



Traditional Management and Diversity of *Opuntia*: General Panorama in Mexico and a Case Study in the Meridional Central Plateau

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Abstract

This chapter shows a general panorama of the biocultural importance of the *Opuntia* genus in Mexico, and a case study directed to illustrate more specifically such relevance. The case study was conducted in one of the regions of Mexico where the highest diversity of species and ethnovarieties of *Opuntia* occur, and where this variation has been strongly rooted in the regional cultures. The *Opuntia* genus comprises more than 200 species, numerous intraspecific taxa, and even more ethnovarieties of cactus pears. It is native to the Americas, with a wide distribution in arid and semiarid lands through subpolar, temperate, subtropical, and tropical regions, from Canada to Patagonia. At least 84 species and numerous intraspecific taxa have been recorded to occur in Mexico; nearly 50 of them are used by different human cultures, and about 15 are cultivated, showing signs of domestication. Nowadays, some Mexican prickly pears like *O. ficus-indica*, *O. streptacantha*, *O. robusta*, *O. cochenillifera*, and *O. auberi* are cultivated throughout the world due to their economic and cultural values as food, ornaments, fodder, health-promoting benefits, as main host plant of cochineal, and for multiple other uses and applications. Some species were introduced to the

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Old World after the European colonization of the Americas and currently are invasive in areas of Australia, Asia, Africa, and Europe, causing severe ecological and economic problems. Since pre-Columbian times, the cactus pear species played agroecological roles in different regions of the Americas. In Mexico, these plants have been used since prehistory by native peoples and currently are important sources of livelihood, outstandingly human food. Fruits and young tender stems of practically all species, and flower buds of some of them, are edible. Their fruits are consumed fresh, and these and other edible parts are prepared in multiple ways in the Mexican cuisine, contributing to diet-nutritious components like amino acids, vitamins, proteins, minerals, dietary fibers, betalains, and phenolic compounds. The young tender cladodes are very much appreciated as vegetables in Mexican cuisine with dozens of recipes developed through history. The mature cladodes are also used to feed livestock; when dried, these are used as firewood. Their easy vegetative propagation and fast growth make *Opuntia* plants favorable for their cultivation, their use in borders of terraces against soil erosion, as live fences, and as main crops in intensive and extensive plantations. Due to their crassulacean acid metabolism (CAM) and water use efficiency, *Opuntia* spp. provide ecological benefits for recovering and improving degraded lands, landscapes rehabilitation, biodiversity preservation, and prevention of desertification. The case study reported in this chapter was conducted in the Meridional Central Plateau of Mexico, a region historically inhabited by different Chichimec Indigenous peoples, which developed a remarkable cultural history of interactions with prickly pears since pre-Columbian times. Then, after the European conquest, peoples of the region maintained traditional use and developed innovations associated with new socio-ecological contexts, strongly influenced by livestock raising and modern agriculture intensification. The study area is a remaining of the cultural region called “Tunal Grande” or “Gran Tunal,” because of the abundance of forests dominated by *Opuntia* spp. The name “Tunal” derives from the word *tuna*, of Caribbean origin but adopted in Spanish to refer to fruits of these plants. The case study documented the local classification of varieties and species of *Opuntia*, their uses, and management forms in the community of Laguna de Guadalupe in the state of Guanajuato. There, we identified 30 traditional varieties of 10 *Opuntia* species managed in two main environmental units: the monte (patches of thorn-scrub and secondary forests) and home gardens. In the monte, people let standing phenotypes of species and varieties that are more valued because of their attributes; in addition, they carry out practices that promote the abundance of these favorable species and varieties. In home gardens, people cultivate the most appreciated species and varieties and practice more intensively human selection that guides processes of domestication. We documented the different uses of species and varieties of *Opuntia*, their economic importance for local people, and their historical and current role as components of the biocultural diversity. We finally discuss the main cultural and economic factors influencing contemporary changes in the local landscape and human culture, and the socio-ecological perspectives for conserving the important biocultural heritage related to *Opuntia*.

Introduction

The *Opuntia* genus of the Cactaceae family comprises more than 200 species, a number that greatly varies according to taxonomic criteria; some authors report up to 350 species (Bravo-Hollis 1978; Guzmán et al. 2003; Chávez-Moreno et al. 2009; Scheinvar et al. 2011; Illoldi-Rangel et al. 2012). *Opuntia* plants are called cactus pears or prickly pears in English, and nopales in Spanish, a term derived from the Nahuatl word *nopalli*, which refers to the cladodes (the entire plant in Nahuatl is called *nopalkuahuitl*) and that was adopted by the Spaniards during the Colonial time in Mexico. Fruits are called *nochtli* in Nahuatl, but *tuna*, the Taino Caribbean term, was the name adopted and diffused by the Spanish conquerors through the Americas. Actually, in some countries (e.g., Peru, Colombia, Ecuador, and Argentina) the entire plants are commonly called *tuna* because of the Spanish adoption of this term. However, because of the wide distribution and human cultural importance of these plants, practically all languages in Mexico have a general term to group all species of *Opuntia* the peoples interact with (Table 1). Although the Nahua and other peoples differentiate the name of the plant, the cladodes, and fruits, several Indigenous languages of Mexico name the entire plant based on the fruit name. Although few Indigenous systems of classification of *Opuntia* have been studied, those available indicate that the most meaningful traits involved in traditional classification are the color and form of cladodes, plant size, spine color, and outstandingly, several attributes of fruits (size, peel and pulp color, flavor, and consistency, among others) (Casas and Barbera 2002; Casas et al. 1999).

The cactus pears have their origins in the Americas (Mazri 2018). The genus is naturally distributed from south of the arctic circle in subpolar areas of Canada and their analogous areas of Patagonia, in Chile and Argentina, through temperate, subtropical, and tropical areas of both hemispheres, including the Caribbean and Galapagos Islands (Bravo-Hollis 1978; Scheinvar 1999; Illoldi-Rangel et al. 2012).

Cactus pears have anatomical, morphological, and physiological adaptations to contrasting environmental conditions, characteristically those with harsh water-deficit stressing areas (Nefzaoui et al. 2014; Prat and Franck 2017; Kumar et al. 2018). Also, cactus pears display wide ranges of plasticity that allow them to cope with environments showing markedly contrasting seasons of the year (Reyes-Agüero et al. 2006). *Opuntia* plants most commonly display spines, which are modified leaves (Glimn-Lacy and Kaufman 2006), but some species or varieties may be spineless, generally associated with human selection. They commonly have fleshy stems, called pads or cladodes, with spines and glochids arranged in areoles (Glimn-Lacy and Kaufman 2006). Leaves are small or absent, the cladodes being the main parts involved in photosynthesis. The stems contain an outer surface cuticle that is thick and waxy, to prevent the water loss in drought conditions (Glimn-Lacy and Kaufman 2006).

Flowers are large, hermaphrodite, composed by several sepals and petals appearing as tepals, and a single pistil with a lobed stigma at the apex (Glimn-Lacy and Kaufman 2006; Arba et al. 2017). The color of the flowers is highly

Table 1 Names of *Opuntia* plants in the main Indigenous languages of Mexico. Each main language may have several variants. Ethnologue (Eberhard et al. 2021) identified nearly 290 languages for Mexico. The different terms annotated are some of the regional names given in a main language

Language	Name of <i>Opuntia</i> plant
Aguacateco (<i>Awakateko, Kayol, Qa'yool</i>)	<i>k'ána</i>
Amuzgo (<i>Tzañcue</i>)	<i>ndua</i>
Chatino (<i>Cha'cña</i>)	<i>bya, yaa, yaa jwle', yaa tii</i>
Chichimeco-jonaz (<i>Ézar</i>)	<i>úp'ó, ují, em'á</i>
Chinanteco (<i>Tsa jujmí</i>)	<i>cha'loo</i>
Chocho (<i>Runixa ngiigua</i>)	<i>kánda</i>
Ch'ol (<i>Winik</i>)	<i>chish-pech, wut petek', petek'</i>
Chontal/Tabasco (<i>Yokot</i>)	No record
Chontal/Oaxaca (<i>Slijuala sihanuk</i>)	<i>labone, lhi'as gabone</i>
<i>Chuj</i>	<i>baj'til</i>
Cochimí (<i>Laymón, Mti'pá</i>)	<i>a</i>
Cora (<i>Nayeeri</i>)	<i>naká, takera</i>
Cucapá (<i>Es péi</i>)	<i>a'</i>
Cuicateco (<i>Dibaku, Dbaku</i>)	<i>yind'itu, ndudu, ndiitu</i>
Guarijío (<i>Makurawe</i>)	<i>jilú, ilacúrugi</i>
Huave (<i>Ikööds</i>)	<i>nüek, nak', nüik, nik'</i>
Huichol (<i>Wixárika</i>)	<i>nakari</i>
Ixcateco (<i>Xwja</i>)	<i>ñunda</i>
Ixil (<i>Ixil</i>)	<i>kaana</i>
Jacalteco (<i>Abxubal</i>)	<i>páak'am</i>
Kakchiquel (<i>K'akchikel, Kaqchikel</i>)	<i>noxti'</i>
Kanjobal (<i>K'anjobal, Q'anjob'al</i>)	<i>a:xí:lh, a'š'i:t</i>
Kekchí (<i>K'ekchí</i>)	<i>noxti'</i>
Kikapú (<i>Kikapooa</i>)	<i>meskupuakaa</i>
Kiliwa (<i>Ko'lew</i>)	<i>'aa, a'a</i>
Kumiai (<i>kumeyaay, Tí'pai, Tipai-ipai, Kamia</i>)	<i>a'a</i>
Lacandón (<i>Hach t'an</i>)	<i>k'oj</i>
Mame (<i>Qyool</i>)	<i>tx'ixj</i>
Matlatzinca (<i>Botuná</i>)	<i>xöt'ö</i>
Maya	<i>pak'am, páak'am, tsutsuy</i>
Mayo (<i>Yoreme</i>)	<i>naabo, nabo taaka, navo</i>
Mazahua (<i>Jñatio</i>)	<i>kijñi</i>
Mazateco (<i>Ha shuta enima</i>)	<i>tu rě nanda, nánta</i>
Mixe (<i>Ayüük</i>)	<i>núum táät tsä'am, táät</i>
Mixteco (<i>Ñuu sávi</i>)	<i>vi'ncha, vi'ndia, bi'ndé</i>
Mochó or motozintleco (<i>Qatok</i>)	<i>a'xí</i>
Nahuatl (<i>Mexicatl</i>)	<i>nopalkuauitl, nopalli</i>
Otomí (<i>Hñähñü</i>)	<i>dokähä, ixcähä, xathä, kähä</i>
Paipai (<i>Akwa'ala</i>)	<i>a'a</i>
Pame (<i>Xigüe, Xi'üy</i>)	<i>nm'u</i>

(continued)

Table 1 (continued)

Language	Name of <i>Opuntia</i> plant
Pápago (<i>Tohono o'odam</i>)	<i>na'abo</i>
Pima (<i>Tohono o'odham</i>)	<i>nava, i'ibi, na'up</i>
Popoloca (<i>Ngigua</i>)	<i>tùchjèkixí, kándá, tùchjèkàndá, túchi kánda</i>
Popoloca (<i>Tuncápxe</i>)	<i>pejtak, to'a</i>
P'urhépecha	<i>pare</i>
Quiché (<i>Q'iché, K'iché'</i>)	<i>machiti, nochiti</i>
Seri (Comcaac)	<i>heel, heel imám</i>
Tacuate	<i>bindia'</i>
Tarahumara (<i>Rarámuri</i>)	<i>erá, napó</i>
Teenek (<i>Téenek</i>)	<i>pak'ak', pots'ots'</i>
Tepehua (<i>Hamásipini</i>)	<i>laklaba'anti</i>
Tepehuano (<i>O'dami</i>)	<i>náboi, náboi jibhiadi</i> (fruit)
Tlahuica (<i>Pjiejakjo, Pjiekak'joo</i>)	<i>mbakijñi</i>
Tlapaneco (<i>Me'phaa, Mè'phàà xkuà ixì ridii</i>)	<i>byáa'</i>
Tojolabal	<i>pejpa</i>
Totonaco (<i>Tachihuün</i>)	<i>ajiit, axit, axilh</i>
Triqui (<i>Guii xihanjhan</i>)	<i>dini, tino</i>
Tzeltal (<i>Winik ate</i>)	<i>pejtak</i>
Tzotzil (<i>Batsil winik</i>)	<i>ch'u</i>
Yaqui (<i>Yoeme</i>)	<i>naboo, naabo, naabujti</i>
Zapoteco (<i>Binizáa</i>)	<i>bia, biao, biaagueta, yága bidxi</i>
Zoque (<i>O'de püt</i>)	<i>nakpat</i>

variable among *Opuntia* species; it could be yellow, cream, yellow-red, or orange through pink or red. It has been discussed that the color variation might be associated with pollinator preferences (Heuzé and Tran 2017). Fruits are ovoid-spherical fleshy berries that may exhibit different colors at maturity, most commonly red, but also orange, yellow, or green peel, and even more variety of pulp colors from different shades of red, purple, violet, green, yellow, to orange. The peel exhibits areoles with spines and glochids (Beccaro et al. 2015; Mazri 2018).

The taxonomic delimitation of *Opuntia* species has been complicated, due to the frequent interspecific hybridizations, polyploidy, human selection in favor of specific traits of fruits, cladodes, plant size, and because of their conflicting phylogenetic positions (Wang et al. 1996; Griffith 2001; Valadez-Moctezuma et al. 2015; Martínez-González et al. 2019). The taxonomic complexity of cactus pears might highlight the complex genetic background of the species of this genus (Samah et al. 2016). Efforts to discriminate cactus pear species by using both morphological traits and molecular markers are currently conducted by several research groups (Caruso et al. 2010).

Nowadays, the cactus pears play important socioeconomic, agronomic, and ecological roles in the agendas of several countries around the world, since a number of species are used for human consumption, medicine, forage, and programs against soil erosion and desertification, ecological restoration, among other purposes. In addition, several biotechnological applications have been recently developed and

performed with these plants as cosmetic, pharmaceutical products and biofuels (Nefzaoui and Ben Salem 2002; Nefzaoui et al. 2014; Valadez-Moctezuma et al. 2015; Mazri 2018). But also, some *Opuntia* species represent severe environmental problems in extent regions of the world where they were introduced and now are aggressive invasive plants (Monteiro et al. 2005; Shackleton et al. 2017; Tesfay and Kreyling 2021).

This chapter aims to show a general panorama of the biocultural importance of the genus *Opuntia* in Mexico, and ethnobotanical information from a case study in one of the regions of this country where the highest diversity of species and ethnovarieties occur, and where this variation has been strongly rooted in the regional cultures, the Meridional Central Plateau. Specifically, we studied the case of Laguna de Guadalupe, Guanajuato, with the purpose to: (1) document the local species and varieties of *Opuntia* recognized by people, their attributes, cultural value, and traditional classification, (2) the uses and management practices carried out on the different species and varieties, those involving human selection, the main targets of selection, and practices used to carry out such selection, and (3) identify the main environmental units where *Opuntia* plants occur, and how these are managed.

Methods

Literature Review

The general panorama of *Opuntia* as Mexican biocultural heritage was reviewed based on literature on taxonomic, biogeographic, ecological, and ethnobotanical issues of the genus among cultural and ecological regions of the territory of the whole country. We generally identified the main different approaches to catalog species of the genus, general information about their use and management, and signs of domestication reported among species of *Opuntia*. Nomenclature of prickly pears among the Indigenous peoples of Mexico involved a careful review of historical, ethnohistorical, linguistic sources, the dictionaries available, as well as direct recording in the field and conversations and consultations with ethnobotanists working in different regions of Mexico. The case study was conducted in an area previously studied, and therefore we collected information on cultural, ecological, and ethnobotanical information of the area and on the role of *Opuntia* in people's life.

Site of the Case Study

The general perspective of *Opuntia* in Mexico comprised most of the territory of the country, while the case study was conducted in the community of Laguna de Guadalupe, which belongs to the municipality of San Felipe, at the state of Guanajuato (Fig. 1). It is part of the Meridional Central Plateau of Mexico (MCPM hereinafter) (Reyes-Agüero et al. 2005a), which is characterized by a semiarid climate, dominated by crassicaule scrub or xerophilous scrub vegetation (Rzedowski 1978) with mesquite (*Prosopis laevigata*), huizaches (*Vachellia schaffneri*), and

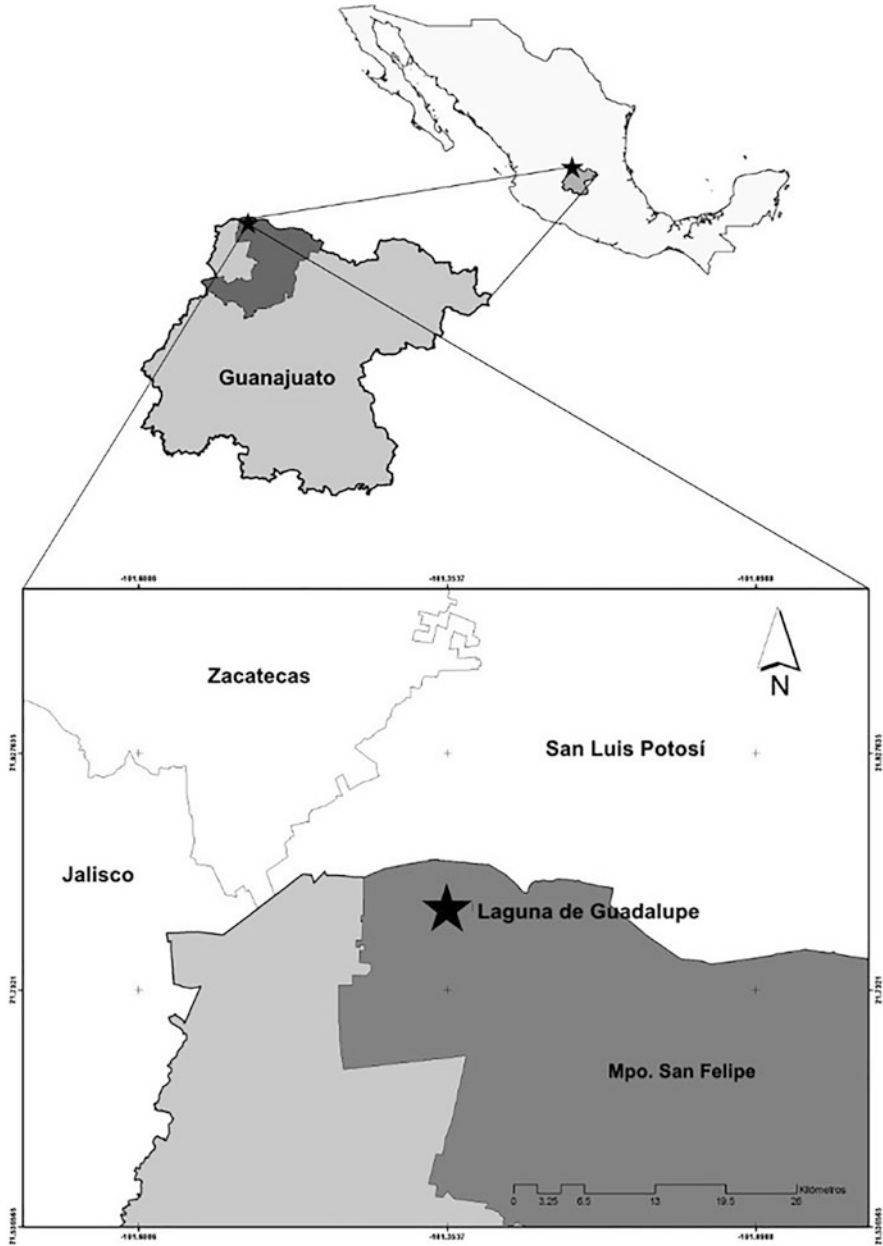


Fig. 1 Location of the study area of Laguna de Guadalupe, Guanajuato, in the Meridional Central Plateau of Mexico (MCPM)

several species of prickly pears like *Opuntia robusta*, *O. streptacantha*, and *O. leucotricha*, among others, being the most abundant plant components (Bravo-Hollis 1978; Reyes-Agüero et al. 2005a).

Laguna de Guadalupe (LG hereinafter) remains as one of the few localities where artisanal products with *Opuntia* are still fabricated. In the community live approximately 3667 people comprising nearly 1000 families, with land mostly on the *ejido* collective property regime. *Ejido* is one of most common types of rural property in Mexico; its main characteristic is the communal type of governmental structure, in which decisions and rules are made by an *Ejido* Assembly in which participate all the recognized local members of the *ejido*, or *ejidatarios*. The *Ejido* comprises 5463.7 ha used as plots for agriculture and 5675.5 ha of forest shrublands, grassland, and secondary vegetation areas, dedicated to common use where the main economic activities are the cultivation of beans and cattle raising.

Ethnobotany of *Opuntia* and the *Nopalera* System in the Case Study

In order to characterize use and management of *Opuntia* species and varieties and the *nopalera* system in LG, we carried out 13 semistructured interviews to *Opuntia* managers, during August–November 2019, when prickly pear fruits and tender cladodes of most of the varieties are available. The questions were oriented to characterize the management of the *nopaleras* (their location, dimensions, management practices, and the *Opuntia* varieties occurring there), the uses and traditional knowledge of the system, especially those aspects linked to the recognition of varieties, their local classification, the phenological stages, and harvesting times.

Additionally, we carried out ethnobotanical walks (Albuquerque et al. 2014) with managers of the main areas where fruits and cladodes are gathered, managed, and cultivated. With the information provided by the managers during the walks, we compiled free listings of the traditional varieties of *Opuntia*, their local names, their abundance perceived by people, and descriptions of their attributes of fruit (color, flavor, consistency, prickly, and skin thickness) and stems (consistency, fiber texture, palatability, and spininess, among others) for each variety.

Participatory Workshop

A participatory workshop was organized with people of LG that are involved in the *Opuntia* management, either for fruits or cladodes. We carried out the workshop using graphic support materials as stimuli to obtain information on the local nomenclature and classification of varieties, their useful parts, their special attributes and uses, the annual cycle of practices, seasons of availability of products, and other cultural aspects of the different varieties of the prickly pears occurring in the area. These activities allowed us to rectify, corroborate, specify, share, and expand the knowledge and experiences of local people in light of the plurality of knowledge, beliefs, and values on the plant species studied. This activity propitiated a space of dialogue and consensus among the attendees (Maxwell 2013).

In the workshop, all the traditional varieties named through the free lists (Smith and Borgatti 1997) were taken up and a classification was carried out from the

ranking of six attributes of the *Opuntia* fruits used by managers to identify them: flavor, consistency, size, skin thickness, spininess, and color. The ranking had values from 1 to 5. For flavor, the scale was generated with 1 being the sourest flavors and 5 being the sweetest. Consistency, 1 the most clearly sandy texture and 5 the juiciest. For size and skin thickness, 1 smaller and thin and 5 larger and thick, and prickly, 1 without spines and 5 with the highest spininess. For recording the attribute color, we used a table of colors characterizing the pulp color. With the values obtained for 30 fruits of *Opuntia* traditional varieties, a nonmetric multidimensional scaling analysis (NMDS) was performed to evaluate the similarities and differences between the varieties according to the attributes identified and management practiced. This analysis was carried out using the “Vegan” package (Oksanen et al. 2019) in R (R Core Team 2020).

Subsequently, based on the ethnobotanical description, photographs and collection of botanical specimens were carried out in the managed spatial units; the identification was corroborated with the studies by Reyes-Agüero et al. (2009) and Reyes-Agüero and Aguirre-Rivera (2011).

Results

Opuntia in Mexican Cultures

Nopales is considered in Mexico to be the Spanish term for *Opuntia*, but these plants receive names in practically all Indigenous languages of this country (more than 290 according to Ethnologue; Eberhard et al. 2021) (Table 1). It is a group of multipurpose plants originated in the Americas, but currently widely distributed throughout the world since some species were deliberately or incidentally brought to the Old World after the European colonization (Palevitch et al. 1993; Casas and Barbera 2002; Caruso et al. 2010; Pinedo-Espinoza et al. 2017; Mazri 2018). *Opuntia* species are deeply rooted in the human cultures of Mexico and form part of landscapes in most of the territory of this country (Bravo-Hollis 1978; Colunga 1984; Colunga-García Marín et al. 1986; Rzedowski 1978, 1993; Toledo and Ordóñez 1993; Hernández-Xolocotzi 1993; Casas and Barbera 2002; Guzmán et al. 2003; Reyes-Agüero 2005; Reyes-Agüero et al. 2005a, b, 2009, 2011). Taxonomists have described about 200 species for Mexico (Bravo-Hollis 1978; Chávez-Moreno et al. 2009; Illoldi-Rangel et al. 2012), but some authors like Guzmán et al. (2003) recorded 270 species and 384 intraspecific taxa. Ethnobotanical studies have reported that at about 50 species of *Opuntia*, and numerous intraspecific taxa are currently used in different regions of Mexico. At least 15 species have clear signs of domestication (Colunga-García Marín et al. 1986; Hernández-Xolocotzi 1993; Casas and Barbera 2002; Reyes-Agüero 2005; Reyes Agüero et al. 2005b; Paz-Navarro 2021) (Table 2).

Their use and management are ancient, as revealed by archeological studies, which have reported that prickly pears were used since the earliest times of human occupation of the Tehuacan Valley (Smith 1967; MacNeish 1967) and Guilá

Table 2 Species of *Opuntia* recorded in Mexico, their use, form of management, and signs of domestication reported in the literature. Uses: 1 = edible fruits, 2 = edible stems, 3 = edible flowers, 4 = fodder, 5 = alcoholic beverages, 6 = house construction, 7 = live fences, 8 = medicine, 9 = ornamental, 10 = adhesive, 11 = fuel, 12 = soap, shampoo, and cream, and 13 = cochineal cultivation

Species	Use	Management type	Domestication	References
<i>O. albicarpa</i>	1, 2, 4	W, C	Yes	This study, Scheinvar (1999), and Paz-Navarro (2021)
<i>O. amyclaea</i>	1, 9	W, C	Yes	Hernández-Xolocotzi (1993) and Soberón et al. (2001)
<i>O. atrispina</i>	9	W, C	No	Konings and Konings (2009)
<i>O. atropes</i>	1, 2, 9, 11, 12	W, M, C	Yes	Bravo-Hollis (1978), Colunga (1984), Hernández-Xolocotzi (1993), and Cornejo-Denman and Arreola-Nava (2008)
<i>O. auberi</i>	2, 3, 8, 9, 13	W, M, C	Yes	Bravo-Hollis (1978), Casas et al. (2001, 2002), and Blancas et al. (2010)
<i>O. azurea</i>	1, 4, 9	W, C	No	Soberón et al. (2001) and Powell and Weedon (2004)
<i>O. bensonii</i>	1	W	No	Bravo-Hollis (1978) and Cornejo-Denman and Arreola-Nava (2008)
<i>O. bravoana</i>	4, 9	W, C	No	Soberón et al. (2001) and Mercado-Muñoz (2014)
<i>O. cantabrigensis</i>	4	W	No	Soberón et al. (2001), Paz-Navarro (2021), and this study
<i>O. cochenillifera</i>	2, 3, 5, 8, 13	W, M, C	Yes	Pennington (1969) and Bravo-Hollis (1978)
<i>O. crassa</i>	1, 11	W, C	Yes	Bravo-Hollis (1978), Colunga (1984), and Hernández-Xolocotzi (1993)
<i>O. chavena</i>	1, 2, 13	W, C	No	Soberón et al. (2001) and Cornejo-Denman and Arreola-Nava (2008)
<i>O. chlorotica</i>	1, 7, 9	W, C	No	Soberón et al. (2001)
<i>O. decumbens</i>	4, 5, 11	W	No	Casas et al. (2001), Casas and Barbera (2002), and Blancas et al. (2010)
<i>O. dejecta</i>	2, 5	W, C	No	Bravo-Hollis (1978)
<i>O. depressa</i>	1, 4, 7, 11	W	No	Soberón et al. (2001) and Casas et al. (2001)

(continued)

Table 2 (continued)

Species	Use	Management type	Domestication	References
<i>O. dillenii</i>	1, 8	W	No	Soberón et al. (2001) and Shirazinia et al. (2019)
<i>O. duranguensis</i>	1, 4, 9	W, C	No	Soberón et al. (2001)
<i>O. excelsa</i>	1, 9	W	No	Soberón et al. (2001) and Cornejo-Denman and Arreola-Nava (2008)
<i>O. engelmani</i>	4	W	No	Soberón et al. (2001)
<i>O. esquirentensis</i>	1	W	No	Casas and Barbera (2002)
<i>O. ficus-indica</i>	1, 2, 4, 5, 8, 10, 11, 12, 13	C	Yes	Bravo-Hollis (1978), Colunga (1984), Casas et al. (2001), Casas and Barbera (2002), Reyes Agüero et al. (2005), and Hernández-Xolocotzi (1993)
<i>O. fuliginosa</i>	1, 2, 11	W, M, C	–	Colunga (1984) and Cornejo-Denman and Arreola-Nava (2008)
<i>O. huajuapensis</i>	1, 2, 3, 4, 5, 8, 9	W	No	Colunga (1984)
<i>O. hyptiacantha</i>	1, 2, 4, 11	W, M, C	Yes	Bravo-Hollis (1978), Colunga (1984), Hernández-Xolocotzi (1993), Paz-Navarro (2021), this study, and Cornejo-Denman and Arreola-Nava (2008)
<i>O. imbricata</i>	1, 2, 4, 5, 8	W	No	Bravo-Hollis (1978), Sánchez-Mejorada (1982), this study, and Cornejo-Denman and Arreola-Nava (2008)
<i>O. jaliscana</i>	1, 2, 11	W, M	–	Bravo-Hollis (1978), Colunga (1984), and Cornejo-Denman and Arreola-Nava (2008)
<i>O. joconostle</i>	1, 11	W, M, C	Yes	Martínez (1993), Hernández-Xolocotzi (1993), Paz-Navarro (2021), and this study
<i>O. karwinskiana</i>	8	W	No	Bravo-Hollis (1978)
<i>O. kleiniae</i>	7	W, C	–	
<i>O. lagunae</i>	1, 4, 8	W		Soberón et al. (2001) and Mercado-Muñoz (2014)
<i>O. lasciacantha</i>	1, 2, 4, 9, 11	W, M, C	Yes	Bravo-Hollis (1978) and Cornejo-Denman and Arreola-Nava (2008)

(continued)

Table 2 (continued)

Species	Use	Management type	Domestication	References
<i>O. leptocaulis</i>	1, 2, 4, 5, 8	W	No	Sánchez-Mejorada (1982), Felger and Moser (1985), and Hernández-Xolocotzi (1993)
<i>O. leucotricha</i>	1, 2, 4, 11	W, M, C	Yes	Bravo-Hollis (1978), Colunga (1984), Soberón et al. (2001), Paz-Navarro (2021), and this study
<i>O. linheimeri</i>	4	W	No	Soberón et al. (2001)
<i>O. littoralis</i>	1, 7, 9	W, C	No	Soberón et al. (2001)
<i>O. lutea</i>	1	W	No	Casas and Barbera (2002)
<i>O. macrorhiza</i>	1, 2, 7	W	No	Chahdoura et al. (2014)
<i>O. megarhiza</i>	1, 7	W	No	
<i>O. megacantha</i>	1, 2, 4, 11	W, M, C	Yes	Colunga (1984), Hernández-Xolocotzi (1993), Paz-Navarro (2021), this study, and Cornejo-Denman and Arreola-Nava (2008)
<i>O. microdasys</i>	7, 8, 9	W, C	No	Soberón et al. (2001), Cornejo-Denman and Arreola-Nava (2008), and Chahdoura et al. (2014)
<i>O. nerpicolor</i>	1, 5	W	No	Sánchez-Mejorada (1982)
<i>O. oricola</i>	1, 7, 9	W, C	No	
<i>O. pachona</i>	1, 2, 4	W, M, C	Yes	Molina-Velázquez (2001)
<i>O. phaeacantha</i>	4	W	No	Soberón et al. (2001)
<i>O. pilifera</i>	1, 2, 3, 4, 11	W, M	No	Bravo-Hollis (1978), Casas et al. (2001), Blancas et al. (2010), and Ojeda-Linares et al. (2020)
<i>O. puberula</i>	4	W	No	Casas et al. (2001)
<i>O. pubescens</i>	7	W, C	No	Cornejo-Denman and Arreola-Nava (2008)
<i>O. pumila</i>	2	W	No	Casas et al. (2001)
<i>O. pycnantha</i>	7	W, C	No	Benavides-Ríos (2016)
<i>O. rastrera</i>	4	W	No	Paz-Navarro (2021) and this study
<i>O. rileyi</i>	9	W	No	Guzmán et al. (2003)
<i>O. robusta</i>	1, 2, 4, 5, 11	W, M, C	Yes	Bravo-Hollis (1978), Colunga (1984), Hernández-Xolocotzi (1993), Reyes Agüero (2005), Paz-Navarro (2021), and this study

(continued)

Table 2 (continued)

Species	Use	Management type	Domestication	References
<i>O. rufida</i>	9	W, C	No	Guzmán et al. (2003)
<i>O. spinulifera</i>	1, 2, 4	W, M, C	No	Scheinvar et al. (2011)
<i>O. spraguei</i>	7	W, C	No	Guzmán et al. (2003) and Mercado-Muñoz (2014)
<i>O. spinulifera</i>	1	W, C	–	Bravo-Hollis (1978)
<i>O. stenopetala</i>	4, 8	W	No	Sánchez-Mejorada (1982)
<i>O. streptacantha</i>	1, 2, 3, 4, 5, 11	W, M, C	Yes	Bravo-Hollis (1978), Colunga (1984), Hernández-Xolocotzi (1993), Reyes-Agüero (2005), Paz-Navarro (2021), and this study
<i>O. stricta</i>	4	W	No	Soberón et al. (2001)
<i>O. tapona</i>	1	W	No	Soberón et al. (2001)
<i>O. tehuantepecana</i>	1, 5, 8	W	No	
<i>O. tomentosa</i>	1, 2, 4, 5, 11, 13	W, M, C	No	Bravo-Hollis (1978) and Cornejo-Denman and Arreola-Nava (2008)
<i>O. tunicata</i>	7, 9	W, C	No	Cornejo-Denman and Arreola-Nava (2008)
<i>O. undulata</i>	1, 7, 11	W, C	Yes	Bravo-Hollis (1978), Colunga (1984), Hernández-Xolocotzi (1993), and Cornejo-Denman and Arreola-Nava (2008)
<i>O. velutina</i>	1, 8, 11	W, M	–	Colunga (1984)
<i>O. violacea</i>	4	W	No	Soberón et al. (2001)
<i>O. wilcoxi</i>	1, 8, 9	W	No	Mercado-Muñoz (2014)

Naquitz, Oaxaca (Flannery 1986), among other sites (MacNeish 1992) more than 10,000 years ago. Together with *Agave*, maize, squashes, avocado, chili peppers, and beans, *Opuntia* are among the most iconic plants used by the Mesoamerican people since prehistory (Casas and Barbera 2002). Remains of prickly pears are abundant in archaeological records, and they were seemingly key plant resources used by the first humans that occupied the area that is currently Mexico (MacNeish 1967, 1992; Bravo-Hollis 1978; Colunga-García Marín et al. 1986; Casas and Barbera 2002; Scheinvar et al. 2011). Together with *Agave* spp. and *Prosopis* spp., *Opuntia* species formed what some authors call “semi-desert triad” (Nava-Martínez 2019) that was a basis for the sustenance of the nomadic groups of those regions (Anaya-Pérez and Bautista-Zane 2008).

Opuntia species play an outstanding role in Mexican cultures, economy, and history (Barros and Buenrostro 1998); their relevance might be consequence but also a cause of the high diversification that has been mentioned above. Among all cactus

pear species, *Opuntia ficus-indica* is the most economically important, with the highest cladode and fruit production. It is considered a domesticated plant, and the identity of its wild ancestors has been under debate (Colunga-García Marín et al. 1986; Palevitch et al. 1993; Labra et al. 2003; Griffith 2004; Reyes-Agüero et al. 2009). However, there are several wild semidomesticated and domesticated species gathered in forests or cultivated in different systems, which provide food and incomes to different sectors of Mexican people (Colunga-García Marín et al. 1986; Reyes-Agüero 2005; Sáenz 2013; Yahia and Saenz 2011).

Fruits of wild species are consumed in different regions of Mexico; however, their small size, sour flavor, thick peel, and spininess have motivated human selection in favor of plants producing larger fruits with sweeter (in some cases sourer) pulp, thinner peel (in some cases thicker), and low spininess. Similarly, the young tender stems are edible, raw or cooked in many ways; stems of all species are edible, but people prefer those species and intraspecific varieties producing tasty stems with good consistency and fewer spines (Colunga-García Marín et al. 1986; Casas and Barbera 2002; Reyes-Agüero 2005; Reyes-Agüero et al. 2011). These attributes, among others, have been favored through processes of human selection practiced by two main management types. One of them is silvicultural, which involves management of wild individuals in forests and agroforestry systems. Through this management, people procure increasing phenotypes with favorable attributes by letting them stand when disturbing the forest for different purposes, sometimes also deliberately propagating the favorable phenotypes in situ (in the original place in forests and agroforestry systems) (Casas et al. 1997; Casas 2001). The other main management type is cultivation, which consists in moving propagules from forests to crop fields, including home gardens, and among anthropogenic environments (Casas et al. 1996, 1997). In all these practices, it is possible to identify that human selection operates actively diversifying varieties of *Opuntia*, according to purposes guided by human culture (Colunga-García Marín et al. 1986; Casas et al. 1997, 2007; Reyes-Agüero et al. 2011). Table 2 summarizes ethnobotanical information reported about use and management types of *Opuntia* species in Mexico, identifying those species with signs of domestication.

The Altiplano Central or Meridional Central Plateau of Mexico (MCPM hereinafter) is placed in the central-northern area of the country, comprising localities of the states of Zacatecas, San Luis Potosí, Aguascalientes, Jalisco, Guanajuato, Querétaro, Hidalgo, Michoacán, and Mexico City. It is a remaining area of the cultural region called “Tunal Grande” or “Gran Tunal,” because of the abundance of *Opuntia*, which are dominant species in forests (Branniff-Cornejo 1999; Rivera-Villanueva et al. 2020). Throughout this region, previous studies have documented the occurrence of 126 variants associated with 18 species (Reyes-Agüero et al. 2005a, b, 2011; Scheinvar and Gallegos 2011). Such diversity highlights the relevance of this region as one of the main centers of human-caused diversification of the genus throughout Mexico and perhaps the continent.

The interaction between humans and *Opuntia* through management and adaptations to the local environments has influenced a high diversification and arising of varieties of prickly pears with differentiated attributes. These varieties are named and

classified by the managers according to their traditional knowledge and criteria. These varieties have been recognized by ethnobotanists as ethnovarieties, local or traditional varieties. The traditional systems of classification are based on perceptible, morphological, physiological, or sensorial attributes and are strongly associated with the local worldview, knowledge, uses, practices, and purposes (Velásquez-Milla et al. 2011; Figueredo-Urbina et al. 2021).

In the MCPM, *Opuntia* species and their traditional varieties are widely distributed and located in different types of forests described as crassicaule scrub or thornscrub. There, it is commonly possible to find areas with high density of prickly pears, called “*nopaleras*” (Bravo-Hollis 1978; Casas and Barbera 2002).

Nopaleras are commonly found on slopes, canyons, depressions, alluvial fans, and plain lands. These have been characterized to harbor a remarkable diversity of species and a high density of *Opuntia* individuals. Some studies have recorded up to 412 plant species associated in these areas (Rzedowski 1965; Reyes-Agüero et al. 1996; del Castillo 2000; Reyes-Agüero and Vallejo 2019). Compared with other xerophytic bushes, *nopaleras* have structural complexity with several strata (González-Espinosa 1999; del Castillo 2000). For instance, the first stratum may be composed by individuals like Joshua tree or *izote* species (*Yucca filifera*, *Y. decipiens*, among others) that surpass the height of the tallest *Opuntia* plants (Rzedowski 1965). A second stratum is composed of shrubby and arboreal cacti species from 1 to 4 m in height. In the boundaries of the states of Guanajuato and Querétaro, frosts are uncommon, and there the *nopaleras* are mainly composed with individuals of *O. streptacantha*. In contrast, in the northern region comprising the states of Zacatecas and Durango, frosts are frequent and intense and there is a lower density of *O. streptacantha* individuals, which are combined with or replaced by species like *O. leucotricha* (Flores-Flores and Yeaton 2003). It has also been recorded that in disturbed sites, *O. streptacantha* is replaced by *O. robusta* populations (Rzedowski 1965; del Castillo 2000; Flores-Flores and Yeaton 2000). Also in this stratum, legume trees such as *mesquites* (*Prosopis juliflora*) or *huizaches* (*Acacia tortuosa*, *A. farnesiana*, among others) are present, varying from scarce to abundant. Although sometimes the density of *Opuntia* plants constrains or limits the development of lower strata, a third stratum can be identified. This is mainly composed of shrubby species with heights ranging from 0.4 to 1.0 m, represented in some places by the “*gatuño*” or “*garabatillo*” (*Mimosa biuncifera*), *Dalea bicolor*, *Agave salmiana* ssp. *crassispina*, and *O. robusta* (Reyes-Agüero and Aguirre-Rivera (2011).

In addition to their biological and ecological importance, the *nopaleras* have been recognized as reservoirs of human cultures. These areas have been the setting of construction of management strategies and techniques, based on ecological experiences and knowledge developed by Indigenous peoples since prehistory. The modern peasant societies have learned the ancient practices and have continued innovating as long as the production systems and their culture have changed. Traditionally, these systems have the capacity of promoting and ensuring biodiversity conservation while procuring subsistence, similar to what has been recorded in other areas of biocultural relevance in Mexico (Toledo and Barrera-Bassols 2008; Berkes 2012; Casas et al. 1997, 2014).

In Mexico, *Opuntia* fruits are consumed fresh or processed into different traditional dishes and products such as juices, jams, candies, and fermented beverages. The cladodes are also prepared in numerous food dishes, for pickles, pills, capsules, body lotions, shampoos, and creams, among other products. Their seeds could be used as agents of flavoring, and in local communities these are commercialized to companies to produce lipsticks and oils for health skin treatments (Pareek et al. 2003; Kaur et al. 2012; Valiente-Banuet et al. 1997; Casas 2002; Dávila-Aranda et al. 2016; Ojeda-Linares et al. 2020, 2021). Stems of *Opuntia* are collected and used fresh or prepared as silage to feed the livestock, while the dead dried stems are collected as firewood.

In such diverse contexts, *Opuntia* species have been under management and processes of human selection. Some species have been under incipient or advanced domestication, which actively promote the diversification of ethnovarieties (Colunga-García Marín et al. 1986, Reyes-Agüero et al. 2005a, b, 2009, 2011).

The MCPM is one of the most relevant centers of diversification of *Opuntia* associated with management and human selection in Mexico. It is therefore an ideal region to characterize the diversity of the *Opuntia* varieties, their uses and management, the way human selection is practiced, and the strategies that are carried out for their maintenance. To address these relevant topics, we conducted studies in the community of Laguna de Guadalupe in the state of Guanajuato (Ojeda-Linares et al. 2020; Paz-Navarro 2021). There, several *Opuntia* species were recorded to be used as food, fodder, and to produce the traditional fermented beverage called *colonche* or *nochoctli* and sweets called *melcocha* and *queso de tuna*.

Management of Spatial Areas of *Opuntia*

A high diversity of *Opuntia* species and varieties occur in Laguna de Guadalupe. During our field trips, 30 traditional varieties belonging to 10 *Opuntia* species were recorded as: *O. albicarpa*, *O. cantabrigensis*, *O. ficus-indica*, *O. hyptiacantha*, *O. joconostle*, *O. leucotricha*, *O. megacantha*, *O. rastrera*, *O. robusta*, *O. streptacantha*, and *Cylindropuntia imbricata* (for some taxonomists, *Cylindropuntia* is a subgenus of *Opuntia*). Through the free list, local varieties were registered by common name, management systems, and ethnobotanical attributes (Table 3). We also identified that the varieties are distributed in two main systems: (1) the *monte* (mount) or *nopaleras*, and (2) home gardens.

The *Monte* or *Nopalera*

The spatial unit considered by the community as *monte* is a semitransformed forest area where crassicaule shrub grows, several useful species cohabit there, among them: *Agave* spp., *Yucca* spp., *Jatropha* spp., *Prosopis* sp., and several species and varieties of *Opuntia*. This type of vegetation is widely distributed in the nearby plains around Laguna de Guadalupe (Fig. 2), and it is the space that gives identity to the community and provides resources that allow sustenance to local people.

Table 3 Traditional varieties of *Opuntia*, management spaces, attributes, and abundance perceived in the case study in Laguna de Guadalupe, Guanajuato

Traditional variety	Species	Management space	Main uses	Flavor	Consistency	Size	Skin thickness	Prickly	Color	Abundance
Clavillina	<i>Cylindropuntia imbricata</i>	Monte (crassicaule shrubs)	Medicinal	1	1	1	5	5	Light green	4
Blanca	<i>Opuntia albicarpa</i>	Home garden	Fresh fruit	4	5	5	1	3	Green	2
Blanca Cristalina	<i>O. albicarpa</i>	Home garden	Fresh fruit	5	5	5	1	1	Green	1
Blanca Espinuda	<i>O. albicarpa</i>	Home garden	Fresh fruit	4	5	5	1	5	Green	1
Burra	<i>O. albicarpa</i>	Home garden	Fresh fruit	5	5	5	1	4	Red	1
Blanca Chapeada	<i>O. albicarpa</i>	Home garden	Fresh fruit	4	5	5	1	1	Light red	1
Blanca Reina	<i>O. albicarpa</i>	Home garden	Fresh fruit	4	5	5	1	5	Green	1
Cuija	<i>O. cantabrigensis</i>	Monte	Forraje	1	3	1	1	5	Purple	4
Amarilla	<i>O. ficus-indica</i>	Home garden	Fresh fruit	5	5	5	1	1	Yellow	1
Colorada or chapeada	<i>O. ficus-indica</i>	Home garden	Fresh fruit	5	5	5	1	1	Red	1
Cascarona	<i>O. hyptiacantha</i>	Monte	Colonche, Queso de Tuna, Melcocha	2	3	3	5	5	Pink	4
Hartona	<i>O. hyptiacantha</i>	Monte	Edible stems	2	1	3	2	5	Carmine	4
Rebusca	<i>O. hyptiacantha</i>	Monte/home garden	Fresh fruit	2	3	3	5	3	Light red	3
Negrta	<i>O. hyptiacantha</i>	Monte	Queso de Tuna, Melcocha	2	2	2	2	3	Dark carmine	4

(continued)

Table 3 (continued)

Traditional variety	Species	Management space	Main uses	Flavor	Consistency	Size	Skin thickness	Prickly	Color	Abundance
Huevo de Gato	<i>O. joconostle</i>	Monte	Fresh fruit	1	4	3	5	3	Light pink	3
Xoconostle Blanco	<i>O. joconostle</i>	Monte/home garden	Fresh fruit	1	4	3	5	3	Light green	3
Xoconostle Rojo	<i>O. joconostle</i>	Monte/home garden	Fresh fruit	1	4	3	5	3	Light red	3
Duraznillo	<i>O. leucotricha</i>	Home garden	Fresh fruit	2	2	1	4	5	Yellow	1
Memela	<i>O. megacantha</i>	Monte	Colonche, Queso de Tuna, Melcocha	3	2	4	2	5	Carmine	4
Jarrita	<i>O. megacantha</i>	Monte	Queso de Tuna, Melcocha	4	5	4	2	3	Light carmine	3
Sangre de Toro	<i>O. megacantha</i>	Home garden	Fresh fruit	5	5	5	1	2	Dark carmine	1
Arrastradilla	<i>O. rasptrera</i>	Monte	Forraje	1	1	1	5	5	Dark carmine	4
Tapona Castilla	<i>O. robusta</i>	Home garden	Fresh fruit	3	3	4	4	1	Dark carmine	1
Tapona Blanca	<i>O. robusta</i>	Monte	Fresh fruit	1	3	4	4	4	Green	1
Tapona Silvestre	<i>O. robusta</i>	Monte	Fresh fruit, edible stems	2	3	4	4	4	Dark carmine	5
Ballita	<i>O. streptacantha</i>	Monte	Colonche, queso de tuna, melcocha	2	1	3	2	5	Light carmine	4

Charola	<i>O. streptacantha</i>	Monte	Colonche, Queso de Tuna, Melcocha	3	1	4	4	4	5	Carmine	4
Cardona	<i>O. streptacantha</i>	Monte/home garden	Colonche, Queso de Tuna, Melcocha, fresh fruit, edible stems	4	2	3	2	2	2	Carmine	5
Cardona Blanca	<i>O. streptacantha</i>	Monte	Fresh fruit	4	2	3	2	2	2	Green	1
Jocotilla or jocoquilla	<i>O. streptacantha</i>	Monte	Forraje	2	4	1	5	3	3	Carmine	1

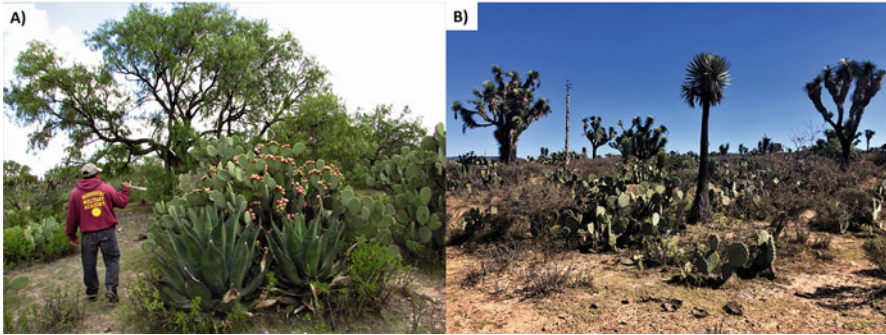


Fig. 2 General aspect of the landscape of the site studied: (a) showing the areas of “monte” or “nopaleras,” which are forest or secondary forest areas where populations of *Opuntia* species are the dominant components; (b) higher areas of *monte*, where individuals of Joshua trees share spaces with *Opuntia* species. (Photos by the authors)

There, we identified 19 traditional varieties of eight *Opuntia* species cohabiting in the *monte* system. The species with the highest number of varieties (five) was *O. streptacantha*, all of them recognized by the local managers of the *monte*.

Some aspects of practices by the gatherers were recorded, for instance, they prefer *O. robusta* cladodes or nopalitos for their consumption as vegetables. On the other hand, *O. streptacantha* fruits are the most valuable to be consumed as fresh fruit. In recent years, an increasing demand for fruits and seeds of this species has generated a growing microindustry dedicated to the collection of fruits of this cactus. The commercial exploitation began transporting nearly 2 tons of prickly pear fruits approximately every third day from September to October. As well, *Opuntia* dead logs are collected to use as firewood; in fact, there are specific ovens for the use of this firewood.

The *monte* are places where extensive ranching techniques are performed; animals like cows, sheep, and goats graze freely, which consequently have an impact on vegetation by browsing, trampling on the ground, and accumulation of manure in particular areas locally named *majadas*. The *majadas* are located in the *monte* system and are composed by high-density clusters of *Opuntia* plants with several species forming patches (Fig. 3). The composition of these areas is the result of a continual silvicultural management performed in situ by the prickly pear fruit collectors. The constant gathering of fruits, for instance, those of *O. streptacantha*, involves a process through which the cladodes with fruits are removed and then the fruits are stored, leaving the cladodes and some fruits on the ground (Fig. 4). Later, because of the vegetative propagation of *Opuntia* species, new individuals emerge from the remains of cladodes dispersed and associated with gathering. The *Opuntia* plants collected through this mechanism are promoted, sometimes incidentally, sometimes deliberately. Therefore, as part of this process dense clusters of *Opuntia* species are formed; then a competition for light and space begins among the resulting plant populations, the people encouraging differentially the growth of some individuals (which may reach 4–5 m), with more bifurcations and a high number of

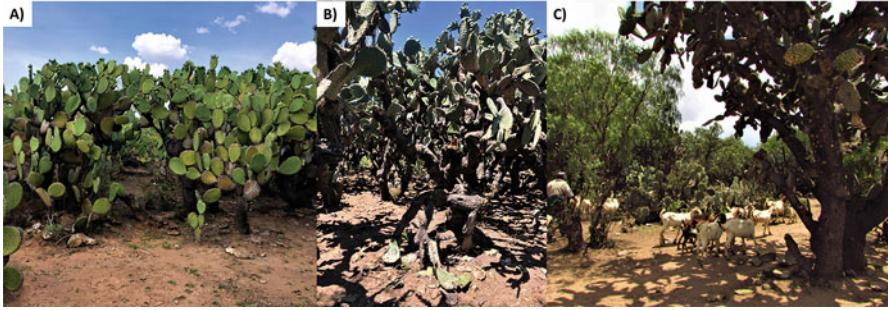


Fig. 3 A close-up view of the high population density that *Opuntia* species may reach in the “majadas”: (a) which are patches of secondary forest where abundance of prickly pears is promoted incidentally or deliberately due to human actions; (b) the inside structure of “majada”; and (c) activities performed inside the “majadas”. (Photos by the authors)



Fig. 4 Aspect of the remains of gathering *Opuntia streptacantha*: (a) showing the gathering of cladodes and fruits resulting from this activity, which eventually become entire plants associated to the “majadas”; (b) a similar principle promotes deliberately or incidentally the abundance of *Opuntia* in patches of forest. (Photos by the authors)

cladodes (870 ± 100). Therefore, through silvicultural and deliberate cultivation activities, local people mold the landscape of the *monte*.

As mentioned above, the *majadas* characteristically have high densities of population of *Opuntia* species; this limits the growth of other species, except the pirul (*Schinus molle*), which is commonly associated with the *majadas*. The average life span of the *majadas* is more than 50 years, as informed by local people, but such form of management is much more ancient. According to local people, as the *majadas* reach this age, gatherers stop frequenting them, mainly because it is more difficult to harvest the fruits due to the height of the individuals and because they perceive changes in the flavor and texture, becoming softer fruits (Fig. 5). The lack of harvest in the *majada* reduces the process of dispersal of cladodes, and the

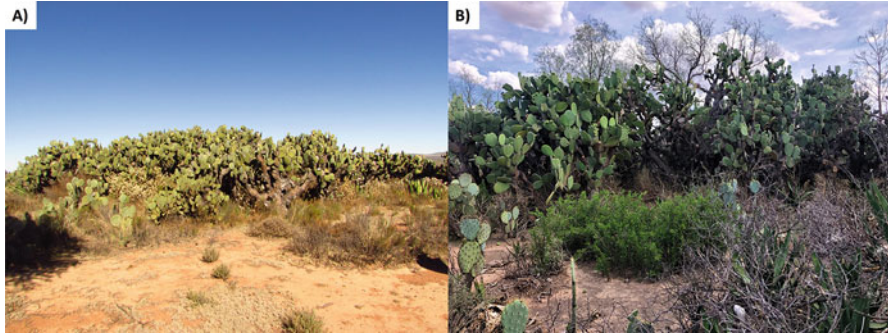


Fig. 5 (a) An old or “mature” *majada*, with ancient individuals of *Opuntia*. The general landscape is modeled through the management of composition and abundance of prickly pears species in the area. (b) A young “*majada*” promoted by human activities. (Photos by the authors)

reduced light availability prevents the propagation of new individuals, which impacts the life span of the *majadas* and gives way to another vegetation type dominated by *S. molle*. The *majadas* provide an optimal microclimate and a physical structure that favors the cattle can stay there generating an accumulating manure or *majada*, which gives the name to this system. The *majadas* have been used for hundreds of years by ancient cultural groups which used them as shelter and to satisfy food needs. Currently, the *majada* play a similar role, and the incorporation of new techniques has allowed the diversification of products obtained from the cactus pear fruits such as *melcocha*, *queso de tuna*, and *colonche*, products that are described ahead.

Home Gardens

The home gardens of LG have an area of approximately 400–1000 m², which are commonly located next to the house where the families live. In these spaces, people cultivate species and varieties of *Opuntia*, and other plants, including medicinal herbs, vegetables, quelites, and ornamental flowers, and chickens are raised. The products of these spaces are mainly intended for self-consumption.

People cultivate *Opuntia* for obtaining nopalitos, fresh fruit, and fuelwood for the direct consumption by the household. However, these spaces are being reduced because the expansion of family buildings is progressively more common, increasing the number of rooms of the house by occupying areas of the home garden.

We registered 15 traditional varieties of prickly pears in homegardens, which correspond to 8 species, most of them of the species *O. albicarpa* (6 varieties). Abundance, in terms of number of individuals, of *Opuntia* in home gardens, is generally lower than that of the *monte* system, since commonly one or two individuals are found per variety in each home garden and each home garden has between four and nine varieties.

In these spaces, it is possible to find species that are part of the forest or secondary forest vegetation. These are individuals that were there before building the house and that are therefore varieties from the *monte* system that they decided not to remove

from the home garden. This is the practice called tolerance by Casas et al. (1997, 2007), Blancas et al. (2010, 2013), and other authors. This practice was identified to occur on varieties such as *cardona* (*O. streptacantha*), *rebusca* (*O. hyptiacantha*), and *xoconostles* (*O. joconostle*). In addition, there are varieties that have been brought from other localities and that are transplanted, such as the *blanca* (*O. albicarpa*), *amarilla*, and *colorada* (*O. ficus-indica*) varieties.

It is rare that varieties from the *monte* system are transplanted to home gardens since it is perceived that these varieties are abundant in the surroundings, and it is therefore unnecessary to have them in the garden. Even so, it may occur when an interesting variety is identified in the *monte*, and when a cactus is transplanted, it is carried out by using cladodes between the months of January to March, so that it manages to generate roots before the rain season starts, thus preventing rotting of the selected individual's propagules. One of the most common maintenance practices is pruning, which is usually annual and is carried out with the objective of preventing the *Opuntia* growing too much, no more than 2.5–3 m in height, as this complicates the collection of *nopalitos* and fruits. Pruning is practiced in both the *monte* systems and home gardens.

Traditional Products of *Opuntia* Species

Prickly pears are used in LG in different ways, as referred to above. In this section, we describe some of the most important uses that are scarcely known and poorly documented. Fruits are harvested from wild, silvicultural managed and cultivated *Opuntia* plants without peeling, their peel is used as fodder and to prepare fertilizers, the seeds are transformed for the production of oils and the pulp for cosmetic dyeing. These new uses have intensified harvesting *Opuntia* fruits. We still do not know the impacts that the change in harvest intensity have, especially on populations from forest and agroforests; therefore, the investigations should be continued to document these aspects. Similarly, harvesting cladodes have been increased associated to their use as fodder, and the impact should be studied.

These are relatively recent uses of *Opuntia*, but some others are ancient and scarcely documented. Some of these forms of use have motivated for centuries management of prickly pears and such management have had implications as mobiles of domestication and diversification of several species, among them, outstandingly, *O. streptacantha*. But both processes and their results require more research. In the following subsections, we describe some of these traditional products in LG and the needs of research for a deeper understanding of their biocultural value.

Prickly Pears and Sweet Products

Through the workshop and semistructured interviews we identified about 30 families that are dedicated to collecting *Opuntia* fruits to transform them into the traditional food products *colonche*, *melcocha*, *queso de tuna* and *miel de tuna*. These foods are commercialized within the town or in the neighboring markets of the municipality of Ocampo, in the state of Guanajuato and in Villa de Arriaga, in the state of San Luis Potosí. The production of these issues generated during the availability season of

prickly pears is relevant, as it contributes to the economic security of the producers for several more months, complementing the main economic activities (rainfed agriculture and cattle arising). But these products may be the main source of income in areas where there is no agricultural production.

Queso De Tuna and Melcocha: *Opuntia* Sweets

Queso de tuna and *melcocha* are traditional Mexican sweets, mainly prepared with *O. streptacantha* fruits. However, when the availability of these fruits decreases, other *Opuntia* fruits are used, mainly *O. hyptiacantha* and *O. megacantha*. The main attributes for the selection of other fruits are a high-density consistency of the pulp, a recognized sweet flavor, a medium-size fruit, few spines, and red color of the pulp.

For producing these issues, the prickly pears are collected in a plastic container and peeled in the collecting site or transported to the house and peeled there. Almost ten plastic containers of 20 l of fruits are required to produce approximately 20 kg of *queso de tuna* or *melcocha*. After peeled, the fruits are moved to a mill called *arnero* in order to squash the fruit pulp and obtain their juice. Then, seeds are removed, and the juice placed in a copper pan, where it is cooked for almost 9 h. It is important for producers to carefully remove all the seeds, because otherwise the cooked product will display a smoky flavor. *Opuntia* logs previously collected in the *monte* are used to maintain the fire for cooking prickly pears juice.

When the pulp starts boiling, the producers (called *melcocheros*) remove the content from the copper pan and places it into a stone or a hardwood container known as *batea* in order to beat this dense paste. This current action will give the paste a harder consistency and a brown color similar to a jam, indeed, *melcocha* is a kind of traditional jam. On the other hand, the *queso de tuna* must be beaten for longer time and more vigorously. After it has been strengthened, the paste is placed in a table and cut into a square or circular shape and stored under cold conditions until it is commercialized in the local and regional markets.

Through the current ethnobiological assessment we identified only three elderly *melcocheros* with an age interval of 65–85 years old in the community, who have maintained this family trade. In fact, this could be one of the last generation of producers, because there is a low interest to continue with these products among young people. Also, because of the current competition generated by the junk food industry, which has displaced traditional foods from the diet and sweets are no the exception. In addition, these products hardly can compete with industrialized facilities in the market, or it is just a product not having a good reception by the consumers.

Colonche: A Traditional Fermented Juice

Colonche is a traditional fermented beverage that can be prepared with fruits of at least 17 cacti species. Colonche is the common name of this beverage in the region of the Southern Mexican Highlands, where it is mainly prepared with several *Opuntia* species, although the most common and favored by the producers and consumers is that prepared with *O. streptacantha* fruits (Ojeda-Linares et al. 2020, 2021). It has a low alcoholic content with an intense magenta color, a thick texture, and a sweet flavor. It is produced during the fruit production season of *O. streptacantha* from August to November. Local



Fig. 6 Colonche production: (a) Producer of the fermented beverage “colonche,” pouring the fermented product from a clay pot, which is the main recipient where the fermentation takes place; (b) another producer with plastic containers for colonche production; and (c) a producer of melcocha with his frinder for extracting the *Opuntia streptacantha* juice. (Photos by the authors)

people have organized the “Colonche Fair,” which is carried out in September. The fermentation to prepare colonche is mostly spontaneous and occurs in clay pots that have been maintained by several generations of the producers (Fig. 6). These pots are extraordinarily important since recent studies demonstrate that they are reservoirs of microorganisms responsible for colonche fermentation; thus, when one of these pots is broken, people make use of its pieces in new fermentation (Ojeda-Linares et al. 2020, 2021). In addition, some people use to inoculate their colonche by using a portion of fermented juice that remained from previous production. This ferment is called *xinaiste*, *pie*, or *semilla*, which hints the concept existing in people’s mind that this material is responsible for starting (and directing) the fermentation process. Colonche can also be prepared with fruits from other species such as *O. hyptiacantha* or *O. megacantha* which have ripening time later than that of *O. streptacantha*, but since they have similar qualities to the latter species, their use allows extending the season of colonche production. This beverage with cacti fruit, receives different names among distinct cultures. It has been reported to be produced in northern Mexico by using fruit of saguaro (*Carnegiea gigantea*), cardón (*Pachycereus pringlei*), and pitaya (*Stenocereus thurberi*). Also, it is produced in southern-central Mexico, using fruits of several species of *Opuntia* and columnar cacti like *Stenocereus stellatus*, *S. pruinosus*, *Escontria chiotilla*, and most importantly, *Pachycereus weberi* (Ojeda-Linares et al. 2020).

Traditional Varieties of *Opuntia*, Classification, and Attributes

In LG, we identified 30 local varieties belonging to 11 species, and we ranked them based on free lists provided by local people. *Opuntia streptacantha*, locally known as *nopal cardón* and its fruit, called *tuna cardona*, is the most valued species in the community. It is the one that has the highest number of uses and that is perceived to have the better attributes.

A classification of the prickly pear fruits based on the phenotypic attributes that people use to identify them, together with the abundance perceived, the management spaces where they are maintained and managed, and the uses they make to the *Opuntia* species and varieties are reported in Table 1.

The ordering of varieties through the NMDS (stress value: 0.0757) shows two groups (Fig. 7). The group at the left of the plot includes the varieties that are clustered according to their attributes, mainly flavor, size, and consistency, also those that are found mainly in home gardens; these are the cases of the *blanca* (*O. albicarpa*), *amarilla*, or *chapeada* (*O. ficus-indica*) varieties, which produce prickly pears much sweeter, larger, and juicier than the rest. We also identified in this cluster three varieties whose provenance is from the *monte* but that are present in home gardens, because they have fruits of large size, sweet taste, and juicy consistency. *Jarrita* (*O. megacantha*) and *cardona* (*O. streptacantha*) varieties have characteristics that make them highly valued and used; therefore, they are present close to people's homes.

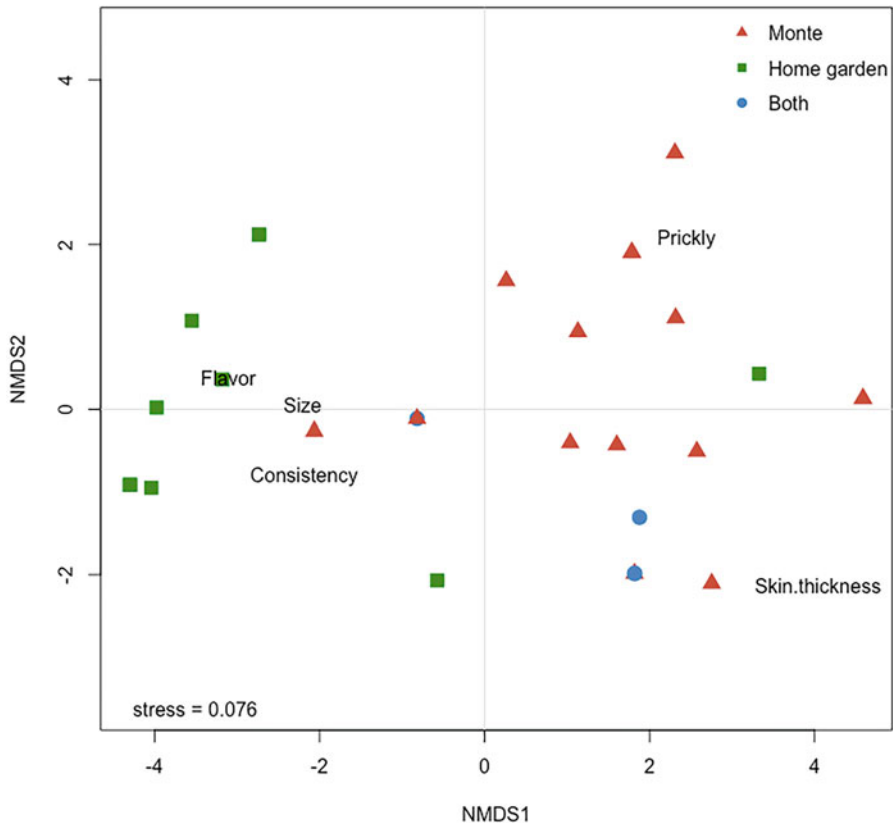


Fig. 7 Nonmetric multidimensional scaling (NMDS) of the attributes used to identify varieties of prickly pears present in monte (triangles), home gardens (squares), and in both (circles) in Laguna de Guadalupe

At the right side of the plot, it is possible to see a group of varieties from the *monte*, except the *duraznillo* variety (*O. leucotricha*), which was found in the home garden because it is small, acidic, and has a high number of spines. This group is characterized by having a greater number of spines and a thicker skin than the varieties grouped on the left. All these features are characteristic of the wild *Opuntia* species. The group of the *monte* prickly pears is more dispersed, with respect to those of home garden, due to their greater variability in attributes of the varieties and species that are part of this group. Another relevant case is *O. joconostle*, which has acid flavor and high skin thickness and is present in the *monte*, but because of its importance in traditional medicine and food, this species is maintained in home gardens.

Conclusion

Traditional knowledge is composed by the complex interactions of collective knowledge; it is based on the characteristics of the group, the type of interactions, and practices performed to maintain the biological resources and ecosystems (Berkes et al. 2000). The body of knowledge is maintained, replicated, and continually innovated by the local human groups. It is stratified, where subgroups due to its characteristics may have a greater depth or specificity on some components of the ecosystems. And it is also dynamic not only with the intrinsic processes of increasing knowledge of all human cultures, but also because of the influence of the changing cultural and ecological contexts where people live and interact with.

In our study, traditional knowledge over *Opuntia* species in LG shows much of the general pattern delineated above. Most of it is generalized among the local population, the inhabitants refer to that knowledge, and practices were inherited from their parents and grandparents. Nevertheless, the group of people called *coloncheros* and those who are involved in the gathering and other uses related to the prickly pear fruits exhibit a specialized knowledge on attributes of species and varieties of this genus. The local producers of *melcocha* and *colonche* are key members of the community due to their extensive knowledge about the diversity of prickly pears, their attributes, and the classification of each one of them. Thus, they recognize a greater number of varieties and specific traits associated with the fruits and also with the *Opuntia* plants than other members of the community. When classification cannot be easily described, the *cardona* prickly pear is used as a point of reference (for comparison of attributes), because it is the most used and appreciated. But outstandingly, they possess specialized knowledge in relation to management of plants in the two main management systems recognized (the *monte* and homegardens), and about the details of techniques used for preparing the products referred to.

To summarize, we identified that traditional knowledge over *Opuntia* species goes through a specialization process in Laguna de Guadalupe. These results are similar to what was reported in other cultural groups as the Ixcatec in the state of Oaxaca (Rangel-Landa et al. 2016) and the Purépechas in Michoacán state (Farfán et al. 2018). So far, the traditional knowledge of *Opuntia* species in Laguna de Guadalupe is maintained and shared by the entire community, which makes it resistant and resilient.

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References

- Albuquerque UP, da Cunha LVFC, De Lucena RFP, Alves RRN, editors. Methods and techniques in ethnobiology and ethnoecology. New York: Springer; 2014.
- Anaya-Pérez MA, Bautista-Zane R. El nopal forrajero en México: del siglo XVI al siglo XX. *Agric Soc Desarrollo*. 2008;5(2):167–83.
- Arba M, Falisse A, Choukrallah R, Sindic M. Biology, flowering, and fruiting of the cactus *Opuntia* spp.: a review and some observations on three varieties in Morocco. *Braz Arch Biol Technol*. 2017;60:e17160568.
- Barros C, Buenrostro I. El maravilloso nopal: sus propiedades alimenticias y curativas. Grijalbo, Mexico City, Mexico; 1998.
- Beccaro GL, Bonvegna L, Donno D, Mellano MG, Cerutti AK, Nieddu G, Chessa I, Bounous G. *Opuntia* spp. biodiversity conservation and utilization on the Cape Verde Islands. *Genet Resour Crop Evol*. 2015;62:21–33.
- Benavides-Ríos EC. Patrones de sensibilidad de las cactáceas ante el cambio climático en la Península de Baja California, México (Master in science dissertation). La Paz: Centro de Investigaciones Biológicas del Noroeste S. C.; 2016.
- Berkes F. Implementing ecosystem-based management: evolution or revolution? *Fish Fish*. 2012;13(4):465–76.
- Berkes F, Colding J, Folke C. Rediscovery of traditional ecological knowledge as adaptive management. *Ecol Appl*. 2000;10(5):1251–62.
- Blancas J, Casas A, Rangel-Landa S, Torres I, Pérez-Negrón E, Solís L, Moreno AI, Delgado A, Parra F, Arellanes Y, Caballero J, Cortés L, Lira R, Dávila P. Plant management in the Tehuacán-Cuicatlán Valley. *Econ Bot*. 2010;64(4):287–302.
- Blancas J, Casas A, Pérez-Salicrup D, Caballero J, Vega E. Ecological and sociocultural factors influencing plant management in Náhuatl communities of the Tehuacán Valley, Mexico. *J Ethnobiol Ethnomed*. 2013;9:39.
- Branniff-Cornejo B. La región septentrional mesoamericana. In: Rojas Rabiela T, Murra JV, editors. *Historia general de América Latina*. Vol. I: Las sociedades originarias. Madrid: Organización de las Naciones Unidas para la Educación, la Ciencia y la Cultura; 1999. p. 229–60.
- Bravo-Hollis H. Las cactáceas de México, vol. 1. Mexico City: Universidad Nacional Autónoma de México; 1978.
- Caruso M, Curró S, Las Casas G, La Malfa S, Gentile A. Microsatellite markers help to assess genetic diversity among *Opuntia ficus indica* cultivated genotypes and their relation with related species. *Plant Syst Evol*. 2010;290:85–97.
- Casas A. Silvicultura y domesticación de plantas en Mesoamérica. In: Rendón B, Rebollar S, Caballero J, Martínez MA, Pérez MA, editors. *Plantas, cultura y sociedad. Estudio sobre la relación entre seres humanos y plantas en los albores del Siglo XXI*. Mexico City: Universidad Autónoma Metropolitana-Iztapalapa/SEMARNAP; 2001. p. 123–57.
- Casas A. Uso y Manejo de Cactáceas Columnares Mesoamericanas. *CONABIO. Biodiversitas*. 2002;40:18–23.
- Casas A, Barbera G. Chapter 9. Mesoamerican domestication and diffusion of cacti. In: Nobel PS, editor. *Cacti: biology and uses*. Los Angeles: University of California Press; 2002. p. 143–62.
- Casas A, Vázquez MC, Viveros JL, Caballero J. Plant management among the Nahuatl and the Mixtec of the Balsas River Basin: an ethnobotanical approach to the study of plant domestication. *Hum Ecol*. 1996;24(4):455–78.

- Casas A, Caballero J, Mapes C, Zárate S. Manejo de la vegetación, domesticación de plantas y origen de la agricultura en Mesoamérica. *Bol Soc Bot Méx (Bot Sci)*. 1997;61:31–47.
- Casas A, Caballero J, Valiente-Banuet A. Use, management and domestication of columnar cacti in south-central Mexico: a historical perspective. *J Ethnobiol*. 1999;19(1):71–95.
- Casas A, Valiente-Banuet A, Viveros JL, Dávila P, Lira R, Caballero J, Cortés L, Rodríguez-Arévalo I. Plant resources of the Tehuacán Valley, Mexico. *Econ Bot*. 2001;55(1):129–66.
- Casas A, Otero-Arnaiz A, Pérez-Negrón E, Valiente-Banuet A. In situ management and domestication of plants in Mesoamerica. *Ann Bot*. 2007;100(5):1101–15.
- Casas A, Blancas JJ, Pérez Negrón E, Torres García I, Vallejo Ramos M, Rangel Landa S, Farfán-Heredia B. Manejo sustentable de recursos naturales: naturaleza y cultura. In: Arias G, Hernández F, Zurita-Zafra M, Uranga López ML, editors. *Sustentabilidad e interculturalidad Paradigmas entre la relación cultura y naturaleza*. Pátzcuaro: Universidad Intercultural Indígena de Michoacán; 2014. p. 10–9.
- Chahdoura H, Barreira JCM, Barros L, Santos-Buelga C, Ferreira ICFR, Achour L. Phytochemical characterization and antioxidant activity of the cladodes of *Opuntia macrorhiza* (Engelm.) and *Opuntia microdasys* (Lehm.). *Food Funct*. 2014;5(9):2129–36.
- Chávez-Moreno CK, Tecante A, Casas A. The *Opuntia* (Cactacea) and *Dactylopius* (Hemiptera: Dactylopiidae) in Mexico: a historical perspective of use, interaction and distribution. *Biodivers Conserv*. 2009;18:3337–55.
- Colunga P. Variación morfológica, manejo agrícola y grados de domesticación de *Opuntia* spp. en el Bajío guanajuatense (Master thesis). Texcoco: Colegio de Postgraduados Montecillos; 1984.
- Colunga-García Marín P, Hernández-Xolocotzi E, Castillo A. Variación morfológica, manejo agrícola y grados de domesticación de *Opuntia* spp. en el Bajío Guanajuatense. *Agrociencia*. 1986;65:7–49.
- Cornejo-Denman A, Arreola-Nava H. Usos actuales y potenciales de las cactáceas de Jalisco. XIX Semana de la Investigación Científica. Avances en la Investigación Científica del CUCBA, Zapopan; 2008. p. 201–8.
- Dávila-Aranda P, Rodríguez-Arévalo I, García-Rojas L, Lecona-Rodríguez A. Ethnobotany and ex situ conservation of plant genetic resources in México. In: Lira R, Casas A, Blancas JJ, editors. *Ethnobotany of Mexico*. New York: Springer; 2016. p. 475–89.
- Del Castillo RF. Composición y estructura de una nopalera bajo situaciones contrastantes de exposición de ladera y herbivoría. *Bol Soc Bot Méx (Bot Sci)*. 2000;65:5–22.
- Eberhard DM, Simons GF, Fennig CD, editors. *Ethnologue: languages of the world*. 24th ed. Dallas: SIL International; 2021.
- Farfán B, Casas A, García-Frapolli E, Moreno-Calles AI, Castilleja A. Ethnoecology of the interchange of wild and weedy plants and mushrooms in Phurépecha markets of Mexico: economic motives of biotic resources management. *J Ethnobiol Ethnomed*. 2018;14(5):1–19.
- Felger R, Moser MB. *People of the desert and sea. Ethnobotany of the Seri Indians*. Tucson: University of Arizona Press; 1985.
- Figueredo-Urbina CJ, Álvarez-Ríos GD, García-Montes MA, Octavio-Aguilar P. Morphological and genetic diversity of traditional varieties of agave in Hidalgo State, Mexico. *PLoS One*. 2021;16(7):e0254376.
- Flannery KV. *Guilá Naquitz*. New York: Academic Press; 1986.
- Flores-Flores JL, Yeaton RI. La importancia de la competencia en la organización de las comunidades vegetales en el Altiplano Mexicano. *Interciencia*. 2000;25(8):365–71.
- Flores-Flores JL, Yeaton RI. The replacement of arborescent cactus species along a climatic gradient in the southern Chihuahuan Desert: competitive hierarchies and response to freezing temperatures. *J Arid Environ*. 2003;55(4):583–94.
- Glimm-Lacy J, Kaufman PB. *Botany illustrated: introduction to plants, major groups, flowering plant families*. New York: Springer; 2006.
- González-Espinosa M. Interacciones entre fenología, elementos bióticos y disturbio por pastoreo en las nopaleras del centro de México. In: Aguirre-Rivera JR, Reyes Agüero JA, editors. *Memoria del VIII congreso nacional y VI internacional sobre el conocimiento y aprovechamiento del nopal*. San Luis Potosí: Instituto de Investigación de Zonas Desérticas, Universidad Autónoma de San Luis Potosí; 1999. p. 342–59.

- Griffith MP. Experimental hybridization in northern Chihuahuan desert region *Opuntia*. *Aliso*. 2001;20:37–42.
- Griffith MP. The origins of an important cactus crop, *Opuntia ficus-indica* (Cactaceae): new molecular evidence. *Am J Bot*. 2004;91(11):1915–21.
- Guzmán U, Arias S, Dávila P. Catálogo de cactáceas mexicanas. Mexico City: Universidad Nacional Autónoma de México (UNAM), Comisión Nacional para el conocimiento y uso de la Biodiversidad (CONABIO); 2003.
- Hernández-Xolocotzi E. Aspects of plant domestication in Mexico: a personal view. In: Ramamoorthy TP, Bye R, Lot A, Fa J, editors. *Biological diversity of Mexico. Origins and distribution*. Oxford, UK: Oxford University Press; 1993. p. 733–56.
- Heuzé V, Tran G. Prickly pear (*Opuntia ficus-indica*). In: *Feedipedia, a programme by INRA, CIRAD, AFZ, Rome*; 2017.
- Illoldi-Rangel P, Ciarleglio M, Sheinvar L, Linaje M, Sánchez-Cordero V, Sarkar S. *Opuntia* in México: identifying priority areas for conserving biodiversity in a multi-use landscape. *PLoS One*. 2012;7(5):e36650.
- Kaur M, Kaur A, Sharma R. Pharmacological actions of *Opuntia ficus indica*: a review. *J Appl Pharm Sci*. 2012;2(7):15–8.
- Konings A, Konings G. *Cacti of Texas in their natural habitat*. Austin: Cichlid Press; 2009.
- Kumar K, Singh D, Singh RS. *Cactus pear: cultivation and uses*. Bikaner: ICAR–Central Institute for Arid Horticulture Bikaner; 2018.
- Labra M, Grassi F, Bardini M, Imazio S, Guiggi A, Citterio S, Banf E, Sgorbati S. Genetic relationships in *Opuntia* Mill. genus (Cactaceae) detected by molecular marker. *Plant Sci*. 2003;165(5):1129–36.
- MacNeish RS. A summary of the subsistence. In: Byers D, editor. *The prehistory of the Tehuacan Valley. Volume 1. Environment and subsistence*. Austin: University of Texas Press; 1967. p. 290–331.
- MacNeish RS. *The origins of agriculture and settled life*. London: University of Oklahoma Press; 1992.
- Martínez M. *Catálogo de nombres vulgares y científicos de plantas mexicanas*. Mexico City: Fondo de Cultura Económica; 1993.
- Martínez-González CR, Gallegos-Vázquez C, Scheinvar L. Re-evaluation of *Opuntia matudae* (Cactaceae). *Phytotaxa*. 2019;423(3):158–70.
- Maxwell JA. *Qualitative research design. An interactive approach*. 3rd ed. Thousand Oaks: Sage; 2013.
- Mazri MA. Cactus pear (*Opuntia* spp.) breeding. In: Al-Khayri J, Jain S, Johnson D, editors. *Advances in plant breeding strategies: fruits*. New York: Springer; 2018.
- Mercado-Muñoz F. *Diversidad y sistemática del género Opuntia s. s., en la región de Los cabos, Baja California Sur, México* (Master in sciences dissertation). La Paz: Centro de Investigaciones Biológicas del Noroeste; 2014.
- Molina-Velázquez, M. *Caracterización, ordenación y clasificación numérica en nopal (Opuntia spp.) mediante atributos morfológicos y físico-químicos* (Master in sciences dissertation). Marín: Universidad Autónoma de Nuevo León; 2001.
- Monteiro A, Cheia VM, Vasconcelos T, Moreira I. Management of the invasive species *Opuntia stricta* in a Botanical Reserve in Portugal. *Weed Res*. 2005;45(3):193–201.
- Nava-Martínez LH. *La Triada del Semidesierto*. *Rev Chicomoztoc*. 2019;1(2):146–80.
- Nefzaoui A, Ben Salem H. Cacti: efficient tool for rangeland rehabilitation, drought mitigation and to combat desertification. *Acta Hort*. 2002;581:295–315.
- Nefzaoui A, Louhaichi M, Ben SH. Cactus as a tool to mitigate drought and to combat desertification. *J Arid Land Stud*. 2014;24:121–4.
- Ojeda-Linares CI, Vallejo M, Lappe-Oliveras P, Casas A. Traditional management of microorganisms in fermented beverages from cactus fruits in Mexico: an ethnobiological approach. *J Ethnobiol Ethnomed*. 2020;16(1):1–12.
- Ojeda-Linares CI, Álvarez-Ríos GD, Figueredo-Urbina CJ, Islas LA, Lappe-Oliveras P, Nabhan GP, Casas A. Traditional fermented beverages of Mexico: a biocultural unseen foodscape. *Foods*. 2021;10(10):2390.

- Oksanen J, Guillaume F, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin P, O'Hara R, Simpson G, Solymos P, Stevens H, Szöcs E, Wagner H. *Vegan: Community Ecology Package. Ordination methods, diversity analysis and other functions for community and vegetation ecologists*, version 2.4-3; 2019.
- Palevitch D, Earon G, Levin I. Treatment of benign prostatic hypertrophy with *Opuntia ficus-indica* (L.) Miller. *J Herbs Spices Med Plants*. 1993;2:45–9.
- Pareek O, Singh R, Vashishtha B. Performance of cactus pear (*Opuntia ficus-indica* (L.) Mill.) clones in hot arid region of India. *J Prof Assoc Cactus Dev*. 2003;5:121–30.
- Paz-Navarro A. Nohpalli: El nopal tunero. Manejo Tradicional de *Opuntia* spp. (Cactaceae) en la localidad de Laguna de Guadalupe, Guanajuato (Bachelor dissertation). Morelia: Licenciatura en Ciencias Ambientales, Escuela Nacional de Estudios Superiores, Universidad Nacional Autónoma de México; 2021.
- Pennington C. *The Tepehuan of Chihuahua: their material culture*. Salt Lake City: University of Utah Press; 1969.
- Pinedo-Espinoza JM, Aguirre-Mancilla CL, Jiménez-Alvarado R, Raya-Pérez JC, Iturriaga G, Ramírez-Pimentel JG, Hernández-Fuentes AD. Bioactive compounds and antioxidant activity evolution during the ripening process of 12 *Opuntia* spp. fruit accessions. *Emir J Food Agric*. 2017;29:138–46.
- Powell AM, Weedin JF. *Cacti of the Trans-Pecos and adjacent areas*. Austin: Texas Tech University Press; 2004.
- Prat L, Franck N. Morphology and anatomy of Platyopuntiae. In: Inglese P, Mondragon C, Nefzaoui A, Sáenz C, editors. *Crop ecology, cultivation and uses of cactus pear*. Rome: FAO; 2017. p. 21–8.
- R Core Team. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing; 2020.
- Rangel-Landa S, Casas A, Rivera-Lozoya E, Torres I, Vallejo M. Ixcatec ethnoecology: biocultural principles of plant management in Oaxaca, Mexico. *J Ethnobiol Ethnomed*. 2016;12:30.
- Reyes-Agüero JA. Variación morfológica de *Opuntia* (Cactaceae) y la relación con su domesticación en la Altiplanicie Meridional de México (Doctoral dissertation). México City: Facultad de Ciencias, Universidad Nacional Autónoma de México; 2005.
- Reyes-Agüero JA, Aguirre-Rivera JR. Agrobiodiversity of cactus pear (*Opuntia*, Cactaceae) in the Meridional Highlands Plateau of Mexico. *J Nat Resour Dev*. 2011;1:1–9.
- Reyes-Agüero JA, Vallejo M. Matorral crasicaule. In: *La biodiversidad en San Luis Potosí*, vol. II. México City: Secretaría de Ecología y Gestión Ambiental de San Luis Potosí, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO); 2019. p. 47–54.
- Reyes-Agüero JA, González-Medrano F, García-Pérez JD. Flora vascular de la Sierra Monte Grande, municipio de Charcas, San Luis Potosí, México. *Bol Soc Bot Méx*. 1996;58:31–42.
- Reyes-Agüero JA, Aguirre-Rivera JR, Hernández HM. Systematic notes and a detailed description of *Opuntia ficus-indica* (L.) Mill. (Cactaceae). *Agrociencia*. 2005a;39:395–408.
- Reyes-Agüero JA, Aguirre-Rivera JR, Flores-Flores JL. Variación morfológica de *Opuntia* (Cactaceae) en relación con su domesticación en la Altiplanicie Meridional de México. *Interciencia*. 2005b;30(8):476–84.
- Reyes-Agüero JA, Aguirre-Rivera JR, Valiente-Banuet A. Reproductive biology of *Opuntia*: a review. *J Arid Environ*. 2006;64:549–85.
- Reyes-Agüero JA, Aguirre-Rivera JR, Carlin-Castelán F, González-Durán A. *Catálogo de las principales variantes silvestres y cultivadas de Opuntia en la Altiplanicie Meridional de México* (no. 634.7750216 C3); 2009.
- Rivera-Villanueva JA, Riojas-López ME, Mellink E. The Tunal Grande and associated tuna groves. Habitat of hunter gatherers. *Rev Col San Luis*. 2020;9(19):151–76.
- Rzedowski J. Relaciones geográficas y posibles orígenes de la flora de México. *Bot Sci*. 1965;29:121–77.
- Rzedowski J. *Vegetación de México*. México City: Limusa; 1978.
- Rzedowski J. Diversity and origins of the phanerogamic flora of Mexico. In: Ramamoorthy TP, Bye R, Lot A, Fa J, editors. *Biological diversity of Mexico. Origins and distribution*. Oxford, UK: Oxford University Press; 1993. p. 129–46.

- Sáenz C. Chapter 7. Industrial production of non-food products. In: Agro-industrial utilization of cactus pear. FAO Rural Infrastructure and Agro-Industries Division, in collaboration with the International Technical Cooperation Network on Cactus (FAO-CACTUSNET). Rome: FAO; 2013.
- Samah S, De Teodoro Pardo CV, Serrato-Cruz MA, Valadez-Moctezuma E. Genetic diversity, genotype discrimination, and population structure of Mexican *Opuntia* sp., determined by SSR markers. *Plant Mol Biol Report*. 2016;34:146–59.
- Sánchez-Mejorada H. Mexico's problems and programmes monitoring trade in common and endangered cacti. *Cactus Succul J Great Brit*. 1982;44(2):36–8.
- Scheinvar L. *Opuntia albicarpa* Scheivar una nueva especie para la ciencia del estado de México. *Rev Jardín Bot Nacl*. 1999;20:267.
- Scheinvar L, Gallegos C. Estado del conocimiento de las especies del nopal (*Opuntia* spp.) productoras de xoconostles silvestres y cultivadas. Informe final. Mexico City: UNAM-CONABIO; 2011.
- Scheinvar L, Olalde G, Sule D. Especies silvestres de nopales mexicanos, proyecto no. GE005. Informe final. México City: Autónoma de México, Instituto de Biología, SNIB-CONABIO, Universidad Nacional; 2011.
- Shackleton RT, Witt ABR, Piroris FM, van Wilgen BW. Distribution and socio-ecological impacts of the invasive alien cactus *Opuntia stricta* in eastern Africa. *Biol Invasions*. 2017;19:2427–41.
- Shirazinia R, Rahimi VB, Kehkhaie VR, Sahebkar A, Rakhshandeh H, Askari VR. *Opuntia dillenii*: a forgotten plant with promising pharmacological properties. *Journal of Pharmacopunct*. 2019;22(1):16–27.
- Smith E. Plant remains. In: Byers D, editor. The prehistory of the Tehuacan Valley. Volume 1. Environment and subsistence. Austin: University of Texas Press; 1967. p. 220–5.
- Smith JJ, Borgatti SP. Salience counts and so does accuracy: correcting and updating a measure for free-list-item salience. *J Linguist Anthropol*. 1997;7:208–9.
- Soberón J, Golubov J, Sarukhán J. The importance of *Opuntia* in Mexico and routes of invasion and impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *Fla Entomol*. 2001;84(4):486–92.
- Tesfay YB, Kreyling J. The invasive *Opuntia ficus-indica* homogenizes native plant species compositions in the highlands of Eritrea. *Biol Invasions*. 2021;23:433–42.
- Toledo VM, Barrera-Bassols N. La memoria biocultural: la importancia ecológica de las sabidurías tradicionales. Barcelona: Icaria Editorial; 2008.
- Toledo VM, Ordóñez MJ. The biodiversity scenario of Mexico: a review of terrestrial habitats. In: Ramamoorthy TP, Bye R, Lot A, Fa J, editors. Biological diversity of Mexico. Origins and distribution. Oxford, UK: Oxford University Press; 1993. p. 757–78.
- Valadez-Moctezuma E, Samah S, Luna-Paez A. Genetic diversity of *Opuntia* spp. varieties assessed by classical marker tools (RAPD and ISSR). *Plant Syst Evol*. 2015;301:737–47.
- Valiente-Banuet A, Casas A, Pickersgill B, Caballero J. Ethnobotany and domestication in Xoconochtil *Stenocereus stellatus* (Cactaceae), in the Tehuacán Valley and La Mixteca, Baja México. *Econ Bot*. 1997;52:279–92.
- Velásquez-Milla D, Casas A, Torres-Guevara J, Cruz-Soriano A. Ecological and socio-cultural factors influencing in situ conservation of crop diversity by traditional Andean households in Peru. *J Ethnobiol Ethnomed*. 2011;7(1):1–20.
- Wang X, Felker P, Paterson A, Mizrahi Y, Nerd A, Mondragon-Jacobo C. Cross hybridization and seed germination in *Opuntia* species. *J Prof Assoc Cactus Dev*. 1996;1:49–60.
- Yahia EM, Saenz C. Cactus pear (*Opuntia* species). In: Yahia EM, editor. Postharvest biology and technology of tropical and subtropical fruits. Cambridge, UK: Woodhead Publishing; 2011. p. 290–331.