

Cuatro Ciénegas Basin: An Endangered Hyperdiverse Oasis

Maria C. Mandujano
Irene Pisanty
Luis E. Eguiarte *Editors*

Plant Diversity and Ecology in the Chihuahuan Desert

Emphasis on the Cuatro Ciénegas Basin

 Springer

Cuatro Ciénegas Basin: An Endangered Hyperdiverse Oasis

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This book series describes the diversity, ecology, evolution, anthropology, archeology and geology of an unusually diverse site in the desert that is paradoxically one of the most phosphorus-poor sites that we know of. The aim of each book is to promote critical thinking and not only explore the natural history, ecology, evolution and conservation of the oasis, but also consider various scenarios to unravel the mystery of why this site is the only one of its kind on the planet, how it evolved, and how it has survived for so long.

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Foreword

Perhaps no landscape in North America has ecological contrasts and visual juxtapositions as dramatic and awe-inspiring as the Cuatro Ciénegas Basin in the Chihuahuan Desert. After miles of travel through hyperarid landscapes dominated by the low-lying xerophilous vegetation known as desert scrub, you arrive at an archipelago of oases unmatched by any habitat for 500 km in any direction. Cool blue waters with an abundance of aquatic life provide a stark contrast to pale gypsum-derived dunes, with cacti such as *Grusonia* which literally crawl across the sands!

You feel as if you have stumbled upon an ecological and evolutionary puzzle as complex as that which Darwin discovered in the Galapagos. That is because the levels of biodiversity in the basin are unusually high compared to any other desert, but its levels of endemism outdistance those of any other habitat complex found elsewhere in the arid regions of the Americas. Diversity and endemism are often negatively correlated, but in Cuatro Ciénegas, this is not the case.

If that puzzle alone were not enough to keep your mind active and your senses attentive, the landscapes and waterscapes of Cuatro Ciénegas face daunting challenges with regard to “whole ecosystem conservation.” We find it difficult—if not disturbing—to see the integrity of this habit complex reduced to a few fragments, for the synergies between the geohydrology, the flora, and the fauna form an indivisible, “unified field” for inquiry and appreciation.

We are now fortunate enough to have some of the finest and most forward-thinking ecologists, biogeographers, and biosystematists in Mexico to help us solve these puzzles. While scientific collaborations have advanced the knowledge of the Basin’s biogeography for over a quarter-century, never have we had such a remarkable synthesis of a single landscape in arid America. I am grateful to the editors and contributors of this volume for their detailed treatment of biogeographic patterns that ripple out from the Basin to the Chihuahuan Desert as a whole. But more than that, their collective lifework on the ecology and evolution of desert and aquatic organisms found in the Cuatro Ciénegas stand as some of the most exciting field research ever accomplished in any of the deserts of North America.

You cannot spend time “beyond the rainbow’s end” in Cuatro Ciénegas without feeling that your own life and sense of what a desert can be have been forever

changed and enriched. While many of us have felt this shift in perception, until now, few of us have had the full scientific context which may explain why we so strongly feel that way.

I am humbled and gratified by the great work that the editors have brought together for this unprecedented volume. The editors were already among my list of heroes before they joined forces for this book; but now they deserve to be honored as “true desert saints.” May the power of their synthesis convince both local communities and national policy-makers that the ecosystem-level conservation and restoration of Cuatro Ciénegas habitat complexes deserve a public investment commensurate with the distinctiveness of this unforgettable landscape.

Sonora, Mexico
March 2019

Gary Paul Nabhan

Preface

Plants are great storytellers, despite their innate silent life. After “Once upon a time...,” they can tell us about the movement of continental masses, the behavior of water, and the vicissitudes of climate through really long-term time-lapses. They can also tell stories of more recent events and even tell us what happened a few days ago. If you “listen” to them, you will hear such stories, and it will be hard to differentiate between fantasy and reality, for plants can tell awesome things about themselves and about the places they live in, as they are such sensitive, green, picky species.

In this book, we recapitulate some stories accumulated by plants that inhabit the Chihuahuan Desert, in Northern Mexico and Southwestern USA, and more specifically of those living in the Cuatro Ciénegas Basin. Stories based on carefully gathered scientific information are presented in 19 chapters in this compendium. These chapters describe aspects of the life history of plants, vegetation distribution, origin and affinities with landforms, and biologically obligated interactions such as water dependence or plant pollination.

Deserts, whose allure deserves to be sensed, have environmental conditions that can be identified and understood simply by looking at plant adaptations such as their reduction of leaves to spines, their different structures that retain water, their cuticles that diminish evapotranspiration, their different photosynthetic paths, physiologies, and complex life cycles and morphologies, including different shapes and number of flowers, fruits, and seeds as well as contrasting reproductive strategies. In the unbelievably beautiful Cuatro Ciénegas Basin—which is at the heart of the Chihuahuan Desert—plant species and vegetation types tell us about a patchy environment resulting from ancient conditions that have been changing for millions of years. In each patch, plants deal with lack of nutrients, high salinity, gypsum soils, or even flooded conditions. No one could expect less from a place located within the Chihuahuan Desert with an elevation of ca. 700 m above sea level and surrounded by very high and steep mountains that were originally covered by an ancient ocean. In the actual basin, complex underground hydrological systems still emerge and create the pools (locally called *pozas*), lakes, creeks, and rivers that make this place

unique not only because of its beauty but also because of its biological history and its ecological characteristics and importance.

Environmental and specific diversity in the Chihuahuan Desert in general, and in the Cuatro Ciénegas Basin in particular, has long been recognized as outstanding. A global ecological overview and in-depth studies of specific processes are reviewed in this book. The Chihuahuan Desert is the largest hot desert in North America and has a complex geologic, climatic, and biogeographical history, which affects today's distribution of vegetation and plants and generates complex phylogeographic patterns. The knowledge of the changing climatic conditions allows the reconstruction of paleogeographic vegetation. The high number of endemic species is related to this complex set of environmental traits. The modern distribution of environments, including aquatic and subaquatic systems, riparian environments, gypsum dunes and gypsum-rich soils, low content of phosphorus and organic matter, and high salinity, combined with an extreme climate demands a set of adaptations to respond to different combinations of these conditions. Plants are distributed in a patchy pattern according to punctual variations, and many of them respond with a considerable morphological plasticity to different resources and conditions. Physiological, morphological, and ecological variability allows the identification of different adaptations to different environments that can be shown in different manners in species and individuals.

Plants tell us their stories through morphology, physiology, all sorts of ecological traits, and, last but not least, their genetics. The authors of the different chapters proved to be nosy enough to ask interesting questions in very different fields and scales, and the stories that plants had to tell are embodied, with a deep scientific insight, in each of them. That is enough to make this book valuable. However, the aim of this book is not only to show what our favorite storytellers tell us about their lives, but also to gather in a single volume information that is relevant to all stakeholders—not only researchers and enlightened public—but specifically decision-makers at all levels. Not even the very adaptable plants of the desert are able to neglect the intense disturbance the Cuatro Ciénegas Basin has been undergoing for more than a decade already, putting plants, as well as all domains of life, in jeopardy. The effects of this disturbance go beyond the scientific interest that Cuatro Ciénegas represents. These effects involve local and regional aspects, including the livelihood and well-being of the people that live in the Chihuahuan Desert.

The consequences of the disturbance of desert ecosystems and in particular of the Cuatro Ciénegas Basin include the loss of water bodies with the concomitant extinction of endemic species, ranging from plants and fishes to bacteria and the stromatolites they form, which are only found in this and few other places in Mexico and in the world. Ecosystem services are being lost, and not even plants, with all their adaptive baggage, can ignore how serious the loss of water can be in an arid zone like this. Aquatic, subaquatic, and riparian plants are quickly disappearing in the Chihuahuan Desert, and punctual dramatic vegetation changes can be observed, and they are described in this book.

As we said, plants are great storytellers and have great stories to tell. We hope the information gathered in this book can help reverse the worst story plants from

Cuatro Ciénegas can tell nowadays: the irreversible disturbance and eventual disappearance of water in one of the most relevant arid lands of the world. Once all ecosystem services are lost, little will remain to be told. We hope this book will help both to understand plant life in Cuatro Ciénegas as much as to reverse the damage that has already been done and to prevent further mismanagement.

This book comprises a foreword by Professor Gary Nabham and 19 peer-reviewed chapters written by expert scientists from Mexico and the USA. The book is organized into three broad sections. The first section includes four chapters that represent a general overview of the origin, evolution, diversity, and floristic composition of the Chihuahuan Desert (Chaps. 1, 2, 3, and 4). The next section comprises nine chapters that provide fascinating examples of the ecology of different plant groups and landforms that are emblematic of Cuatro Ciénegas Basin, as well as of different desert species subject to management and use (Chaps. 5, 6, 7, 8, 9, 10, 11, 12, and 13). For instance, deserts are frequently viewed as not having any resources for human societies, because agriculture and cattle raising are limited. However, local dwellers have found ways to use a rich diversity of wild species, as it happens with *candelilla* from which wax to prevent the early maturation of citric, among other uses, is extracted. Wild species are an important source of resources for the rural inhabitants of arid and semiarid regions, and Cuatro Ciénegas is not an exception. The last section includes six chapters that describe the environmental problems that are risking the preservation of riparian vegetation in Cuatro Ciénegas such as invasive species and water overexploitation and about scientific strategies that may support or lead to conservation (Chaps. 14, 15, 16, 17, 18, and 19). Along the reading of the chapters in this last section, you will find why the Chihuahuan Desert is so special, and how cacti were identified as the most important group in specific environments like *bajadas*, characterized by high diversity values, while gypsophytes and gypsovagues of different phylogenies including species with restricted distribution and endemics proved to constitute one of the most diverse gypsophyllous floras in the world. Sexual reproduction, clonality, floral biology, life history, and germination were studied for several species of which very little was known, providing useful information for the recovery of the Cuatro Ciénegas populations. Riparian species, that form a discrete landscape that indicates the presence of water, are losing their habitat as the water bodies desiccate, but proved to be good colonizers of newly opened habitats formed by the drastic disturbance of underground water system. Thus, they are found colonizing numerous sinkholes formed due to the subsurface water flow of water, as well as the dry beds of the now dry water bodies. Germination patterns and morphological and ecological variations of these species, as well as the interactions among them, can help explain their colonizing ability in an unusual succession process. Genetic analysis of native and invasive species helped understand their distribution and differentiation as well as their invasive potential.

This book is the fourth in a series of books on the ecology, natural history, biodiversity, evolution, conservation, and geology of Cuatro Ciénegas and the surrounding Chihuahuan Desert. The first book, edited by Valeria Souza, Gabriela Olmedo-Álvarez, and Luis E. Eguiarte (2018), described the general natural and

physical settings of Cuatro Ciénegas, including 9 chapters dealing with general aspects of the ecology, natural history, geological history, climate, and the microbiology of the area, including a brief description of the different scientific research programs that have been conducted in the valley. In the second book in the series, edited by Felipe García-Oliva, James Elser, and Valeria Souza, and also published in 2018, the ecosystem ecology and geochemistry of Cuatro Ciénegas were carefully described in 12 chapters, again with emphasis, but not exclusively, on micro-organism and the aquatic systems. The third book of the series analyzed the rich animal diversity in Cuatro Ciénegas and contiguous Chihuahuan Desert, and was carefully edited by Fernando Alvarez and Margarita Ojeda and published in 2019. In 14 chapters, the animal diversity and biogeographical patterns of diversity were described and analyzed, ranging in studies from the helminth parasites and soil microarthropods to birds and mammals. The future two books in this series will deal with the astrobiological relevance of Cuatro Ciénegas and the conservation perspectives of this beautiful but endangered valley.

We are sure that you will enjoy reading the series and will discover all sorts of interesting and amazing details from our favorite silent storytellers.

Mexico City, Mexico

María C. Mandujano
Irene Pisanty
Luis E. Eguiarte

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Chapter 1

Diversity and Uniqueness at Its Best: Vegetation of the Chihuahuan Desert



José Alejandro Zavala-Hurtado and Monserrat Jiménez

Abstract About 10,500 years ago at the beginning of the Holocene, the first humans in the north of Mexico found themselves in the middle of an aridification process that culminated about 4000 years ago in the modern Chihuahuan Desert, which is the largest desert in North America and the second most diverse on Earth with about 3400 plant species, including cacti that reach their greatest diversity in this region. Nearly 25% of the species are endemic, most notably in the Cuatro Ciénegas Basin with 86 plant taxa. The climate is hot-dry with summer rain. Most of the region has calcareous soils, although there are important outcrops of gypsum in patchy arrangements throughout the region. These environmental pressures have generated a variety of adaptive strategies among the organisms evolving here, resulting in great species' richness. Creosote bush (*Larrea tridentata*) dominates in the driest sites, frequently accompanied by lechuguilla (*Agave lechuguilla*) and tarbush (*Flourensia cernua*); in the *bajadas* (lowlands) we find the less drought-tolerant plants such as yuccas (*Yucca* spp.) and sotol (*Dasylyrion wheeleri*). Grasslands integrate grass and shrub mosaics, with species such as bush muhly (*Muhlenbergia porteri*), bluegrass (*Bouteloua gracilis*), and purple three-awn (*Aristida purpurea*). In gypsum outcrops a diverse flora with several endemics is found. The vegetation is highly variable, responding to water availability, physical–chemical and biological dynamics of soils and fires, among other factors. Currently, there are serious pressures modifying the natural dynamics of the desert, such as the indiscriminate extraction of water, agricultural and livestock practices, water and soil contamination, and invasive species that threaten this unique place.

Keywords Arid lands · Cuatro Ciénegas Basin · Desert plants communities · Cacti · Endemic plants

to Carlos Montaña and Francisco González-Medrano, in memoriam

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In the Beginning

The groups of hunters that inhabited what is now the north of Mexico and the Southeastern United States some 10,500 years ago, in the Early Holocene (Epstein 1980), had the sight of vast wooded areas. In these woods a transition was already taking place from the mesic subalpine forest, dominated by (Pinaceae) *Picea* and limber pine (*Pinus flexilis*), to a more xeric forest with *Pinus edulis*, *Pseudotsuga menziesii*, and (Fagaceae) *Quercus gambelii* (Van Devender et al. 1977). In this forest matrix, elements characteristic of the current Chihuahuan Desert, such as (Asparagaceae) *Agave lechuguilla*, *Dasyllirion* sp., *Nolina* sp., *Yucca rostrata*, *Y. torreyi*, (Cactaceae) *Echinocereus dasyacanthus*, *Opuntia macrocentra*, (Leguminosae) *Acacia roemeriana*, and (Ephedraceae) *Ephedra aspera*, among others, were already there (Wells 1966, 1977).

A constant decrease in humidity, despite some intervals of increasing humidity in the Late Holocene, generated the expansion of the desert, and it is estimated that the Chihuahuan Desert acquired its current characteristics only about 4000 years ago (Polyak and Asmerom 2001). Thus, it is one of the youngest deserts on Earth.

The Physical Scenario

The Chihuahuan Desert is the largest in North America and, together with the Great Sandy-Tanami Desert of Australia and the Namib-Karoo of Southern Africa (Olson and Dinerstein 1998) is among the most diverse deserts worldwide. Its extension is shared by the USA (New Mexico and Texas) and Mexico (Chihuahua, Coahuila, Durango, Zacatecas, San Luis Potosí, and Nuevo León), ignoring political borders and intended walls. As happens with almost any natural system, the precise definition of its limits is practically impossible (Gleason 1926); different criteria (climate, soil, vegetation, vertebrates) have been used to demarcate its boundaries (Granados-Sánchez et al. 2011), but there is not a consensus regarding the extension of the Chihuahuan Desert. Area estimations go from 350,000 km², using climatic criteria based on the De Martonne aridity index (Schmidt Jr. 1979), to 507,000 km² from the distribution of its flora (Goettsch and Hernández 2006), and up to 629,000 km² when the adjacent Central Plateau is included as part of this ecoregion in a conservation proposal (Dinerstein et al. 2001). For this reason, the biodiversity evaluations of the Chihuahuan Desert can vary widely, although in this chapter an extension of 507,000 km² is taken as reference.

Chihuahuan Desert covers an altitudinal range of 1000–2000 m asl, although within the region there are mountain ranges of up to 3050 m. The largest area of the desert is composed of calcareous soil on limestone, although some parts of the mountains are of igneous origin (Ferrusquía-Villafranca 1993). There is an important presence of alluvial fans with deep soil and localities with gypsum outcrops (Ochoterena et al. 2020, this volume). It is also common to find endorheic basins or

“bolsones” (González-Medrano 2012). The climate is dry with very hot summers and cold winters. The average annual rainfall is 235 mm, most of which occurs during the summer.

Diversity of Plant Communities

Although a first visual impression of the Chihuahuan Desert could consider it a somewhat monotonous ecosystem with a high predominance of only a few species, it harbors an extraordinary richness of plant species. This richness is clearly related to high environmental heterogeneity. There have been 3382 species reported (Henrickson and Johnston 2007), of which almost a quarter (826 species) are endemic to the region (Villarreal-Quintanilla et al. 2017). This plant richness has been systematized into different types of vegetation considering the patterns of coexistence of groups of species in different patches with particular environments (Table 1.1). These habitats are defined fundamentally by the type of substrate, geomorphology, and microclimatic variations of temperature and precipitation. This characterization of vegetation types varies with different authors; up to 17 different types of vegetation have been proposed in the Chihuahuan Desert (Johnston 1977). However, Rzedowski (1965, 1978) and González-Medrano (2012), authors with greater experience and recognized expertise in the definition of vegetation types, at a general level and specifically of arid ecosystems, recognized three general types of desert plant communities for the Chihuahuan Desert. Difference in criteria and conceptions of the vegetation is reflected in the fact that the three types of vegetation recognized by these authors are not fully equivalent. Considering both proposals, the three general vegetation types are:

1. Microphyllous desert scrub (Fig. 1.1) is found in alluvial fans and foothill depressions, on calcareous sedimentary material derived from limestone or, in some cases, igneous rock. The substrates are coarse-textured loams on gravelly plains and slopes (Schulz and Muldavin 2015). It is also known as Chihuahuan Desert scrub (Brown 1982). This scrub is the most conspicuous and extensive along the Chihuahuan Desert and is dominated by shrubby species with small leaves that may have thorns. The most conspicuous and abundant component is the creosote bush (Zigophyllaceae) *Larrea tridentata* and, to a lesser extent, the tarbush (Compositae) *Flourensia cernua*. Other important elements of this scrub are: (Fouquieriaceae) *Fouquieria splendens*, (Compositae) *Zinnia acerosa*, *Parthenium incanum*, (Euphorbiaceae) *Jatropha dioica*, (Koeberliniaceae) *Koeberlinia spinosa*, (Leguminosae) *Prosopis glandulosa*, *Mimosa aculeaticarpa*, *M. zygophylla*, *Acacia berlandieri*, *A. farnesiana*, *A. tortuosa*, *Eysenhardtia polystachya*, (Asparagaceae) *Agave lechuguilla*, *A. scabra*, *Yucca carnerosana*, and *Y. filifera*, among others (Granados-Sánchez et al. 2011, Ezcurra et al. 2020, this volume; Flores Vázquez et al. 2020, this volume). Also noteworthy are the cacti with several species of *Ariocarpus*, *Astrophytum*,

Table 1.1 Main traits of vegetation types in the Chihuahuan Desert

| Type of vegetation | Physiognomy | Representative species | Distribution in the Chihuahuan Desert ^a | Main threats ^b |
|-----------------------------|------------------------|---|---|-----------------------------------|
| Microphyllous desert scrub | Shrubby | <i>Larrea tridentata</i> , <i>Flourensia cernua</i> , <i>Fouquieria splendens</i> , <i>Zinnia acerosa</i> , <i>Astrophytum spp.</i> , <i>Coryphantha spp.</i> | Is the vegetation matrix of the Chihuahuan Desert in plains, alluvial fans, basins, piedmont | OG, CC, LUC, HS, P, IPC, HF |
| Rosetophyllous desert scrub | Arboreal rosette | <i>Agave spp.</i> , <i>Yucca spp.</i> | Bolsón de Mapimí, Durango; trans-Pecos, Texas; Cuatro Ciénegas and mountain range, Coahuila | OG, CC, LUC, HS, P, IPC, HF |
| Lechuguillal | Arboreal rosette | <i>Agave lechuguilla</i> , <i>Hechtia glomerata</i> , <i>Agave striata</i> , <i>Yucca carnerosana</i> , <i>Agave asperima</i> | Coahuila; South of Zacatecas; North of San Luis Potosí | OG, CC, LUC, HS, P, IPC, HF |
| Izotal | Arboreal rosette | <i>Yucca carnerosana</i> , <i>Yucca filifera</i> , <i>Yucca rigida</i> , <i>Larrea tridentata</i> , <i>Cylindropuntia imbricata</i> , <i>Cylindropuntia leptocaulis</i> | Potosino-Zacatecano plateau | OG, CC, LUC, HS, P, IPC, HF |
| Crassicaulous desert scrub | Thorny tall succulent | <i>Myrtillocactus geometrizans</i> , <i>Cylindropuntia imbricata</i> , <i>Cylindropuntia tunicata</i> , <i>Opuntia leucotricha</i> , <i>Opuntia streptacantha</i> , <i>Stenocereus griseus</i> | South and Southeast of San Luis Potosí; South and Southeast of Zacatecas | OG, CC, LUC, HS, P, IPC, HF |
| Grassland | Perennial grasses | <i>Bouteloua gracilis</i> , <i>Bouteloua curtipendula</i> , <i>Bouteloua eriopoda</i> , <i>Bouteloua barbata</i> , <i>Aristida adscensionis</i> , <i>Aristida curvifolia</i> | North of Chihuahua; Southwest Arizona; South New Mexico and Texas; Margin of the Sierra Madre Oriental; North of Coahuila | OG, CC, F, WM, LUC, SE, HS, P, HF |
| Halophytic vegetation | Herbaceous and shrubby | <i>Acacia greggii</i> , <i>Allenrolfea occidentalis</i> , <i>Atriplex canthocarpa</i> , <i>Atriplex canescens</i> , <i>Clappia suaedifolia</i> | Bolsón de Mapimí, Chihuahua; Cuatro Ciénegas Coahuila; Trans-Pecos, Brewster Co., Texas; Vanegas, San Luis Potosí | CC, F, WM, LUC, HS, M, P, CP, HF |

(continued)

Table 1.1 (continued)

| Type of vegetation | Physiognomy | Representative species | Distribution in the Chihuahuan Desert ^a | Main threats ^b |
|--------------------------------------|-------------|---|---|----------------------------------|
| Gypsophilous vegetation | Herbaceous | <i>Tiquilia hispidissima</i> , <i>Atriplex canescens</i> , <i>Calylophus hartwegii</i> , <i>Ephedra torreyana</i> , <i>Frankenia jamesii</i> , <i>Bouteloua breviseta</i> , <i>Mentzelia perennis</i> | Cuatro Ciénegas, Coahuila; Mazapil, Zacatecas; Los Cerritos, San Luis Potosí; Río Nazas, Durango; Chihuahua center; Southwest and Northwest of Nuevo León; North of San Luis Potosí; Bolsón de Mapimí, Durango; Río Grande, Texas | CC, F, WM, LUC, HS, M, P, CP, HF |
| Chaparral | Shrubby | <i>Quercus intricata</i> , <i>Quercus mohriana</i> , <i>Quercus vaseyana</i> , <i>Quercus laceyi</i> , <i>Quercus hypoxantha</i> , <i>Quercus pringlei</i> , <i>Fraxinus greggii</i> , <i>Arctostaphylos pungens</i> | Sierra El Carmen, Coahuila; Brewster Co., Trans-Pecos, Texas; Río Grande, Chihuahua | CC, F, LUC, HS, P, CP, HF |
| Montane woodlands | | | | |
| Pynion-Juniper low-stature woodlands | Arboreal | <i>Pinus cembroides</i> , <i>Juniperus monticola</i> , <i>Juniperus deppeana</i> , <i>Juniperus flaccida</i> , <i>Arbutus xalapensis</i> , <i>Pinus greggii</i> | Southeast of Arizona and Southwest New Mexico; Sierra de Parras, Sierra El Carmen and South of Coahuila | F, CC, LUC, HS, P, HF |
| Coniferous forests | Arboreal | <i>Cupressus arizonica</i> , <i>Juniperus pachyphlaea</i> , <i>Pinus arizonica</i> , <i>Pinus ayacahuite</i> , <i>Populus tremuloides</i> , <i>Pinus teocote</i> , <i>Acer brachypterum</i> , <i>Quercus gravesii</i> | Sierra El Carmen, Coahuila; Bolsón de Mapimí, Santa Elena canyon, Chihuahua | F, CC, LUC, HS, P, HF |
| <i>Abies</i> forests | Arboreal | <i>Abies</i> sp., <i>Pinus ayacahuite</i> , <i>Populus tremuloides</i> , <i>Pseudotsuga menziesii</i> , <i>Abies coahuilensis</i> , <i>Pinus arizonica</i> | Low part of Coahuila; South of Zacatecas; North of San Luis Potosí | F, CC, LUC, HS, P, HF |

(continued)

Table 1.1 (continued)

| Type of vegetation | Physiognomy | Representative species | Distribution in the Chihuahuan Desert ^a | Main threats ^b |
|---------------------|-------------|--|--|---------------------------|
| Riparian vegetation | Arboreal | <i>Populus nigra</i> , <i>Salix babylonica</i> , <i>Prosopis glandulosa</i> , <i>Cercidium texanum</i> , <i>Chilopsis linearis</i> | Río Grande and tributaries, Texas | CC, WM, LUC, HS, P, HF |

^aBecause of the amplitude of distribution of most vegetation types, only some representative sites are shown

^bMain threats: *OG* Overgrazing; *CC* Climatic change; *F* Fires; *WM* Water management; *LUC* Land use change; *SE* Shrub encroachment; *HS* Human settlements; *M* Mining; *P* Air, water, and soil pollution; *IPC* Illegal plant collection; *HF* Habitat fragmentation



Fig. 1.1 Microphyllous desert scrub of *Larrea tridentata* (creosote bush) near Van Horn, Texas. Photo by Leaflet, licensed under the Creative Commons Attribution-Share Alike 3.0 Unported (<https://creativecommons.org/licenses/by-sa/3.0/deed.en>) license

Coryphantha, *Echinocactus*, *Echinocereus*, *Escobaria*, *Ferocactus*, *Lophophora*, *Mammillaria*, *Opuntia*, and *Turbincarpus* (Granados-Sánchez et al. 2011; Flores Vázquez et al. 2020, this volume). Creosote bush scrub has increased its extension, particularly in the last 150 years, by invading large areas previously occupied by grasslands, mainly in the north of the Chihuahuan Desert (Alvarez et al. 2011).

2. Rosetophyllous desert scrub (Fig. 1.2) is found in hills formed of sedimentary material, mainly limestone, although it is also found on rocky substrates of igneous origin. This scrub is dominated by plants with succulent leaves arranged in



Fig. 1.2 Rosetophyllous desert scrub. Izotal of *Yucca carnerosana* near San Luis Potosí. Photo by Tomás Castelazo, licensed under the Creative Commons Attribution-Share Alike 2.5 Generic license

the form of a rosette, in individuals with arboreal physiognomy (e.g., *Yucca* spp.) or without an apparent stem, with leaves emerging from the base of the plant (e.g., *Agave* spp.). They form high density patches of individuals on hills with limestone substrates. Within this type of vegetation, several different types of communities have been described:

- Lechuguillal, a desert scrub established in lower parts of the limestone slopes, usually below 1400 m. The dominant species is (Asparagaceae) *Agave lechuguilla*, frequently accompanied mainly by *Agave striata*, *Yucca carnerosana*, and (Bromeliaceae) *Hechtia glomerata* (González-Medrano 2012). Other relevant species are (Asparagaceae) *A. asperrima*, *Dasyilirion cedrosanum*, *Nolina parviflora*, *Y. rigida*, (Scrophulariaceae) *Buddleja marrubiiifolia*, (Euphorbiaceae) *Euphorbia antisyphilitica*, *Jatropha dioica*, (Fouquieriaceae) *Fouquieria splendens*, (Cactaceae) *Opuntia stenopetala*, and (Compositae) *Parthenium argentatum*, among others (Granados-Sánchez et al. 2011). This scrub is also rich in herbaceous species such as (Compositae) *Eupatorium calophyllum*, *Verbesina pedunculosa*, *Zaluzania triloba*, *Ageratum corymbosum*, *Zinnia acerosa*, (Poaceae) *Bouteloua curtipendula*, (Polemoniaceae) *Loeselia coerulea*, (Brassicaceae) *Lesquerella fendleri*, and (Linaceae) *Linum scabrellum*, among others (González-Medrano 2012).
- Izotal, a type of arboreal community dominated physiognomically by the *Yucca* genus that is generally established in relatively deep soil or caliche on alluvial fans.

3. Crassicaulous desert scrub (Fig. 1.3) is found mainly in the south and center of the Chihuahuan Desert, on substrate of igneous material (rhyolites or basalt). Physiognomically, they are thorny, tall succulent plants with a predominance of cacti. Among the dominant species are (Cactaceae) *Myrtillocactus geometrizans*, *Cylindropuntia imbricata*, *Cylindropuntia tunicata*, *Opuntia leucotricha*, *Opuntia streptacantha*, *Stenocereus griseus*, *Echinocactus platyacanthus*, *Stenocactus multicostatus*, (Euphorbiaceae) *Jatropha dioica*, *Euphorbia maculata*, (Asparagaceae) *Yucca carnerosana*, *Agave lechuguilla*, (Compositae) *Verbesina oreopola*, *Parthenium incanum*, *Gymnosperma glutinosum*, (Leguminosae) *Mimosa zygophylla*, *Eysenhardtia polystachya*, (Poaceae) *Bouteloua curtipendula*, *Bouteloua gracilis*, *Stipa eminens*, (Convolvulaceae) *Dichondra argentea*, (Anacampserotaceae) *Talinopsis frutescens*, (Oleaceae) *Menodora coulteri*, and (Nyctaginaceae) *Boerhavia intermedia*, among others (González-Medrano 2012).

In the Chihuahuan Desert we find other types of vegetation that occupy smaller areas than the three mentioned above, but which are important for their contribution to plant diversity and constitute peculiar environmental scenarios for the evolution of different lineages of desert plants (Pinkava 1984; Meyer 1986; Granados-Sánchez et al. 2011; Moore and Jansen 2007):

4. Grasslands (Fig. 1.4a) are dominated by perennial grasses, “zacates,” in flat lowlands with relatively more developed soil and higher humidity conditions (Granados-Sánchez et al. 2011). They occupy about 20% of the surface of the Chihuahuan Desert, although it is estimated that between 25 and 50% of the cur-



Fig. 1.3 Crassicaulous desert scrub with *Opuntia* sp., *Cylindropuntia imbricata*, *Myrtillocactus geometrizans*, *Agave* sp., and *Prosopis glandulosa* near San Luis Potosí. Photo by Evelyn M. Rosas-García



Fig. 1.4 Gypsophilous vegetation with *Dasyilirion cedrosanum* in Cuatro Ciénegas, Coahuila. Photo by Eduardo Casas Hernández

rent desert scrubs were grasslands in the past (Dinerstein et al. 2001). Among the dominant grass species are (Poaceae) *Bouteloua gracilis*, *B. curtipendula*, *B. eriopoda*, *B. barbata*, *Aristida adscensionis*, *A. curvifolia*, *A. purpurea*, *Hilaria mutica*, *Eragrostis lehmanniana*, *Sporobolus airoides*, and *S. palmeri*, among others (Granados-Sánchez et al. 2011). Currently, stands where the grassland species are interspersed with individuals of microphyllous species are frequently found, particularly *Larrea tridentata*, forming ecotones between the two types of vegetation. These transition zones are evidence of the process of invasion of the creosote bush over the grassland (Dinerstein et al. 2001; Gibbens et al. 2005; Alvarez et al. 2011; Moreno de las Heras et al. 2016).

5. Halophytic vegetation is distributed throughout the Chihuahuan Desert, frequently around dry lakes, beaches, or in salt flats at the bottom of basins with internal drainage. Various salts, derived from weathering and filtration of mineral material or salty sediment, accumulate in the soil (Hendrickson 1977). Halophytic vegetation accounts for the lowest number of species in the Chihuahuan Desert; they are primarily herbaceous plants although some shrubs can be found. The dominant species include (Leguminosae) *Acacia greggii*, *Prosopis glandulosa*, (Amaranthaceae) *Allenrolfea occidentalis*, *Atriplex acanthocarpa*, *A. canescens*, *Salsola tragus*, *Suaeda mexicana*, (Compositae) *Clappia suaedifolia*, (Poaceae) *Cynodon dactylon*, *Distichlis spicata*, *Sporobolus airoides*, (Solanaceae) *Lycium berlandieri*, and (Aizoaceae) *Sesuvium verrucosum*, among others (Granados-Sánchez et al. 2011). The majority of these species present some physiological

mechanism to face conditions of high salinity. Some accumulate salts in their tissues, while others reduce the concentration of salts by increasing their intake of water, which may imply an increase in the succulence or the deep vertical extension of their roots in order to exploit water tables (Hendrickson 1977).

6. Gypsophilous vegetation (Fig. 1.4) is found in outcrops of gypsum-rich substrate that sustain a community of endemic plants with a grassland appearance (Rzedowski 1955; Luévano 2009). Gypsum deposits on the Chihuahuan Desert are widely dispersed but well localized, ranging from less than one hectare to several km² in extension, and they have developed a diverse endemic flora that presumably has evolved through several million years, resulting in at least 200 species and plant varieties restricted to gypsum substrates on the Chihuahuan Desert (Moore and Jansen 2007; Ochoterena et al. 2020, this volume). Among the gypsophilic species found in these communities we can mention (Boraginaceae) *Tiquilia hispidissima*, (Amaranthaceae) *Atriplex canescens*, (Onagraceae) *Oenothera hartwegii*, (Ephedraceae) *Ephedra torreyana*, (Frankeniaceae) *Frankenia jamesii*, (Poaceae) *Bouteloua brevisetata*, *Sporobolus nealleyi*, *Sporobolus airoides*, (Loasaceae) *Mentzelia perennis*, (Boraginaceae) *Nama carnosus*, (Nyctaginaceae) *Acleisanthes lanceolata*, and (Compositae) *Sartwellia flaveriae*.
7. Chaparral consists of evergreen scrub characterized by plants with sclerophyllous leaves that have settled at mid elevations of the mountains (ca. 2000 m), often between grasslands and pine forests. These communities are dominated by oak species, such as (Fagaceae) *Quercus intricata*, *Q. mohriana*, *Q. vaseyana*, *Q. laceyi*, *Q. hypoxantha* and *Q. pringlei*, as well as other species such as (Oleaceae) *Fraxinus greggii*, (Ericaceae) *Arctostaphylos pungens*, (Berberidaceae) *Berberis trifoliolata*, (Rhamnaceae) *Ceanothus pauciflorus*, *Condalia ericoides*, (Rosaceae) *Cowania plicata*, *Cercocarpus montanus*, (Asparagaceae) *Dasylyrion* sp., *Nolina erumpens*, *Yucca carnerosana*, (Garryaceae) *Garrya ovata*, (Rhamnaceae) *Condalia ericoides*, (Anacardiaceae) *Rhus microphylla*, *R. trilobata*, and *R. virens* (Muldavin et al. 2004; Granados-Sánchez et al. 2011).
8. Montane woodlands: within the surface of the Chihuahuan Desert there are several mountain ranges above 1500 m with temperature, humidity, and soil conditions that allowed the establishment of wooded communities with a temperate affinity. Depending on altitude, slope orientation and inclination, as well as on the substrate, different types of forest communities can be recognized (Muldavin et al. 2004; Granados-Sánchez et al. 2011):
 - In the relatively lower parts with gentle slopes and shallow soil, still under xeric conditions, there are pinyon-juniper low-stature woodlands dominated by the pinyon pine, *Pinus cembroides*, which can form associations with (Cupressaceae) *Juniperus monticola*, *J. deppeana*, *J. flaccida* and different tree species such as (Ericaceae) *Arbutus xalapensis*, (Pinaceae) *Pinus greggii*, *P. edulis*, (Fagaceae) *Quercus chihuahuensis*, *Q. deserticola*, *Q. emoryi*, *Q. laeta* and (Asparagaceae) *Yucca carnerosana*.

- At higher altitudes up to 2300 m, on steep slopes and mountain tops, on igneous and karstic substrates, with climate patterns from temperate to cold, and with higher humidity, coniferous forests are established. The characteristic species of one of the modalities of these forests at an altitude of 2000 m are (Cupressaceae) *Hesperocyparis arizonica*, *Juniperus deppeana* var. *deppeana*, (Pinaceae) *Pinus arizonica*, *P. ayacahuite*, and (Salicaceae) *Populus tremuloides*. At higher altitudes, between 2300 and 3000 m, there are pine-oak forests, characterized by *Pinus arizonica*, *P. teocote*, (Sapindaceae) *Acer saccharum* var. *sinuosum*, *Cupressus* sp., *Juniperus* sp., (Fagaceae) *Quercus gravesii*, *Q. hypoleucoides*, and *Q. muehlenbergii*, among other species.
 - In the highest mountain ranges, above 2500 m, under a temperate-humid climate regime, high and closed fir (*Abies*) forests are established. The characteristic arboreal species are (Salicaceae) *Populus tremuloides*, (Pinaceae) *Abies* sp., *Pinus ayacahuite*, and *Pseudotsuga menziesii*, being also *Abies coahuilensis* and *Pinus arizonica*.
9. Riparian vegetation: arboreal plant communities established on the banks of streams and rivers are among the least studied communities in the Chihuahuan Desert (Soykan et al. 2012), despite being considered sites with high diversity. The dominant tree species are (Salicaceae) *Populus nigra*, *Salix babylonica*, (Leguminosae) *Prosopis glandulosa*, *Cercidium texanum*, and (Bignoniaceae) *Chilopsis linearis*. The invasive (Tamaricaceae) *Tamarix ramosissima* is also frequently found. Among the shrub species, (Compositae) *Baccharis glutinosa*, *Chloracantha spinosa*, (Leguminosae) *Prosopis juliflora*, and (Cannabaceae) *Celtis pallida* can be recognized (Cornell et al. 2008). Herbaceous ensemble is represented by many endemic species such as (Cyperaceae) *Carex potosina*, (Poaceae) *Bouteloua kayi*, (Potamogetonaceae) *Potamogeton clystocarpus*, (Compositae) *Helianthus neglectus*, *Chromolaena bigelovii*, (Caryophyllaceae) *Drymaria pachyphylla*, (Convolvulaceae) *Bonamia ovalifolia*, (Phyllanthaceae) *Phyllanthus ericoides*, (Gentianaceae) *Eustoma barkleyi*, (Lythraceae) *Ammannia grayi*, (Onagraceae) *Oenothera arida*, (Papaveraceae) *Argemone turnerae*, and (Solanaceae) *Solanum davisense* (Villarreal-Quintanilla et al. 2017). The diversity of these communities increases with the integration of elements of nearby associations, such as grasslands and scrubs (Soykan et al. 2012).

The Dynamic Nature of Chihuahuan Desert Communities

The Chihuahuan Desert communities present a high variability in their spatial and temporal dimensions, which contributes to their high biological diversity. This variability is driven primarily by the input of water, which is scarce and has unpredictable fluctuations at different time scales (Noy-Meir 1973). In addition, plants respond in different ways, depending on their life history characteristics and in different circumstances of their environmental envelope, mainly related to the

availability of water and nitrogen, which has been reported as a limiting element in arid ecosystems (Ladwig 2014).

The variety of landforms present in the region is also a determining factor of diversity. A study conducted in the south of the Chihuahuan Desert (Montaña 1990) shows the relationship between landforms and diversity of species and life forms in different types of vegetation. He found significant differences in species richness between landforms. Lowlands, hills, and mountains were the most diverse landforms, and the beaches and inter-dunes plains, the poorest. Foothills and dunes showed intermediate values. Although no significant differences in the composition of life forms between landforms were found, landforms actually differed in the relative cover of life forms. These differences would be a consequence of patterns of spatial and temporal distribution of species, regulated by the hydrological and radiation dynamics in the different landforms throughout the Chihuahuan Desert landscape. The author suggests that the lack of differentiation in the life forms' spectra between landforms would be an expression of the relatively young age of the Chihuahuan Desert.

One of the most notorious processes in the dynamics of Chihuahuan Desert communities is the continuous and accelerating invasion of microphyll shrub species, mainly the creosote bush, *Larrea tridentata*, and the honey mesquite, *Prosopis glandulosa*, over grassland communities. This process has been documented since 1858 (Gibbens et al. 2005). It has caused changes in the patterns of primary production, reduction of biodiversity, and an increase in wind and water erosion (Moreno de las Heras et al. 2016). It has been proposed that these changes, which some authors (Van Auken 2000; Ladwig 2014; Caracciolo et al. 2016) consider irreversible, are due to factors such as temperature increase, overgrazing, and poor management practices (Ladwig 2014). This would have caused alterations in soil characteristics and the dynamics of the seed bank that are reflected in the exacerbation of the asymmetry in the competitive capacity of grasses and shrubs (Montaña et al. 1995).

The Uniqueness of Cacti

The Chihuahuan Desert has the greatest richness of cacti species on Earth. Currently, 329 species have been reported (including five hybrids), of which 229 are endemic to the region (Hernández et al. 2004). This extraordinary diversity is not apparent to the naked eye, since the populations of most species are made up of small individuals that are difficult to observe. This has made completing an exhaustive inventory of the species actually present in the region problematic. Most of the registered species belong to the genera *Mammillaria* (79 species), *Opuntia* (46), *Coryphantha* (36), and *Echinocereus* (30) (Hernández et al. 2004).

The great diversity of cacti in the patches of vegetation that make up the types of the Chihuahuan Desert communities described above is inevitably related to the high environmental heterogeneity that characterizes the region, in geomorphology, solar radiation regime, water and nutrient availability, and soil (Goettsch and

Hernández 2006), as well as conditions generated by coverage of other plants. A large part of cactus species shows specific and restrictive habitat preferences, in addition to limited dispersal ability, which limits their distribution to only certain patches. However, there are more generalist species, such as opuntias, which have a wide distribution in the Chihuahuan Desert.

The adequate conditions for the establishment of several species of cacti in the harsh environment of the desert are generated by the coverage of other plants, the nurse plants, which favor microenvironments with higher humidity, less extreme temperatures, nutrient accumulation, and protection against predators, compared to the microenvironment found in unsheltered areas (Pérez-Sánchez et al. 2015). Although the importance of facilitating interactions in the determination of patterns of coexistence in desert communities has been documented for several species, there is still a long way to go to cover the extraordinary diversity of cacti in the Chihuahuan Desert (Muro-Pérez et al. 2011).

A Glimpse of the Uniqueness of the Cuatro Ciénegas Basin

The Cuatro Ciénegas basin (CCB) is a unique and extraordinary place in the Chihuahuan Desert, as it is highlighted in this volume (Ezcurra et al. 2020; Flores Vázquez et al. 2020; Ochoterena et al. 2020) and in companion books. This basin of only about 2000 km² has the highest number of endemic plant taxa (86), of a total of 902 plant species throughout the Chihuahuan Desert (Villarreal-Quintanilla et al. 2017). An area of 840 km² is under the Mexican regime of Flora and Fauna Protection Area (INE 1999).

CCB has an intricate water network with underground interconnections. At a superficial level, these systems form ponds, rivers, and lakes, building up a great diversity of terrestrial, aquatic, and semi-aquatic environments (Meyer 1973; Wolaver et al. 2006; Souza et al. 2012; Pisanty et al. 2013). The substrate is limestone, and the topography is very rough.

Pinkava (1984) recognizes eight major vegetation types for the CCB: (1) sacaton grasslands on the saline basin floor, (2) aquatic and semi-aquatic habitats, (3) gypsum dunes, (4) transition zone, (5) desert scrub on the *bajadas*, (6) chaparral, (7) oak-pine and oak woodlands, and (8) montane forests. Although these groups roughly correspond to those described previously in this chapter for the entire Chihuahuan Desert, they are not fully equivalent. Pinkava's desert scrub (5) encompasses microphyllous and rosetophyllous desert scrub, and his transition zone (4) is a kind of transition between the microphyllous desert scrub and the herbaceous vegetation of the halophytic communities. Grasslands (1), chaparral (6), woodlands (7), and montane forests (8) do correspond with those described for the Chihuahuan Desert. The gypsophyllous vegetation (3) found mainly in the surroundings of the Churince water system is noteworthy. In addition, associated with bodies of water, aquatic and semi-aquatic vegetation (2) can be found, including species such as (Nymphaeaceae) *Nymphaea ampla*, (Characeae) *Chara* spp., (Typhaceae) *Typha*

domingensis, (Cyperaceae) *Eleocharis* sp., and (Juncaceae) *Juncus torreyi* (INE 1999).

Diversity and Uniqueness Under Threat

The Chihuahuan Desert has a long history of human intervention, with increasing intensity and extension, that has necessarily modified the spatial and temporal patterns of natural communities. Perhaps the most notorious disturbance agents so far are changes in regimes from agriculture, grazing, and induced fires, as well as the overexploitation of aquifers in the region (Dinerstein et al. 2001). In addition, there is strong pressure from plant collecting, mainly cacti and other species such as *Fouquieria splendens* (CONABIO 2014).

Likewise, air and water pollution, mining, human settlement development, introduction of invasive species (Colin and Eguiarte 2020, this volume), and of course climate change are generating new scenarios for the coexistence and evolution of the species that inhabit the Chihuahuan Desert (Hultine et al. 2016).

The challenge of maintaining ecological and evolutionary processes in a matrix of inevitable pressures of human societies is huge. There is no proposal for an integrated solution. Here we only make a call to try to incorporate the knowledge of patterns and processes of the natural systems of the Chihuahuan Desert into whatever we intend to do with this unique and diverse ecosystem.

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