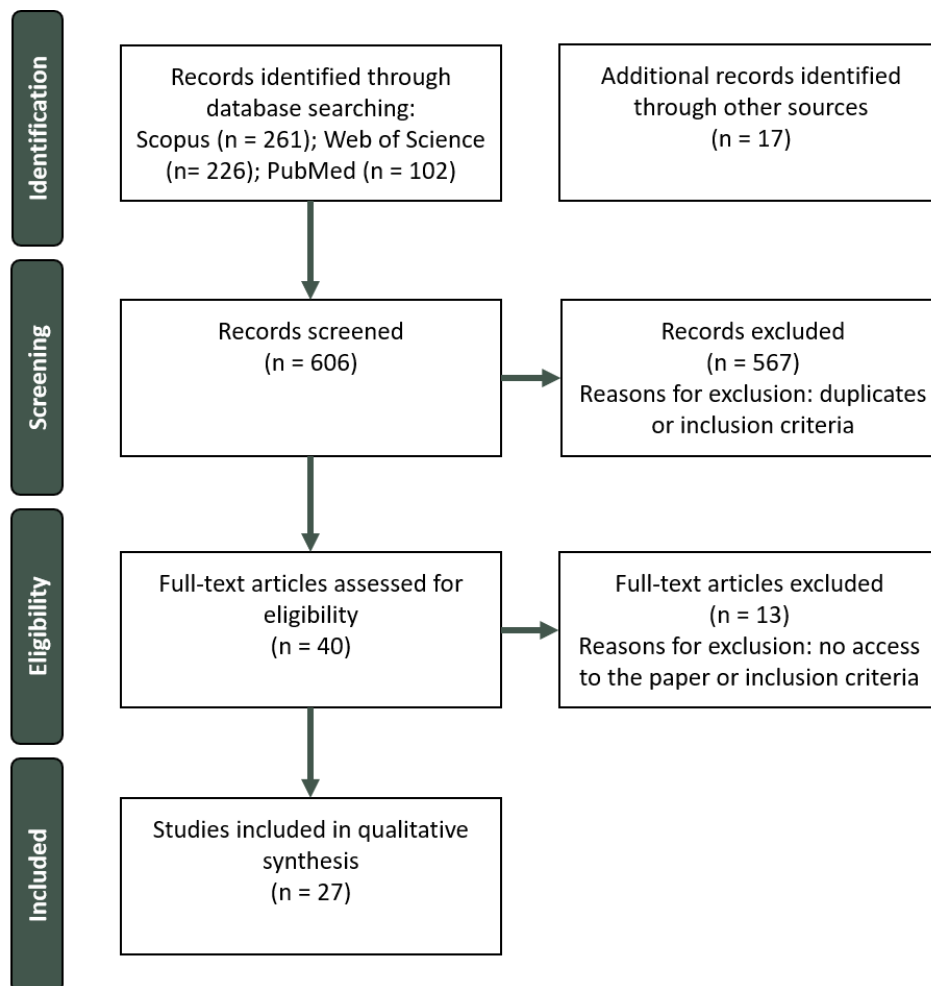
272 Literature review confirmed that there is a serious lack of up-to-date information on peyote's

273 biology, ecology and propagation. Detailed analysis and review of the retrieved literature is

274 beyond the scope of this paper, as my main aim was to collate all the available data and distill it

275 to simple and easy-to-follow principles which form the basis of these first harvesting guidelines

276 for peyote.



277 **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.

317 Discussion

318 There is a considerable knowledge gap when it comes to peyote conservation and ecology.

319 Books and hundreds of publications have been written about peyote over the 500 years of its

320 written history (and archaeological evidence shows that it's been used as early as 6000 years

321 ago, (El-Seedi et al. 2005). Peyote has been portrayed as a medicine, sacrament, the devil (e.g.

322 some early Spanish writings (Dawson 2016), psychotomimetic agent, trade commodity, drug,

323 ethnographic curiosity – but considerably little has been written about it as a cactus, a

324 vulnerable species in need of protection in its native habitat.

325 This study is filling in this gap by developing and implementing methodology for surveying

326 peyote populations in Texas, USA, establishing baselines for different ecoregions and

327 understanding the primary habitat characteristics.

328 I have collected data from 294 plants and surveyed 1.21ha of land in the Tamaulipan thorn-

329 scrub and the Chihuahuan desert – two ecoregions of Texas where peyote grows. Finding

330 peyote in the field is not an easy task, even narrowing it down to the sites with appropriate

331 soils (gray-white sandy loam) and geology (limestone) and geography (escarpment). I have

332 developed my methodology with the aim to be unbiased and statistically rigorous, and have

333 produced repeatable, unbiased definitions of the sampling universe and established transects

334 according to criteria independent of the previously known locations of populations. Most of the

335 transects that I surveyed had no peyote plants on them – although occasionally plants were

336 growing just a few metres off a transect. In fact, more than 90% of transects in STx and 84% in

337 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 550m². 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 cm³) compared to STx (21cm³), 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-

382 West-facing slopes and tops of the mountains, but never on North-facing slopes. Further
383 research, with a larger sample size, is needed to verify this observation. It would be even more
384 informative for elucidating relationships between plant distribution and environmental
385 variables if I compare areas where plants occur (presences) and where they don't (absences).
386 However, none of the environmental variables turned out significant in my analysis.

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

394 My original idea has been to compare peyote populations that have never been harvested, that
395 have been harvested legally, and some that have been illegally harvested. Once I arrived for my
396 fieldwork in Texas, I realized that I had seriously overestimated what can be done in two
397 months. Because most of peyote populations grow on private land, it was necessary to obtain
398 permissions and consent from the landowners to do research. Conservation work on private
399 lands is a relatively new and promising field (Drescher & Brenner 2018), which is especially
400 relevant to the context of Texas, where 96% of land is privately owned ("Texas Land Trends"
401 2019). It takes much longer that a few weeks to gain trust from the local landowners, especially
402 when it comes to discussing sensitive and controversial topics such as peyote conservation.

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

407 Peyote is situated in a very peculiar position because of its listing as a Schedule 1 in the USA.
408 The Texas DPS and the federal DEA have extensive regulations regarding *who* can harvest, and
409 *where*, yet there are no regulations on *how or what plants* to harvest, as is usually the case with
410 other heavily harvested plant species, such as ginseng (McGraw et al. 2013; Schmidt et al.
411 2019), frankincense (Lemenih & Kassa 2011), hoodia (Wynberg 2010), cork oak (Gil & Varela
412 2008; Oliveira & Costa 2012) and many others.

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

418 The current state of knowledge about peyote populations does not yet allow quantification of
419 what level of harvesting would be 'sustainable'. What I collated and distilled from the published
420 literature, and learned from doing fieldwork, are the necessary first steps, a set of common-
421 sense rules that are easy to apply in harvesting practice. As our knowledge increases, these
422 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 through 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 (Cortés-Olmos, 2017 and Ortiz-Montiel & Alcantara-García, 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.

Acknowledgements

I gratefully acknowledge my supervisors Prof. Martin Terry and Dr. Colin Clubbe for their support and guidance throughout the study, and providing valuable comments and suggestions for this manuscript. Imperial College London and Cactus Conservation Institute provided funding for travel and equipment. Prof. Norma Fowler and Carolyn Whiting were instrumental

487 in developing the appropriate survey methodology, and special thanks to Norma Fowler for her
488 contribution to the statistical analysis.

489

490 **Supporting information**

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

496

497

498 Literature cited

- 499 Anderson EF. 1996. *Peyote: The divine cactus*. University of Arizona Press.
- 500 Bárcenas Luna RT. 2015. Chihuahuan Desert cacti in Mexico: an assessment of trade,
501 management, and conservation. priorities. Part II. Prickly trade: trade and conservation of
502 Chihuahuan Desert cacti. TRAFFIC North America, World Wildlife Fund, Washington,
503 DC. http://www.traffic.org/speciesreports/traffic_species_plants5.pdf.
- 504 BBNP peyote is now extirpated (i.e. made locally extinct) – Cactus Conservation Institute -
505 Trout Keeper. (2019.). Available from
506 [https://cactusconservation.org/blog/2019/06/30/bbnp-peyote-is-now-extirpated-i-e-made-](https://cactusconservation.org/blog/2019/06/30/bbnp-peyote-is-now-extirpated-i-e-made-locally-extinct/)
507 [locally-extinct/](https://cactusconservation.org/blog/2019/06/30/bbnp-peyote-is-now-extirpated-i-e-made-locally-extinct/) (accessed August 27, 2019).
- 508 Cortés Capano G, Toivonen T, Soutullo A, Di Minin E. 2019. The emergence of private land
509 conservation in scientific literature: A review. *Biological Conservation* **237**:191–199.
- 510 Dawson AS. 2016. *Peyote in the Colonial Imagination*. *Peyote: History, Tradition, Politics, and*
511 *Conservation*. Edited by Beatrice C. Labate and Clancy Cavnar. Santa Barbara:
512 Praeger:43–62.
- 513 Drescher M, Brenner JC. 2018. The practice and promise of private land conservation. *Ecology*
514 *and Society* **23**. Available from <https://www.ecologyandsociety.org/vol23/iss2/art3/>
515 (accessed July 21, 2019).
- 516 Dyck E. 2016. *Peyote and Psychedelics on the Canadian Prairies*. *Peyote: History, Tradition,*
517 *Politics, and Conservation*:151–70.
- 518 El-Seedi HR, Smet PAGMD, Beck O, Possnert G, Bruhn JG. 2005. Prehistoric peyote use:
519 Alkaloid analysis and radiocarbon dating of archaeological specimens of *Lophophora*
520 from Texas. *Journal of Ethnopharmacology* **101**:238–242.
- 521 Feeney K. 2017. *Peyote as Commodity: An Examination of Market Actors and Access*
522 *Mechanisms*. *Human Organization* **76**:59–72.
- 523 Feeney KM. (2016). *Peyote & the Native American church: an ethnobotanical study at the*
524 *intersection of religion, medicine, market exchange, and law*. Doctoral dissertation.
525 Washington State University
- 526 For Indian Church, a Critical Shortage. 1995, March 20. *The New York Times*. Available from
527 <https://www.nytimes.com/1995/03/20/us/for-indian-church-a-critical-shortage.html>
528 (accessed August 27, 2019).
- 529 Gil L, Varela MC. 2008. Technical Guidelines for genetic conservation of Cork oak (*Quercus*
530 *suber*). Bioersivity International.
- 531 Goettsch B et al. 2015. High proportion of cactus species threatened with extinction. *Nature*
532 *Plants* **1**. Available from <http://www.nature.com/articles/nplants2015142> (accessed July
533 21, 2019).
- 534 Texas Land Trends. (2019). Available from <http://txlandtrends.org/> (accessed August 27, 2019).

- IBM SPSS Software. 2019, May 14. Available from <https://www.ibm.com/uk-en/analytics/spss-statistics-software> (accessed August 27, 2019).
- Jay M. 2019. *Mescaline: a global history of the first psychedelic*. Yale University Press.
- Klein MT, Kalam M, Trout K, Fowler N, Terry M. 2015. Mescaline Concentrations in Three Principal Tissues of *Lophophora williamsii* (Cactaceae): Implications for Sustainable Harvesting Practices. *Haseltonia* **20**:34–42.
- La Barre W. 1975. *The peyote cult*. Archon Books, Hamden, Conn.
- Labate BC, Cavnar C. 2014. *Prohibition, religious freedom, and human rights: Regulating traditional drug use*. Springer.
- Labate BC, Cavnar C. 2016. *Peyote: History, Tradition, Politics, and Conservation*. ABC-CLIO.
- Lemenih M, Kassa H. 2011. Management guide for sustainable production of frankincense: a manual for extension workers and companies managing dry forests for resin production and marketing. CIFOR.
- Margulies JD, Bullough L-A, Hinsley A, Ingram DJ, Cowell C, Goettsch B, Klitgård BB, Lavorgna A, Sinovas P, Phelps J. 2019. Illegal wildlife trade and the persistence of “plant blindness.” *Plants, People, Planet*.
- McGraw JB, Lubbers AE, Van der Voort M, Mooney EH, Furedi MA, Souther S, Turner JB, Chandler J. 2013. Ecology and conservation of ginseng (*Panax quinquefolius*) in a changing world: Ecology and conservation of ginseng. *Annals of the New York Academy of Sciences* **1286**:62–91.
- McGraw JB, Souther S, Lubbers AE. 2010. Rates of Harvest and Compliance with Regulations in Natural Populations of American Ginseng (*Panax quinquefolius* L.). *Natural Areas Journal* **30**:202–210.
- Milner-Gulland EJ, Rowcliffe JM. 2007. *Conservation and sustainable use: a handbook of techniques*. Oxford University Press.
- Moher D, Liberati A, Tetzlaff J, Altman DG, Group P. 2010. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement.
- Morgan GR, Stewart OC. 1984. Peyote trade in South Texas. *The Southwestern Historical Quarterly* **87**:269–296.
- Myerhoff BG. 1976. *Peyote Hunt: The Sacred Journey of the Huichol Indians*. Cornell University Press.
- Oliveira G, Costa A. 2012. How resilient is *Quercus suber* L. to cork harvesting? A review and identification of knowledge gaps. *Forest Ecology and Management* **270**:257–272.
- PRISM Climate Group, Oregon State U. (n.d.). Available from <http://www.prism.oregonstate.edu/normals/> (accessed August 27, 2019).
- Prue B. 2014. Prevalence of reported peyote use 1985–2010 effects of the American Indian Religious Freedom Act of 1994. *The American journal on addictions* **23**:156–161.
- Prue B. 2016. Protecting the Peyote for Future Generations: Building on a Legacy of Perseverance. *Peyote: History, Tradition, Politics, and Conservation*:129.

- 574 QGIS Development Team. (2019). QGIS Geographic Information System. Available from
575 <https://qgis.org/en/site/index.html> (accessed February 23, 2019).
- 576 Rojas-Aréchiga M, Flores J. 2016. An overview of cacti and the controversial peyote. *Peyote:*
577 *History, Tradition, Politics, and Conservation*. Edited by Beatrice C. Labate and Clancy
578 Cavnar. Santa Barbara: Praeger:21–42.
- 579 Salas JS, Pérez GM, Castellón EE, Aranda MG, Ávila JAA. 2011. Registro de una nueva
580 localidad de *Lophophora williamsii* (cactaceae) a punto de extinción por saqueo en
581 coahuila, mexico. *Journal of the Botanical Research Institute of Texas* 5:685–687.
- 582 SAS Studio. (2019). Available from https://www.sas.com/en_gb/software/studio.html (accessed
583 August 27, 2019).
- 584 Schaefer SB, Furst PT. 1996. *People of the Peyote: Huichol Indian History, Religion & Survival*.
585 UNM Press.
- 586 Schmidt JP, Cruse-Sanders J, Chamberlain JL, Ferreira S, Young JA. 2019. Explaining harvests
587 of wild-harvested herbaceous plants: American ginseng as a case study. *Biological*
588 *Conservation* 231:139–149.
- 589 Schultes R, Hofmann A. 1980. *The Botany and Chemistry of Hallucinogens*. Charles C Thomas
590 Publisher, LTD, Springfield. Available from
591 <http://public.eblib.com/choice/publicfullrecord.aspx?p=631142> (accessed August 27,
592 2019).
- 593 Stewart OC. 1987. *Peyote religion: A history*. University of Oklahoma Press.
- 594 Terry M, Mauseth JD. 2006. Root-shoot anatomy and post-harvest vegetative clonal
595 development in *Lophophora williamsii* (cactaceae: cactaceae): implications for
596 conservation. *SIDA, Contributions to Botany* 22:565–592.
- 597 Terry M, Trout K. 2013. Cultivation of peyote: a logical and practical solution to the problem of
598 decreased availability. *Phytologia* 4.
- 599 Terry M, Trout K, Williams B, Herrera T, Fowler N. 2011. Limitations to natural production of
600 *Lophophora williamsii* (Cactaceae) I. Regrowth and survivorship two years post harvest
601 in a South Texas population. *Journal of the Botanical Research Institute of Texas*:661–
602 675.
- 603 Terry M, Trout K, Williams B, Herrera T, Fowler N. 2012. Limitations to natural production of
604 *Lophophora williamsii* (Cactaceae) II. Effects of repeated harvesting at two-year intervals
605 in a South Texas population. *Journal of the Botanical Research Institute of Texas*:567–
606 577.
- 607 Terry M, Trout K, Williams B, Herrera T, Fowler N (2014). Limitations to natural production of
608 *Lophophora williamsii* (cactaceae) III. Effects of repeated harvesting at two-year
609 intervals for six years in a South Texas population *Journal of the Botanical Research*
610 *Institute of Texas*:541–550.
- 611 The Controlled Substances Act. (1970). Available from [https://www.dea.gov/controlled-](https://www.dea.gov/controlled-substances-act)
612 [substances-act](https://www.dea.gov/controlled-substances-act) (accessed August 27, 2019).

- 613 The IUCN Red List of Threatened Species. (2019). Available from
614 <https://www.iucnredlist.org/en> (accessed July 21, 2019).
- 615 TNRIS - Texas Natural Resources Information System. (2019). Available from <https://tnris.org/>
616 (accessed July 21, 2019).
- 617 TxDPS - Texas Department of Public Safety. (2019). Available from <https://www.dps.texas.gov/>
618 (accessed August 27, 2019).
- 619 United Nations Treaty Collection. (2019). Available from
620 [https://treaties.un.org/Pages/ViewDetails.aspx?src=TREATY&mtdsg_no=VI-](https://treaties.un.org/Pages/ViewDetails.aspx?src=TREATY&mtdsg_no=VI-16&chapter=6&clang=_en)
621 [16&chapter=6&clang=_en](https://treaties.un.org/Pages/ViewDetails.aspx?src=TREATY&mtdsg_no=VI-16&chapter=6&clang=_en) (accessed August 27, 2019).
- 622 USGS.gov | Science for a changing world. (2019). Available from <https://www.usgs.gov/>
623 (accessed July 21, 2019).
- 624 Web Soil Survey - Home. (2019). Available from
625 <https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm> (accessed July 21, 2019).
- 626 Wynberg RP. 2010. Navigating a way through regulatory frameworks for Hoodia use,
627 conservation, trade and benefit sharing. Wild Product Governance: Finding Policies That
628 Work for Non-Timber Forest Products:309–26.
- 629 Xian G, Homer C, Rigge M, Shi H, Meyer D. 2015. Characterization of shrubland ecosystem
630 components as continuous fields in the northwest United States. Remote Sensing of
631 Environment **168**:286–300.

632

633

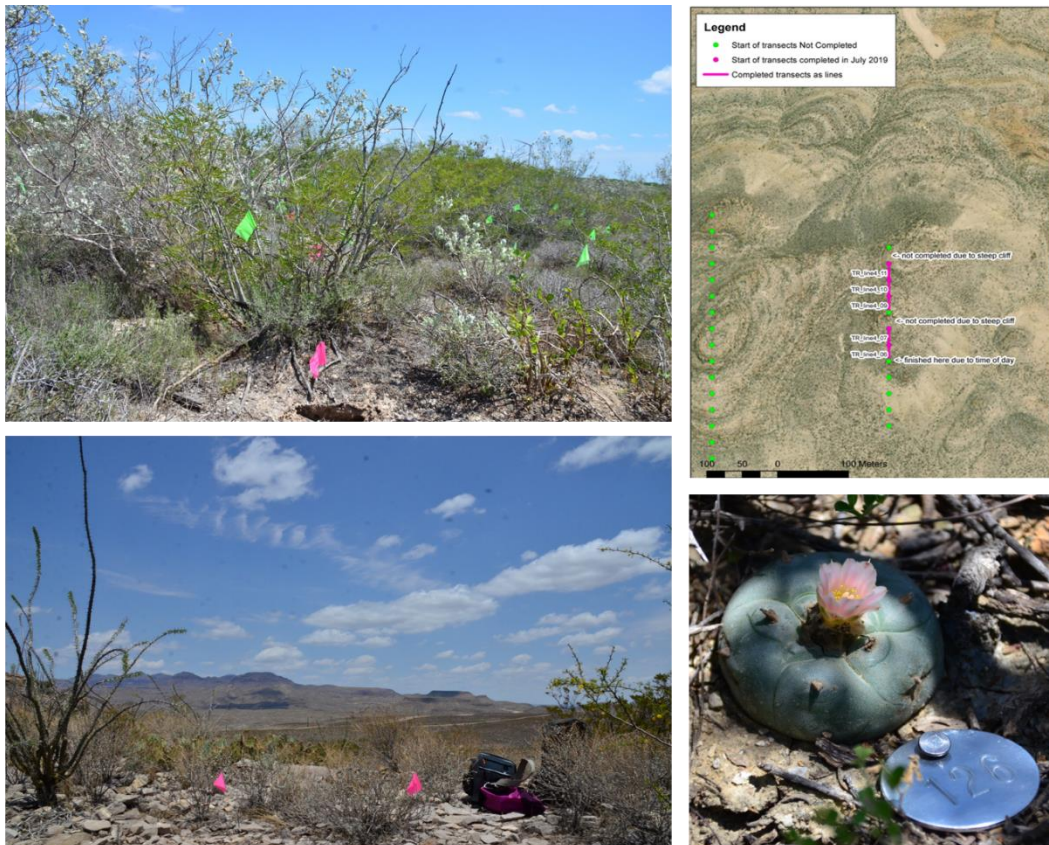
SUPPORTING INFORMATION

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), *Dasyllirion texanum* (Texas sotol), *Agave lechuguilla* (lechuguilla), *Fouquieria splendens* (ocotillo), *Dasyllirion 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

647 present. Ferns and fern allies, such as *Astrolepis* spp. (cloakferns), *Cheilanthes* spp. (lipferns) and *Selaginella lepidophylla*
 648 (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.

649

650

651 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	<i>D. long axis (mm)</i>	<i>D. short axis (mm)</i>	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.

652

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

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

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

655

656

657 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	cm ³	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).

661 ***Literature search terms***

662 Scopus

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

664 Web of Science Core Collection

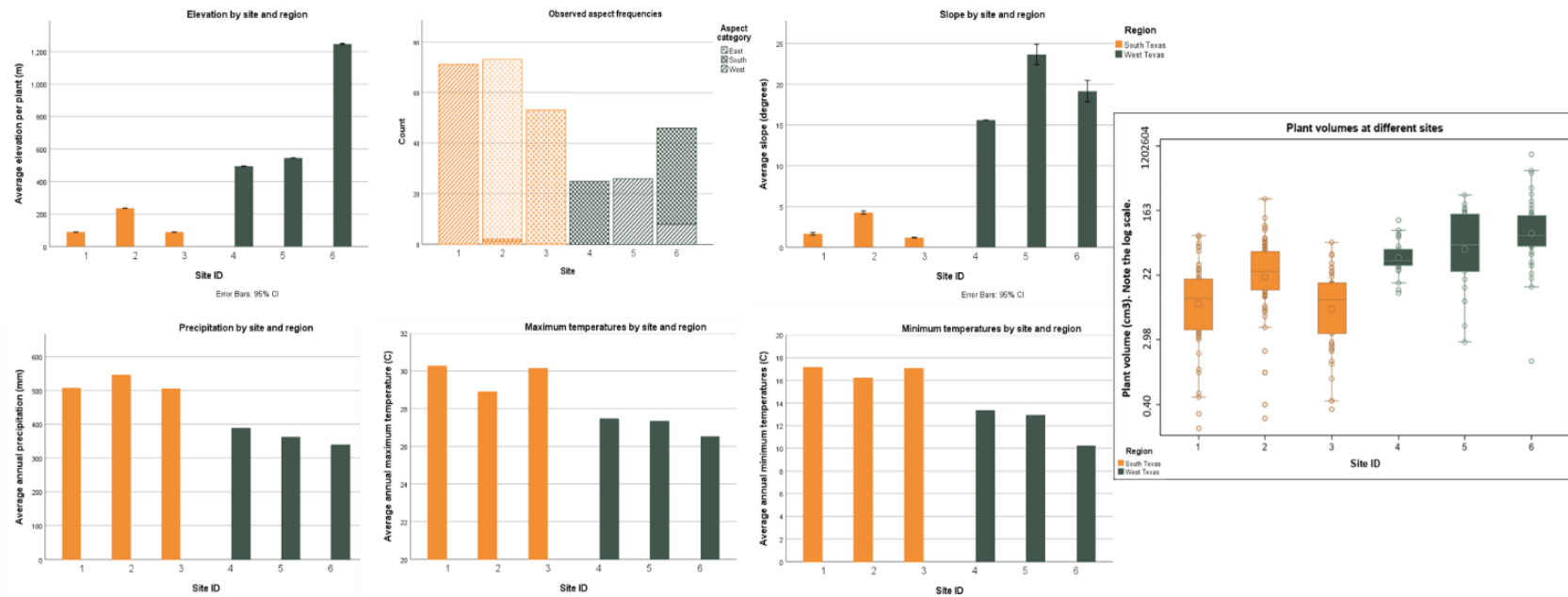
665 (Lophophora williamsii) OR TOPIC: (peyote)

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

667 PubMed

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

669 Appendix III: Results



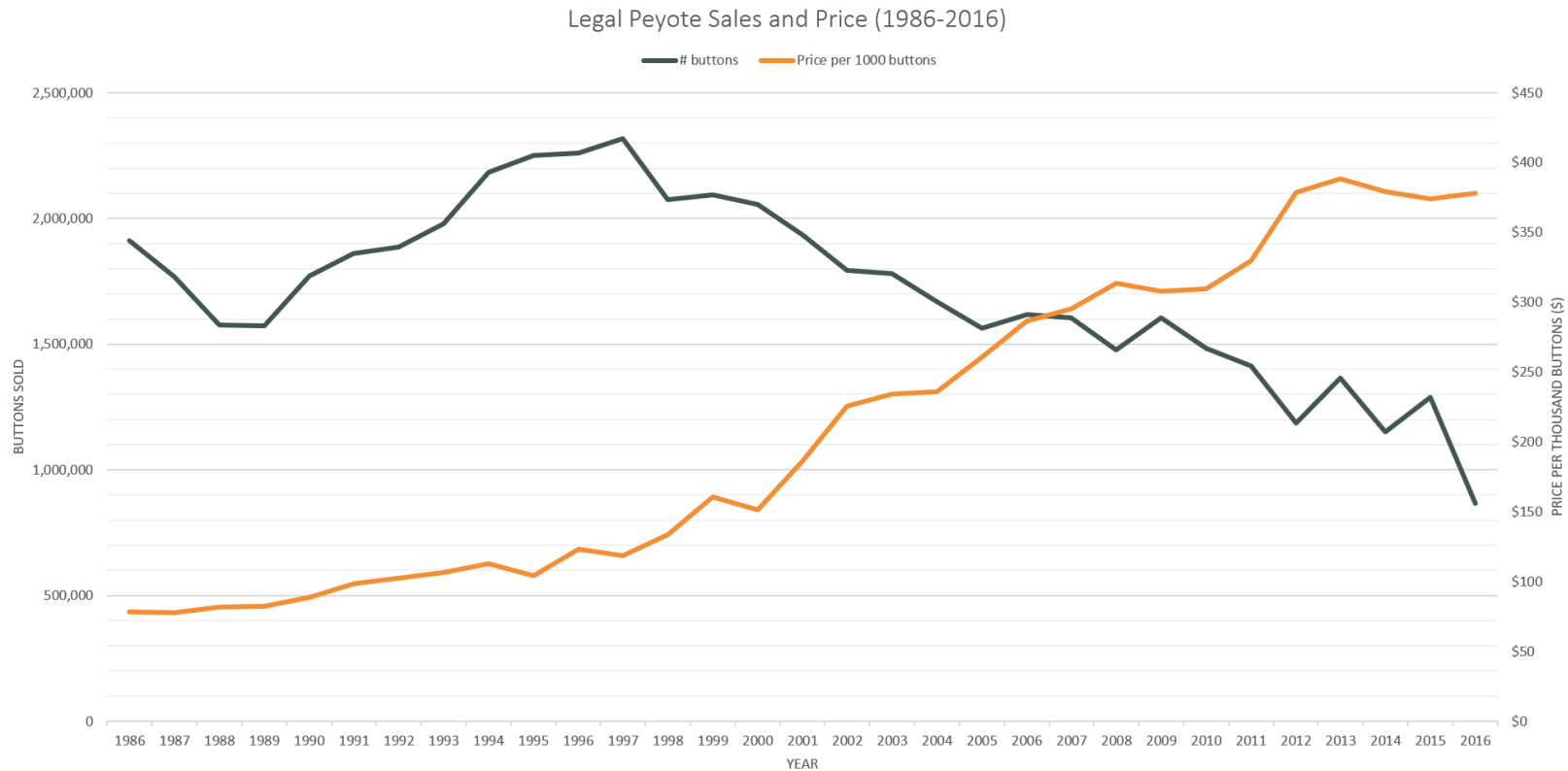
S.Fig. 3. Environmental variables and plant volume at different sites. West Texas is generally colder, dryer and has higher elevations compared to South Texas. In West Texas, where peyote mostly grows on the mountain slopes, aspect is much more important – plants are commonly found on the South-West 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.

670



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 underneath) 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.

672 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.

673

674

675 **Appendix V. Model analyses**

676 Supplementary Table 3. Results from the general linear model for log (plant volume). *significance at P=0.0085 (Bonferroni
677 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

678

679 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

680

681

682 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

683