The phylogeographic structure of Lycianthes dejecta and Lycianthes peduncularis is explained by Pleistocene oscillations and reveals a new lineage

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Research Article

Keywords: Baja California, Chihuahuan Desert, Disjunction, Phylogeography, Pleistocene fluctuations, Transmexican Volcanic Belt

Posted Date: June 17th, 2025

DOI: https://doi.org/10.21203/rs.3.rs-6521389/v1

Additional Declarations: No competing interests reported.

Abstract

Diversification of xerophilous linages in Mexico is result of the expansion and isolation due by the geological and climatic events in the past 15 Ma. *Lycianthes dejecta* and *L. peduncularis* have a sister relationship. Both are endemic to the xerophilous scrubs of Mexico and have disjunct populations. We anticipate they represent phylogeographically structured linages. The objectives were first, analyzing their genetic variation, structure and genealogical relationships. Second, described the demographic history and inferred they paleodistribution. Two cpDNA (*rpl*32-*trn*L and *ycf*1) regions were amplified and sequenced for 137 individuals and 16 populations. The data matrix included 92 individuals of 10 populations of *Lycianthes dejecta* and 45 individuals of six populations of *L. peduncularis*. The haplotype network included 22 haplotypes. *Lycianthes dejecta* and *L. peduncularis* formed two haplogroups within each. Our results showed phylogeographic structure in both species. The highest genetic differentiation for *L. dejecta* was found in Baja California (BC). The populations of *L. peduncularis* isolated showed moderate levels of differentiation. The demographic history exposed expansion in the Chihuahuan Desert (CHD) populations of *L. dejecta*. In contrast, in *L. peduncularis*we found no evidence of population expansion or reduction. In both species, we observed contraction and expansion of its suitable climatic conditions. Orography and Pleistocene glacial cycles shaped the diversity and genetic structure of *Lycianthes dejecta* and *L. peduncularis* in the CHD. The evidence suggested that the BC population should be considered as an independent lineage. Transmexican Volcanic Belt (TVB) played a filter role in both species.

Introduction

Expansion and isolation patterns during the glaciations cause genetic differentiation, local adaptation, demographic changes and distribution shifts (Loera et al. 2017; Martínez de León et al. 2022; Gutiérrez-Ortega et al. 2023). These patterns have promoted the diversification of the plant linages in the Mexican Transition Zone (MTZ) and in the Chihuahuan Desert (CHD; Hernández-Hernández et al. 2014; Gutiérrez-Ortega et al. 2018; Vásquez-Cruz et al. 2020). Understanding and describing these processes provides valuable information on how genetic variation and diversification of lineages have arisen.

The aridification of North America started after the origin and development of the Rocky Mountains (RM) and the Sierra Madre Occidental (SMOc), 15 Ma during the middle Miocene (Wilson and Pitts 2010; Graham 2011). In Mexico, xerophilous vegetation occupy 536,713 km^2 or 27.46% of its territory (Ricker et al. 2022). However, the community is discontinuous, and they are divided into three biogeographic provinces: the Baja Californian Desert (BC), the CHD and the Sonoran Desert (SD, Morrone et al. 2019). Further, aridity has promoted diversity in Mexico (Hernández-Hernández et al. 2014; Gutiérrez-Ortea et al. 2018). Phylogeographical evidence suggests that the Pleistocene refugia and vicariance events are important for the evolutionary history of the xerophytic lineages (Morrone et al. 2022). The climatic changes during the Pleistocene affected their distribution, expanding and contracting the populations (Loera et al. 2017; Scheinvar et al. 2017; Contreras-Negrete et al. 2021). Also, geographic barriers isolated populations and affected their genetic diversity and structure (O'Connell et al 2016; Provost et al. 2021; Romero-Soler et al. 2021).

The CHD is the youngest, largest, and most biodiverse desert in North America (Riddle and Hafner 2006; Zavala-Hurtado and Jiménez 2020). It ranges from the southwestern United States of America to Central Mexico and it is surrounded by the Transmexican Volcanic Belt (TVB), the SMOc, the Sierra Madre Oriental (SMOr) and the RM (Morrone 2019). Geological and climatic events of the Miocene-Pliocene and Pleistocene promoted the biodiversity of the region (Scheinvar et al. 2020; Sosa et al. 2020). The CHD is recognized as a biogeographic province and is divided in two subprovinces: Chihuahuan (CH) and Mexican Plateau (MP). Further, each subprovince includes districts. Trans-Pecos and Mapimian districts belong to CH and Mexican Southern Arid (MSA), Salada and Tehucán-Cuicatlán Valley (TCV) districts are included in MP. These divisions are supported by endemics elements and the genetic structure of several species (Vázquez-Cruz and Sosa 2016; Scheinvar et al. 2017; Díaz-Cárdenas et al. 2019; Morrone et al 2022).

The TCV is the southernmost portion of the CHD and it is included in the MP (Morrone et al. 2022). The valley is isolated from the rest of the CHD by the TVB. The formation of the TVB started with Cenozoic geodynamics in south-central Mexico (Dávalos-Álvarez et al. 2007; Ferrari et al. 2012). However, on the Neogene the tectonic activity gave the current its configuration (Medina-Sánchez et al. 2020). Finally, the formation of TCV and the late Pleistocene climate changes configured the biotic composition of the area (Valiente-Banuet et al. 2000). The lineages in the valley resulted from vicariance and dispersal processes (Vásquez-Cruz and Sosa 2020). Today, the valley represents a hotspot of plant diversity and endemism, it contains between 10 and 11.4% of the Mexican flora and around 2684 species are endemic (Dávila et al. 2002; Sosa and De Nova 2012). The combination of isolation and the heterogeneity environmental promoted the evolution of the flora in the TCV (Soto-Trejo et al. 2024).

The Baja California Peninsula situated in northwestern Mexico and is recognized as a biogeographic province with eight districts (Morrone 2021). Most of the peninsula is covered by xerophilous scrubs and the high mountains had dry forest, oak forest, and pine

forest (Rzedowski 2006). Also, the province is a hotspot for plant richness and endemism (Riemann and Ezcurra 2005, 2007). Its formation started on 12 Ma and the drift of the Baja California microplate began 6 Ma (Umhoefer et al. 2020). The biotic composition of the peninsula resulted from both geological events during the last 5 Ma and the climate Pleistocene changes occurred over the past 2.5 Ma (Dolby et al. 2015). The BC drift promoted vicariant events in plants (Riddle et al. 2000). Likewise, dispersal events through glacial cycles occurred after it reached its current position, 3 Ma (Breslin et al. 2022).

Lycianthes series *Meizonodontae* Bitter comprise eight species and two varieties [*Lycianthes acapulcensis* (Baill.) D'Arcy, *L. ciliolata* (M.Martens & Galeotti) Bitter, *L. dejecta* (Fernald) Bitter, *L. hintonii* E.Dean, *L. moziniana* var. *margaretiana* E.Dean, *L. moziniana* (Dunal) Bitter var. *moziniana, L. moziniana* var. *oaxacana* E.Dean, *L. peduncularis* (Schltdl.) Bitter, *L. starbuckii* E.Dean and *L. rzedowskii* E.Dean]. The series is characterized by geophytic life form and developmental sympodial units with one or two leaves and a solitary flower (Dean 2004). Also, the group is monophyletic and is composed of three clades (Särkinen et al. 2013; Anguiano-Constante 2025). Its distribution goes from Mexico to Costa Rica. All taxa inhabit Mexico and occur along the pine-oak, tropical dry forest and xerophilous shrub (Anguiano et al. 2018). *Lycianthes dejecta* and *L. peduncularis* are sister species and represent the sister group of the remaining species which form the series (Anguiano-Constante 2025).

Lycianthes dejecta and *L. peduncularis* are endemic of Mexico and inhabit in xerophilous shrub (Anguiano et al. 2018). Both species are easy to distinguish from the rest of the series. *Lycianthes dejecta* is an erect to decumbent herb with a thick and long root. It is distinguished by its multi-angulate-dendritic trichomes, reniform leaf, solitary flower, poricidal anthers, enlarged calyces and ovoid to conic green fruit with purple to black stripes (Dean 2004; Fig. 1A-E). It is common along the CHD, the SMOr, the SMS, and the TVB, with isolated populations in BC and TCV (Anguiano et al. 2021; Dean et al. 2020). In contrast, *L. peduncularis* is a prostrated herb and has a thick and long root. Likewise, it is distinguished by its simple trichomes, spathulate leaf, solitary flower, poricidal anthers, small calyces, and round green fruit with maroon to black stripes (Dean 2004; Fig. 1F-J). It is distributed in the CHD on the MSA and TCV. Its distribution is dissected by the TVB (Anguiano et al. 2021; Dean et al. 2021). Both are pollinated by bees and seed dispersal is probably mediated by birds or mammals (Dean 2004; Albuquerque et al. 2006).

The evolutionary history of the *Lycianthes* series *Meizonodontae* is associated with the orogeny and Pleistocene climate changes in Mexico. It has been suggested that the MTZ embodies a diversification scenario for *L. moziniana* (Anguiano et al. 2021a, 2023). Also, the speciation and effects of geological and climatic events in the CHD has been documented before (Scheinvar et al. 2020). In the province, incipient processes have been observed where two populations are in transition (Angulo et al. 2014; Martínez de Leon et al. 2022). On the other extreme, the process that generates the distinct groups that we ultimately recognize as species occurred in the CHD (De-Nova et al. 2020).

Here we focused on *Lycianthes dejecta* and *L. peduncularis* clade. Both species are endemics of Mexico and mainly distributed on the CHD with isolated population in the BC and TCV. We hypothesized that *L. dejecta* and *L. peduncularis* have accumulated genetic variation and structure between populations at each side of the TVB and the one population of *L. dejecta* that is isolated in BC. Also, we anticipated that the variation is due to the climatic events of the Pleistocene. The objective of this work was to analyze the phylogeographic structure across the populations in both species. Likewise, we evaluated the demographic history and paleodistribution to determine the causes of the genetic variation. Our results will show how genetic variation in both species is. Also, we will propose in what way the isolated populations should be treated. Finally, we will contribute to understanding the process that promotes the diversification in the series.

Materials and methods

Plant material and DNA isolation, amplification, and sequencing

Leaf tissue samples were collected from 137 individuals from 16 populations. The samples correspond to 92 individuals of 10 populations of *Lycianthes dejecta* and 45 individuals of six populations of *L. peduncularis* (Table 1; Online Resource 1). The sampling represents the whole distribution of both species. In addition, the population were selected using the biogeographic provinces of Mexico (Morrone et al. 2019). Also, emphasis was placed on collecting isolated populations and populations that occur in different subprovinces and districts proposed for the CHD (Morrone et al. 2022). Each population has an herbarium specimen voucher deposited in the IBUG and MEXU (codes according to Thiers 2022).

Table 1

Localities, samples and diversity index of *Lycianthes dejecta* and *L. peduncularis*. Abbreviations: Hd, haplotype diversity; N, number of samples; π, nucleotide diversity; BC, Baja California; CHD, Chihuahuan Desert; MSA, Mexican Southern Arid; OH, Oaxacan Highlands; S, Saladan; SL, Sierra de la Laguna; SMS, Sierra Madre del Sur; TCV, Tehuacán-Cuicatlán Valley; TVB, Transmexican Volcanic Belt.

Taxa	Location	Code	Geographical coordinates	Sample	Provice	Distric	*N*	Hd	π	Haplotypes
Lycianthes dejecta	La Paz, Baja California Sur	BC	23° 42'9.88"N 109° 59' 8.86"W	MAC et al. 900	BC	SL	10	0.6 (SD ± 0.131)	0.0004 (SD ± 0.00011)	H6, H7, H8
Lycianthes dejecta	Ojuelo, Jalisco	JAL	21° 48' 57.46"N 101° 48' 58.24"W	JPB 1118	CHD	MSA	10	0.467 (SD ± 0.132)	0.00028 (SD ± 0.00008)	H3, H11
Lycianthes dejecta	Zaragoza, Nuevo León	NL	23° 58' 13.05"N 99° 44' 32.12"W	MAC et al. 888	CHD	S	10	0.533 (SD ± 0.18)	0.00036 (SD ± 0.00014)	H2, H3, H4, H5
Lycianthes dejecta	Ezequiel Montes, Querétaro	QRO	20° 44' 48.06"N 99° 57' 0.17"W	MAC 896	CHD	MSA	7	0.667 (SD ± 0.16)	0.00046 (SD ± 0.00014)	H3, H9, H10
Lycianthes dejecta	Zaragoza, San Luis Potosí	SLP	22° 6' 3"N 100° 41' 40.5"W	MAC & GML 405	CHD	MSA	9	0	0	H1
Lycianthes dejecta	Calvillo, Aguascalientes	AGS	21° 58' 33.54"N 102° 39' 4.19"W	MAC et al. 980	CHD	MSA	8	0.733 (SD ± 0.12)	0.00055 (SD ± 0.00013)	H4
Lycianthes dejecta	Tepeapulco, Hidalgo	HGO	19° 48' 26.3"N 98° 31' 45.4"W	MAC et al. 985	TVB	--	11	0.327 (SD ± 0.153)	0.0002 (SD ± 0.0009)	H3, H11
Lycianthes dejecta	Tolcayuca, Hidalgo	HGO	19° 58' 30" N 98° 56' 38.61" W	MAC et al. 1040	TVB	--	9	0	0	H3
Lycianthes dejecta	Caltepec, Puebla	PUE	18° 21' 51.43" N 97° 26' 21.81" W	MAC et al. 1025	CDH	TCV	12	0.167 (SD ± 0.134)	0.0001 (SD ± 0.00008)	H3, H15
Lycianthes dejecta	Súchil, Durango	DGO	23° 39' 50.21" N 103° 56' 53.55" W	MAC et al. 1010	CDH	S	4	0.667 (SD ± 0.204)	0.0004 (SD ± 0.00012)	H3, H5
Lycianthes peduncularis	Vizarron, Queretaro	QRO	20° 47' 25.4"N 99 43' 23.6"W	DSC & AP 881	CHD	MSA	7	0.81 (SD ± 0.130)	0.00169 (SD ± 0.00041)	H17, H18, H19, H20
Lycianthes peduncularis	Tehuacan, Puebla	TEH	18° 21' 51"N 97° 26' 21.8"W	MAC et al. 342	CHD	TCV	10	0	0	H16
Lycianthes peduncularis	Mitla, Oaxaca	MITL	16° 55' 42.6"N 96° 21' 26.2"W	GML & JLP 1069	SMS	OH	9	0.556 (SD ± 0.165)	0.00037 (SD ± 0.00013)	H16, H18, H22
Lycianthes peduncularis	Chalcatongo, Oaxaca	CHAL	17° 02' 38.2"N 97° 33' 49.4"W	JLP & GML 504	SMS	OH	4	0.5 (SD ± 0.265)	0.00031 (SD ± 0.00016)	H18, H21
Lycianthes peduncularis	Tlaxiaco, Oaxaca	TLAX	17° 15' 37.9"N 97° 39' 48.7"W	JLP & GML 505	SMS	OH	2	1 (SD ± 0.5)	0.00123 (SD ± 0.00061)	H18, H22
Lycianthes peduncularis	Puebla, Puebla	PUE	18° 56' 32.8"N 98° 07' 11.8"W	MAC et al. 1008	TVB	--	13	0.154 (SD ± 0.126)	0.00009 (SD ± 0.00008)	H16, H18, H22

Genomic DNA was isolated following the protocol of Doyle and Doyle (1987). Two cpDNA (*rpl*32-*trn*L and *ycf*1) regions were amplified and sequenced. Both regions have been shown to be variable and informative in Solanaceae (Särkinen and George 2013; Morris and Shaw 2018). An Applied Biosystems 2720 thermocycler (Applied Biosystems, Foster City, CA, USA) was used to execute the polymerase chain reactions (PCRs). The amplified PCR products were sequenced at the Laboratorio Nacional de Identificación y Caracterización Vegetal (LaniVeg), Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, Jalisco, Mexico. SEQUENCHER v.4.1.2 (Gene Codes Corporation, Ann Arbor, MI, USA) was used to edit the regions sequences and PhyDE to align them (Müller et al. 2005), using the MUSCLE method (Edgar 2004). The cpDNA fragments were concatenated with Mesquite 3.31 (Madison and Madison 2017). All sequences were deposited in GenBank (PP579424 – PP579515, PP579516 – PP579560, PP964639 - PP964730 and PP9664590 – PP964638).

Genetic diversity, genealogical relationships and phylogeographical structure

For each species, population and geographic group we calculated the genetic diversity, haplotype diversity (*Hd*), nucleotide diversity (π) and number of haplotypes with DNASP v.6 (Rozas et al. 2017). We built a haplotype network for visualizing the relationships among cpDNA (*rpl*32-*trn*L and *ycf*1) using statistical parsimony (Clement et al. 2000) in PopART v.1.7 (population analysis with reticulate trees; Leigh and Bryant 2015). The gaps were treated as single evolutionary events, and loops were resolved following Pfenninger and Posada (2002). Indices for singleton haplotypes (h_S) and total haplotypes (h_T) unordered and haplotypes frequency of the alleles singletons (v_S) and haplotypes frequency of the alleles totals (v_T) ordered were estimated using PERMUT v.1.0 (Pons and Petit 1996). The parameter N_{ST} estimates the genetic similarities among haplotypes, whereas G_{ST} calculates allelic frequencies. A significant value of N_{ST} indicates that the most similar haplotypes are also close to each other geographically. The significant difference between the N_{ST} and G_{ST} values was tested with 10,000 permutations.

Pairwise comparisons of fixation index values among populations (F_{ST}) were calculated using ARLEQUIN v.3.5.2.2 (Excoffier and Lischer 2010). Three analyses of molecular variance (AMOVAs) were performed (Excoffier et al. 1992) using ARLEQUIN v.3.5.2.2 (Excoffier and Lischer 2010). The molecular structure was determined based on the F_{ST} values. We defined four grouping criteria for *Lycianthes dejecta*: (1) a single group, to determine the amount of variation partitioned among and within population; (2) populations growing in mainland Mexico and population isolated in Baja California; (3) BC, CHD and TVB to determine the variation among biogeographic provinces and (4) to test if the TVB influenced the structure within *L. dejecta* (BC, CHD, TVB and TCV). For *L. peduncularis* we defined three grouping criteria: (1) a single group, to determine the amount of variation partitioned among and within population; (2) populations that are on the north side of the TVB and the south side (Mexican Southern Arid district (MSA) and TCV + Sierra Madre del Sur (SMS); Morrone 2017, Morrone et al. 2022); (3) populations grow in different biogeographic provinces (CHD, TVB and SMS) to determine the variation among biogeographic provinces. The Tamura and *Nei* model with 10,000 permutations was used to determine the significance of each AMOVA.

Alternatively, we implement an approach to define groups geographically homogeneous to identify genetic barriers. The most probable number of groups (*K*) was determined by repeatedly running the analysis of spatial analysis of molecular variance in SAMOVA v.1.0 (Dupanloup et al. 2002). Two to eight groups and the run with the highest F_{CT} value were chosen (Dupanloup et al., 2002). The values of *K* were explored with 100 simulations for each run. The parameters F_{CT} and F_{SC} maximize the genetic variance among groups and among populations within groups, respectively.

Demographic history

The historical population expansion of *Lycianthes dejecta* and *L. peduncularis* was analyzed with the neutrality tests Tajima´s D (*D*; Tajima 1989) and Fu´s (F_S; Fu 1997) to explore the population size variation under neutral mutations using 10,000 permutations in ARLEQUIN v.3.5.2.2 (Excoffier and Lischer 2010). The pairwise distribution differences under population expansion were examined in DNASP v.6 (Rozas et al. 2017). All tests were carried out at the level of species and population groups.

We estimated the nucleotide substitution models of each species based on the Akaike information criterion in JModelTest v2.1.10 (Darriba et al. 2012). In BEAST v2.6.6, we conducted a coalescent Bayesian Skyline Plot analysis to infer the changes in the effective population size (*Ne*) through the time for each species and population groups (Bouckaert et al. 2019). The analysis was executed with 100 million generations, sampling every 10,000 steps, and using a relaxed lognormal clock model. The mutation rate was 3×10^{-9}, based on molecular dating analyses in Solanaceae (Särkinen et al. 2013). Then, the results of each run were visualized in TRACER v1.7

(Rambaut et al. 2018) to corroborate the effective sample size (ESS > 200) and build the Bayesian Skyline plots (BSP, Drummond et al. 2005).

Geographical data

Geographical data of each species were obtained from 31 Herbaria (either in person or using digital images) ANSM, CFNL, CIIDIR, CIMI, DAV, F, GBH, GUADA, HCI, HGOM, HUAA, HUAP, HUAZ (not in index herbariorum, Herbario de la Universidad Autónoma de Zacatecas), IBUG, IEB, INEGI, MEXU, MO, NY, OAX, P, QMEX, QNCE, SERO, TEX, UCR, UNL, UNSIJ (not in index herbariorum, Universidad de la Sierra Juarez, Oaxaca), US, WIS, XAL and ZEA (codes according to Thiers 2023). Also, we included data of three electronic databases (Global Biodiversity Information Facility (GBIF, http://www.gbif.org), Missouri Botanical Garden (Tropicos, http://www.tropicos.org) and Southwest Environmental Information Network (SEINet, http://www.swbiodiversity.org) and the information in the studies by Anguiano et al. (2018, 2021), Dean (2004) and Dean et al. (2020).

We constructed a database for each species with the information contained in the label. The database for *Lycianthes dejecta* includes 125 and for *L. peduncularis* 104 records were incorporated. These databases were curated, first removing the duplicate, ambiguous and cultivated records. Then records were eliminated manually by the spatial autocorrelation of the distribution points projecting in a grid of 1 ×1 km in QGIS Las Palmas v.2.18.3 (QGIS Development Team 2017). We only conserved one point of each 1 ×1 km grid. Finally, the databases include 99 records of *L. dejecta* and 75 records of *L. peduncularis* (Online Resource 2).

Climatic data and paleodistribution

Climatic data for the Present (30 arc s), Middle Holocene (MH; 30 arc s) and LGM (2.5 arc min) layers were obtained from the WorldClim database, v.1.4 (Hijmans et al. 2005; http://www.worldclim.org). The Present, MH, and LGM were based on the CCSM4 (Community Climate System Model, v.4) models. The 19 layers of the LGM were resampled to 30 arc s in QGIS Las Palmas v.2.18.3 (QGIS Development Team 2017). The present layers were trimmed out to the accessible area (M) (Soberón and Peterson, 2005; Barve et al. 2011). The M was adjusted to the CHD province proposed by Morrone et al (2022) using the terrestrial ecoregion of the world (Olson et al. 2001) where the species inhabit plus a buffer of 10 km. All layers of the past (MH and LGM) were cut to the extent of Mexico. Using the present point of the species we extracted the values of the whole 19 climate variables. Then, to select the variables, the correlation of the variables was evaluated for each species with Pearson correlation using a 0.05 level of significance in the corrplot R package. After, we calculated the variance inflation factor for correlated variables and excluded the highly correlated variables using threshold of 0.9 in the usdm R package in RStudio version 1.3.1093 (RStudio Team 2020).

We constructed an ecological niche model (ENM) for each species. For *Lycianthes dejecta* we used 99 records and nine climatic layers (BIO3, BIO6, BIO7, BIO9, BIO12, BIO13, BIO14, BIO18 and BIO19) and for *L. peduncularis* we included 75 records and seven layers (BIO2, BIO3, BIO9, BIO15, BIO16, BIO18 and BIO19). Samples collected between 2010–2022 were used to validate the models of *L. dejecta* (20) and *L. peduncularis* (7). The ENM was projected onto past climatic conditions (LGM and MH) using MAXENT v.3.3.3K (Phillips et al. 2006). Twenty samples collected between 2010–2022 were used to validate the models. Each model was replicated ten times, and we applied maximum training sensitivity plus specificity as threshold rule. The rest of the parameters used were those of the basic configuration. Finally, the models were evaluated using under the curve values.

Results

Genetic diversity, genealogical relationships and phylogeographical structure

The aligned dataset included *rpl*32-*trn*L (658 bp) and *ycf*1 (1,011bp) totaled 1,669 bp. The polymorphic sites for *Lycianthes dejecta* matrix were 22. The haplotype diversity (*H*d) of *L. dejecta* was 0.688 (SD ± 0.051) and the nucleotide diversity (π) was 0.00177 (SD ± 0.00031). The polymorphic sites for the *L. peduncularis* matrix were eight. The *Hd* of *L. peduncularis* was 0.588 (SD ± 0.077) and π was 0.00096 (SD ± 0.00024).

The most parsimonious network illustrated the relationships between the 22 haplotypes. The two species were separated by 10 mutation steps and two unsampled haplotypes (Fig. 2). The network of *L. dejecta* contains 15 haplotypes distributed on two haplogroups (BC and CHD; Fig. 2). The group BC (*Hd* = 0.6 and π = 0.0004) includes three haplotypes (H6-H8) and corresponds to the population occurring in the BC province. In the CHD group (*Hd* = 0.612 and π = 0.00061) founded 12 haplotypes. These populations were

distributed in the CHD and TVB provinces. The H3 was the most frequent (50 individuals) haplotype of *L. dejecta* (54% of the individuals and 70% of the populations). BC and CHD groups were separated by 10 mutation steps and one haplotype unsampled (Fig. 2). *Lycianthes peduncularis* network includes seven haplotypes and was divided into two groups (MSA and TCV + SMS). The MSA (*Hd* = 0.8 and π = 0.000165) had three haplotypes (H17, H19 and H20). The TCV + SMS (*Hd* = 0.44 and π = 0.0031) included four haplotypes (H16, H18, H21 and H22). The H16 was the most frequent (28 individuals) haplotype of *L. peduncularis* (62% of the individuals and 50% of the populations). The two groups were separated by four mutation steps (Fig. 2).

Genetic diversity across all populations of *Lycianthes dejecta* (h_T = 0.662, se = 0.1413, v_T = 0.6686, se = 0.3775) was higher than the within population average value (h_S = 0.322, se = 0.0963, v_S = 0.086, se = 0.0282). *Lycianthes dejecta* showed population subdivision. The F_{ST} value (0.8619) indicated population structure (Table 2). Lastly, the permutation results were high and significantly suggests phylogeographical structure (N_{ST} = 0.874, se = 0.0657, G_{ST} = 0.514, se = 0.1226; P < 0.05). For *L. peduncularis* the genetic diversity across all populations (h_T = 0.773, se = 0.1117, v_T = 0.787, se = 0.3446) was higher than the within population average value (h_S = 0.488, se = 0.1545, v_S = 0.387 se = 0.18). The value of F_{ST} was 0. 6228 (Table 2). These values and the distribution of genetic diversity revealed population structure and subdivisions. The permutation results were high and significantly suggest phylogeographical structure (N_{ST} = 0.509, se = NC, G_{ST} = 0.369, se = 0.1247; P < 0.05).

Table 2
Results of the analysis of molecular variance (AMOVA) and the spatial analysis of molecular variance (SAMOVA) on *Lycianthes dejecta* and *L. peduncularis*. Abbreviations: BC, Baja California; CHD, Chihuahuan Desert; MSA, Mexican Southern Arid; SMS, Sierra Madre del Sur; TVB, Transmexican Volcanic Belt; TCV, Tehuacán-Cuicatlán Valley. $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

	d.f	Sum of squares	Variance	Percentage	Fixation indices
Lycianthes dejecta					
AMOVA					
No groups defined					
Among populations	8	116.522	1.43223 Va	86.91	Fst 0.861911***
Within populations	83	17.902	0.21569 Vb	13.09	
Total	91	134.424	1.64792		
Two groups (CHD and BC)					
Among groups	1	90.46	4.86112 Va	89.56	Fsc 0.61945***
Among populations within groups	7	26.061	0.3511 Vb	6.47	Fst 0.96026***
Within populations	83	17.902	0.21596 Vc	3.97	Fct 0.895558*
Total	64	202.523	6.44147		
Three groups (BC, CHD and TVB)					
Among populations	2	91.576	1.75683 Va	72.5	Fsc 0.67631***
Among populations within groups	6	24.946	0.45065 Vb	18.6	Fst 0.91099***
Within populations	83	17.902	0.21569 Vc	8.9	Fct 0.72501*
Total	91	134.424	2.42317		
Four groups (BC, CHD, TVB and TCV)					
Among populations	3	92.827	1.22211 Va	61.46	Fsc 0.7185***
Among populations within groups	5	23.694	0.55053 Vb	27.69	Fst 0.89152***
Within populations	83	17.902	0.21569 Vc	10.85	Fct 0.61464*
Total	91	134.424	1.98833		
SAMOVA					
Four groups					
Among groups	3	113.991	2.45555 Va	90.94	Fsc 0.1837***
Among populations within groups	5	2.531	0.02896 Vb	1.07	Fst 0.92012***
Within populations	83	17.902	0.21569 Vc	7.99	Fct 0.9094**
Total	91	134.424	2.7002		
Lycianthes peduncularis					
AMOVA					
No groups defined					
Among populations	5	21.975	0.56758 Va	62.29	Fst 0.62286***

	d.f	Sum of squares	Variance	Percentage	Fixation indices
Within populations	39	13.403	0.34367 Vb	37.71	
Total	44	35.378	0.91125		
Two groups (MSA and TCV + SMS)					
Among groups	1	17.487	1.38089 Va	75.26	Fsc 0.24271***
Among populations	4	4.488	0.11015 Vb	6	Fst 0.81268***
Within populations	39	13.403	0.34367 Vc	18.73	Fct 0.75265**
Total	44	35.378	1.83471		
Three groups (CHD, TVB and SMS)					
Among populations	2	18.009	0.53608 Va	50.92	Fsc 0.33487***
Among populations within populations	3	3.966	0.17303 Vb	16.44	Fst 0.67356***
Within populations	39	13.403	0.34367 Vc	32.64	Fct 0.5092**
Total	44	35.378	1.05278		
SAMOVA					
Three groups					
Among groups	2	20.930	1.13262 Va	76.69	Fsc 0.00163***
Among populations within groups	3	1.044	0.00056 Vb	0.04	Fst 0.76729***
Within populations	39	13.403	0.34367 Vc	23.27	Fct 0.76691**
Total	44	35.378	1.47685		

When all populations of *Lycianthes dejecta* were considered as a group, the genetic variation among populations was 86.91%. The remaining 13.09% of variation was found within populations (Table 2). The highest value of F_{ST} (0.96), generated by AMOVA, grouped populations into BC and CHD groups. The SAMOVA recorded the highest value of F_{CT} (0.909) with $K = 4$ (NL + QRO + JAL + HGO + PUE + DGO, AGS, SLP and BC; Table 1, 2). All paired F_{ST} values were significant. The BC relative to TCV and TVB had the greatest differentiation (Table 3). *Lycianthes peduncularis* had 62.29% genetic variation among populations and 37.71% within populations. The highest value of F_{ST} by AMOVA was obtained when grouped MSA and TCV + SMS (0.812) and of F_{CT} (0.767) by SAMOVA was obtained with $K = 3$ (QRO, CHAL, TEH + TLAX + MITL + PUE; Table 1, 2). All paired F_{ST} values were significant between MSA and TCV + SMS groups (Table 3).

Table 3
Pairwise comparisons of F_{ST} values among groups of *Lycianthes dejecta* (BC, CHD, TVB and TCV) and *L. peduncularis* (TCV + SMS and MSA). Abbreviations: BC, Baja California; CHD, Chihuahuan Desert; MSA, Mexican Southern Arid; SMS, Sierra Madre del Sur; TVB, Transmexican Volcanic Belt; TCV, Tehuacán-Cuicatlán Valley. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Lycianthes dejecta				
Groups	BC	CHD	TVB	TCV
BC	--			
CHD	0.8832***	--		
TVB	0.9671***	0.0622**	--	
TCV	0.9625***	0.051**	0.0261**	--
Lycianthes peduncularis				
Groups	TCV + SMS	MSA		
TCV + SMS	--			
MSA	0.7763***	--		

Demographic history

The D_T and F_S index for *Lycianthes dejecta* were negative and not significant (Table 4). The pairwise distribution differences showed bimodal distribution (Fig. 3a). For the BC population the D_T, and F_S, were negative and not significant. The CHD populations have negative values of D_T and F_S, but the first was not significant and the second was significant (Table 4). For BC and CHD populations, the pairwise distribution differences showed unimodal distribution (Online Resource 3). At the species level and CHD population, the BSP inferred an increase of *Ne* on the last 20,000 BYP (Fig. 3b; Online Resource 3). In contrast, the BSP of BC showed stability on the last 3,000 BYP (Fig. 3c).

Table 4
Summary statistics of demographic analysis by two groups of *Lycianthes dejecta* (BC and CHD) and *L. peduncularis* (TCV + SMS and MSA). Abbreviations: N, number of individuals; Nh, number of haplotypes; Hd, haplotype diversity; π, nucleotide diversity; D_T, Tajima's D; F_S, Fu's; BC, Baja California; CHD, Chihuahuan Desert; MSA, Mexican Southern Arid and SMS Sierra Madre del Sur; TVB, Transmexican Volcanic Belt; TCV, Tehuacán-Cuicatlán Valley. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

Lycianthes dejecta			
Parameters	BC	CHD	Total
N	10	82	92
Nh	3	12	15
Hd	0.711	0.612	0.688
π	0.0004	0.00061	0.0017
D_T (*P*)	-0.183 (0.361)	-1.307 (0.078)	-0.936 (0.156)
F_s (*P*)	-0.271 (0.321)	-6.772^{**} (0.0014)	-2.338 (0.215)
Lycianthes peduncularis			
Parameters	TCV + SMS	MSA	Total
N	38	7	45
Nh	4	3	7
Hd	0.44	0.81	0.588
π	0.0031	0.00169	0.00096
D_T (*P*)	-0.602 (0.295)	0.649 (0.693)	-0.3371 (0.34)
F_S (*P*)	-0.94 (0.218)	0.494 (0.601)	-0.536 (0.438)

The D_T and F_S index for *Lycianthes peduncularis* were negative and not significant (Table 4). The pairwise distribution differences showed bimodal distribution (Fig. 4a). TCV + SMS had values of D_T and *FS* that were negative and not significant. The MSA showed positive and no significant value of D_T and F_S (Table 4). For the two groups the pairwise distribution differences showed unimodal distribution (Online Resource 4). Based on the BSP the *Ne* increase on the last 20,000 YBP in *L. peduncularis* (Fig. 4b). The MSA and TCV + SMS populations had similar trends of stability at 20,000 and 3,000 YBP, respectively (Online Resource 3).

Paleodistribution

Expansion and contractions were observed over the climatic conditions during the last 20,000 YBP for the ENM of *Lycianthes dejecta* (Fig. 5a-c). During LGM the estimated condition was smaller than the other scenarios (Fig. 5c). On the MH an expansion occurred for the optimum condition estimated (Fig. 5b). Finally, at the present the estimation showed a contraction (Fig. 5a). Interestingly, at the level of populations climatic condition during MH suggested an expansion in the BC and CHD. In contrast, we detected a contraction on the TVC and TVB and then an expansion. *Lycianthes peduncularis* ENM showed expansion of the climatic conditions over during the last 20,000 YBP (Fig. 5d-f). For the populations the pattern was similar, expansion in the TVC + SMS and expansion and a contraction on the MSA in the present scenario (Fig. 5e-f). Also, we observed an expansion in the TVB (Fig. 5d).

Discussion

Diversification of Solanaceae Juss. is dated around 66 – 56 Ma and has its actual distribution since 56-33.9 Ma (Särkinen et al. 2013; Deana et al. 2023). *Capsicum* L., *Lycianthes, Physalis* L. and *Solanum* L. reached their modern distribution on the Neogene (23 – 2.6 Ma; Deana et al. 2023). Their diversification coincides and could be promoted by the orogenic and climatic events of the last 80 Ma on the Anden region and MTZ (Mastretta-Yanes et al. 2015; Perez-Escobar et al. 2022). Also, empirical data suggests that species richness

and endemism of the four genera are concentrated in America and especially in the mountains (Anguiano-Constante et al. 2021; Murillo-Pérez et al. 2022; Barboza et al. 2022). *Lycianthes* series *Meizonodontae* diverged around 2.5 Ma and the clade of *L. dejecta* and *L. peduncularis* formed 1-0.5 Ma (Särkinen et al. 2013; Anguiano-Constante 2025). Recently, biogeographic analyses suggested that the complex history of MTZ promoted the diversification of the group (Anguiano-Constante et al. 2018, 2021a, 2025). *Lycianthes dejecta* and *L. peduncularis* are partially restricted to the CHD and inhabit the xerophilous scrubs.

The genetic diversity of *Lycianthes dejecta* was higher (*Hd* = 0.688) than *L. peduncularis* (*Hd* = 0.588). We observed the same pattern with the values of π between both species (0.00177 and 0.00096, respectively). Genetic diversity depends on the evolutionary history of the populations, the reproductive system and environmental heterogeneity (Booy et al. 2000). The value of *Hd* in *L. dejecta* could be explained by the connection of their population in mainland Mexico and the isolation of the BC population. Also, the *Hd* in *L. peduncularis* suggested genetic exchange between populations. High values of both species implied a historical connection of its populations. Low values of π are evidence of a rapid speciation or recent colonization (Zink et al. 2002). Except for the BC population, we could interpretate that the populations in both species has recently diverged. Similar levels of genetic diversity were found in other perennial plants that inhabit in the CHD, for example: *Hunnemannia fumariifolia* Sweet (Sosa et al. 2009), *Berberis trifoliolata* Moric. (Angulo et al. 2017), *Agave lechuguilla* Torr. (Sheinvar et al. 2017) and *Ephedra compacta* Rose (Loera et al. 2017).

The genetic diversity in *Lycianthes dejecta* and *L. peduncularis* was found among the populations 86.91 and 62.29%, respectively. The AMOVA and SAMOVA result suggested a differentiation of the populations (Table 2). Evidence indicates that populations distributed in BC and MSA are distinct genetic groups from *L. dejecta* and *L. peduncularis*, respectively. Likewise, both species showed phylogeographic structure based on G_{ST} and N_{ST} values. In both species the values of N_{ST} were greater than G_{ST} and the permutation test was significant [*L. dejecta* (N_{ST} 0.874 > G_{ST} 0.514); *L. peduncularis* (N_{ST} 0.509 > G_{ST} 0.369)]. These results are supported by the complexity of geological and climatic events that occurred in the CHD. As well, the TVB formation since 12 Ma, the drift of the BC (5 Ma) and the Last Glacial Maximum (20,000 YBP) played an important role on the structuring the genetic variation and diversification on several lineages (Scheinvar et al. 2020; Breslin et al. 2022; Arenas et al. 2023).

Haplotype network of those sister species was constituted with four groups and 22 haplotypes (Fig. 2). Two principal groups include the haplotypes distributed into *Lycianthes dejecta* (H1-H5 and H9-H15) and *L. peduncularis* (H16, H18, H21 and H22). Both species are divided by 10 mutation steps and two haplotypes unsampled. A third group (H6, H7 and H8) is separated by 10 mutation steps and one haplotype unsampled with respect to *L. dejecta* and by 12 mutation steps and two haplotypes unsampled with respect to *L. peduncularis*. Remarkably, the separation of BC group (H6, H7 and H8) is comparable with the distance between *L. dejecta* and *L. peduncularis*. The last group (H17, H19 and H20) had a relationship and shared haplotypes with *L. peduncularis*. The network reveals genetics structure in both species and the presence of a different linage in *L. dejecta*.

Phylogeographic structure of Lycianthes dejecta

The analysis of *Lycianthes dejecta* identified differences between BC and CHD populations. The F_{ST} value (0.861) suggested that *L. dejecta* is structuring. The BC population is the most different from other populations (Table 3). In contrast, *L. dejecta* showed minimum genetic variation across the CHD (Table 3). The BC population obtained high values of *Hd* and π (Table 4). The evidence could be interpreted as that there was no genetic flow between mainland and BC populations. Haplotypes H6, H7 and H8 correspond to the population that inhabits the Sierra La Laguna, Baja California Sur (Fig. 2b). The first populations of the Sierra La Laguna were collected in 1993 (*J.L. León de la Luz 6962*, HCIB) and identified as *Solanum dejectum* Fernald. It was later included in the checklist of the vascular plants of Baja California as *L. dejecta* (Rebman et al. 2016). Also, in the taxonomic treatment of *Lycianthes* of Mexico and Guatemala the populations were added in the description of *L. dejecta* (Dean et al. 2020). Moreover, the type collection of *L. dejecta* (*E. Palmer 347*, GH) was collected near the city of Durango. Remarkably, The CHD population must be treated as *L. dejecta*. Contrary to, the BC population is differentiated from mainland populations and should not be considered as *L. dejecta*.

The Sierra La Laguna is a district of the BC and exhibits high levels of endemism (González-Abraham et al. 2010; Morrone et al. 2021). Levels of endemism in the BC are the results of environmental heterogeneity and Pleistocene glaciation (Riemann and Ezcurra 2007). The BC population could be a linage isolated by the historical peninsula drift event (6-2.5 Ma; Umhoefer et al. 2020), before the divergence of *L. dejecta* and *L. peduncularis* clade. In addition, BC population differs from *L. dejecta* by its decumbent stem growth, indument with simple trichomes or glabrous, reflexed calyx appendages, and ovoid and light green fruit. Plant species such as *Fouquieria* DC., *Mammillaria* Hawk., *Milla* clade and *Quercus* section *Virentes* Loudon show a pattern of dispersal or vicariance resulting of the separation of the BC and the Glacial cycles of the Pleistocene (Gándara et al. 2014; Cavender-Bares et al. 2015; Soto-Trejo et al. 2022; Chincoya et al. 2023).

Neutrality tests in CHD population show signs of recent population expansion according to F_S values (Table 4). Contrary to the BC population there is no statistically significant evidence of expansion or selection (Table 4). Interestingly, the pairwise distribution differences of *L. dejecta* were bimodal, reflecting the haplotypes network (Figs. 2, 3a). The first curve indicated the CHD group and the second separated by 10 different mutation steps represented the BC group (Fig. 3a). Likewise, the bimodal distribution suggested a historical event of divergence. The BSP showed an increase in *Ne* since 20,000 BYP in *Lycianthes dejecta*. In contrast, the BC population showed stability in the last 3,000 BYP (Fig. 3c). Demographics show that BC and mainland populations have been trapped up in different scenarios.

The ENM showed expansion and contraction of favorable climatic condition for *Lycianthes dejecta* across the time within the CHD (Fig. 5a-c). This would explain the *Hd* and F_{ST} values across the CHD. The expansion caused contact among the populations and the contractions promoted its isolation. Together, modeled the genetic variation in the populations of the CHD. The population of TCV is the southernmost and is divided by the TVB from the population of CHD. The ENM for the LMG showed that the climatic conditions were present in the southernmost part. However, during the MH they were not favorable (Fig. 5b-c). The answer of this scenario is the lowest level of *Hd* and π supporting a recent recolonization (Table 1). The other disjunction population is BC. The climatic conditions demonstrated that the BC population has been separated by more than 20,000 YBP (Fig. 5a-c). This assertion is supported by the haplotype network and genetic differences (Fig. 2; Tables 3, 4). Additionally, the favorable climatic conditions of the BC population showed an expansion in the last 6,000 YBP on the MH (Fig. 5b). However, based on the demographic inferences, this population is in balance. The contrasting scenarios and the high values of *Hd* and π could demonstrate that the population is evolving separately (Fig. 3; Table 1).

Phylogeographic structure of Lycianthes peduncularis

The distribution of *Lycianthes peduncularis* is along the CHD. However, the TVB causes a discontinuity in its distributions. *Lycianthes peduncularis* showed differences between MSA (H16, H18 and H21-H22) and TCV + SMS (H17, H19-H20) populations. The F_{ST} value (0.622) suggested intermedial connection among its population. Also, the populations divided by the TVB showed genetic differences and are separated by four mutational steps (Fig. 2; Table 3). The genetic structure of *L. peduncularis* is congruent with the natural division of the MP subprovince in CHD (Morrone et al. 2022). Other plants showed similar structure in the subprovinces (Gándara and Sosa 2014; Vásquez-Cruz and Sosa 2016; Sosa et al. 2019). Moreover, genetic diversity was highest (*Hd* 0.81 and π 0.00169) on the MSA population than the other populations (Tables 1, 4). High values of genetic diversity were found in areas that had stable climatic conditions during glacial periods and recent populations that colonized after the glacial period had lowest values (Loera et al. 2017). This suggests that the genetic structure found in *L. peduncularis* resulted by physical and climatic isolation.

The demographic results of *Lycianthes peduncularis* and its groups show no significant evidence of expansion, population reduction of natural selection. However, the D_T and F_S values for the specie level and TCV + SMS populations were negative and could suggest a slight tendency towards population expansion (Table 4). In contrast, the positive values in MSA population could inferred a deficiency of alleles due to a bottleneck (Table 4). The bimodal distribution in the mismatch distribution is congruent with the haplotype network. This finding justifies a historical separation event. Interestingly, the MSA shows similar bimodal distribution this could be due to the bottleneck. Also, the BSP suggests that *L. peduncularis* is expanding from 20,000 YBP (Fig. 4b). In contrast, the MSA and TCV + SMS populations had stability (Online Resource 4). Finally, *L. peduncularis* and its groups may be in demographic equilibrium.

The ENM of *L. peduncularis* showed a partial connection of the favorable climatic conditions across the TVB in the LGM. Following a disjunction and scenarios of expansion. The genetic differences between MSA and TCV + SMS populations confirm the historical separation by TVB (Fig. 2; Tables 3). Afterwards, the climatic conditions on the MH contracted in the MSA population. In contrast, the TCV + SMS are involved in expansion. The present condition suggests a connection between both populations. First, the high value of genetic diversity in the MSA population indicates refugia (Tables 1, 4). Second, our results showed that the H18 was in both populations this demonstrated genetic flow between populations (Fig. 2). Third, the mismatch distribution could imply the recent connection and the low genetic diversity of the intermediate population in Puebla, Puebla (TVB) propose recent colonization (Table 1; Online Resource 4). Remarkably the TVB role as a filter during Pleistocene oscillations for *L. peduncularis* populations.

Conclusion

Orography and climatic events around Mexico contributed to the diversity and genetic structure of *Lycianthes dejecta* and *L. peduncularis*. Different levels of genetic differentiation were observed. The BC population is most differentiated. We propose that the BC population is evolving separately and should be considered as an independent lineage. Also, the origin of the BC lineage could be

before the divergence of *L. dejecta* and *L. peduncularis* clade. In contrast, the populations of both species in mainland Mexico show moderate genetic variation. Moreover, the genetic diversity and demographic history indicates that the populations of both species diverged recently. Our paleodistribution results suggest that the variation and structure of *L. dejecta* and *L. peduncularis* is due to the Pleistocene glacial cycles and the presence of the TVB. First, the climatic oscillation promoted contraction and expansion in the populations of mainland Mexico. Second, the TVB acts as a filter and creates differences between the populations that are on one side and the other.

Declarations

Acknowledgments

We are grateful to the curators of the herbaria ANSM, CFNL, CICY, CIIDIR, CIMI, CIQRO, DAV, F, GBH, GUADA, HCIB, HGOM, HUAA, HUAP, HUAZ (not in index herbariorum, Herbario de la Universidad Autónoma de Zacatecas), IEB, INEGI, MEXU, OAX, QMEX, SERBO, UNL, UNSIJ (not in index herbariorum, Universidad de la Sierra Juárez, Oaxaca), XAL and ZEA. Likewise, we thank the staff of F, MO, NY, P, TEX, UC, UCR, US, WIS, Tropicos, GBIF, SEINET for access to specimen images and data. Special thanks to Jon Rebman, curator of the herbarium of the San Diego Natural History Museum (SD), José Luis León De La Luz and Reymundo Domínguez Cadena curator and assistant curator of the HCIB. Juan Ortiz Brunel, Luis Manuel Cardona Cruz, Jorge David López Pérez, María de la Luz Pérez López and Guadalupe Munguía Lino assisted during fieldwork.

Author contributions M. A. A-C, conceived the idea, collected the samples, carried out the lab work and executed the analysis. D. S-C collected the samples and assisted in the analysis. E. R-S collected the samples and assisted in the analysis. A. R, contributed to the conception and development of the study. All wrote and edited the draft and approved the final version.

Funding This research was supported by the Secretaria de Ciencias, Humanidades, Tecnología e Inovación (SECIHTI) with a scholarship (855486/2020-000026-02NACF-19054) to the first author. This study was also supported by the Laboratorio Nacional de Identificación y Caracterización Vegetal (LaniVeg) and the Universidad de Guadalajara which provided economic support for visiting herbaria and carrying out field work.

Data availability The datasets presented in this study can be found in online repositories. The accession numbers of the DNA sequence on NCBI (https://www.ncbi.nlm.nih.gov/) are as follows PP579424 – PP579515, PP579516 – PP579560, PP964639 - PP964730 and PP9664590 – PP964638.

Conflict of interests: The authors declare no competing interests.

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Figures

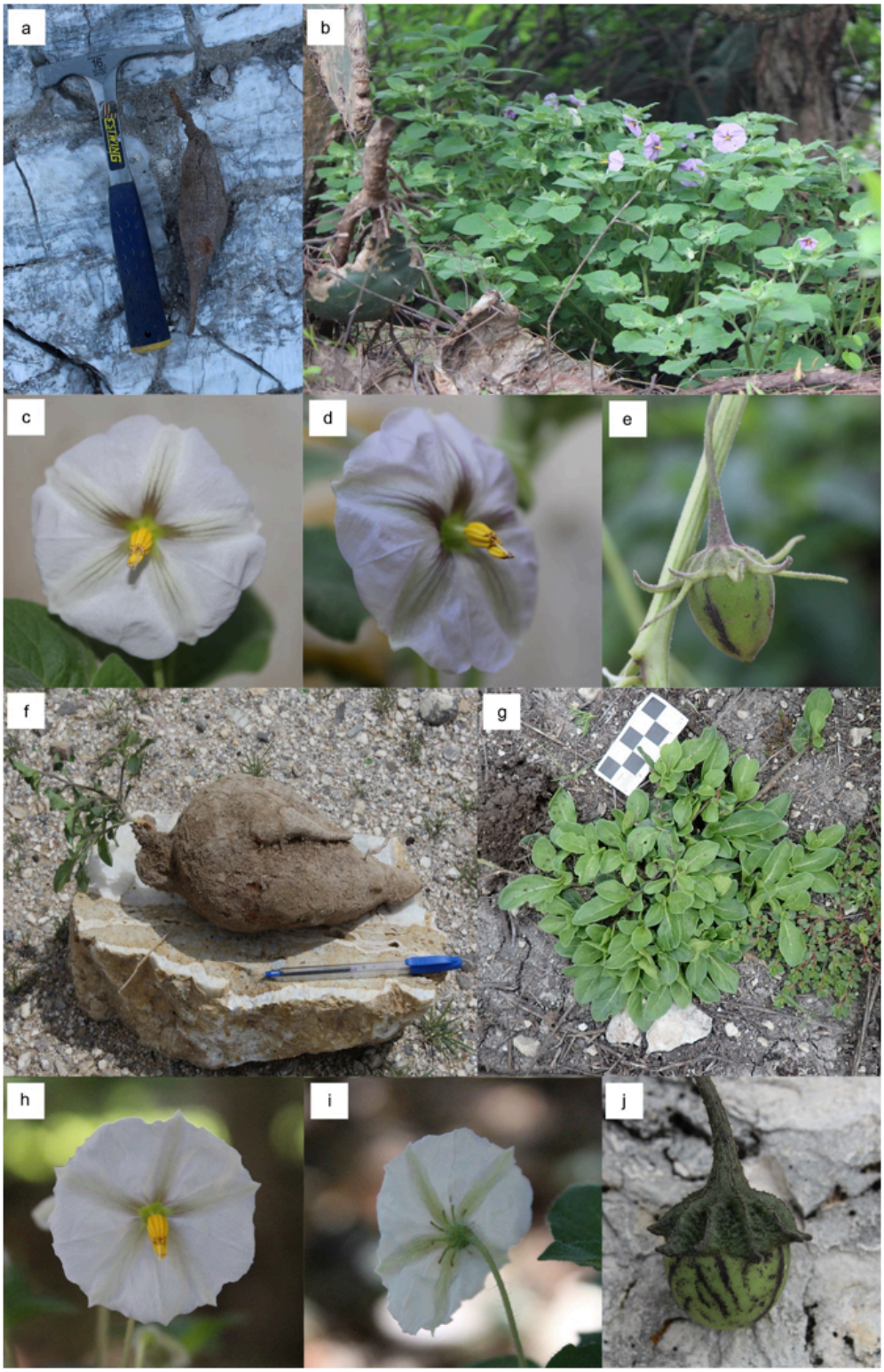

Figure 1

Lycianthes dejecta (a-e) and *L. peduncularis* (f-j). (a) Root. (b) Herbaceous habit. (c) Corolla front view. (d) Corolla lateral view (e) Fruit. (f) Root. (g) Prostrate habit. (h) Corolla front view. (i) Corolla back view. (j) Fruit. Photographs by Marco Antonio Anguiano Constante, except (b) by José Belem Hernández Díaz and (g) by Daniel Sánchez.

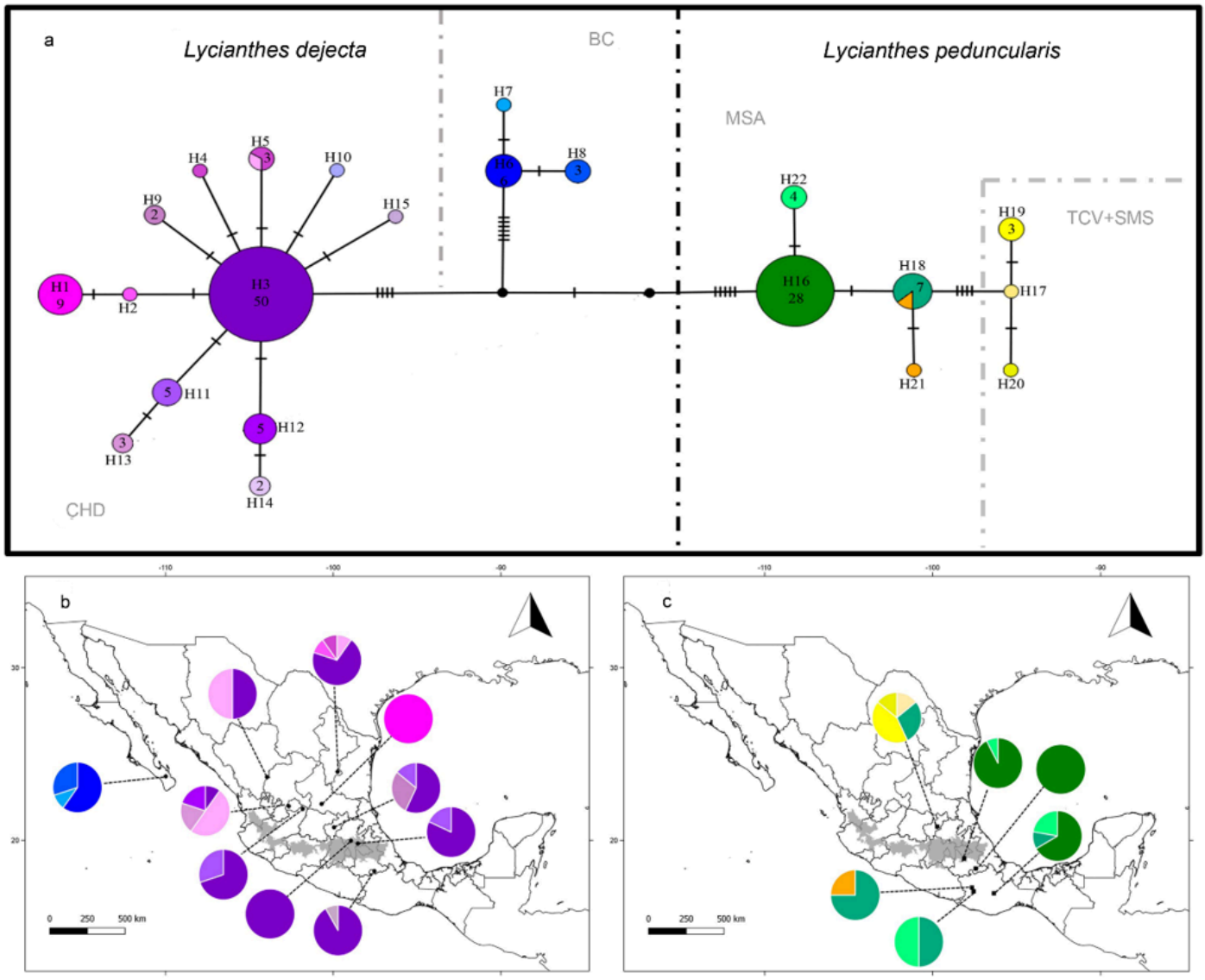

Figure 2

Distribution and relationship of 22 haplotypes found in *Lycianthes dejecta* and *L.peduncularis*. (a) Haplotype network. Black dots represent unsampled haplotypes and black dash represent the mutation steps. The frequency of each haplotype is represented by the size and number of the circle. Dotted lines delimit the species and BC group. (b) Distribution map of haplotypes in *L. dejecta*. (c) Distribution map of haplotypes in *L. peduncularis*. The gray polygon shows the TVB (Morrone et al. 2017). Sampled individuals and haplotypes by population are shown in Table 1.

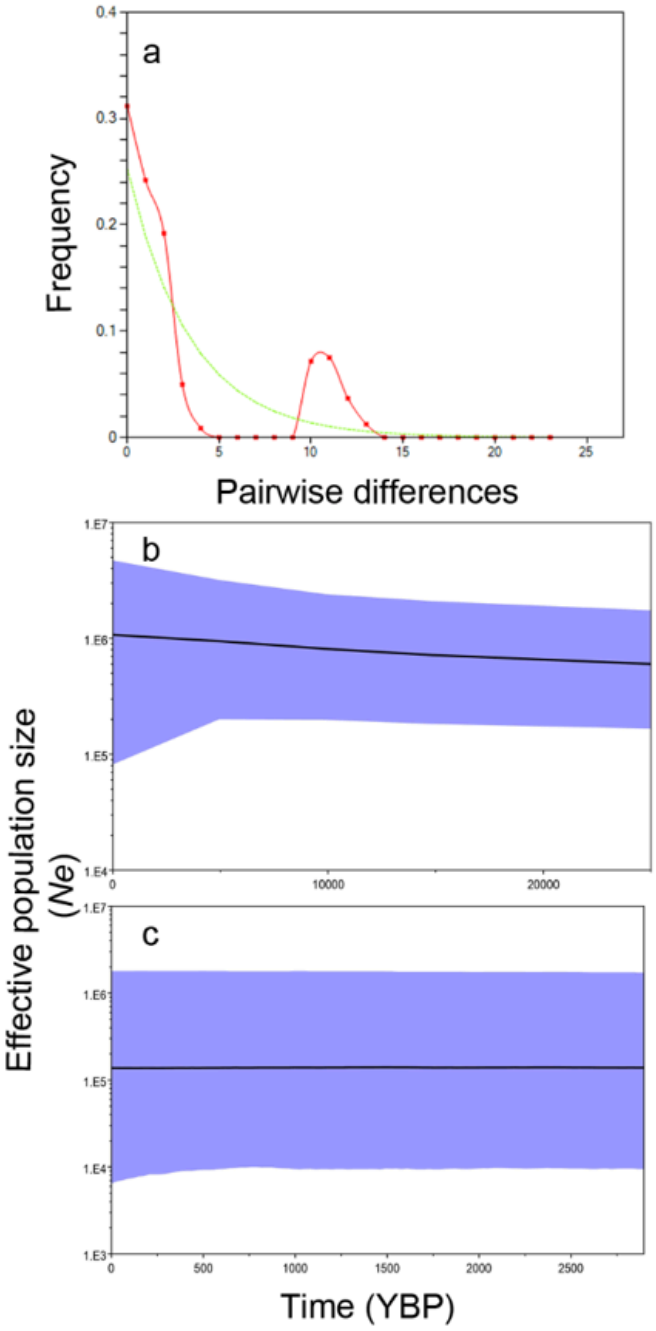

Figure 3

Demographic history of *Lycianthes dejecta*. (a) Mismatch distributions with sudden demographic/population expansion model of *L. dejecta*. The green dotted line shows the frequency observed, and the red continuous line shows the frequency expected. (b) Variation in the effective population size (*Ne*) of *Lycianthes dejecta*. (c) The *Ne* of BC population. The blue line represents the mean, and the blue area represents the limits of the 95% highest posterior density interval.

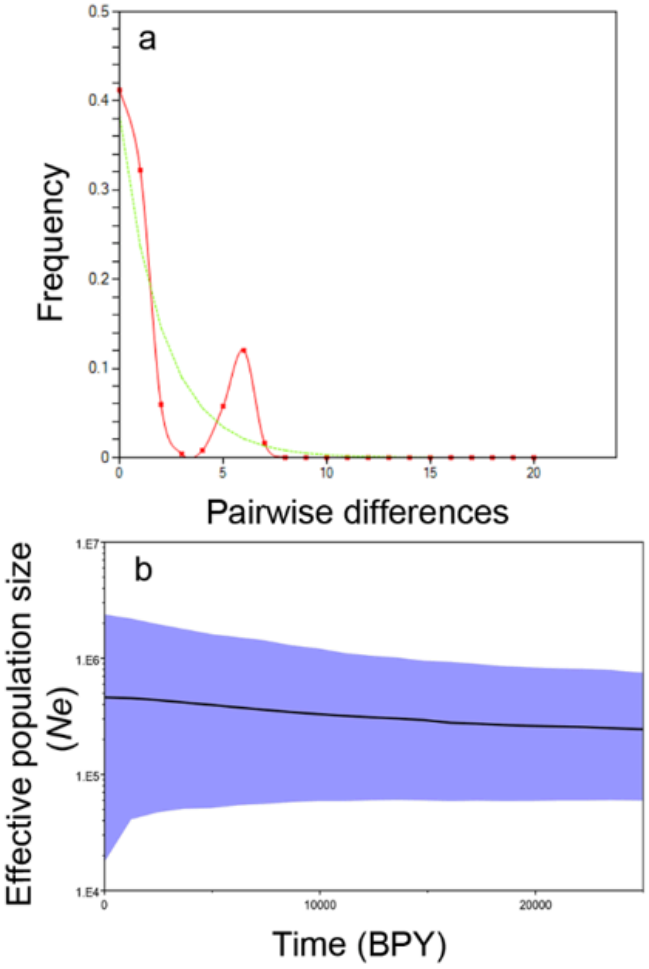

Figure 4

Demographic history of *Lycianthes peduncularis*. (a) Mismatch distributions with sudden demographic/population expansion model of *L. peduncularis*. The green dotted line shows the frequency observed, and the red continuous line shows the frequency expected. (b) Variation in the effective population size (*Ne*) of *L. peduncularis*. The blue line represents the mean, and the blue area represents the limits of the 95% highest posterior density interval.

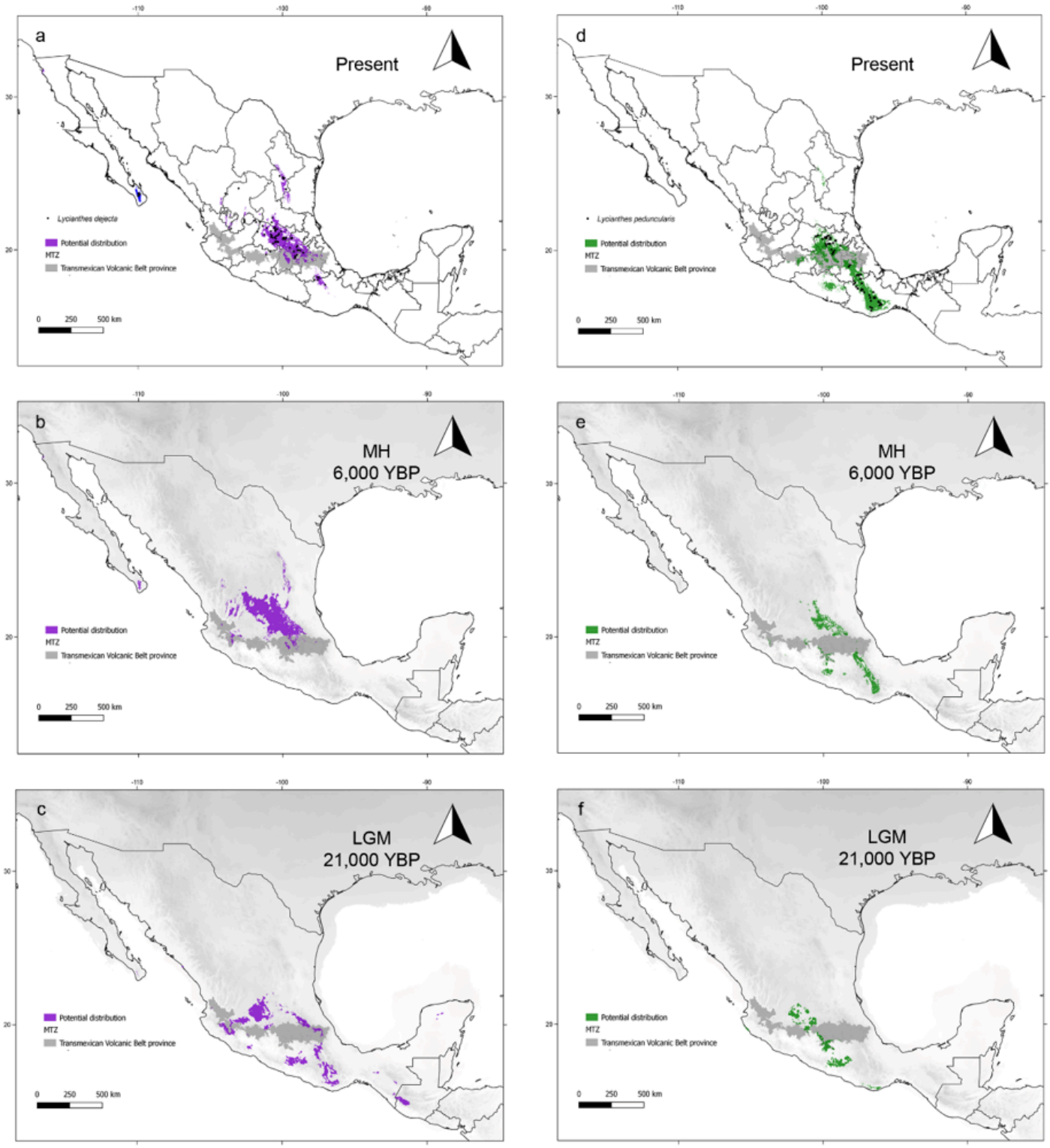

Figure 5

The ecological niche model obtained in MAXENT under the climatic models. (a) Current distributions of *Lycianthes dejecta* (black dots) and potential distribution (purple area) with present estimation. (b) Estimation of the potential distribution (purple area) projected to the Middle Holocene (MH, 6,000 YBP) using Community Climate System Model (CCSM4). (c) Estimation of the potential distribution (purple area) projected to the Last Maximum Glacial (LGM, 21,000 YBP) using Community Climate System Model (CCSM4). (d) Current distributions of *L. peduncularis* (black squares) and potential distribution (green area) with present estimation. (e) Estimation of the potential distribution (green area) projected to the Middle Holocene (MH, 6,000 YBP) using Community Climate System Model

(CCSM4). (f) Estimation of the potential distribution (green area) projected to the Last Maximum Glacial (LGM, 21,000 YBP) using Community Climate System Model (CCSM4). The gray polygon shows the TVB (Morrone et al. 2017).

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