Robert W. Jones
C. Patricia Ornelas-García
Rubén Pineda-López
Fernando Álvarez *Editors*

Mexican Fauna in the Anthropocene

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Editors

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Editors
Robert W. Jones
Facultad de Ciencias Naturales
Universidad Nacional Autónoma de Querétaro
Juriquilla, Mexico

Rubén Pineda-López
Facultad de Ciencias Naturales
Universidad Autónoma de Querétaro
Juriquilla, Querétaro, Mexico

C. Patricia Ornelas-García
Colección Nacional de Peces
Instituto de Biologia
Universidad Nacional Autónoma de México
Ciudad Universitaria
Ciudad de México, Mexico

Fernando Álavarez
Colección Nacional de Peces
Instituto de Biologia
Universidad Nacional Autónoma de México
Ciudad Universitaria
Ciudad de México, Mexico

ISBN 978-3-031-17276-2 ISBN 978-3-031-17277-9 (eBook)
https://doi.org/10.1007/978-3-031-17277-9

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Foreword

The Anthropocene is known as the geological epoch whose main characteristics of change are the results of human activity, from the origin of agriculture to the present day, and we do not know for how much longer this perturbation can no longer be sustainable for the human race. It is a time marked by technological advances that have generated huge imbalances in ecosystems, fragmenting, polluting, and destroying them. Human intelligence and its capacity to modify the environment are outstanding, but this capacity has not been accompanied by an awareness of the long-term consequences of these modifications. In the same way that we build cities, we annihilate natural spaces and extirpate plants and animals. We have polluted the oceans, cleared much of our forests, caused faunal extinction (defaunation), and in general depleted the natural resources. All this started with apparently simple and innocuous actions by a very small human population a few thousand years ago, which has been accelerated in the last hundred years, putting all life on Earth at risk.

Some of the consequences are the drastic environmental imbalances in natural ecosystems, global warming, and the effects of pollution by agrochemicals, plastics, and microplastics. The present great threats to biodiversity include an increasing number of species in danger of extinction combined with the decline in the abundance of populations of many animals due to the loss of their habitats. This represents by some the sixth great mass extinction event of the planet. Significant decreases in abundance have been detected in many animal groups. Besides the well-known threats to large vertebrates, now even many small-sized fauna, such as insects and other arthropods, are recognized as threatened. Their reduction of populations causes important effects on ecosystem functions, such as pollination and the reduction of population control of pest species. Whole ecosystems are being threatened, such as coral reefs and tropical forests. Additionally, in marine ecosystems, decreases have been observed in useful species for man and for the maintenance of ecosystems, such as sharks and many fish species. For birds, losses of 30% in their abundance have been estimated in the last 50 years, and the impact on ecosystems is clearly significant but difficult to determine.

The present book has 27 chapters written by national and international authors examining the actual state, threats, and future of Mexican fauna in the face of the various and current ecological, social, and economic threats unique to the country. It presents not only a panorama of the present state and threats to distinct faunal taxonomic groups, but their associated ecosystems and processes associated with human impacts; a work that elucidates the details and magnitude of the problems and provides guidelines to carry out actions to reduce the consequences for the fauna of Mexico.

Teresa García Gasca
Rectora
Universidad Autónoma de Querétaro,
Santiago de Querétaro, Querétaro, México

Contents

Part I Introduction

Part II Faunal Groups

Part III Ecosystems

Part IV Processes

Contributors

Verónica Aguilar-Sierra Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, Mexico

Yuri V. Albores-Barajas Consejo Nacional de Ciencia y Tecnología/ Universidad Autónoma de Baja California Sur, La Paz, B.C.S, Mexico

Javier Alcocer Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Estado de México, México

R. Carlos Almazán-Núñez Laboratorio Integral de Fauna Silvestre, Facultad de Ciencias Químico-Biológicas, Chilpancingo de los Bravo, Guerrero, México

Javier Alvarado-Díaz Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México

Fernando Álvarez Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, México

León F. Álvarez-Sánchez Unidad de Informática Marina, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, México

Dan Anderson University of California, Davis, CA, USA

Rafael Ávila-Flores División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco, Villahermosa, Tabasco, México

M. Delia Basanta Centro de Ciencias Genómicas, Universidad Nacional Autónoma de México, Cuernavaca, Morelos, México

Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, Ciudad de México, México

Jorge L. Becerra-López Facultad de Ciencias Biológicas, Universidad Juárez del Estado de Durango, Gómez Palacio, Durango, México

Rosa Gabriela Beltrán-López Colección Nacional de Peces, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Colección Ictiológica del Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, Mexico

Julio S. Bernal Department of Entomology, Texas A&M University, College Station, TX, USA

Beatriz Bolivar-Cimé Instituto de Investigaciones Forestales, Universidad Veracruzana, Parque Ecológico El Haya, Xalapa, Veracruz, México

José Luis Bortolini-Rosales Departamento de Biología Comparada, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, México

Omar Calva Posgrado en Biociencias, Universidad de Sonora, and UMAE, Hermosillo, Sonora, México

José A. Castillo-Guerrero Centro Universitario de la Costa Sur, Universidad de Guadalajara, San Patricio-Melaque, Jalisco, CP, México

Diana G. Cordero-Torres Facultad de Ciencias Biológicas, Universidad Juárez del Estado de Durango, Gómez Palacio, Durango, México

María del Coro Arizmendi Laboratorio de Ecología, UBIPRO, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Estado de México, México

Alan P. Covich Institute of Ecology, Odum School of Ecology, University of Georgia, Athens, GA, USA

Horacio de la Cueva CICESE, Ensenada, B.C., México

Alexander Czaja Facultad de Ciencias Biológicas, Universidad Juárez del Estado de Durango, Gómez Palacio, Durango, México

Rodolfo Dirzo Department of Biology, Stanford University, Stanford, CA, USA

Brenda Durán Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, México

William R. Elliott , Georgetown, TX, USA

Elva Escobar Briones Laboratorio de Biodiversidad y Macroecología, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, México

Juan F. Escobar-Ibáñez Gnósis – Naturaleza con Ciencia A.C, Guadalajara, Jalisco, México

Doctorado en Ciencias de la Sustentabilidad, Instituto de Estudios Superiores de la Ciudad de México “Rosario Castellanos”. Center Gustavo A. Madero, México City, México

Maestría en Ciencias en Biosistemática y Manejo de Recursos Naturales y Agrícolas, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, Jalisco, México

José L. Estrada-Rodríguez Facultad de Ciencias Biológicas, Universidad Juárez del Estado de Durango, Gómez Palacio, Durango, México

Ana B. García-Andrade Laboratorio de Macroecología Evolutiva, Red de Biología Evolutiva, Instituto de Ecología, Xalapa, Veracruz, México

Mirna G. García-Castillo Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, México

Benigno Gómez Gómez El Colegio de la Frontera Sur, San Cristobal de las Casas, Chiapas, México

Emma P. Gómez-Ruiz Parque Ecológico Chipinque, A.B.P. San Pedro Garza García, Nuevo León, México

Alejandro Gordillo-Martínez Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México City, México

Roger Guevara Biología Evolutiva, Instituto de Ecología, A.C. (INECOL), Xalapa, México

Miguel Ángel Guzmán Díaz Departamento de Agricultura Sociedad y Ambiente, El Colegio de la Frontera Sur, Tapachula, Chiapas, México

Norma Hernández-Camacho Universidad Autónoma de Querétaro, Faculty of Natural Sciences, Queretaro, México

Johnattan Hernández-Cumplido Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, UNAM, Ciudad de México, Mexico

Mircea G. Hidalgo Mihart División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco, Villahermosa, Tabasco, México

María Luisa Jiménez Colección de Arácnidos e Insectos (CARCIB), Programa de Planeación Ambiental y Conservación, Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S, México

Robert W. Jones Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, México

Lynna M. Kiere Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México City, México

Nalleli E. Lara Díaz Laboratorio de Zoología, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, México

Carlos A. López González Laboratorio de Zoología, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, México

Issachar L. López-Cuamatzi Centro de Investigaciones Tropicales (CITRO), Universidad Veracruzana, Xalapa, Veracruz, México

Juan C. López Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, Mexico

M. Cristina MacSwiney-González Centro de Investigaciones Tropicales (CITRO), Universidad Veracruzana, Xalapa, Veracruz, México

Juan Maldonado Carrizales Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México

Alejandra Martínez de Castro Dubernard Departamento de Agricultura Sociedad y Ambiente, El Colegio de la Frontera Sur, San Cristóbal, Chiapas, México

Juan E. Martínez-Gómez INECOL, Xalapa, Veracruz, CP, México

Enrique Martínez-Meyer Instituto de Biología, Universidad Nacional Autónoma de México, México City, México

Samuel Meacham Centro Investigador del Sistema Acuífero de Quintana Roo A.C. (CINDAQ), Solidaridad, Quintana Roo, México

Rodrigo A. Medellín Instituto de Ecología, UNAM, Ciudad de México, México

Eduardo Mendoza Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, México

Mariana Munguía-Carrara Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, México

Adolfo G. Navarro-Sigüenza Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México City, México

C. Patricia Ornelas-García Colección Nacional de Peces, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, México

Carlos Palacios-Cardiel Laboratorio de Aracnología y Entomología, Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S, México

Eduardo Palacios CICESE Unidad La Paz, La Paz, B.C.S, México

José G. Palacios-Vargas Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México and Unión Mexicana de Agrupaciones Espeleológicas (UMAE), Mexico City, México

Gabriela Parra-Olea Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, Ciudad de México, México

Carlos Pedraza-Lara Ciencia Forense, Facultad de Medicina, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, México

A. Townsend Peterson Biodiversity Institute, Kansas, KS, USA

Reese Brand Phillips , Anchorage, AK, USA

Rubén Pineda-López Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, México

Javier Ponce-Saavedra Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México

David A. Prieto-Torres Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México

Ana F. Quijano-Ravell Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México

Benjamín Quiroz-Martínez Laboratorio de Ecología Numérica y Análisis de Datos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, México

Patricia Ramírez-Bastida Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México

Aurelio Ramírez-Bautista Centro de Investigaciones Biológicas (CIB), Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, México

Jorge L. Reyes Díaz Laboratorio de Zoología, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, México

Hugo E. Reyes-Aldana Department of River Ecology, Helmholtz Centre for Environmental Research – UFZ, Magdeburg, Germany

William D. Rodríguez Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, Jalisco, México

Octavio R. Rojas-Soto Red de Biología Evolutiva, Instituto de Ecología A. C., Xalapa, Veracruz, México

Romeo A. Saldaña-Vázquez Instituto de Investigaciones en Medio Ambiente Xabier Gorostiaga, S.J. Universidad Iberoamericana Puebla, San Andrés Cholula, Puebla, México

Guillermo Salgado-Maldonado Laboratorio de Helmintología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, México

Luis A. Sánchez-González Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, México City, México

Uriel J. Sánchez-Reyes Instituto Tecnológico de Ciudad Victoria, Ciudad Victoria, Tamaulipas, México

Michael F. Schmidt Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, Mexico

Raúl Sierra Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, D.F., México

Cecilia Soldatini CICESE Unidad La Paz, La Paz, B.C.S., México

Lislie Solís-Montero Departamento de Agricultura Sociedad y Ambiente, El Colegio de la Frontera Sur, Tapachula, Chiapas, México

Angel Fernando Soto Pozos Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, Ciudad de México, México

Ireri Suazo-Ortuño Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México

Ek del Val de Gortari Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, México

David Valenzuela-Galván Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Cuernavaca, México

Alfonso Valiente-Banuet Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, México City, México

Rémy Vandame Departamento de Agricultura Sociedad y Ambiente, El Colegio de la Frontera Sur, San Cristóbal, Chiapas, México

Margarita Vargas-Sandoval Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia Michoacán, México

David Chamé-Vázquez Laboratorio de Aracnología y Entomología. Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S, México

Leopoldo Vázquez-Reyes Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México

Enriqueta Velarde Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Boca del Río, Veracruz, México

Julián A. Velasco Instituto de Ciencias de la Atmósfera y Cambio Climático, Universidad Nacional Autónoma de México, México City, México

Carlos H. Vergara Departamento Química y Biología, Universidad de las Américas-, Puebla, México City, México

José L. Villalobos Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, México

Veronica Zamora-Gutierrez CONACYT- Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional Unidad Durango (CIIDIR), Instituto Politécnico Nacional, Mexico City, Mexico

Salvador Zamora-Ledesma Universidad Autónoma de Querétaro, Faculty of Natural Sciences, Queretaro, México

Part I
Introduction

Chapter 1
The Mexican Fauna in the Anthropocene, Where Do We Go from Here?

Robert W. Jones, C. Patricia Ornelas-García, Rubén Pineda-López, and Fernando Álvarez

Contents

1.1 Introduction

Several terms in the last decades have had a significant impact on the way we think and act, among these are biodiversity, climate change, sustainable development, mass extinction, conservation, and recycling. All of these, however, can be combined to define a new reality in the times that human development has reached every corner of our planet and provoked substantial changes in natural cycles and processes, which have been called the “Anthropocene”. Some authors propose that the activities of man since the second half of the eighteenth century, at the onset of the industrial revolution, have produced changes at a planetary scale modifying the atmosphere’s composition, transforming more than half of the land surface of the planet, creating accelerated species extinction rates, and even producing measurable

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R. W. Jones (✉) · R. Pineda-López
Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro,
Juriquilla, Querétaro, Mexico
e-mail: rjones@uaq.mx

C. P. Ornelas-García
Colección Nacional de Peces, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico

F. Álvarez
Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_1

changes in the geology of the planet (Dirzo et al. 2014; McCauley et al. 2015; Young et al. 2016).

Defining "Anthropocene" proves to be a very difficult task, since many angles have to be considered when one attempts to either develop or accept a definition. The construction of the term denotes that it refers to a geological epoch, with marked shifts in Earth's state (Lewis and Maslin 2015), with a specific biota and/or well-defined strata or rock series. It is believed that man's impact on the planet has left and will continue to leave for centuries to come, an indelible mark on the Earth's surface and atmosphere.

The notion of a global-scale human-induced change of the planet is not new; it has been around for some 150 years, since the Italian priest Antonio Stoppani in 1873 talked about the human impact on the Earth referring to it as the "Anthropozoic Era" (Lucchesi 2017). Subsequently, many other authors and thinkers have arrived at a similar idea, producing a variety of definitions and describing a wide array of impacts at very different scales. Several important modern revisions are now available for the interested reader (e.g., Oldfield et al. 2014; Lewis and Maslin 2015), amid hundreds of publications. The effect of having this variety of interpretations around the same idea has prevented the emergence of single concept of "Anthropocene," although they converge on the same idea that human activities have radically changed the Earth's surface and its biodiversity.

A second challenge that has arisen regarding the concept of Anthropocene is to establish its limits, primarily when were the first effects visible? As Lewis and Maslin (2015) discuss, several starting points are possible as the geological stratigraphic markers needed to indicate the transition between epochs is not clear. Another problem is that the limits of the Holocene, as the preceding epoch, would have to be revised to accommodate the new period. It seems clear that hundreds or thousands of years into the future, the impact of man on the Earth's surface will be readily recognizable; however, given the pace that events are occurring now, the onset of the new epoch remains under debate.

Despite the definition problems and temporal uncertainties, it appears unquestionable that a planetary change is occurring. The editors of the present volume, as zoologists, saw the need to present an overview of what has and could occur to the diverse fauna of Mexico. To achieve this goal, we have invited experts of different zoological groups to explore the state of the art in their fields and to present alternative disturbance scenarios on what this fast rate of change will mean for our current faunal diversity, their ecosystems, and processes. We think that this is a significantly important idea since Mexico harbors around 10% of the world's species and the fate of this important fraction of the biota will have wide-ranging consequences.

The definition of the Anthropocene used herein is that proposed by Smith and Zeder (2013). These authors place the onset of the Anthropocene at the Pleistocene-Holocene, approximately 11,000 to 9000 years B.P. and defined as "when evidence of significant human capacity for ecosystem engineering or niche construction behaviors first appear in the archeological record on a global scale." Their criteria are based principally on ecological variables and thus most easily relate to the factors and causes that significantly impact animal species and their communities.

Thus, the Anthropocene epoch used herein is an “early” Anthropocene concept and is considered coeval with the start of the Holocene, starting roughly 11,000 years B.P (Doughty 2010). This period is at the dawn of the origins of agriculture and the domestication of animals and plants worldwide. Ellis et al. (2021) considered that these technological developments together with other land transformation practices were already significantly shaping the Earth’s biosphere at this time.

1.2 History of the Anthropocene in Mexico

An overview of major environmental periods of the Anthropocene in Mexico can be roughly divided into three periods. The first is development of agriculture and greater social organization and technology of human indigenous societies from 11,000 to 1600 B.P. In fact, human populations had established in the northeastern portion of Yucatan Peninsula by 13,500 B.P., where multiple remains have been discovered in flooded caves (Hubbe et al. 2020). And by at least by 8000 B.P., humans were already impacting the environment based on carbon accumulation in strata that suggests selective use of fire by humans as well as the presence of pollen grains of an early maize subspecies and other early cultivars that have been found in central, western Mexico (Zizumbo-Villarreal and Colunga-García 2010).

This initial period of land transformation was followed by the development of greater complexity of indigenous cultures and their impact of land transformations due to more intense agriculture practices, population growth, and urbanization of indigenous cultures, up to the Spanish colonization starting in the fifteen century. In a recent study, they detect at least seven ecoregions in Mexico densely occupied before the European arrival. Thus, regions correspond to two in the Yucatan Peninsula (Plain and Hills and Northwestern Plain of the Yucatan Peninsula) and five in Central and Southern Mexico (Interior depressions, Gulf of Mexico, Transversal Neo—Volcanic System, Mexican High Plateau, and Sierra Los Tuxtlas) (Gónzalez-Abraham et al. 2015).

Using the Olmec culture as a starting point around 1600 B.P., the subsequent period is marked by several indigenous cultures that thrived and greatly transformed the natural landscape, especially in the Yucatan Peninsula with the Maya, in the Central Valleys of Oaxaca with the Zapoteca and later in Central Mexico by the Aztec. The population size of these societies is controversial. Population estimates of Mexico at the time of European arrival are highly variable ranging from 3 to over 50 million (Koch et al. 2019), with intermediate estimates for Mexico based on a synthesis of various methods and models that are calculated at 17.2 million (Denevan 1992). To maintain such populations, even at the lower size estimates, as well as the evident social stratification of the various cultures, required efficient and large-scale agricultural practices. These included extensive water management systems, including canals and wetland raised plots (“*chinampas*”), as well as terracing of highlands and diverse agroforestry practices (Fedick 2010; Canuto et al. 2018). Crop diversity was high and as many as 500 food plants were probably used (Fedick 2010; Casas et al. 2016). Despite the diversity and sophistication of agricultural practices, significant erosion of soils is evident from many sites (González-Arqueros et al. 2017; Anselmetti et al. 2007). Per capita land use estimates for the Americas are calculated at 1.04 ha with Mexican estimates of within this range of 0.57–1 ha based on the "*milpa*" land use system (Koch et al. 2019). These land use levels combined with population estimates indicate that a significant area of highland and tropical forests was modified or converted to croplands or fields during the last millennial.

Besides habitat alteration due to urbanization and agricultural activities, harvesting of wildlife for food was also practiced and an important part of the pre-Columbian diet of indigenous societies in central México and presumably elsewhere (Zizumbo-Villarreal et al. 2016). Besides their use as food, animals had important religious and ritual values (jaguar; Fig. 1.1). In Mexico, there is considerable evidence of the transport of animal for symbolic-religious purposes that lingered on in the Native American cultures after the conquest (Valadez 1994; De la Garza 1999; Olivier 1999). For example, animals were part of the tributes given to by subjugated tribes to the Aztecs and included terrestrial vertebrates, fish and even invertebrates such as centipedes, scorpions, arachnids, snails, and shells (Durán 1581 quoted by Haemig 1978; Moctezuma 1985; Olivier 1999). Besides the transport for tributes and religious purposes, indigenous societies domesticated various species including stingless bees, turkeys, Psittaciformes (parrots, parakeets, macaws), and song birds such as the mocking bird (Valadez 1999). In addition, upon the arrival of the conquistadores in Tenochtitlan (Mexico City), they reported finding extensive gardens and a zoo with "countless" animals exotic to the Aztec homeland (Ixtlilxochitl, cited in Haemig 1978, Blanco et al. 2009). According to Hernán Cortés's *Segunda Carta de Relación* (1522), in the zoo of the supreme leader, Moctezuma, there were 600 men dedicated exclusively to the care of the zoo animals, including veterinarians to care for the sick individuals. This transport and domestication of animals are factors that can explain anomalous distribution patterns of some species found in Latin America. For example, the Great-Tailed Grackle *Quiscalus mexicanus* ("*zante*" or "*teotlzanatl*") was brought by the

Fig. 1.1 A "cuauhxicalli" or basalt vessel from the Mexica culture in the form of a feline on display at the National Museum of Anthropology in Mexico City (Wikepedia.org)

emperor Ahuitzotl from the tropical regions of the Gulf Coast to the Mexico City Valley (Bernardino de Sahagún, in Haemig 1978). This species became established in the Valley and currently continues its expansion in North America, mainly in human-altered ecosystems (Wehtje 2003). Another example of pre-Hispanic translocation corresponds to the goodeid fish species *Allotoca catarinae*, whose translocation was associated with settlements of the P'urhépecha culture around 1900 years ago in the Lerma river basin in the Transversal Neo-Volcanic System (Corona-Santiago et al. 2015).

The second period began when the Spanish arrived in the sixteenth century. They did not find a pristine landscape with scattered human settlements, but entered a continent with a sizable population living in anthropized landscapes. One of the first and most devastating introductions that European colonization brought to Mexico was Old World human diseases. The impact of the epidemics on the indigenous populations wrought by the introduction of these European diseases was monumental. Approximately 90% of the indigenous population was estimated to have been lost in Mexico by 1650 (Koch et al. 2019). The enormous population loss also meant a large reduction in agricultural activity and land use leading to a marked regrowth of secondary vegetation (Dull et al. 2013; Koch et al. 2019). On a continental scale, this expansion of secondary growth and reforestation of previously agricultural lands throughout the Americas has been argued to have been on such a scale as to have resulted in a worldwide reduction in atmospheric CO_2 and subsequent global cooling (Dull et al. 2013; Koch et al. 2019). In Mexico, this means that the colonization by the Spanish beginning in the sixteenth century initiated within a newly transformed landscape with a greatly reduced and socially transformed indigenous populations.

Another change in land use brought by the Spanish was through the introduction of grazing domesticated animals including cattle, horses, donkeys, mules, goats, and sheep as well as barnyard animals such as chickens and pigs. Having few domesticated animals, these were readily adopted by the native populations. The Spaniards also brought new crops including wheat, barley, sugar, bananas, temperate fruits, and many vegetables, although maize, beans, and other native crops remained preferred food crops of the indigenous populace.

European livestock were so successful that by 1550, there were flocks of up to 300,000 sheep in parts of central Mexico. This phenomenon caused a food and clothing revolution for the indigenous populations, but also brought major conflicts with indigenous farmers due to overgrazing that caused severe soil erosion, especially in the Mezcal and Mixteca regions (García 1999). Following the initial boom in livestock farming, land use and occupation of the land were more clearly defined, and fences or stone walls were built that separated different land uses and spatially delimited pastures (García 1999).

Despite these changes in agriculture, ownership of land was heavily favored for the Spanish colonists. At first, land was not as important as labor, which was conscripted from indigenous inhabitants ("*encomienda*") to favored Spanish colonists, who also received most of the land grants (Butzer 1992). As the "*encomienda*" system was gradually phased out, increasing numbers of land grants were given to

Spanish settlers for sheep and cattle raising which became the major source of rural income (Prem 1992). The Spanish crown initially respected indigenous community lands in the granting of land grants, but many previously indigenous occupied lands were often abandoned due to the continued epidemics which were usually acquired be Spanish settlers (Butzer 1992).

By the late colonial period, extensive degradation was evident in many Mexican ecosystems (Skopyk and Melville 2018). The causes for this degradation are debated and clearly multifactorial including the shift from indigenous land use practices to colonial Spanish agricultural land use, overgrazing (Fisher et al. 2003), climate change (Skopyk 2017), population settlement patterns (Fisher et al. 2003), and loss of forest cover (Street-Perrott et al. 1989), among others.

Following Mexican Independence in 1821, there was little change in the land use practices and increasing consolidation of ownership by Spanish descendants, with further land degradation. This was heightened during the dictatorship of Porfirio Díaz established in 1876, when land and water resources were monopolized for industrial production and haciendas were further consolidated (Schumacher et al. 2019). The growth of large "*haciendas*" lead to industrialization of agricultural practices and further loss of the more sustainable, biodiverse land practices used by indigenous peoples (Schumacher et al. 2019).

The final period starts with the Mexican Revolution and its change in land use, together with the industrialization of agricultural production, exponential population growth, and urbanization of Mexico, during the twentieth and twenty-first centuries. The unjust social, economic, and land tenure conditions that ignited the Mexican Revolution in 1910 resulted in sweeping land reform. The new laws established after the revolution allowed the State to convert the "*haciendas*" into communal land, or "*ejidos,*" a communal land tenure system similar to that used in pre-Hispanic times, which is a unique form of land ownership (Schumacher et al. 2019). An "*ejido*" is formed when land is granted to a group of individuals for their use, which in practice is divided into family parcels, over a portion of the land grant. Currently, slightly more than half of the surface of Mexico is in possession of "*ejidos*" or agrarian communities and includes mountains, extensive forests, arid regions and is often within national and state designated protected areas (Morett-Sánchez and Cosío-Ruiz 2017; Schumacher et al. 2019). As such, most ecosystems in Mexico are social property and are the primary source of livelihood for the "*ejiditarios.*" The land use of "*ejidos*" is mainly dedicated to agricultural activities, including farming and livestock grazing, but also direct resource extraction including firewood, construction materials, and harvesting of wild plants and animals, among others (Flores-Rodríguez 2008; Morett-Sánchez and Cosío-Ruiz 2017; Schumacher et al. 2019). The "*ejidos*" and their rural Mexican areas, in general, are important regions of environmental heterogeneity formed by different crop lands, minimally managed ecosystems, areas of secondary vegetation, and remnants of natural vegetation (Fig. 1.2). Although these regions are often clearly disturbed, they can maintain significant biological diversity (Hiley et al. 2016; Blasio-Quintana and Pineda-López 2020; Cruz-Elizalde et al. 2022).

Fig. 1.2 Heterogeneous landscape of Ejido el Madroño, in municipality of Pinal de Amoles, Querétaro. In foreground, minimally managed and favored agaves and piñon pines in area also used for cattle grazing, with mixed oak-pine forest fragments in background including small, settlement clearings

However, although "*ejidos*" have been one of the most resilient communities of the world and have been adapted to a myriad of economic and societal changes, the living conditions of many of the "*ejiditarios*" have worsened during the twenty-first century (Barnes 2009; Morett-Sánchez and Cosío-Ruiz 2017; Schumacher et al. 2019). Importantly, legislatorial changes in 1998 permitted the ownership of "*ejidal*" property to being legally transformed to private property, resulting in massive growth of peri-urban areas around the urban cores of Mexican cities (Schumacher et al. 2019). These conditions and changes in rural Mexico have led to increasing migration of "*ejiditarios*" and the rural poor to large cities in search of factory jobs or migration to the USA and Canada (Morett-Sánchez and Cosío-Ruiz 2017). This together with continued population growth during the latter part of the twentieth century has resulted in an incessant increase in levels of urbanization (Fig. 1.3), continued deforestation, further industrialization of agricultural production with increasing environmental contamination and negative impacts of established and new exotic species (SEMARNAT 2016).

Despite that the Mexican territory has been modified by man for more than 4000 years (Somerville et al. 2021), and markedly so within the last 70 years, there are important positive accomplishments in environmental protection. Government environmental agencies have been created and evolved in various sectors including the Department of Environment and Natural Resources (Secretaría del Medio Ambiente y Recursos Naturales, SEMARNAT), under which is the National Commission of Natural Protected Areas (CONANP), and the National Commission for the Knowledge and Use of Biodiversidad (CONABIO), among other national, state, and local agencies. Important environmental laws were founded in 1988 in the General Law on Ecological Equilibrium and Environmental Protection (LGEEPA) which is enforced by the Federal Attorney for Environmental Protection (PROFEPA).

Currently, CONANP administers 183 federal natural protected areas (NPAs) accounting for 90,942,124 hectares in addition to 371 areas voluntarily destined for

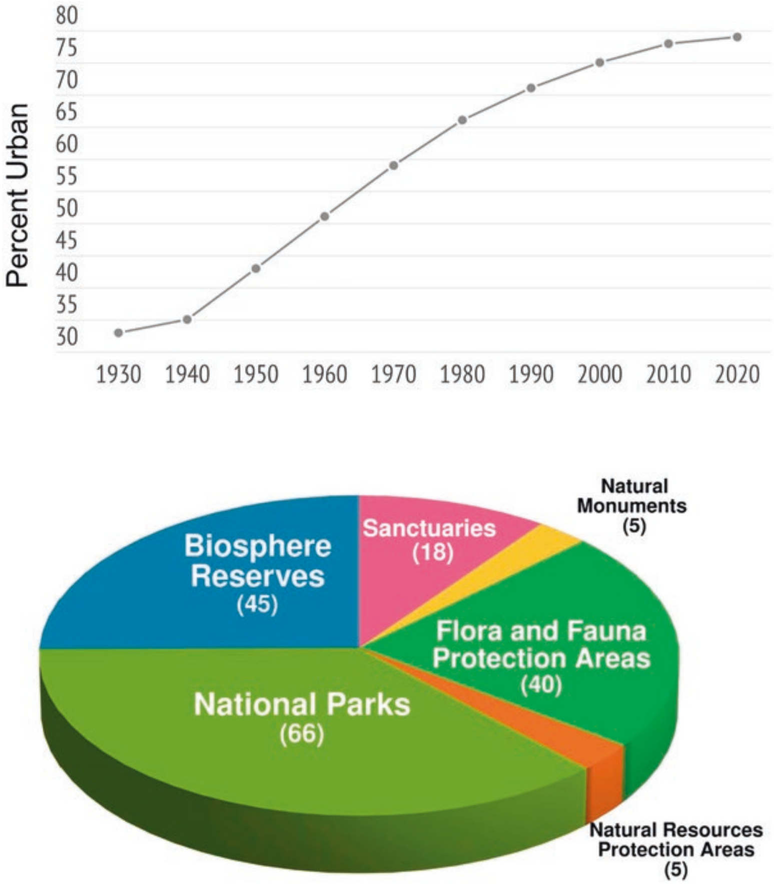

Fig. 1.3 Top. Growth of percent urban population growth in Mexico (INEGI, Censo de Población y Vivienda 2020); bottom. Number (parentheses) and types and numbers of protected areas in Mexico (CONANP 2022)

conservation, with a total area of 604,906 hectares (CONANP 2022). Of these areas, more than 95% were created after 1995 (Ocampo et al. 2014). Of the NPAs, 21,483,510 hectares correspond to terrestrial ecosystems, representing 10.93% of the national land area, whereas the protected marine surface comprises 69,458,613 hectares, corresponding to 22.05% of the national territory of marine waters (Fig. 1.3; CONANP 2022). Although these agencies and the protected areas suffer political, social, and economic challenges and despite the unremitting trends that continue through urbanization and habitat destruction as seen throughout the world, what is remarkable is that even today, the diversity of species Mexico, including its fauna, is still very high. However, as is articulated in the present volume, almost all faunal groups and the ecosystems that maintain them are imperiled.

1.3 Final Remarks

There appears to be a growing acceptance of the term Anthropocene by the scientific community and the general public. With this, the recognition that the physical and biological changes on the planet we are now experiencing are comparable to the other five major extinction events in geological time. This acceptance is evidenced by the creation of new scientific journals such as Anthropocene, The Anthropocene Review, Elementa: Science of the Anthropocene, Anthropocene Science, Anthropocene, among others, which have been created in the last 5 years to cope with an increasing number of studies on this topic. In the present volume, we use the term to focus the exploration of a wide range of topics related to the past and current conservation status of major faunal groups in Mexico and a prognosis of future challenges and the expanding threats inherent within the context of the unique physical, biological, and cultural aspects of the nation. We also hope to reach a broad audience beyond academics to promote ideas and awareness of the apparently, irreversible trajectory the world has embarked and in particular, in reference to the unique and diverse fauna of Mexico. As the mounting evidence of negative impacts on biodiversity and invaluable ecosystem functions continues to accumulate in the different realms, the question becomes, Where do we go from here? Our discussion as a society will have to shift from the efforts to confirm the existence of the Anthropocene to a more proactive attitude, in which we incorporate understanding of local, regional, and global processes of the human impacts threatening biodiversity and on the associated ecosystem services in order to formulate viable strategies to mitigate the consequences.

Acknowledgments This present book is part of an inter-institutional research project begun in 2015 called the Network of Biology, Management and Conservation of Native Fauna in Anthropized Environments (REFAMA, Red de Biología, Manejo y Conservación de Fauna Nativa en Ambientes Antropizados), supported by Consejo Nacional de Ciencia y Tecnología (CONACyT) of Mexico. The present work is the fifth in a series of books initiated by REFAMA concerned with the conservation and management of fauna in anthropized environments and the first in English. We thank Springer Publishing for consideration and encouragement in the formulation of the idea for this work.

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Part II
Faunal Groups

Chapter 2
The Fauna of Arachnids in the Anthropocene of Mexico

Javier Ponce-Saavedra, María Luisa Jiménez, Ana F. Quijano-Ravell, Margarita Vargas-Sandoval, David Chamé-Vázquez, Carlos Palacios-Cardiel, and Juan Maldonado-Carrizales

Contents

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/978-3-031-17277-9_2.

J. Ponce-Saavedra (✉) · A. F. Quijano-Ravell · M. Vargas-Sandoval · J. Maldonado-Carrizales
Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo,
Morelia, Michoacán, Mexico
e-mail: javier.ponce@umich.mx

M. L. Jiménez
Colección de Arácnidos e Insectos (CARCIB). Programa de Planeación Ambiental y Conservación. Centro de Investigaciones Biológicas del Noroeste, S.C. Instituto Politécnico Nacional, La Paz, B.C.S, Mexico

D. Chamé-Vázquez · C. Palacios-Cardiel
Laboratorio de Aracnología y Entomología, Centro de Investigaciones Biológicas del Noroeste, S.C, La Paz, B.C.S, Mexico

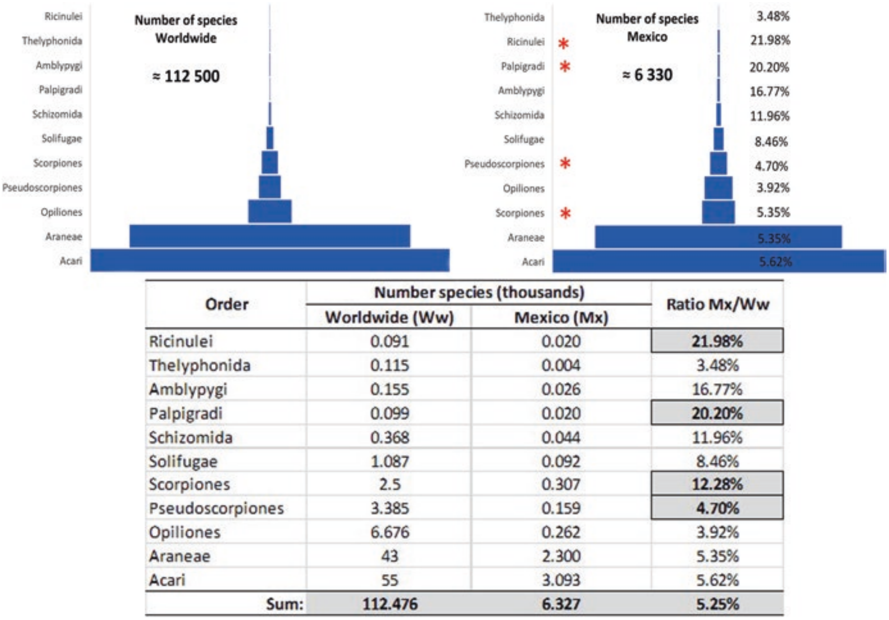
R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_2

2.1 Introduction

The arachnids are arthropods of the Chelicerata group with the first appendages called “chelicerae” which have a preoral position and alimentary function (Ubick et al. 2005). This characteristic is distinctive for arachnids when compared to insects, myriapods, and crustaceans whose first preoral appendages are the antennae and have sensorial function. In Mexico, there are 11 orders of the class Arachnida, from the minute mites to large scorpions, spiders, or vinegaroons (Francke 2014).

After the largest groups of insects (Coleoptera, Lepidoptera, Diptera, and Hymenoptera), the arachnids are the most species diverse animals on the earth and considered a “mesodiverse” group with almost 112,476 described species, constituting 10.22% of the total 1.1 million described species (Fig. 2.1).

The arachnids are present in all the varied ecosystems of Mexico, from arid or semiarid environments to humid tropical rainforests and wetlands and even aquatic systems where they often feed on fully aquatic organisms. They are found in soil, leaf litter, under rocks or logs, under tree bark, on plant leaves and other vegetation, in caves, and virtually all ecosystems of Mexico. Almost all ecosystems have their distinct composition of arachnid fauna, a result of local endemism levels that are remarkably high. However, there is very little information about the effects of anthropic activities and the progressive destruction of natural habitats on these small animals.



Order	Number species (thousands)		Ratio Mx/Ww
	Worldwide (Ww)	Mexico (Mx)	
Ricinulei	0.091	0.020	**21.98%**
Thelyphonida	0.115	0.004	3.48%
Amblypygi	0.155	0.026	16.77%
Palpigradi	0.099	0.020	**20.20%**
Schizomida	0.368	0.044	11.96%
Solifugae	1.087	0.092	8.46%
Scorpiones	2.5	0.307	**12.28%**
Pseudoscorpiones	3.385	0.159	**4.70%**
Opiliones	6.676	0.262	3.92%
Araneae	43	2.300	5.35%
Acari	55	3.093	5.62%
Sum:	**112.476**	**6.327**	**5.25%**

Fig. 2.1 Comparative number of species by order of Arachnids in the world and in Mexico. (* Country with most species diversity on the world)

They are remarkable predators, and their ecological role is important for the dynamics of terrestrial systems. They are predators of invertebrates including insects and other arachnids, and likewise, are important prey items for other small animals such as lizards, snakes, frogs, rodents, bats, and birds. Mites, ticks, spiders, and scorpions can be anthropic organisms and are common in urban environments. Most species are without negative interactions with humans, although some spiders, mites, or scorpions are important pests in agroecosystems, in livestock production, or in public health.

Arachnids are generally not recognized as beneficial organisms. However, if we consider that these organisms are important in keeping much of insect populations at low densities in natural environments, as well as in or around our houses and gardens, this is of great benefit to us. In addition, there are several forms which the humans obtain other benefits of the arachnids, e.g., drugs obtained from venom of spiders and scorpions for medicinal formulations or therapeutic use.

2.2 The "Small Arachnids"

The "small arachnids"groups (Fig. 2.2) are so named because of their low species richness and/or reduced body size. Most authors include in this group the orders: Amblypygi, Palpigradi, Pseudoescorpiones, Schizomida, Solifugae, Thelyphonida, and Ricinulei based on their low species richness. The remaining orders are the "large arachnids"with higher species richness: Acari, Araneae, Opiliones, and Scorpiones (Harvey 2003, 2013).

The species number of each order included as "small arachnids"in the world and Mexico are very small (Fig. 2.1). Of these, the Palpigradi, Pseudoescorpiones, Schizomida, and Ricinulei are minute organisms, most of a few millimeters in body size, whereas Solifugae and Thelyphonida are relatively large animals (>5 cm).

Palpigradi (microwhip scorpions; Fig. 2.2a) are small, poorly sclerotized, and fragile arachnids that dwell in moist or dry stable habitats, living in the interstitial spaces of soil. In dry soils, they can be found under stones taking advantage of the more tolerable conditions of humidity and temperature. Palpigradi are capable of preying on minute organisms, including bacteria when they live in caves (Smrž et al. 2013). There are only 99 recorded species in the world while for Mexico there are a notable total of 18 recorded species (18.2%).

Pseudoscorpionida (pseudoscorpions; Fig. 2.2b) are small arthropods, generally 2–10 mm in body length that occur in most terrestrial ecosystems and are easily recognized by their pincer-shaped pedipalps, much like the scorpions but without a tail with a venomous sting. However, some pseudoscorpions have venom glands in their pedipalps. They are among the oldest recorded terrestrial lineages (≈ca. 400 million years ago; Harms and Dunlop 2017). These small arachnids have a total of 3600–3800 described species (Wriedt et al. 2021; Harvey 2013) and are a medium diverse order of arachnids alongside Solifugae (camel spiders) and Opiliones (harvestmen). Mexico has 167 recorded species (4.4% of the world diversity) in 18

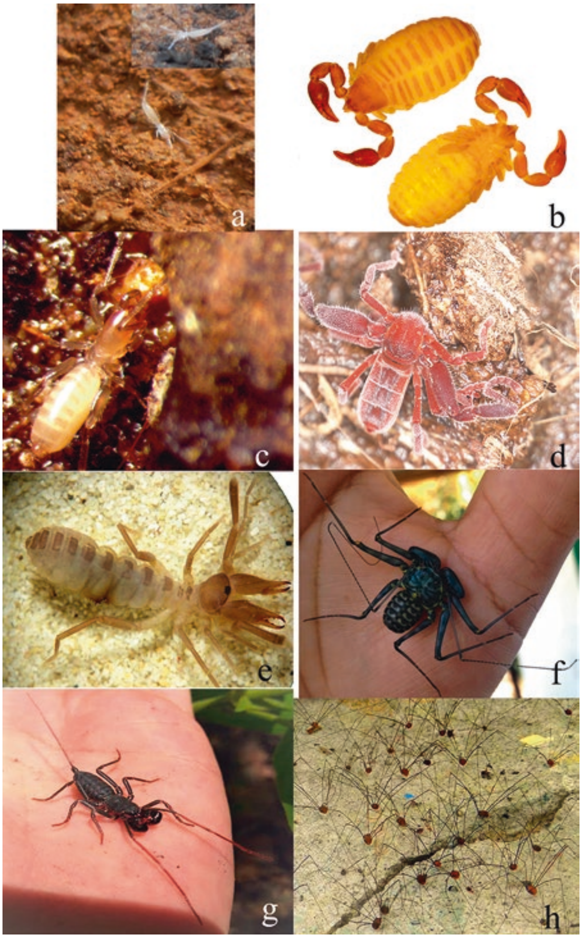


Fig. 2.2 Eight orders of Arachnids of Mexico. (**a**) Palpigradi, family Eukoeneniidae from Nocupétaro, Michoacán; (**b**) Pseudoscorpiones, family Chernetidae from Uruapan, Michoacán; (**c**) Schizomida, genus *Stenochrus*, family Hubbardiidae from "Villas de la Loma," Morelia, Michoacán; (**d**) Ricinulei: *Pseudocellus olmeca*, family Ricinoididae from "Parque jaguarundi," Veracruz; (**e**) Solifugae: family Ammotrechidae from Morelia, Michoacán; (**f**) Amblypygi: *Phrynus purhepechas* family Phrynidae from La Huacana, Michoacán; (**g**) Thelyphonida: *Mastigoproctus* sp. family Thelyphonidae from Charo, Michoacán. (**h**) "Daddy long legs" order Opiliones: *Leiobunus* sp. from Morelia, Michoacán. (Photos by Javier Ponce-Saavedra except (a) family Eukoeneniidae from Nocupétaro by Ernestor Oliveros-Guzmán; (**d**) *Pseudocellus olmeca* by Alejandro Valdez-Alarcón; (**f**) *Phynus purhepechas* by Ana F. Quijano-Ravell)

families (Villegas-Guzmán 2015). Pseudoscorpions occur primarily in leaf litter habitats, soil, tree bark, or under rocks and caves.

Schizomida (Fig. 2.2c) are an order with 368 species worldwide while in Mexico there are two families, Hubbardiidae and Protoschizomidae, the latter, as well as five genera are endemic to the country (Monjaraz-Ruedas et al. 2019; Monjaraz

Ruedas unpublished data). There are 44 registered species, several of them recently described. They inhabit soil with high humidity and organic matter and found under rocks or associated with roots. Several species inhabit relatively small, horizontal caves, sometimes with human disturbance. There are few records of Schizomida due to its minute body length and their appearance as "white ants" that makes them go unnoticed, as well as the lack of taxonomists for the group.

Ricinulei (Fig. 2.2d) are the least diverse order of arachnids in the world with only 91 current species classified all in the suborder Neoricinulei (Valdez-Mondragón 2017) Valdez-Mondragón and Juárez-Sánchez 2021). Ricinulids have appearance of ticks and have a typical frontal plate named "cuculus" covering the chelicerae. They are best represented in Mexico in the tropical rainforest, mainly Chiapas and Veracruz. *Pseudocellus* (Fig. 2.2a) is the only recorded genus, and it is endemic to the country with currently 20 valid species. Most of these are epigean and others inhabit caves with distinct troglomorphisms (Valdez-Mondragón and Juárez-Sánchez 2021).

In Mexico, the arachnids of order Solifugae (Fig. 2.2e) are known as "mata venados" or "madres de alacrán." In other countries, they are named as "camel spiders," "sun spiders," or "wind scorpions"; however, they are neither spiders nor scorpions. They are common elements of arid, semiarid, and temperate environments around the world, although knowledge of camel spiders biology is limited. The solpugids are mostly crepuscular or nocturnal arachnids with powerful two-segmented chelicerae, fast running speeds and are great predators of invertebrates and small vertebrates (Punzo 1998; Beccaloni 2009; Santibañez-López et al. 2021). Solifugae is a relatively small order with over 1100 described species, about 200 of which occur in North America (Harvey 2003; Cushing et al. 2015) and 92 species recorded from 24 states of Mexico, mainly in the north (Harvey 2013; Medina-Soriano and Vázquez-Rojas 2016). Solpugids hide during the day under stones or in crevices. Females are capable of burrowing in loose soil for protection during gestation.

Most of the amblypygids are relatively small (ca. 5 cm including legs and pedipalps), fast runners, easily recognized by their first very elongated legs with strong pedipalps with big spines used for predation (Fig. 2.2f). In Mexico, there are three genera (*Acanthophrynus*, *Paraphrynus,* and *Phrynus*) and 26 species, 16 of which are endemic. This group has cryptic species so greater diversity is expected in the country.

The vinegarroons or whip scorpions (order Thelyphonida; Fig. 2.2g) make up a poorly studied arachnid group in Mexico. There are 121 species recorded worldwide. They are nocturnal and are typically found under logs, stones, and in underground burrows during the daytime. Their common name refers to the capacity to produce a mixture of acetic acid (vinegar) and caprylic acid as a defensive mechanism. Vinegarroons are emblematic neotropical arachnids with one genus of large animals of more than 60 mm of body length (*Mastigoproctus*). In Mexico, there are six species which have records mainly from the center, northwestern, and northeastern portions of the country and only one species registered from Chiapas from the Lancandon tropical forest of Chiapas (Harvey 2013; Barrales-Alcalá et al. 2018).

2.3 The Opilionids

The order Opiliones (Fig. 2.2h) is third in diversity among the arachnids with 6676 described species worldwide (Catalogue of life 2021). They are known as "harvestmen" and can be distinguished by their cephalothorax and abdomen joined throughout all its width giving the body an ovoid and compact appearance with external segmentation with characteristically long legs, hence the common name of "Daddy long legs." There is significant variation in morphological appearance unlike most other groups of arachnids. Kury and Cokendolpher (2000) recorded 283 species for Mexico; however, this figure included more than 50 non-described species. Later, Francke (2014) adjusted this number to 238, with the current figure of 262 described species (unpublished data by Cruz-López J. A). There are four suborders, all represented in Mexico: Eupnoi with 4 families (66.6% of the worldwide) with ≈8% of recorded species; Dyspnoi with 1 family and 8 species (2.13%); Laniatores with 6 families (23.07%) and ≈3.5%; and Cyphophthalmi with 1 family and ≈1.0% of total described species.

They have a variety of eating habits and a wide range of food items. They are generally considered omnivorous organisms, which is a very notable feature among arachnids. The diet of the group includes small arthropods and other invertebrates, including other opilionids, living or dead and plants and fungi. They can consume carrion, be predators, and capture live prey or consume organic matter of the soil. Opilionids inhabit mainly tropical and temperate forests and some species are gregarious.

2.4 The Scorpions

The order Scorpiones (scorpions; Fig. 2.3) is a group of arachnids that have nocturnal or crepuscular habits. Most scorpions are between 15 and 60 mm in length, although there are some that reach more than 120 mm or more. They are distinctive from other arachnids for their body with a tail and sting associated to venom glands and two ventral sensitive structures called "pectines". In general, they remain hidden and at rest during the day, under stones, logs, cracks, or any object that offers them protection. Other species dig their burrows in the ground, which can be relatively superficial, whereas others are found at depths greater than 1 m (Polis 1990; Warburg and Polis 1990; Ponce-Saavedra et al. 2006; Quijano-Ravell et al. 2012; Francke 2014).

Scorpions are predators of small invertebrates (mollusks, insects, arachnids, and arthropods, in general). Some species can eat small vertebrates such as lizards or rodents and can withstand long periods of starvation without any noticeable effect (Polis 1990). In desert areas, they survive with very little water, obtaining what they need from their prey. In other areas, they require drinking water from time to time,

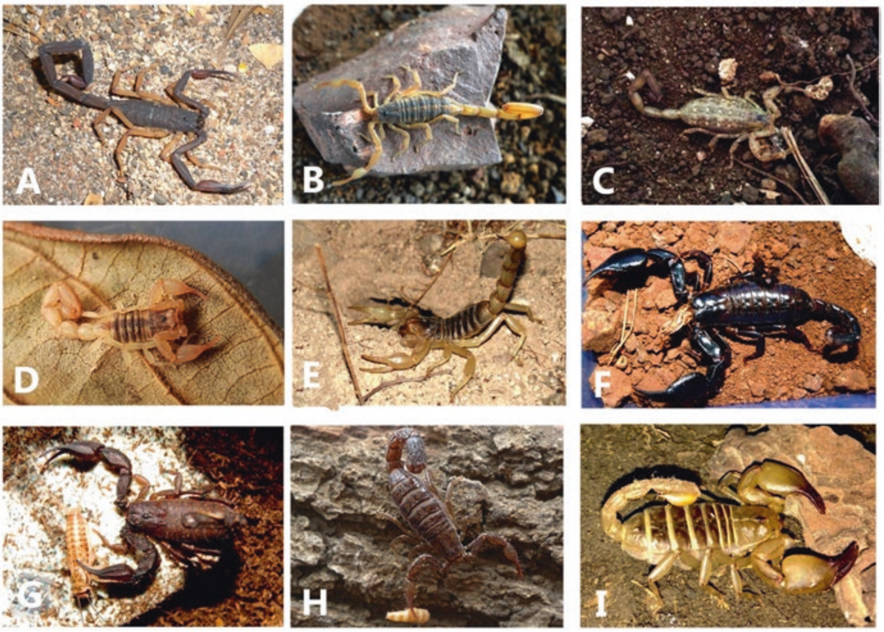


Fig. 2.3 Scorpion species of some families from Mexico: (**a**) adult ♂*Centruroides gracilis* Latreille, 1804 (Buthidae); (**b**) adult ♂ *Centruroides ornatus* Pocock, 1902 (Buthidae); (**c**) adult ♀ *Centruroides* "thorelli group" (Buthidae); (**d**) adult ♂ *Chaneke hofereki* Kovarik, Teruel & Lowe, 2016 (Buthidae); (**e**) adult ♀ *Hoffmannihadrurus gertschi* (Soleglad, 1976) (Hadruridae); (**f**) adult ♀ *Kolotl poncei* (Francke y Quijano-Ravell, 2009) (Diplocentridae); (**g**) adult ♀ *Megacormus franckei* Kovařík, 2019 (Euscorpiidae); (**h**) adult ♂ *Konetontli acapulco* (Armas & Martin-Frias, 2001) (Vaejovidae); (**i**) adult ♀ *Nullibrotheas allenii* (Wood, 1863) (Chactidae). (Photos by de Ana F. Quijano-Ravell except (G) by Rolando Teruel)

to supplement their metabolic requirements, which makes them search for wet areas during the night. Consequently, it is common to see scorpions in areas near natural or artificial water sources, which unfortunately, such areas are preferred by humans (Polis 1990; Ponce-Saavedra et al. 2016).

The life cycle of scorpions includes in most cases, a time of year when mating occurs, although other species may have more than one annual reproductive period. These periods are characterized by significant displacement because males search for females (Polis 1990; Quijano Ravell and Ponce-Saavedra 2016). Usually, this period occurs before the rainy season and in some places also coincides with the time of higher temperatures, so it is common to associate the observation that there are "more scorpions" in the hot, dry season (Ponce-Saavedra 2003; Quijano Ravell and Ponce-Saavedra 2016).

2.4.1 Scorpion Diversity

There are 23 families and 226 genera with 2632 species in the world (Rein-Ove 2021). The updated record for Mexico includes eight families, 38 genera, and 317 species (Updated November 2021, Francke Unpublished data). The family with the greatest generic relative diversity in Mexico is Vaejovidae with around 58%, followed by Typhlochactidae 18%, Diplocentridae 14%, and Buthidae 9%. Regarding species, Vaejovidae has the 53%, followed by Diplocentridae with 19% and Buthidae has 17% (Tables 2.1 and 2.2).

In Mexico, the diversity of species is high, some species live from sea level to altitudes above 2500 m above sea level (Ponce-Saavedra et al. 2016). There are published records of scorpion species for all states.

In other countries, some scorpions can inhabit places of higher altitude; for example, in the Andes area of Peru and Argentina, the genus *Orobothriurus* spp. reaches up to 4910 m above sea level (Mattoni et al. 2012). In Mexico, there are several species of Vaejovidae and Diplocentridae families with records between 2500 and 3000 m above sea level.

Table 2.1 Families of scorpions recorded in Mexico, including the number of genera and species with general distribution worldwide (Rein-Ove 2021)

Family	No. Gen.	No. Esp.	Distribution
Buthidae C.L. Koch, 1837	95	1248	This family is found around the world (not found in Antarctica and New Zealand) and is found in tropical, subtropical, and partly in temperate habitats
Chactidae Pocock, 1893	15	209	This family is known from North America, Central America, and South America
Diplocentridae, Karsch, 1880	10	134	North America (Mexico, Southwestern USA [Texas, New Mexico, and Arizona]), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua) and South America (Colombia, Venezuela), Caribbean (Greater & Lesser Antilles), Asia (Egypt, Iran, Israel, Jordan, Lebanon, Oman, Saudi Arabia, Syria, Yemen)
Euscorpiidae Laurie, 1896	6	91	Are widespread in central and southern Europe, and Africa (Mediterranean coast), North America (Mexico), Central America (Guatemala), South America (Brazil, Peru, Venezuela)
Hadruridae Stahnke, 1974	2	9	Members of this family are found in North America (USA and Mexico)
Superstitionidae Stahnke, 1940	1	1	Members of this family are found in western New Mexico, Arizona, extreme southern Nevada, and southern California in the United States. It is also found in Baja California, Baja California Sur, and Sonora in Mexico
Typhlochactidae Mitchel, 1971	4	11	The family is endemic to eastern Mexico
Vaejovidae Thorell, 1876	25	223	Are found in North America (Southwestern Canada, the United States, and Mexico) and Central America (Guatemala)

Table 2.2 Families, number of genera, and species with distribution in Mexico

Family	Genera	Species	Distribution
Buthidae C.L. Koch, 1837	2	53	Almost all Mexican territory.
Chactidae Pocock, 1893	2	3	Baja California Sur
Diplocentridae, Karsch, 1880	3	59	Almost all Mexican territory
Euscorpiidae Laurie, 1896	2	9	Chiapas, Guanajuato, Hidalgo, Oaxaca, Pueblo, Querétaro, San Luis Potosí, Tamaulipas, and Veracruz.
Hadruridae Stahnke, 1974	2	9	Baja California, Baja California Sur, Guerrero, Oaxaca, Puebla, Sonora
Superstitionidae Stahnke, 1940	1	1	Baja California, Baja California Sur, Sonora
Typhlochactidae Mitchel, 1971	4	11	Oaxaca, Tamaulipas
Vaejovidae Thorell, 1876	22	164	All Mexican territory except in the Yucatán Peninsula
Total	38	309	

Scorpions can inhabit different ecosystems, from deserts, semiarid, or humid environments as well as rocky hills. Others, such as the species of the genus *Chaneke* (Buthidae) or species of “Thorelli group” or the minute genus *Konetontli* (Vaejovidae), have specialized niches and consequently are micro-endemic species (Prendini 2001; Santibañez-Lopez et al. 2016).

2.4.2 *Synanthropic scorpions*

The family Buthidae, mainly the genus *Centruroides* as well as some species of the Vaejovidae family, such as *Vaejovis nigrescens* or *Thorellius cristimanus,* have records in the urbanized zones and the inner or peri-domiciliary area of houses, although the scorpions whose sting produces dangerous poisoning have been better studied.

The distribution observed in noxious species of Mexico is largely associated with anthropization of the environment and several ecological factors associated with these species. The species of the genera *Centruroides* are of medical importance to humans and are strongly opportunistic and readily capable of invading disturbed environments. The invasion of habitats disturbed by human impact by these species of is well known in Brazil and Mexico, but also in other regions of the world (Lourenço 2018).

Of the 2632 species of scorpions worldwide, almost 50 are dangerous to humans. In Mexico, only the genus *Centruroides* of the family Buthidae have species of importance for public health. This is because they possess neurotoxic peptides that

Table 2.3 List of species of scorpions in Mexico with importance for public health

Species	Distribution
Centruroides balsasensis Ponce-Saavedra y Francke, 2004	Estado de México, Guerrero, Michoacán
Centruroides bonito Quijano-Ravell, Teruel y Ponce-Saavedra, 2016	Guerrero
Centruroides chamela Ponce-Saavedra y Francke, 2011.	Jalisco
Centruroides elegans (Thorell, 1876).	Jalisco
Centruroides hirsutipalpus Ponce-Saavedra y Francke, 2009.	Colima
Centruroides huichol Teruel, Ponce-Saavedra y Quijano-Ravell, 2015.	Nayarit
Centruroides infamatus (Koch, 1844)	Aguascalientes, Guanajuato, Jalisco, Michoacán, Zacatecas
Centruroides limpidus (Karsch, 1879)	Estado de México, Guerrero, Michoacán, Morelos, Puebla, Querétaro
Centruroides mascota Ponce-Saavedra y Francke, 2011.	Jalisco
Centruroides meisei Hoffmann, 1932	Guerrero, Oaxaca
Centruroides noxius Hoffman, 1932	Nayarit
Centruroides ornatus Pocock, 1902	Guanajuato, Jalisco, Michoacán
Centruroides poncei Teruel, Kovarik, Baldazo-Monsivais y Hoferek, 2015.	Guerrero, Oaxaca
Centruroides ruana Quijano-Ravell y PonceSaavedra, 2016	Michoacán
Centruroides sculpturatus Ewing, 1928.	Sonora
Centruroides suffusus Pocock, 1902	Durango
Centruroides tecomanus Hoffmann, 1932.	Colima, Jalisco, Michoacán, Guerrero
Centruroides villegasi Baldazo-Monsivaiz, Ponce-Saavedra y Flores-Moreno, 2013.	Guerrero
Centruroides vittatus (Say, 1821)	Chihuahua, Coahuila, Durango, Nuevo León
Centruroides pallidiceps Pocock, 1902	Sinaloa, Sonora

may produce a lethal sting for humans and other mammals. Of the 51 species recorded of *Centruroides* in Mexico, only 20 species are considered in the category of importance for public health (Ponce-Saavedra et al. 2016; Riaño-Umbarila et al. 2017; González-Santillána and Possani 2018; Table 2.3). Scorpion stings are considered a serious and widespread health problem in various parts of the world, particularly in tropical and subtropical countries, being an important cause of mortality, primarily in children and older adults (Kassiri et al. 2012; Vahdati and Moradi 2012).

Scorpionism affects 16 states in the center and western portion of the country, where around 400,000 cases are registered annually. In 2020, 266,467 cases of scorpion sting poisoning were recorded nationwide. In first place for scorpion stings is the State of Guanajuato with 45,291 cases, followed by the states of Jalisco and Guerrero with 43,963 and 39,369, respectively, which in total represent 48.27% of cases in the year (SINAVE/DGE/ Salud 2020). Deaths from this cause have been declining due to timely care and treatment with a commercially available, specific antidote. Currently, the treatment against scorpion stings in Mexico is very efficient. It consists of the application of a polyvalent Fabotherapic-antivenom that is produced from the hyperimmunization of horses with the venom of four dangerous species of scorpions. Its mode of action is through interfering and neutralizing circulating toxins and those accumulated in the organs and tissues (Espino-Solis et al. 2009; SINAVE-2020; Norma Oficial Mexicana NOM-033-SSA2-2011; Santibañez-López et al. 2015; Ponce-Saavedra et al. 2016).

2.4.3 Scorpion Conservation

Scorpions have high levels of endemism, and their distributions are typically narrow, making them particularly vulnerable to changes in their environment. Unfortunately, little is known about the status of scorpion conservation worldwide (Ureta et al. 2020). Scorpions are not emblematic or flag species for protected natural areas and are generally considered as noxious fauna mainly due to their dangerous stings rather than species of conservation importance. However, in all protected natural areas these animals are present, so that are at least some species are indirectly protected within established Natural Protected Areas (Martínez-Tejada and Ponce-Saavedra 2020). There are areas of the country with a high diversity of scorpions, such as the Mexican states of Baja California Sur, Coahuila, Guerrero, Oaxaca, Morelos, Michoacán, and Yucatán but none of these areas is under protection by an NPA. A few areas with less species are in Coahuila, Oaxaca, Puebla, and Morelos which do overlap with the existing NPAs and include the following: Cuatro Ciénegas, Don Martín, Tehuacán-Cuicatlán, and Corredor Biológico Chichinautzin (Ureta et al. 2020).

Some species have specific adaptations and requirements, which limit their distributions and represent examples of microendemisms, which per se represents a relevant characteristic of those species that must be protected. The ancient existence on earth, their great adaptive capacity as terrestrial organisms, in addition to their presence in most of the natural and anthropized terrestrial ecosystems, makes scorpions interesting organisms for various purposes in conservation biology, including their usefulness in detecting changes in the habitats and ecosystems in which they are found (Ureta et al. 2020; Martínez Tejada and Ponce-Saavedra 2020).

2.5 Mexican Spiders: Current Knowledge and Perspectives

Among arachnids, spiders are one of the most successful groups in terms of evolutionary radiation, adaptation, and ecological plasticity (Mammola and Isaia 2017). They are the second most diverse order of arachnids after mites, with 49,550 known species in the world (Coddington and Levi 1991; WSC 2021). Their excellent adaptive capabilities have allowed them to live in many environments, conquering all terrestrial habitats and even aquatic habitats, e.g., *Argyroneta aquatica.* In their habitats, spiders are one of the main predators of insects, and they also serve as prey to other species in trophic networks (Turnbull 1973; Polis and Yamashita 1991). Their success primarily is due to the use and production of several types of silk for diverse functions and the employment of venom (toxins) for prey capture (Foelix 2011).

The order Araneae is diverse in Mexico, yet it has only been partially studied. Some regions have been well sampled, and some spider families are relatively well known, whereas other regions or families have been neglected for decades. In this work, we review the spider diversity in Mexico, and we briefly discuss recent studies of spider diversity and conservation, conservation challenges of threatened, and medical importance species. For this work, we sorted all Mexican spider records from the World Spider Catalog 2021 (WSC version 21.5, May 2021). From this, we created a database with the distribution of all species for each state of Mexico. All information was obtained from taxonomic publications downloaded from WSC. We discarded non-taxonomic papers to retrieve the number of families, genera, and species per state. All figures were made with R Studio Desktop. Information of recent studies of diversity, habitats, and ecological aspects, as well as endangered and spiders of medical importance in México, is also provided.

2.5.1 Taxonomy and Diversity

In Mexico, spiders of considerable size, conspicuous coloration, or medical importance were known by native people since the pre-Hispanic period (Barrera and Hoffmann 1981). "*Epeira mexicana*" Lucas (1833) was the first Mexican spider described (Hoffmann 1976), *nomen oblitum* under *Verrucosa arenata* (Walckenaer, 1841). Then, European and US researchers made the most contributions with more than 207 taxonomic works (Hoffmann 1976). Pickard-Cambridge (1891–1899) and his nephew, Pickard-Cambridge (1900) made the main taxonomic contributions at the end of the XIX century and the beginning of the last century. Both described and illustrated many spider genera and thousands of species from Mexico in the monumental work *Biologia Centrali-Americana*. Then, US researchers usually single-authored or in collaboration papers, described a myriad of species in their taxonomic revisions where they included Mexican species. Among them, Gertsch, Levi, Banks, Chamberlin, Platnick, and several others made outstanding contributions and described more than one thousand species distributed in the country. In the last four decades, Mexican researchers have addressed faunistic and taxonomic studies (Fig. 2.4a). For example, in a series of publications about Agelenidae, Maya-Morales and Jiménez (2013, 2016, 2017), and Maya-Morales et al. (2017) described 58 new Mexican species (Fig. 2.4b).

Although many type specimens of Mexican species are deposited in foreign collections, there are 13 formal arachnid collections housed in Mexican institutes and

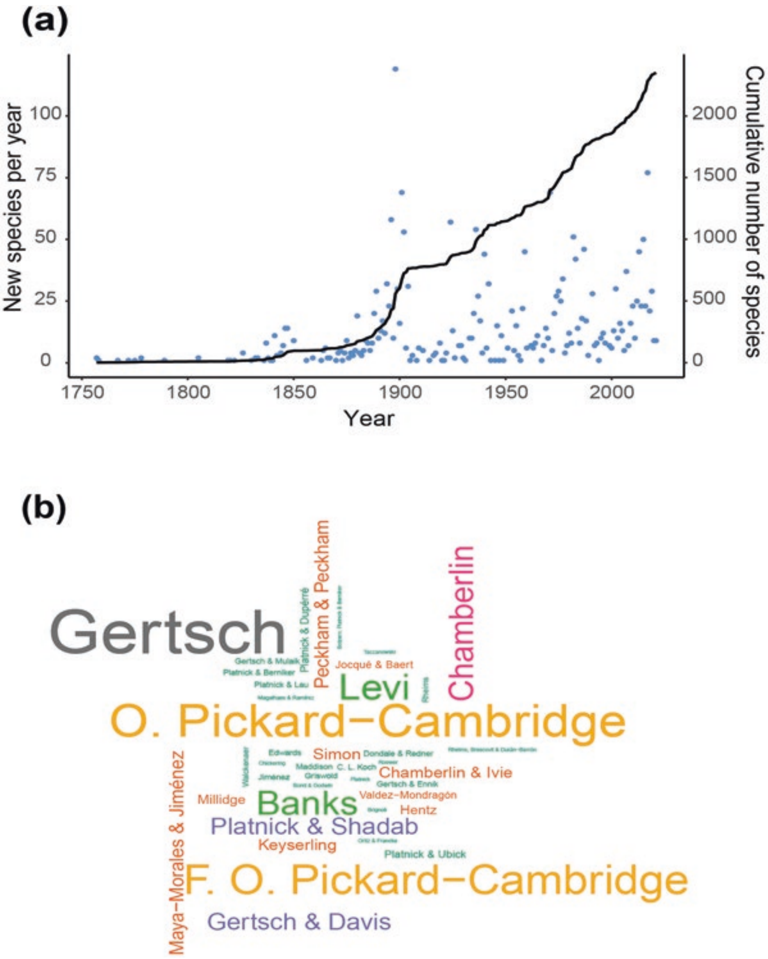


Fig. 2.4 (**a**) Number of spider species described each year between 1757 and 2021 (point) and cumulative number of species valid in Mexico (line). (**b**) Most prolific taxonomists (font size), by number of descriptions of Mexican spiders

universities. The three main collections are Colección Nacional de Arácnidos (acronym CNAN) at Universidad Nacional Autónoma de México (UNAM) with approximately 52,000 specimens, followed by Colección de Arácnidos del Sureste de México (ECOTAAR) at El Colegio de la Frontera Sur (ECOSUR) with 35,490 specimens, finally the Colección Aracnológica (CARCIB) at Centro de Investigaciones Biológicas del Noroeste S.C. which have 18,660 specimens. The three collections hold representatives of all extant orders of arachnids. The CNAN stored specimens of 61 families, 247 genera, and 398 spider species (Brescovit et al. 2017), ECOTAAR holds 52 families, 240 genera, 299 species, and 412 morphospecies (Ibarra-Núñez, 2003, personal communication), and CARCIB holds specimens of 38 families, 132 genera, and 230 species (Jiménez 2004, unpublished data).

These three collections are registered in the Secretaría del Medio Ambiente y Recursos Naturales y Pesca (SEMARNAT).

Hoffman (1976) published the first Mexican spider checklist and listed 50 families with 1598 species. Jiménez (1996) recorded 62 families and 2506 species, Jiménez and Ibarra-Nuñez (2008) enumerated 65 families and 2368 species, while Francke (2014) stated that 66 families and 2295 species have distribution in the country. Here, we registered 2345 species, 455 genera, and 70 families with distribution in Mexico. In other words, roughly 4.7% of all the spiders currently known (49,564 species, see WSC 2021, July 15, 2021) are in Mexico. Moreover, 70 of the 129 families, including the recently described family Myrmecicultoridae, are distributed in Mexico.

Interestingly, 26 genera and approximately 1405 species (58.8%) are known only from Mexico, most of them seem to be endemic. Recent examples include the genera *Califorctenus* Jiménez, Berrian, Polotow & Palacios-Cardiel, 2017, and *Cabolena* Maya Morales & Jiménez, 2017 from Baja California Sur (Fig. 2.5a, b), and the species *Loxosceles malintzi* from Puebla, Morelos, and Guerrero (Valdez-Mondragón et al. 2018a, b) and *Phonotimpus pennimani* from Chiapas (Chamé-Vázquez et al. 2018; Fig. 2.5c, d). Of the total of 2345 species, roughly 14.8% of species are shared between Mexico and the United States, 2.9% are distributed in North America, and 2.2% are known with distributions from Mexico to Panama. Besides, we found that around 27 species were introduced accidentally (exotic species), of which the impact of these species on the native fauna is unknown.

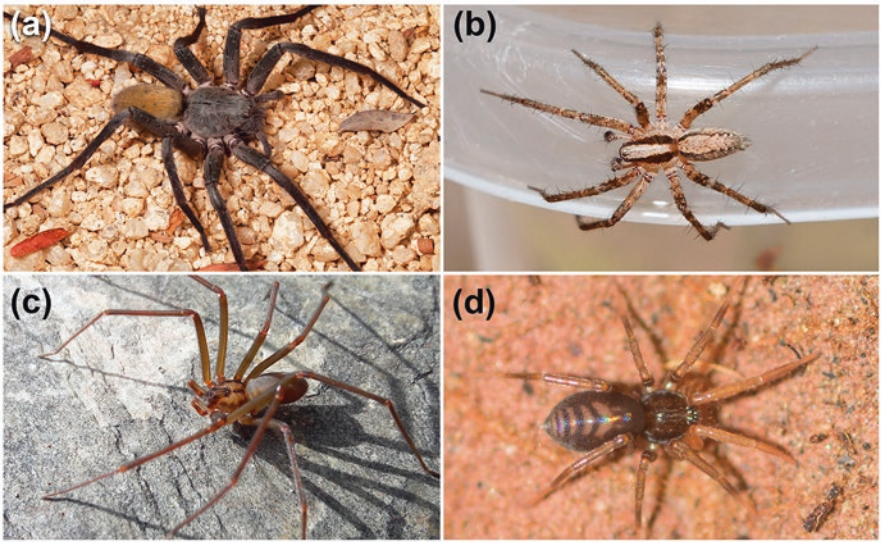


Fig. 2.5 (**a**) Male of *Califorctenus cacachilensis* Jiménez et al. 2017. (**b**) Female of *Cabolena huiztocatl* Maya-Morales and Jiménez 2017. (Source: Maya-Morales). (**c**) Male of *Loxosceles malintzi* Valdez-Mondragón et al. 2018a, b. (Source: Valdéz-Mondragón). (**d**) Female of *Phonotimpus pennimani* Chamé-Vázquez, Ibarra-Núñez, and Jiménez 2018

The families with higher species richness in Mexico are Salticidae (266), Araneidae (200), Pholcidae (175), Gnaphosidae (169), Theridiidae (120), Agelenidae (107), and Oonopidae (104). In comparison, Atypidae, Barychelidae, Hexurellidae, Liocranidae, Myrmecicultoridae, Nemesiidae, Paratropididae, and the introduced families Desidae and Dysderidae have one genus and one species recorded in Mexico (Fig. 2.6a). The family Myrmecicultoridae is monotypic, containing the single genus *Myrmecicultor* Ramírez, Grismado & Ubick, 2019 that in turn contains the single species *M. chihuahuensis* Ramírez, Grismado and Ubick, 2019, which is known from USA and Mexico (state of Coahuila and Aguascalientes). The genera with a high number of species are *Habronattus* (57), *Novalena* (48), *Pardosa* (40), *Loxosceles* (39), *Araneus*, and *Mermessus* (38 each one), *Phidippus* (37), and *Anospicus* (36). These genera are among the most diverse, and they have been taxonomically reviewed in North America.

The southern states of Chiapas (183 genera, 379 species), Veracruz (185, 360), and Guerrero (139, 291) are the regions with high diversity of genera and species, while Aguascalientes (78), Tlaxcala (18, 19), and Zacatecas (24, 31) are the regions with the least documented spider diversity (Fig. 2.6b). This is a general pattern in many arthropod groups such as Formicidae, Papilionidae, Cerambycidae, Diplopoda that are also more diverse in southern states. Clearly, Mexico and especially southern Mexico harbor diverse fauna and flora. Nevertheless, there is sampling bias in the spider numbers since the southern states, the northeastern states of San Luis Potosí and Tamaulipas and Baja California Baja California Sur have been more extensively sampled than the remaining states.

Eleven Mexican states have local spider checklists; Chiapas and Quintana Roo were the first states with checklists (Salas-Suárez and Beutelspacher-Baigts 2011; Ibarra-Núñez 2013), while Hidalgo was the latest (Orozco Gil and Desales-Lara 2021). The number of species reported by these works is different from our tally because we used primary data from taxonomic papers and discarded papers that did not have compelling evidence for species designations (e.g., did not include illustrations or photographs).

Currently, there are 1399 valid species of fossil spiders known globally (Dunlop et al. 2020). Most of the species known were described from Burmese, Baltic, and Dominican amber. In Mexico, 22 spiders have been described from Chiapas amber (Dunlop et al. 2020), most of them studied by Petrunkevitch (1963, 1971). In the Chiapanecan amber, fossil records of 16 extant families are known. Among them, the family with the most species described is Theridiidae (five species see Dunlop et al. 2020).

2.5.2 Diversity Studies, Habitats, and Ecological Aspects

Most spider studies can be included into three broad categories: those conducted in natural environments, those in agroecosystems, and those of synanthropic species (associated with human habitats). Although the National Commission of Natural

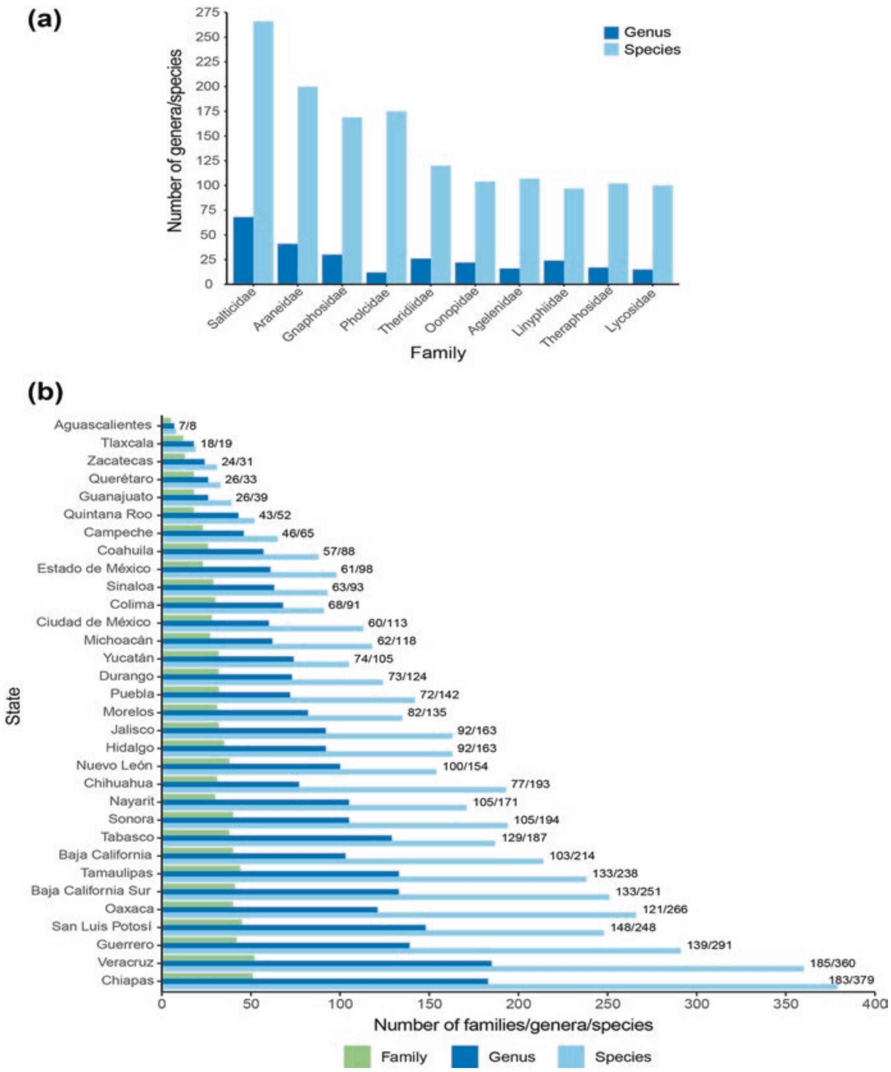


Fig. 2.6 (**a**) Spider families with the highest number of genera and species in Mexico. (**b**) Number of spider families, genera, and species per state in Mexico

Protected Areas (CONANP) administers 182 Natural Protected Areas (ANP), few comprehensive spider inventories have been carried out in these sites. Spider assemblages have been studied in Área de Protección de Flora y Fauna (APFF) Médanos de Samalayuca (Jiménez et al. 2020), APFF Cuatrociénegas (Bizuet-Flores et al. 2015), Reserva de la Biósfera (RB) Volcán Tacaná (Ibarra-Núñez et al. 2011; Maya-Morales et al. 2012), RB El Triunfo (Campuzano et al. 2019), RB Los Tuxtlas (Álvarez-Padilla et al. 2020), RB Sierra La Laguna (Jiménez 1988), and RB Archipiélago de Revillagigedo (Jiménez 1991). In these areas coexist different plant formations, among them: temperate forest, tropical humid forest, xeric scrublands (including dune vegetation), wetlands (oases), tropical mountain cloud forests, and others. Moreover, these ANP were established because they are significant areas of Mexico harboring high biodiversity with a high proportion of relict and endemic species. Furthermore, most of these areas are fragile environments with complex biogeographic and evolutionary characteristics. Indeed, spider inventories were part of baseline studies useful to decision makers for establishing some natural protected areas; for example, the studies carried out in the RB Sierra de La Laguna in Baja California Sur (Jiménez 1988) and RB Revillagigedo Islands in Colima (Jiménez 1991).

Apart from previous studies, researchers have made several spider inventories throughout Mexico. Most of these studies analyzed diversity patterns of spider assemblages, change in abundance, and taxonomic composition of species through space or time. Nevertheless, most studies focus on a local or short temporal scale and some focus on a particular taxonomic group or guild. Rivera-Quiroz et al. (2016) highlighted several of these studies. Furthermore, Rivera-Quiroz et al. (2016) and Álvarez-Padilla et al. (2020) suggest adopting a protocol for online documentation of spider diversity of Mexico. Such a protocol can expedite the species identification process by allowing for comparisons of morphospecies from different studies. Moreover, the suggested standardized sampling protocol can allow meaningful taxonomic and spider community comparisons.

Furthermore, Rivera-Quiroz et al. (2016) and Álvarez-Padilla et al. (2020) demonstrated that this new protocol speeds up the recognition of new species.

Most studies made in agroecosystems have focused on spider diversity in coffee (Ibarra 1990; Ibarra-Núñez and García-Ballinas 1998; Pinkus-Rendón et al. 2006), cocoa (Lucio-Palacio and Ibarra-Núñez 2015; De la Cruz-Pérez et al. 2009, 2015), corn (Martínez-Martínez et al. 2016; Santiago-Pacheco et al. 2017), avocado (Guzmán-García et al. 2017), and mango and citrus (Jiménez and Tejas 1996). Some of these studies evaluated the influence of agricultural intensification (Marín and Perfecto 2013) or different management scenarios on the diversity or abundance of spider assemblages (Pinkus-Rendón et al. 2006; Lucio-Palacio and Ibarra-Núñez 2015). Moreover, some studies suggest that spiders, as generalist predators, can influence insect populations; hence, spiders are potentially important natural enemies of insect pests in Mexican agroecosystems (Ibarra 1990; Moreno-Mendoza et al. 2012).

Arthropods are commonly associated with human habitats. Among them, spiders are recognized as synanthropic. In these habitats, synanthropic spiders benefit from the abundance of prey and stable microclimatic conditions. Moreover, they are usually free from competitors and predators. In Mexico, studies of synanthropic spiders were conducted in cities of Baja California Sur (Jiménez 1998); State of Mexico (Desales-Lara et al. 2013); Guerrero (Rodríguez-Rodríguez et al. 2015); Tamaulipas (Salazar-Olivo and Solís-Rojas 2015); Jalisco (Cupul-Magaña and Navarrete-Heredia 2008); Mexico City (Durán-Barrón et al. 2009); and Michoacán (Maldonado-Carrizales and Ponce-Saavedra 2017). Although some include biological observations, most of studies present species checklists. Surprisingly, spiders of medical significance, e.g., *Latrodectus* and *Loxosceles,* usually are found in houses. In addition, introduced spiders usually are among the most common synanthropic spiders.

Despite these studies, the spider diversity of many natural protected areas remains unexplored. In addition, the number of spider inventories in the agroecosystems is also low, and many types of crops and plantations need to be explored. Moreover, studies focused on the function of spiders in limiting insect populations in Mexico require study. Finally, the impact of invasive spiders on native species needs to be documented as well as how prevalent spiders of medical importance are in houses.

2.5.3 Threatened or Endangered Spiders

Tarantulas (Theraphosidae) are the largest and most colorful, long-lived spiders and are also the most popular spiders as exotic pets (Mendoza and Francke 2020; Pérez-Miles 2020). Tarantulas inhabit tropical and subtropical environments and can be found in caves or anthropogenic habitats too (West 2005; Rojo 2004; Mendoza 2014; Mendoza and Francke 2018, 2020). Currently, there are 152 genera and 1014 theraphosids described worldwide, of which 17 genera and 102 species are known from Mexico (WSC 2021). Among Mexican tarantulas, the genera *Brachypelma* Simon 1891 ("red legs tarantula") and *Tliltocatl* Mendoza and Francke 2020 ("red rump tarantula") due to their bright coloration, docile behavior, and longevity have been illegally traded in massive quantities for decades (Rojo 2004; Mendoza and Francke 2017; Cooper et al. 2019; Mendoza 2020).

The genus *Brachypelma* (eight species) occurs only in Mexico, while *Tliltocatl* (seven species, originally in *Eurypelma* or *Brachypelma* and transferred recently by Mendoza and Francke 2020) is found in Mexico, Guatemala, Belize, and Costa Rica. Species of these genera were categorized as endangered or threatened species at national and international levels because most species have limited geographic distribution, are sensitive to habitat loss, and are illegally collected and traded (Mendoza 2020; Mendoza and Francke 2020).

Fortunately, several species, mainly of *Brachypelma* genus, are protected by the Convention on International Trade in Endangered Species (Appex II of CITES), International Union for Conservation of Nature (IUCN, Red List of Threatened Species) and by SEMARNAT (Norma Oficial Mexicana, NOM-059-SEMARNAT-2010). Unfortunately, illegal trade continues, and tarantulas are shipped in poor conditions (in plastic bags or small containers). Many of them die before reaching their destination due to dehydration or asphyxia (Rojo 2004; Mendoza 2020). Although México is one of the few countries that relates the sustainable conservation and management of native tarantulas, the demands exceed the legal supply. Therefore, many species, even undescribed ones, are extracted in large quantities from their natural habitat and sold illegally.

2.5.4 Spiders of Medical Importance

The World Health Organization listed the following genera as spiders of medical interest: *Latrodectus* Walckenaer, *Loxosceles* Heineken & Lowe, *Sicarius* Walckenaer, *Hexophthalma* Karsch, *Phoneutria* Perty, and *Atrax* O. Pickard-Cambridge (Ramos-Rodríguez et al. 2019). In México, 42 species (1.8%) of the 2345 known spider species are of medical importance. The genera *Loxosceles* (Sicariidae) and *Latrodectus* (Theridiidae) are spiders of medical concern due to their poisonous bite. The former is commonly known as “violin spiders,” “recluse spiders,” or “brown recluse spiders,” whereas the latter is known as “black widow spiders” or “capulina spiders.”

Currently, the genus *Latrodectus* comprises 31 species globally, of which three are found throughout Mexico: *L. mactans* Fabricius 1775, *L. hesperus* Chamberlin and Ivie 1935, and *L. geometricus* Koch 1841. The lats one is a synanthropic, and cosmopolitan species introduced into America (WSC 2021). The three *Latrodectus* species are recorded together (sympatric) in the states of Baja California Sur, Chihuahua, Coahuila, and Hidalgo The species, *L. mactans* and *L. geometricus* are recorded in 27 states, while *L. mactans* is the only species recorded in Tabasco and Ciudad de Mexico (Cabrera-Espinoza and Valdez-Mondragón 2019; Cabrera-Espinosa 2020).

The genus *Loxosceles* comprises 141 species worldwide, of which 39 are known from Mexico. Among them, *L. reclusa* Gertsch & Mulaik 1940 and *L. rufescens* (Dufour 1820) are introduced species (Valdez-Mondragón et al. 2018a, b; WSC 2021). Mexico harbors the highest diversity of *Loxosceles* globally (WSC 2021). In the country, recluse spiders can be found from sea level to 2200 m above sea level. Moreover, these spiders are also found in desert environments (xeric scrub, and deserts) and tropical forests (low deciduous forest, cloud forests, and tropical rain forest; Valdez-Mondragón et al. 2018a, b). All Mexican states have at least one recorded species of *Loxosceles*, although Baja California Sur and Sonora have the highest diversity (5 species; Valdez-Mondragón et al. 2018a, b). From an epidemiological viewpoint, Guanajuato (392) and Jalisco (101) have the highest records of specimens of *Latrodectus*, while Guerrero, Morelos (35), and BCS (30) have the highest records of *Loxosceles* (Valdez-Mondragón et al. 2018a, b).

In humans, *Loxosceles* bites (loxoscelism) result in necrotic cutaneous lesions caused by a rare enzyme (sphingomyelinase D). Occasionally, envenomation may cause systemic damage at the internal organ level (Ramos and Méndez 2008; Vetter 2008; De Moura et al. 2011). In addition, the bite of *Diaea* sp. (Thomisidae), *Anyphaena* sp. (Anyphaenidae), *Zorocrates guerrerensis* (Zoropsidae), and *Kukulcania* cf. *tractans* (Filistatidae) may also cause cutaneous lesions (Ramos 2014, 2018; Sánchez-Vega et al. 2016*). Latrodectus* bites (latrodectism) result in muscle pain, cramps, and occasionally a fatal outcome caused by its highly potent neurotoxin (α-latrotoxin; Garb et al. 2004). Although cases of envenomation have been documented, the biological, physiological, and ecological aspects of Mexican *Loxosceles* and *Latrodectus* remain unstudied. However, as an initial step, recent efforts toward the integrative taxonomy of *Loxosceles* and *Latrodectus* have been published (Valdez-Mondragón et al. 2018a, b; Cabrera-Espinoza and Valdez-Mondragón 2019).

2.5.5 *Anthropic Effects on Spiders*

Even though spiders play a crucial ecological role in any ecosystem (Jiménez, 1996), few Mexican studies have partially addressed anthropic changes or perturbation's impact on spider communities, populations, or species. Most Mexican researchers have studied the effect of land use change on spider communities (diversity, composition, abundance, and guilds). Mostly, such studies compare the spider communities of relatively pristine habitats versus disturbed habitats or relative pristine habitats versus temporal or permanent agroecosystems (e.g., Pinkus-Rendon et al. 2006; Ibarra-Núñez et al. 2011; Lucio-Palacio and Ibarra-Núñez 2015). Some of these studies highlight that the management or the complexity of those transformed landscapes might play an essential role in the persistence of spider communities, since each species response different to perturbation. However, most species are sensitive to any intensity or frequency of perturbation. Urbanization could be considered the most drastic land use change, yet some spiders seem to exploit anthropic environments, especially invasive and synanthropic species (e.g., Jiménez 1998; Maldonado-Carrizales and Ponce-Saavedra 2017; Maldonado-Carrizales et al. 2021a, b). Furthermore, the spider communities that inhabit these anthropic environments are impacted by the same biotic and abiotic factors as those involved in spider communities of disturbed habitats or agroecosystems.

2.5.6 *Final Considerations*

Studies on spiders in Mexico have increased considerably in the last decades, and Mexican and international researchers have made valuable contributions. However, the destruction or modification of the habitat by human-initiated wildfires, deforestation, landscape fragmentation, indiscriminate use of insecticides, unsustainable agricultural practices, and global climatic change will lead to the disappearance of many spiders and arthropods in general before they can be known. Moreover, it seems that national reforestation programs, the implementation of biological corridors, and the natural protected areas have not been enough to reverse biodiversity loss. Still, even with reduced funding, new generations of arachnologists are publishing valuable studies contributing to the knowledge of spiders in Mexico.

2.6 Mexican Mites and Ticks

Within all taxa that make up the Arachnida, mites traditionally have been treated with the systematic category of subclass. Members have a series of shared traits that characterize the group: the prosome and the opistosome are fused widely and this union is not visible; therefore, that two tagmas are recognized as one region called the idiosome. In their life cycle, they present several well-differentiated development stages: larva, protonymph, deutonymph, tritonymph, and adult. The larvae, the first ontogenetic stage, possessing three pairs of legs. Most of the mite species are small (from 0.001 to 30 mm, most less than 1 mm), which has remarkable success in diversification due to the possibility of establishing themselves in all habitats; consequently, they live in all kinds of terrestrial, freshwater, and marine environments.

Their way of feeding varies, since some can feed on solid particles and have internal digestion, whereas others require liquid food, usually as animal parasites or herbivores associated with plants, and even some are predators. Their adaptive versatility and genetic plasticity have allowed for the modification of mouthparts and capacity to adapt to almost all forms of feeding.

Free-living mites can be found in all habitats on the planet. Other mites have formed symbiotic associations (commensal, parasite, and pheric) with invertebrates and vertebrates. Parasites are very important as they can cause direct damage (scabies, exsanguination, paralysis) or indirect damage (vectors of disease pathogens such as Lyme, rickettsiosis, and Erlickiosis). In the case of those that live associated with plants, most species are harmless, however, due to man-made management of agriculture, some species come to cause damage to crop, impacting producers sometimes with very serious economic losses or total loss of crops.

Throughout their evolution, beginning with their origin estimated at approximately 400 million years ago, their capacity of adaptation has led them to great diversification, so there is no habitat where a species is not found. Thus, mites are the most diverse and abundant within the arachnids. As of 2011, there was a worldwide total of 55,000 described species (Zhan 2011), but with a prediction that there may be up to a million species.

Despite the controversy of the monophyletic origin of mites and their relationship with other groups of arachnids, phylogenies have recently been made using molecular characters that support their descent from a common ancestor (Lozano-Fernandez et al. 2019) and the classification in large groups proposed by Krantz and Walter (2009) who group them into two large monophyletic groups in the taxonomic level of superorders Parasitiformes which include Ixodida, Holothyrida, Opilioacarida, and Mesostigmata orders and Acariformes with the orders Trombidiformes (suborders Prostigmata and Sphaerolichida) and Sarcoptiformes (suborders Oribatida, including Astigmata and Endeostigmata) (Vázquez-Rojas et al. 2016).

Regarding the worldwide diversity of Parasitiformes, 12,070 species have been described, these include the ticks (Ixodida) with 3 families and 900 species, the Opilioacarida with one family and 40 species, the Holothyrida with 3 monotypic families with 30 species and the Mesostigmata, the most diverse group with 70 families and 11,000 species (Zhan 2011).

In Mexico, species of all orders of Parasitiformes have been recorded, except Holothyrida. Opilioacarida is one of the best-studied groups in our country of which 36 species are known (Vázquez 1999; Pérez et al. 2014; Vázquez-González et al. 2016; Vázquez and Klompen 2015; Ojeda and Gasca-Pineda 2019).

The Mesostigmata also have a very large number of species with 671 recorded species (Villegas-Guzmán et al. 2008, 2009, 2011; Ujvári 2011; Vargas-Sandoval et al. 2013; Chaires-Grijalva et al. 2013; Pérez et al. 2014; Colín-Martínez and García-Estrada 2016; Ojeda and Gasca-Pineda 2019; Valerio-Salgado et al. 2019; Ramos-Lima et al. 2021).

The Ixodida mites (ticks), the only order in which they are all obligate hematophagous parasites, cause great economic damage; they are also the number one disease vectors among all arthropods. Due to their great medical and veterinary importance, they have been widely studied, but there is still a lot of wild fauna to be explored. Two of the three families have been recorded in Mexico with 38 species of Argasidae and 76 of Ixodidae (Pérez et al. 2014; Guzmán-Cornejo et al. 2016, 2019; Light et al. 2020).

Mites of the superorder Acariformes comprise two orders, Sarcoptiformes with two suborders, the first Oribatida with 162 families and 11,000 species, Astigmata (part of Oribatida) with 71 families and 5000 species and the Endeostigmata suborder with 10 families and 100 species. On the other hand, the order Trombidiformes has the Sphaerolichida suborder with two families and 21 species and the Prostigmata suborder, which is one of the most diverse, has 149 families and approximately 25,000 species (Zhan 2011).

In Mexico, the order Trombidiformes have two suborders: Prostigmata, which represents a very varied and diverse group which 1334 species and the Sphaerolichida suborder with five recorded species (Paredes-León and Morales-Malacara 2014; Pérez et al. 2014; Vázquez-González et al. 2016; Bucio-Soto et al. 2016; Ayala-Ortega et al. 2019a, b; Morales-Felipe et al. 2019; Ojeda and Gasca-Pineda 2019; Light et al. 2020).

Finally, within the order Sarcoptiformes, there are two suborders, first Oribatida, including Astigmata mites, which is a diverse taxon that currently has 900 recorded species but being such a large group there is still much systematic work to do (Pérez et al. 2014; Ojeda and Gasca-Pineda 2019). The Endeostigmata second suborder have been recorded 33 species (Pérez et al. 2014).

Most of the studies of mites in Mexico are faunistic by locality, state, region, crop, or by host. Even so, knowledge is advancing, since 2014 when Pérez and collaborators recorded 2625 species, thus having increased between registered and descriptions to a total of 3093 in acarofauna species of Mexico, increasing from 4.8% to 5.8% of total known species worldwide. By groups, those with the highest percentage respect to worldwide described species are Opiliacarida (90%), Endeostigmata (33%), Sphaerolichida (23.8%), Ixodida (12.6%), and the rest oscillate between 5% and 7% (Table 2.4).

The conservation status of mites is directly related to the conservation status of the ecosystems, fauna, and flora they inhabit. The small size and highly specific feeding biology of mites make them have great species richness and ecological diversity, with a wide variety of life histories, trophic habits, and reproductive patterns. The role that mites fulfill is fundamental to the functioning of ecosystems through their actions as predators, decomposers, herbivores among others, which makes them very important to maintain the important components in the conservation of ecosystems.

Table 2.4 Number of known mite species in worldwide and Mexico

	Worldwide Zhang (2011)	Pérez et al. (2014)	2021	% Mexico
Parasitiformes	12,070	615	821	6.8
O. Ixodida	900	100	114	12.6
O. Holothyrida	30	0	0	0
O. Opilioacarida	40	8	36	90
O. Mesostigmata	11,000	507	671	6.1
Acariformes	41,121	2010	2272	5.5
O. Trombidiformes	25,021	1209	1339	5.4
SO. Prostigmata	25,000	1208	1334	5.3
SO. Sphaerolichida	21	1	5	23.8
O. Sarcoptiformes	16,100	801	933	5.7
SO. Oribatida	11,000	435	544	4.9
Astigmata	5000	351	356	7.12
SO. Endeostigmata	100	15	33	33
Total	53,191	2625	3093	5.8

O order, *SO* suborder

Rainforests, deserts, agroecosystems, and coastal ecosystems are in a serious threat due to accelerated urban and tourist development, as well as the indiscriminate use of pesticides, changes in land use, forest clearing, and forest fires. These all constitute serious threats to the conservation of mites, with species that are not yet known and/or dependent on other species of animals or plants in danger of extinction. The biodiversity of mites is directly related to the conservation of species with which they are associated, and with healthy ecosystems, so actions that benefit conservation and sustainable management of agroecosystems and natural ecosystems contribute to the conservation of mites. The conservation actions that should be implemented in favor of the mites are the same that we must do for the conservation of the planet.

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Chapter 3
Mexican Insects in the Anthropocene

Benigno Gómez Gómez, Ek del Val de Gortari, and Robert W. Jones

Contents

3.1 Introduction

Terrestrial insects are the most species diverse animal group with a total world biomass greater than ten-fold that of all wild terrestrial mammals and birds (Gaston 1991; Bar-On et al. 2018). As such, they lag far behind larger vertebrates in the percentage of species that have been described and of which we have knowledge of their basic life histories or population parameters. Also, whereas the decline of the vertebrate fauna has been well documented for many taxonomic groups (Dirzo et al. 2014; Young et al. 2016), evidence of insect decline has been harder to document

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/978-3-031-17277-9_3.

B. G. Gómez
El Colegio de la Frontera Sur, San Cristobal de las Casas, Chiapas, Mexico

E. del Val de Gortari
Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Morelia, Mexico

R. W. Jones (✉)
Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, Mexico
e-mail: rjones@uaq.mx

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_3

and, until recently, had not attracted much attention. As stated by Raven and Wagner et al. (2021), “We have been slow to recognize that insects, too, are declining rapidly.”

Recently, this appreciation changed with the report of a 75% decline over 27 years in total flying insect biomass in protected areas of Germany by Hallmann et al. (2007). This research galvanized the scientific community and led to numerous reports and reviews of insect declines worldwide, which ignited a global media storm proclaimed as the “Insect Apocalypse” (Vogel 2017; Saunders et al. 2019). Although there is still a need for more quantitative data (Saunders et al. 2019; Wagner 2020), there is general acknowledgment that the precipitous declines we have witnessed and documented in the vertebrate world, appear also to be happening with insects (Dirzo et al. 2014; Eggleton 2020; Wagner 2020; Cardoso et al. 2020; van Klink et al. 2020; Wagner et al. 2021; Raven and Wagner 2021; Janzen and Hallwachs 2021). If these declines are as serious as the evidence suggests, then the consequences are alarming. Insects make up much of the lower trophic levels of terrestrial ecosystems, upon which the higher levels depend. Insect losses portend serious disruptions of terrestrial ecosystem function, and loss of essential ecosystem services such as pollination, organic matter decomposition, and insect population regulation, among others (Yang and Gratton 2014; Eggleton 2020).

The scientific evidence for insect decline in Mexico is limited. However, many environmental-related issues of Mexico leave little doubt that insect losses reported for other regions of the globe are also occurring there. These include the following: a general loss of 50% of the country’s natural vegetation cover and 32% loss in forest cover as of 2011 (Sarukhán et al. 2017); continued deforestation rates with an 8.1% decrease in tree cover from 2000 to 2020 (Global Forest Watch 2022); a 1.1% annual population growth rate, and high rates of urbanization; limited support and funding for established protected areas; continued reliance on insecticides as primary pest control measures with continued use of banned chemicals and/or using non-recommended dosages Hernández-Antonio and Hansen 2021; serious contamination of practically all the watersheds of the central and northern regions of the republic (Martínez Austria et al. 2019); and general combined effects of climate change in relation to forest fires, drought, desertification, and loss of soils (Becerril-Pina et al. 2015; Martínez-Meyer and Velasco this volume Chap. 20).

As for many countries located within the tropics, one of the limitations of evaluating the threats and potential loss of insect species in Mexico is the lack of basic taxonomic information for the majority of taxa. Most of the estimations of the percentages of undescribed to described species in taxonomic groups for Mexico are “educated guesses” within specific taxa by taxonomic specialists. For species diverse taxa, estimates of undescribed species can vary from 15% (Butterflies) to greater than 50% (Hymenoptera, Orthoptera, Coleoptera) (Heraty et al. 2003; Barrientos 2004; Anderson and O’Brien 1996; Navarrete-Heredia et al. 2002; Llorente-Bousquets et al. 2014).

Given the enormity of the task of sufficiently describing the biological roles and importance of the highly diverse and poorly known insect fauna of a megadiverse country such as Mexico, we focus on selected topics and case studies concerning insect species or communities unique to the country. By focusing on a subset of insect species, we sought to describe some of the general life-history aspects, evolutionary background, and conservation status or importance in sufficient detail so that they could serve as apt examples for illustrating the roles and continuing importance of insects in Mexican ecosystems and culture. With this approach, we present three examples. The first concerns the emblematic, internationally known, and intensely studied monarch butterfly *Danaus plexippus* (L.) which completes an extraordinary annual migration of up to 4800 km to overwinter in aggregated populations in highly restricted mountain habitats in central Mexico. The second is a taxonomic group, the dung beetles (Scarabaeinae), which is historically one of the best studied groups in Mexico. The third group is an ecological community, the highly diverse, highly endemic, and poorly studied community of insects inhabiting leaf litter and soil of montane forests, with emphasis on leaf litter weevils.

3.2 Conservation Status and Future of the Monarch Butterfly, *Danaus plexippus* (L.): A Mexican Perspective

Animal migrations have fascinated humans since time immemorial. In the case of a migrating insect, this appeal also elicits astonishment since we strive to understand how such small creatures such as butterflies, moths, and dragonflies are able to travel thousands of kilometers every year (Ward 1987; Satterfield et al. 2020). One of the best-known examples is *Danaus plexippus* (L.), the Monarch butterfly, which accomplishes a journey of more than 4000 km every fall, traveling from southern Canada and the United States to central Mexico. Conservation efforts in Mexico have focused on the conservation of the winter roosting site in the highlands of the state of Michoacán, where the butterflies aggregate each year. This area was designated in 2000 as the Monarch Butterfly Biosphere Reserve (MBBR) and a UNESCO World Heritage Site in 2008. These high-elevation Mexican fir forests are unique because they provide the ideal conditions for monarch survival during winter. The monarch butterflies form dense clusters (Fig. 3.1) that are attached to and completely cover fir branches and stems where they are protected from extreme temperatures, hail, strong winds, and snow by an insulating microclimate formed by the forest canopy. This microclimate prevents butterflies from freezing but is cool enough to also prevent the exhaustion of lipid reserves that would occur at higher temperatures (Williams and Brower 2015).

The MBBR is inhabited by several local communities that have managed and lived from the forest since pre-Columbian times. Understandably, there have been some conflicts between local landowners and conservation managers (Ramírez et al. 2003). Several NGOs (local and international) and governmental departments have initiated different projects to try to coordinate conservation efforts and tourism (Ramírez et al. 2015). Most successful projects are those that have included local people from the beginning and that take into consideration traditional knowledge and resource management. Presently, several communities are conscious about the importance of forest conservation for monarchs and have developed conservation and restoration plans in order to coordinate their traditional way of living with forest-monarch conservation (Fig. 3.1).

Fig. 3.1 (**a**) Tourist entrance to Monarch Butterfly Sanctuary, in the Monarch Butterfly Biosphere Reserve, and part of community of the Ejido San Mateo Almomoloa, Michoacan (Wikimedia CC). (**b**) Winter roosting site on fir tree in Monarch Butterfly Biosphere Reserve (CONANP 2019)

Monarch migratory populations at winter roosting sites in the state of Michoacán, in the central plateau region, have declined in recent years. In 1997, the butterfly overwintering roosting area covered 18.7 ha, reached the lowest monarch area covered in 2014 with less than 1 ha, and has only partially recovered to 2.1 ha by 2021 (MBF 2021). These declines have put the conservation community on alert. Several factors appear responsible for monarch population decline. These include a lethal combination of (1) a decrease in monarch larvae host plants ("milkweed," *Asclepias* spp.) throughout the monarch's North American distribution, in part because the plants are often regarded as agricultural weeds, (2) an increase of pesticide use in agricultural fields throughout North America, and (3) to a decrease and fragmentation of forest cover in general and specifically in overwintering sites in Mexico (Brower et al. 2012).

An important emerging factor to be considered for monarch butterfly conservation in Mexico is the fact that fir forests (*Abies*) are under severe stress due to climate change. It has been predicted that the suitability of climatic conditions for firs survival within the MBBR will decrease by 70% by the year 2030 (Sáenz-Romero et al. 2012). This indicates that current hibernating sites will not be suitable for sheltering monarchs in the near future. However, recently, new colonies have been found in other temperate forests of the Sierra Nevada, south of MBBR, suggesting that monarch butterflies may be already tracking new sites with more adequate conditions to spend the winter under sheltered conditions (Pérez-Miranda et al. 2020). Forest restoration in the present overwintering area now includes assisted migration efforts to enhance plant survival and planting tree saplings with higher drought tolerance from lower altitudinal forests under nurse shrubs (Carbajal-Navarro et al. 2019; Sáenz-Romero et al. 2021).

Also, it has become increasingly relevant for Mexico to address the migratory trajectory throughout the country in order to understand the causes of decline. For example, Mora Alvarez et al. (2019) have identified two deadly points where monarchs cross two high-speed freeways in northern Mexico. They calculated that ca. 200,000 butterflies were killed in those two spots during 15- and 20-day periods in a single year. The mitigation measures they propose are to better enforce vehicle speed during the migration period, to construct deflection structures to raise the height of crossing monarchs, and to manage nearby habitat to decrease the potential for monarch to descend to roost near crossing points. Monarch conservation in the long term will require further emphasis on the safety of the migratory route and to augment nectar sources for the migrating adults as well as secure more roosting sites along the migration route.

3.3 Mexican Dung Beetles in the Anthropocene (Coleoptera: Scarabaeidae: Scarabaeinae)

The Scarabaeinae is a group of Coleoptera that are generally known as dung beetles (Fig. 3.2a), even though their feeding habits extend beyond vertebrate droppings for feeding and reproduction (coprophagy). This feeding habit is complemented or replaced with other nutritional activities such as necrophagy, mycetophagy, carpophagy, and even predation (Halffter and Halffter 2009; Larsen et al. 2009; Sánchez-Hernández et al. 2019). These beetles are a widely distributed group of insects, found in almost all ecosystems, from sea level to altitudes above 4000 m with greatest diversity found in tropical and subtropical regions (Scholtz et al. 2009). Thanks to their various mechanical actions during manure burial, they provide important environmental services such as recycling and reincorporating nutrients into the soil, generating benefits such as nitrogen retention, the reduction of greenhouse gases, the release of gases, drainage and aeration of the soil by bioturbation, control of mammalian gastroenteric parasites, secondary zoochory (seed dispersal) and pollination, among others (Nichols et al. 2008; Simmons and Edwards 2011; Penttilä et al. 2013; Lumaret et al. 2020). These arthropods have been noted to be sensitive to structural changes in habitats caused by disturbances, often exhibiting drastic transformations in their development and distribution in modified landscapes (Sánchez-Hernández et al. 2020). These characteristics have led different authors to consider these beetles as indicators of change in the biological diversity of ecosystems in the Anthropocene (Halffter and Favila 1993; Favila and Halffter 1997; Davis et al. 2001; Halffter and Arellano 2002; McGeoch et al. 2002; Spector 2006; Otavo et al. 2013).

Dung beetle declines are caused by a variety of factors and are not necessarily the same everywhere. It largely depends on the biogeographic region, as well as the types of anthropogenic pressures that are exerted (Lumaret et al. 2020). Among the negative impacts, the destruction of forests accompanied by defaunation processes reduces both the habitats where they develop and the food resources for the beetles

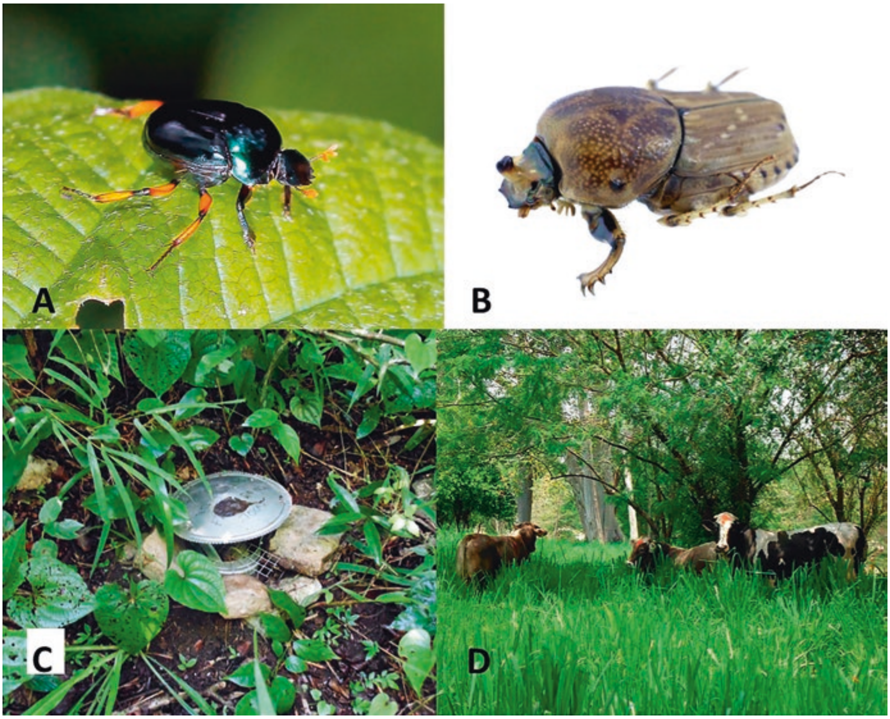

Fig. 3.2 (**a**) *Canthon femoralis* (Chevrolat) a Mexican dung beetle (Photo B. Gómez) (**b**) The exotic dung beetle *Euoniticellus intermedius* Reiche of Afro-Asiatic origin, now a dominate dung beetle in Mexico. (Photo credit: David McClenaghan, CIRSO). (**c**) Baited dung trap used to monitor populations of dung beetles (Photo B. Gómez). (**d**) Modified tropical silvopastoral grazing system in Mexico, now a dominant habitat for dung beetles. (Photo B. Gómez)

(Scholtz et al. 2009; Dirzo et al. 2014; Mendoza and Camargo-Sanabria 2019). Another is intensive agricultural methods that employ mechanization and chemical products which generally have a greater impact on dung beetles when compared to traditional agricultural practices that use draft animals (Hutton and Giller 2003). Also, the widespread use of antiparasitic veterinary products in livestock, whose residues end up in animal manure, also negatively affects dung beetles (Martínez et al. 2017). Even the application of selective herbicides in grazing areas has added to the decrease in dung beetles (Lobo 2001; Carpaneto et al. 2007; Lumaret et al. 2020). In an attempt to compensate for the deficiency in beetle ecosystem services, mainly the removal of animal manure, some countries have introduced exotic dung beetles. These species invariably have high reproductive rates, which makes them successful invaders that unfortunately can also reduce the diversity and abundance of native populations, sometimes leading to extirpation of native species (Pokhrel et al. 2020; Lumaret et al. 2020). Finally, accelerated climate change of the Anthropocene brings negative consequences for dung beetles. This is because temperature plays an important role in the bioecology of species, affecting their latitudinal and altitude distributions. These changes in dung beetle distributions and their associates modify interspecific interactions that can lead to the extinction of more specialized species (Parmesan 2006; Dortel et al. 2013; Maldaner et al. 2021).

Some 6200 species of dung beetles are known in the world (Sánchez-Hernández et al. 2018), of which 294 are distributed in Mexico (Sánchez-Hernández et al. 2020). The best-known fauna of Mexican ecosystems is that which is distributed in the center-south portion of the country, mainly in the tropical zones of the states of Veracruz and Chiapas. The temporal distribution of adults reaches the highest values of richness and abundance during the months of the rainy season (Deloya et al. 2007; Mora-Aguilar and Montes de Oca 2009; Rodríguez-López et al. 2019). In less disturbed Mexican forests, dung burrowing species dominate over dung crawlers (rollers); generalist feeding species (copronecrophagous) predominate over coprophagous and necrophagous species; and nocturnal species are more abundant than diurnal (Halffter et al. 1992). However, the conversion of forests into pastures and new cultivation areas can cause drastic changes in microhabitats. The result is a higher proportion of small Scarabaeinae species with diurnal preferences and rolling habits (Pineda et al. 2005; Quintero and Halffter 2009).

Mexican dung beetles during the Anthropocene are experiencing losses in diversity and altered ecological interactions similar to what is occurring globally. Various investigations in the rainforest of Mexico have found a positive relationship between a preserved or little disturbed habitat and the diversity of dung beetles. Changes in land use and the structure of primary vegetation result in a reduction in taxonomic diversity and ecological functioning of beetle communities (Halffter et al. 1992; Reyes-Novelo et al. 2007; Navarrete and Halffter 2008; Díaz et al. 2010; Barragán et al. 2011; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; Rivera et al. 2021). Fragmentation caused by human activities in the Central Plateau of Chiapas is leading to biotic homogenization in dung beetle assemblages, with a high proportion of rare and opportunistic species (Sánchez-Hernández et al. 2022). In the Lacandon Rain Forest (Chiapas), the diversity of species within the landscape depends on the canopy cover, soil temperature, and the geographical distance between fragmented sites, and results have found that the large-bodied nocturnal paracoprid species (dung burrowers) are the most sensitive to anthropogenic impacts (Navarrete and Halffter 2008; Barragán et al. 2011; Rös et al. 2012). In the more temperate mountainous landscapes of the Mexican Transition Zone, which extend along narrow cordilleras, dung beetles are in contact with ecosystems of diverse and different biogeographic histories and ecological characteristics. The species dynamics of dung beetles appear to differ here than in lowland tropical landscapes. The variegated landscape and natural disturbances of these mountainous areas have allowed a better adaptation of their typical specie assemblages to these changing conditions, exhibiting a sufficiently robust ecological behavior, so that they appear less affected by anthropogenic disturbances. However, because of the modification of the habitat in these areas, the biota is modified with the invasion of species, mainly those that come from lower altitudes (Halffter et al. 1995; Arriaga-Jiménez et al. 2018).

In the Anthropocene, changes in land use in Mexico generally begin with deforestation and fragmentation of forests to open new agricultural, livestock, and urban areas. Due to their adaptability to exploit agricultural areas, dung beetle populations come in contact and are affected by the intensified and inadequate use of dewormers and insecticides for livestock, and herbicides for weed control (Martínez et al. 2017). The expansion in the use of macrocyclic lactones (mainly ivermectin) for the treatment of endo and ectoparasites of cattle in tropical regions can have an ecotoxic effect by reducing populations and negatively impacting the reproductive biology and ethology of dung beetles (Pérez-Cogollo et al. 2018). In livestock regions such as those of Yucatan, pastures where cattle are treated with these types of dewormers present less diversity of the characteristic dung beetle community compared to those without treatment (Basto-Estrella et al. 2014a, b). However, a differential effect has been found throughout the Mexican territory. On the one hand, in northern Mexico, *Canthon (Canthon) humectus* (Say, 1831) and *Copris incertus* Say, 1835, may be negatively affected by ivermectin (Ochoa-García et al. 2019; Villada-Bedoya et al. 2019) while in southwestern Mexico there is evidence of the lethal and sublethal effect on *Onthophagus landolti* Harold, 1880, an abundant paracoprid species with a wide geographical distribution (Rodríguez-Vivas et al. 2020). However, there are data suggesting that *Canthon (Canthon) indigaceus chevrolati* Harold, 1868, a species that inhabits livestock systems in the Mexican tropics, may show tolerance/resistance to both ivermectin and moxidectin (Rodríguez-Vivas et al. 2020).

Another factor that is impacting the dynamics of dung beetles in Mexico is invasive exotic species, mainly the African *Digitonthophagus gazella* (Fabricius 1787) and the Afrotropical *Euoniticellus intermedius* (Reiche 1849; Fig. 3.2b). These species were introduced to the United States to fill the gap in the ecosystem service of local dung beetles: the removal of manure from livestock areas. The subsequent process of introduction, dispersion, and colonization carried out by these invasive coprophagous species has been extensively studied in Mexican territory (Rivera-Cervantes and García-Real 1991; Lobo 1996; Kohlmann 1994; Lobo and Montes de Oca 1997; Montes de Oca and Halffter 1998; Morales et al. 2004). The data reveal that these invasive species can establish themselves and become dominant species in open sites with livestock presence in arid and semi-arid ecosystems in northern Mexico. Intensive livestock practices increase the abundance of exotic species of dung beetles and are indicative of pastures with intensive management (Anduaga 2004; Barragán et al. 2021). In the tropical zone of southern Mexico, invasive species are distributed mainly along livestock corridors in coastal areas, silvopastoral systems, mainly with tropical dry forest, and transformed landscapes (Fig. 3.2d). In these ecosystems, the invasive beetles compete with the local fauna but apparently without having an impact on the loss of native species, which are associated with fragments of nearby forests (Arellano et al. 2008).

In Mexico, the effects of climate change on the bioecology, distribution, and diversity of dung beetles have been little studied. These insects are one of the groups that are possibly one of the most vulnerable to the increase in temperature as their diversity is negatively related to altitude (Deloya et al. 2007; Escobar et al. 2007; Gómez et al. 2017; Ortega-Martínez et al. 2020).

It is necessary and urgent to understand the effects of natural and anthropogenic processes that affect dung beetles within the Anthropocene. The change in land use to open agricultural areas has turned out to be one of the main drivers of change in the dynamics and loss of diversity of the Scarabaeinae. However, it is possible to minimize the impact with crops and practices that are friendly to biodiversity, such as rustic cacao plantations, shade-grown coffee, low-density cattle ranching with moderately managed pastures where native vegetation is preserved, and the rational use of dewormers, insecticides, and herbicides (Pineda et al. 2005; Deloya et al. 2007; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; Barragán et al. 2021). On the other hand, the recovery of the original forest cover and the accompanying large mammals is crucial to maintain the taxonomic and functional diversity of dung beetles in tropical forests (Rivera et al. 2020, 2021).

Protected natural areas play a very important role in maintaining over 90% of the diversity of dung beetles in a region, with Biosphere Reserves being those that present greater environmental heterogeneity and protect a greater diversity of biota (Sánchez-Hernández et al. 2020). Conservation efforts through Protected Natural Areas would be much more important and effective when linked to the landscape or ecosystem scale, such as the Archipelago Reserves proposal (Moctezuma et al. 2018). In this sense, the resulting connectivity is prioritized, which may be more relevant than the actual quality of the habitat itself to conserve functionally diverse beetle assemblages (Ortega-Martínez et al. 2020). Unfortunately, and despite its characteristics as a bioindicator group, in Mexico dung beetles are not included among the priority groups within the monitoring programs that support the management of protected areas, underestimating their importance when compared to larger, more charismatic species of vertebrates and plants (Sánchez-Hernández et al. 2020).

3.4 Leaf Litter Insects of Montane Forests: Loss of Hyper-diverse Assemblages

A well-known biodiversity pattern for Mexican montane fauna is the inverse relationship between high species richness with relatively low levels of endemism in the tropical lowlands, compared to lower overall richness contrasting with greater levels of endemism at higher elevations (Peterson et al. 1993; Laurance et al. 2011). However, this is not the case for certain invertebrates inhibiting tropical montane leaf litter where abundance and diversity of arthropods are high, and both the species richness and endemism are generally greater than that in lowland tropical forest litter (Nadkarini and Longino 1990; Longino and Colwell 2020). Presumably, the greater accumulation and slower degradation of litter in the cooler, moist environment of montane forests (Leija-Loredo et al. 2018) affords more energy and resources for the maintenance and evolution of this arthropod community. Also, ant abundance, a key soil predator guild, is notably less in cloud forests than lowland forests (Longino et al. 2014).

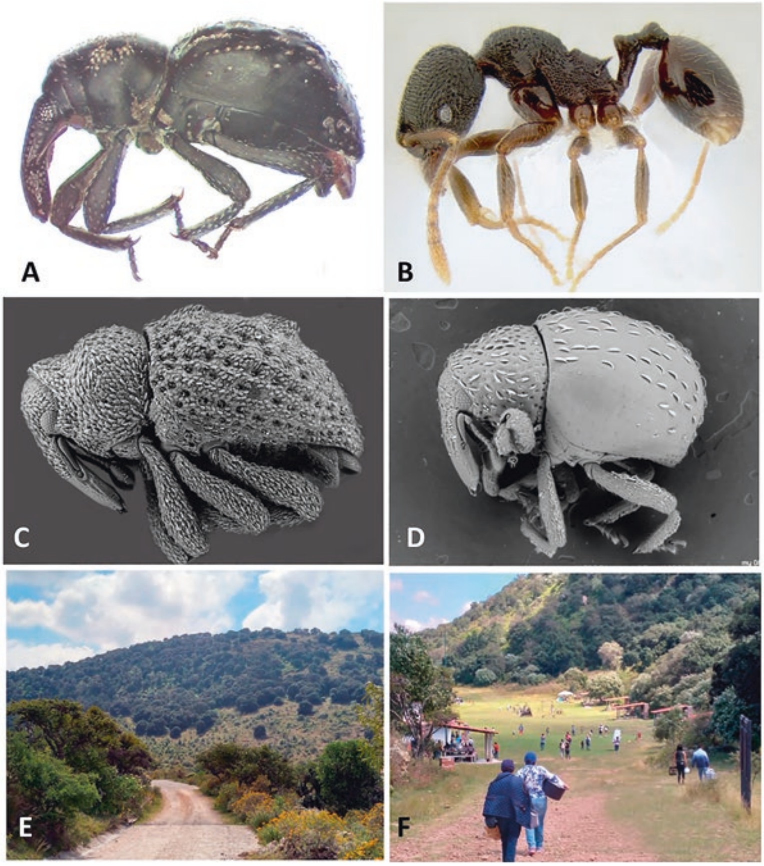

Fig. 3.3 Examples of insect fauna of leaf litter and habitats: (**a**) *Theognete tuberosa* Anderson (Coleoptera: Curculionidae), Sierra Gorda Biosphere Reserve, near Pinal de Amoles, Queretaro, in leaf litter of cloud forest, length 3.6 mm. (Photo R.W. Jones); (**b**) *Stenamma ignotum* Branstetter (Hymenoptera: Formicidae), Cerro Mirador, Oaxaca, in leaf litter of humid montane forest, 990 m, length 1.9 mm. (Photo credit: Michael Branstetter, www.antweb.org); (**c**) undescribed Cryptorhynchinae genus (*Acalles/Tylodinus*) (Coleoptera: Curculionidae), El Cielo Biosphere Reserve, in leaf litter of cloud forest, 1429 m, length 2.9 mm. (Photo R.W. Jones); (**d**) undescribed species of *Eurhoptus* (Coleoptera: Curculionidae), La Barreta Municipal Park, Querétaro, in leaf litter of montane forest, 2500 m, length 1.6 mm. (Photo R.W. Jones); (**e**) montane forest fragment of approximately 20 ha, La Barreta Municipal Park, Querétaro. (Photo R.W. Jones); (**f**) tourist area of La Barreta Municipal Park, Querétaro adjacent to forest fragment. (Photo R.W. Jones)

There are numerous examples of "hyper-diversity" of insect taxa from Mexican leaf litter. Anderson (2010) took on the mammoth taxonomic task of describing the species from a single montane leaf litter genus, *Theognete* (Coleoptera: Curculionidae; Fig. 3.3a), which prior to his study had a single described species. After an intensive collection effort, he described a total of 93 new species from humid montane forests from Mexico and Central America, of which 78 (83%) were from Mexico, and 77 (98%) were collected from a single state (Anderson 2010). Endemic altitudinal specialists are also found in ants. Branstetter (2013) revised the Middle American clade of the leaf litter-inhabiting ants of the genus *Stenamma* (Formicidae, Myrmicinae; Fig. 3.3b). To a previous total of seven species, he added 33 new species, of which 21 were reported from Mexico. Likewise, Luna-Cozar et al. (2014) described 32 species from leaf litter of the genus *Tylodinus* (Curculionidae) found exclusively in cloud forests of the state of Chiapas. In a similar region, Barrios-Izás et al. (2016) described the new genus *Plumolepilius* (Curculionidae), along with nine of its species from leaf litter of cloud forests in Guatemala and Chiapas State, México. New genera and species have also been described from Hemiptera in leaf litter (Brailovsky and Peredo 2009).

Species richness and endemism levels on individual mountains peaks of the Mexican highlands are often high, and many insect species are undescribed (Fig. 3.3c, d). Jones et al. (2008) reported a total of 56 species of leaf litter weevils (Curculionidae) from a single mountain peak in Chiapas. These were found at high densities (>15 individuals per m^2 of litter) of which 95% were undescribed. In a similar study of three montane oak forests in Central Mexico, Jones et al. (2022) reported a total of 49 species of leaf litter weevils of which 88% represented undescribed taxa. Species similarity between these sites was low and less 26% of the species were shared among the three oak forests, with only 16% shared between the two closest sites separated by only 24 km. In addition, for both these studies, most weevil species (>90%) were wingless (apterous) indicating low powers of dispersion, and virtually nothing is known of their biology. These examples of weevils of leaf litter can be considered as an indicator group for other poorly collected and studied arthropods from soil and leaf litter of montane forests with “micro-endemic” distributions in Mexico and Central America. These groups include many other, often wingless beetle families and true bugs, among others, as well as other arthropods, such as spiders, mites, and related groups of Arachnids (see Chap. 2).

Unfortunately, cloud and temperate forests have been heavily impacted by land use changes in Mexico, with oak forests and cloud forest having been reduced by approximately 50% from their original extension and presently occupy only 1% of the national territory (Ramírez-Marcial et al. 2001; Challenger and Soberón 2008; Sarukhán et al. 2017; Jiménez-García and Peterson 2019). Deforestation rapidly affects the macroinvertebrate community of cloud forests, and full recovery of invertebrate fauna after logging may take more than 100 years (Negrete-Yankelevich et al. 2007), this assuming that wingless species can repopulate logged areas from less disturbed, surrounding areas. Furthermore, the impacts of climate change are predicted to be most severe in these forests (Ponce-Reyes et al. 2012; Rojas-Soto et al. 2012; Janzen and Hallwachs 2021). The high-moisture environment that underlines the ecology of cloud forests depends on cloud cover, which is affected by rising temperatures that result in less cloud cover and its occurrence at increasingly higher altitudes, consequently leading to reduced forest area and disturbances of ecosystem functioning (Laurance et al. 2011; Janzen and Hallwachs 2021). Based on modeling of climate and the limits of cloud forest conditions, Ponce-Reyes et al.

(2012) predict that a minimum of 68% of cloud forests of Mexico will be lost by 2080. Given the highly endemic and high percentage of altitude specialists of the leaf litter arthropods, it can be assumed that a similar percentage of mostly undescribed arthropods of these Mexican forests will likewise be lost.

Conservation of montane forests and cloud forests, in particular, is recognized as a priority need in conservation efforts in Mexico (González-Espinosa et al. 2012; Moctezuma et al. 2018). Clearly, increasing the number and area of formally protected areas of montane forests is needed (López-Arce et al. 2019), as well as insuring adequate management of the protected montane forests now in existence. A number of studies have identified and prioritized cloud forest areas for potential formal protection (Toledo-Aceves et al. 2014; Ponce-Reyes et al. 2012; Rojas-Soto et al. 2012; Jiménez-García and Peterson 2019; López-Arce et al. 2019).

Besides expansion of designation of protected montane forest areas, there is also a need for novel conservation and restoration strategies with an intent toward sustainable exploitation for inhabitants of the regions where these montane forests exist (González-Espinosa et al. 2012). With a view toward insects, one conservation strategy is protecting small areas, which, although incapable of maintaining populations of larger vertebrate fauna, may preserve sufficient viable populations of arthropods of montane origin. An example of a small-scale conservation effort is the La Joya-La Barreta Park in the state of Querétaro. This is a small park administered at the municipality level, embedded within the ejido La Barreta and is within a densely populated region with high pressure from the urban development (Hernandez-Sandoval et al. 2000). The park is a popular picnic and camping area for residents of Queretaro City and region (Fig. 3.3f) which provides employment for a number of individuals of the ejido and some commerce from the tourist traffic through the town. In addition, the protected vegetation of the park provides water capture, erosion control, and animal grazing within the watershed (Hernández-Sandoval et al. 2000). Within the five vegetation types of the park, there is a small fragment of approximately 20 ha of humid oak forest (Fig. 3.3e). Despite its size, there are apparently viable populations of endemic arthropod leaf litter inhabitants of this forest (Fig. 3.3d). This is not to suppose that the original diversity of the arthropod inhabitants that was present in a larger expanse of the original vegetation is conserved, but even such small, moderately disturbed montane fragments may maintain a portion of the original insect fauna (Jones et al. 2022). These small reserves may be incorporated into the larger landscape-level concepts such as the concept of the archipelago reserves, designed to protect montane entomofauna and beta-diverse ecosystems (Moctezuma et al. 2018).

3.5 Conclusions

The examples presented here illustrate the present status and some of the principal threats to insect diversity in Mexico. Of these, land use changes and climate change are the two most important factors that overlay other varied causes of insect species loss (Wagner et al. 2021). With its highly reduced, single forest overwintering site in high altitude mountains of central Mexico, the monarch butterfly exemplifies how land use changes and climate change interact and threaten this important emblematic species. Yet, despite the recognition of the economic and social importance of the species at the local, national, and international levels, problems of deforestation continue even within the Monarch Butterfly Biosphere Reserve (Flores-Martínez et al. 2019). In addition, the effects of climate change have already started to push the temperate fir forests of the monarch's mountain habitat upward, reducing the area and changing the unique environmental conditions of their overwintering sites. Deforestation also affects dung beetles, which have greatest diversity in complex, biodiverse forests, and climate change is affecting the habitat specialists of this group. In addition, pesticides are impacting dung beetles through an unusual route in which antiparasitic treatments given to domestic animals pass onto their larval food source, animal dung. In the final example, the continued deforestation of temperate and cloud forests together with a progressively drier, hotter climate doom the majority of the microendemic insects of these forests to extinction before they can be described.

The dearth of basic taxonomical and ecological information of the great majority of Mexican insects limits management options and the inclusion of insects in conservation initiatives. This is clearly not a new problem and shared by all countries residing within the tropics (Paknia and Koch 2015) and will not be solved in time to adequately describe and document the majority of the threatened biodiversity of Mexican insects. To repeat the lament of insect taxonomists the world over, there is a need for more trained taxonomists and the creation of positions to employ them (Kim and Byrne 2006; McClain 2011), together with the preservation and expansion in the number of well-curated, natural history collections (Paknia and Koch 2015). These collections are not only of value for conservation purposes but are also a fundamental resource for the identification and study of insects of economic, medical, and forensic importance which are areas of research that are still in the development stage in Mexico. Of particular importance for agriculture is the identification of the diverse natural enemies of insect pests found on wild hosts and the many ancient domesticated races of Mexican cultivars (see Chap. 25, this volume). These can offer novel, biological-based pest management options to reduce the reliance on chemical control.

Fortunately, there has been greater support recently for collections and databases through collection improvement grants from the Mexican National Commission for the Knowledge and Use of Biodiversity (CONABIO 2016). Additional hope comes from a growing understanding among the Mexican populace that insects are more than just pests and that they play a fundamental role in the functioning of all terrestrial and freshwater ecosystems of Mexico. This realization has been especially promoted in social media platforms and the popular press in relation to the crisis of pollinators, especially bees (see Chap. 24, this volume). It is hoped that the present interest in this essential insect group can be a springboard to promote basic taxonomic and ecological research of insects that will further open new opportunities and international cooperation for greater study of the mostly unknown insect fauna of Mexico.

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Chapter 4
Threats and Conservation Status of Freshwater Crayfish (Decapoda: Cambaridae) in Mexico

Carlos Pedraza-Lara, José Luis Villalobos, and Fernando Álvarez

Contents

4.1 Introduction

Approximately 10% of the world's species inhabit freshwater ecosystems, although they occupy less than 1% of the earth's surface (Strayer and Dudgeon 2010). Freshwater resources sustain a rapidly growing human population, and their overexploitation is leading to a freshwater biodiversity crisis (Vörösmarty et al. 2010). As a consequence, growing evidence shows that freshwater taxa are at greater risk of extinction than other groups, such as terrestrial vertebrates (Darwall et al. 2011; Ricciardi and Rasmussen 1999). Given this, increasing the knowledge of the distribution and conservation status of freshwater species is fundamental for their conservation (Darwall et al. 2011).

C. Pedraza-Lara (✉)
Ciencia Forense, Facultad de Medicina, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico
e-mail: pedraza@cienciaforense.facmed.unam.mx

J. L. Villalobos · F. Álvarez
Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_4

Previous studies have found that threats to crayfish worldwide are set to increase both in magnitude and extent (Richman et al. 2015). Therefore, there is an urgent need to understand the extinction risk and threats faced by freshwater crayfish. In this study, we assess the extinction risk of native Mexican crayfish species described up to 2022.

Freshwater crayfish comprise about 670 species worldwide and occur in all continents except for Antarctica and continental Africa (Crandall and De Grave 2017). They inhabit four main habitat types: streams, ponds/lakes/large rivers, caves, and burrows (Crandall and Buhay 2008). Species inhabiting a specific habitat type show distinctive morphological adaptations. For example, cave dwellers (stygobitic) commonly show a lack of pigmentation and eye loss, and elongated limbs and sensory structures, whereas stream-dwellers are intolerant to low oxygen levels in the water. In general, crayfish are preferably nocturnal, mainly omnivorous, and play a key role in freshwater trophic webs (Reynolds et al. 2013; Alvarez and Villalobos 2016). Most species are gonochoric and sexually dimorphic, but hermaphroditism, intersexuality, and parthenogenesis have been described for several species (Yazicioglu et al. 2016). They have direct development with yolky-rich eggs and eclosion of juveniles. Females display brood care. They are used by human communities as a food source or as a bait to fish other animal species in several regions and have been model organisms for a variety of studies.

Freshwater crayfish are grouped in two superfamilies: Astacoidea and Parastacoidea. Astacoidea shows an holarctic distribution and Parastacoidea a semi-pantropical distribution, including Australasia, South America and Madagascar (Crandall and De Grave 2017). Astacoidea is composed by three families, Astacidae with 4 genera and 20 species, Cambaridae with 14 genera and 449 species, and Cambaroididae with 1 genus and 6 species. Parastacoidea is composed of one family, Parastacidae, which includes 15 genera and 198 species (Miranda et al. 2018). Native species of crayfish in North America belong to Astacidae (6 spp.) and Cambaridae, which is endemic to the region. In Mexico, all native crayfish species belong to the family Cambaridae, and 97% (59 of 61 spp.) are endemic to the country with a major hotspot of diversity in the center and south of Mexico.

The Cambaridae inhabits all types of freshwater bodies along the eastern slopes of Mexico and the Trans-Mexican Volcanic Belt (TMVB). Two genera naturally occur in Mexico: *Cambarellus* with 12 species and *Procambarus* with 47, whereas *Faxonius virilis* has been introduced to some localities in the state of Chihuahua, probably from populations located further in North America. Three species of *Cambarellus* are described from the Northern Plateau, whereas the rest inhabit lentic water bodies along the TMVB. Conversely, most of the species of *Procambarus* inhabit several river basins along the gulf coast (Fig. 4.1), from the Río Bravo in the north to the Usumacinta basin in the south. Only two species in the genus inhabit localities from the Pacific slope, *Procambarus digueti* (Bouvier, 1897) (Fig. 4.1a), from the tributaries of the Chapala Lake in the Lerma basin, and *Procambarus bouvieri* (Ortmann, 1909) (Fig. 4.1c) from the highlands of the Balsas basin.

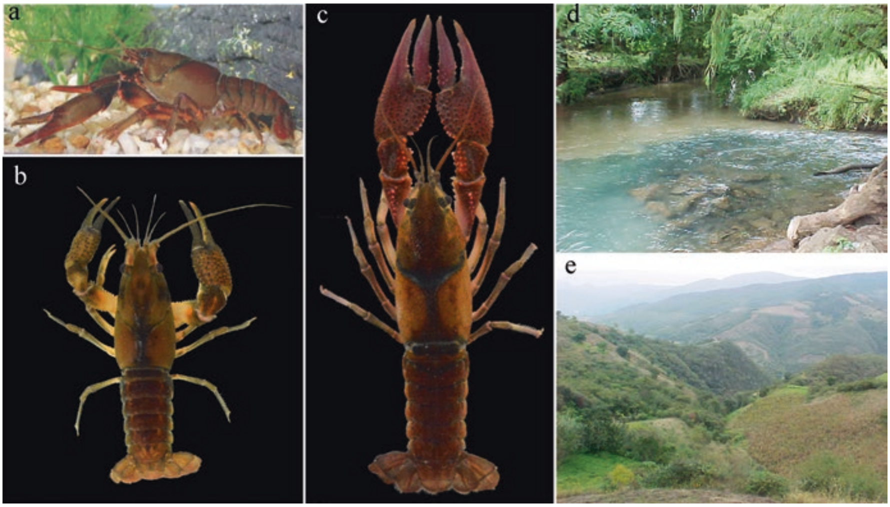

Fig. 4.1 Some examples of Mexican Crayfish species and their habitats. (**a**) *Procambarus digueti*; (**b**) *P. hoffmanni*; (**c**) *P. bouvieri*; (**d**) the Camécuaro river (at the right of the picture), habitat of *P. digueti*, joining to the Duero river, which shows contrasting habitat conditions in terms of pollution and physical modifications; (**e**) common conditions surrounding the habitat of several species dwellers of headwater streams (a small stream running down between hills), showing some modifications such as agriculture and livestock

4.2 Current Threats and Conservation Challenges

4.2.1 Introduced Species

Three crayfish species have been introduced into Mexico. Although naturally occurring in the Río Bravo basin, *P. clarkii* was translocated to distinct locations and from there it has spread to regions in the states of Baja California, Chiapas, Coahuila, Chihuahua, Durango, Nuevo León, Sonora, and Tamaulipas (Campos and Rodríguez-Almaraz 1992; Hernández et al. 2008).

Two more exotic crayfish represent a threat for native species. Populations of *Faxonius virilis* (native to the east part of the USA and southern Canada but now found widely in both countries) have now become established in northern Mexico in at least two localities (Campos-González and Contreras-Balderas 1985; Alvarez and Villalobos 2015). Although presently not showing a widespread distribution, the invasive potential of this species has been shown by its spread in non-native basins in other countries and justifies the need to avoid its translocation to other localities.

Furthermore, the Australian redclaw crayfish, *Cherax quadricarinatus*, brought to Mexico for aquacultural purposes, has escaped and established populations in Jalisco, Morelos, Nayarit, Nuevo León, San Luis Potosí, Sinaloa and Tamaulipas, and has been recently reported in the Sierra Gorda Biosphere Reserve, Querétaro (Rodríguez-Almaraz et al. 2018; Álvarez et al. 2014). Mendoza-Alfaro et al. (2011) reviewed the status of *C. quadricarinatus* in Mexico. Studies describing the possible impact on local environments and on native crayfish are urged in these zones, especially in the Pánuco watershed, a region harboring a striking diversity of Mexico's crayfish. This is especially true for *P. roberti*, endemic to the Media Luna Valley, in San Luis Potosí where *C. quadricarinatus* has invaded. Sampling of *P. roberti* showed a marked decline in populations from 2004 when compared to those in 2019. Individuals were very rare in the Lagoon, whereas in the outlet channels, a low abundance of individuals was observed. In contrast, *C. quadricarinatus* now has a thriving population in the Lagoon, which could be explained by a possible displacement of *P. roberti* by the exotic species. From the Media Luna Valley, there are high probabilities for dispersal of *C. quadricarinatus* to the rest of the Pánuco basin, inhabited by a high number of endemic crayfish species. Farming of the redclaw crayfish is part of an active aquaculture plan by the Mexican government at a national scale, so founding and spread of new populations from additional points in additional basins is expected in the near future if this program keeps operative. New feral populations have been established even in natural reserves, where native species inhabit, such as *Procambarus xihui*, endemic to the Sierra Gorda Biosphere Reserve.

4.2.2 Freshwater Extraction and Increased Rate of Desiccation

Freshwater extraction is a common practice in the habitats of a number of crayfish species. Many of them inhabit mountain springs, surviving surrounded by human activities such as dwelling construction, livestock raising, and agriculture, which routinely use water either directly from springs and stream headwaters, or indirectly from extraction by wells. Water extraction directly from water bodies has been observed in sampling efforts and has probably caused the complete dry-up of some localities. The spread of such activities seems to be on the rise, aided by human population growth in these locations, or the rise in economic activities highly dependent on water availability.

Cambarid populations inhabiting headwater stream ecosystems are especially sensitive to rainy conditions, as short and severe periods of drought may represent a high risk of extinction (Boulton 2003). The last decade along the Sierra Madre Oriental has been dryer than preceding decades (Seager et al. 2009). The most severe drought recorded from this region was during 2010–2015, with the year 2012 being the most intense (Mendoza-Villa et al. 2018). Climatic predictions at a regional scale indicate that naturally occurring sub-decadal droughts will be made more frequent and widespread by anthropogenic climate change (Seager et al. 2009). Impacts driven by climate change are expected to be substantial on headwater stream ecosystems, which makes diagnosing and planning for conservation an urgent task (Durance and Ormerod 2007). From this perspective, the conservation of the rivers' headwaters, as well as the maintenance of seasonal water regimes, is of utmost importance to preserve endemic species, especially those that have very narrow distributions. This is especially true for several species of the genus *Procambarus* that inhabit springs and mountain streams under high pressure from human activities, like agriculture and livestock raising (see Fig. 4.1e).

4.2.3 Pollution

Freshwater ecosystems in central Mexico are among the most disturbed habitats, severely altered by industrial, urban, crop, and livestock waste waters. In mountainous regions, unregulated mining and crop activities are important pollutants of small streams. Agriculture pollutes water with pesticides, greatly affecting crayfish populations to the extent of local extinction in the points receiving such discharges. Pollution is more relevant in aquatic ecosystems along the TMVB, habitat of most of the species of *Cambarellus*. But pollution is occurring in the habitats of several of *Procambarus* too. For example, *Procambarus digueti*, an inhabitant of the TMVB, at the Tangancicuaro Valley, part of the Duero basin before its junction to the Chapala lake. Only two localities have been recorded for the species in the last 20 years of samplings, corresponding to two oligotrophic and isolated springs, which are now channelized or polluted by urban and crop activities shrotly after its origin (pers. obs.; García et al. 2004) (see Fig. 4.1e).

Other highly endemic species illustrate the imperiled state of many Mexican crayfish. After extensive sampling along the Pánuco basin, *Procambarus strenthi* has only been found at the type locality, Santa Anita spring, close to Ciudad Valles, San Luis Potosí, and along the outlet stream extending approximately 100 m. Beyond that point, sugarcane monocultures begin, and no crayfish have been recorded further on. Water conditions change rapidly from oligotrophic in the spring to highly turbid in the downstream river, suggesting strong pollution associated with the surrounding cultures. Similar conditions have been observed for the only population found to date of *P. villalobosi* in a small basin from the Pánuco watershed. Similarly, the species has only been recorded from its type locality, composed by a small stream running along a small cave by ca. 50 m and emptying to a small shallow reservoir (around 12 m^2). Beyond that point, a small channel less than 1 m wide is formed and within 50 m is dammed into a small pool with no outlet. The locality is surrounded by agricultural fields, and a small town is located a bit higher in the mountain. Water is not clear when running underground, which makes us suppose some level of water pollution is already present. After the small cave, the habitat is strongly modified, and water becomes dirtier. Crayfish have been recorded only from the cave, possibly because conditions at the surface are non-suitable. As a troglophile, but non-stygobitic species, the habitat inside the cave is probably the only one available to date for the species.

4.2.4 Vulnerable and Restricted Habitats

Six species have been recorded exclusively in subterranean habitats, five of them showing troglomorphic (cave) adaptations. Cave systems not only have high levels of endemism due to the low dispersal ability of many cave-dwelling species but are also sensitive to environmental changes by disturbances directly to the cave or from the surrounding land cover, which may drive climatic changes within the underground system (Boulton 2020). Most Mexican cave-adapted crayfish have been recorded from one locality only. A paradigmatic case is *Procambarus xilitlae*, endemic to the bottom of the Sótanos de las Huahuas, San Luis Potosí, more than 420 m underground. Specimens have only been sampled on three occasions. In 1979, the first collected specimens motivated its description (Hobbs and Grubbs 1982), later, in 1981, allowed a more detailed description of genitalia (Hobbs and Grubbs 1986), and recently, in 2020, a sampling effort recorded some new specimens (pers. obs.). The population was observed as very scarce, inhabiting only some small, shallow ponds (less than 2 m long and around 15 cm deep) and composed by a few individuals. That is the case of most other species of troglobites, considered ‘short-range’ endemics (Harvey 2002) for which disturbances coming from water extraction, climate change, tourism and deforestation of the surrounding lands, could mean a loss of water infiltration and the greatest threat to their extinction.

Some species in the genus *Procambarus* inhabit low-altitude, high-order rivers, or the habitats associated with them, such as *P. clarkii*, *P. hoffmanni* (Fig. 4.1), *P. toltecae,* or *P. acanthophorus*. However, around 20 crayfish species inhabit headwater stream ecosystems or the springs from which these rivers originate and, in most cases, consist of small portions of streams harboring corresponding small populations. Headwater streams might be especially vulnerable to disturbances in the surrounding catchment, which correlates with a higher risk of biodiversity loss (Lowe and Likens 2005). Locally, populations inhabiting headwater stream ecosystems are especially sensitive to human disturbances, as these can easily drive populations to local extinction due to the small size of their distribution and corresponding population sizes. In fact, Mexico is considered as a hotspot of climate change-vulnerable crayfish species (Hossain et al. 2018), most of them restricted to such vulnerable habitats.

4.2.5 Habitat Modification (Channelization, Damming, Desiccation)

Drastic habitat modifications are observed for *Procambarus* species inhabiting headwater streams with oligotrophic conditions. As an example, *Procambarus bouvieri* inhabits only its type locality, a spring ca. 16 m^2 and a small outlet stream, which is dammed after about 100 m. The spring is located in a small locally protected area but surrounded by the second-largest city of the state of Michoacán. Historically, no individuals have been located in or downstream from the dam in all the surveys carried out in the area. Similar cases have been recorded for a number of species in the genus. Almost all *Cambarellus* species inhabit greatly modified ecosystems, especially through damming and channelization. However, members of this genus are probably tolerant to such modifications as the ecological requirements of this group are often found in lentic conditions. This does not mean that all levels of such disturbances can be tolerated by these species, as exemplified by the only two species of crayfish extinct to date, *C. alvarezi* and probably *C. areolatus*. *Cambarellus alvarezi* was endemic to a single location, the spring of Ejido El Potosí, Galeana, in the state of Nuevo Leon, Mexico (Rodríguez-Almaraz and Campos 1994). This spring no longer exists, having undergone reduction due to water extraction, and since 1994 has been permanently dry. Furthermore, this species has been surveyed additional times, over a period of 4–5 years within the only known habitat, but no specimens have been found. The most recent visit to the site in 2009 confirmed there was no surface water at Ejido El Potosí. The other species, *C. areolatus,* was also known from its type locality, near Parras, Coahuila; however, this location has now been flooded and is artificially managed. Recent surveys have found no specimens, and further survey work is planned. Here, *C. areolatus* is considered as critically endangered, although its situation probably corresponds to the status of extinct.

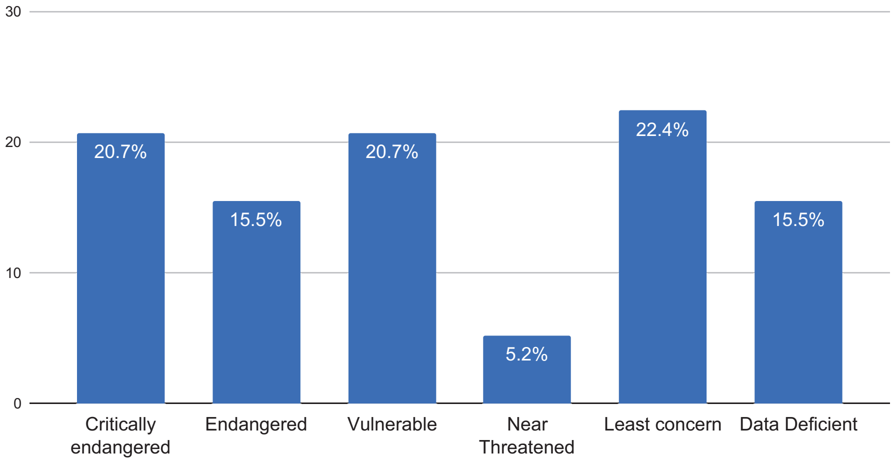

Fig. 4.2 Percent of native extant species of crayfish in Mexico assigned to a conservation status (CR, EN, VU), to other categories (NT, LC) or considered as data deficient

4.3 Conservation Status

Our analysis on the major threats faced by crayfish fauna in Mexico reveals an alarming situation. One species is definitely extinct in nature (Fig. 4.2), one more is probably in a similar situation after in situ confirmation (*C. areolatus*), and one additional species faces a very likely scenario of extinction in the short term (*C. chihuahuae*). Of the 58 species of cambarids native to Mexico and extant to date, more than half are assigned to a conservation status (33 species, 56.9%) either as CR, EN, or VU.

One species of Cambaridae is extinct in Mexico, *Cambarellus alvarezi* (EX) (Table 4.1). Its habitat, the spring of Ejido El Potosi, has been completely dry for nearly 30 years and has been lost as well as several other freshwater endemic species from the site. The fate of this species resembles that of many other, whose habitats have somehow endured the incoming disturbances for some time, but if such trends are maintained at the regional and local scales, these habitats could become unsustainable in a relatively short time.

Twelve native species of Cambaridae are found to be critically endangered (CR) (Table 4.1), which corresponds to 20.7% of the extant native species in Mexico. Assignation to such conservation status for most of these species is justified by criterion B1 (Extent of Occurrence, EOO), as they have only been recorded from one locality and the EOO is less than 100 km^2. Sometimes, such reduced occurrence is explained by the specificity of their habitats, that is why several of them inhabit only one cave location, and they are assumed to be unable to sustain populations in surface habitats, as they are cave adapted. In addition, strong disturbances have been recorded in their only locality, which represents a high risk of extinction. This is the case of *P. adani*, and *P. xilitlae*. As previously mentioned, any disturbance directly in the caves or in the surrounding lands could affect the population and hence pose a high risk of extinction for these species. Their localities are already affected by human activities such as deforestation, direct modification of cave habitats, climate change, or an increased rate of desiccation at a regional scale, which threatens the conservation of their populations in the short term.

Two species of the genus *Cambarellus* are also in this category, *C. chihuahuae* and *C. areolatus*. *Cambarellus chihuahuae*, previously occurring in several spring habitats in the Guzman desert basin, Chihuahua, had been considered extinct by previous IUCN evaluations because the habitat of all populations known to that date had been documented to be dried up, as a consequence of the intense water extraction carried out in the region for crop irrigation (Alvarez et al. 2010). However, some years later, one additional population was discovered in Ojo Solo spring (Carson et al. 2015). The locality, however, is still under great danger and is possibly affected by the same disturbances causing the extinction of the rest of its neighbour springs. Efforts are being made to build a refuge under protection, but the species is evidently under great risk of extinction in the short term if no additional efforts are taken to ensure the prevalence of this last natural population. In the case of *C. areolatus*, the drastic habitat modification and the failure to recover

Table 4.1 Species of Cambaridae from Mexico, major threats affecting their conservation and updated status of conservation based on IUCN criteria

	Threats								IUCN status and criteria	
Species	1	2	3	4	5	6	7	8	9	10
1. *Cambarellus* (*Cambarellus*) *alvarezi* Villalobos, 1952	•	•				•			EX	–
2. *Cambarellus* (*Cambarellus*) *areolatus* Faxon, 1885	•	•		•		•			CR	B1
3. *Cambarellus* (*Cambarellus*) *chapalanus* Faxon, 1898		•	•	•	•		*	•	VU	–
4. *Cambarellus* (*Cambarellus*) *chihuahuae* Hobbs, 1980	•	•		•		•			CR	A2, B1, B2a,b,c,
5. *Cambarellus* (*Cambarellus*) *lermensis* Villalobos, 1943		•	•	•	•		*		LC	–
6. *Cambarellus* (*Cambarellus*) *moi* Pedraza-Lara, Ortíz-Herrera and Jones, 2021		•	•	•	•	•			VU	B1
7. *Cambarellus* (Cambarellus) *montezumae* de Saussure, 1857			•	•	•	•	*	•	VU	B1
8. *Cambarellus* (*Cambarellus*) *occidentalis* Faxon, 1898			•				*		LC	–
9. *Cambarellus* (*Cambarellus*) *patzcuarensis* Villalobos, 1943		•	•		•		*	•	VU	B1
10. *Cambarellus* (*Cambarellus*) *prolixus* Villalobos and Hobbs, 1981		•	•		•		*	•	CR	B1
11. *Cambarellus* (*Cambarellus*) *zacapuensis* Pedraza-Lara and Doadrio, 2015		•	•	•			*		LC	–
12. *Cambarellus* (*Cambarellus*) *zempoalensis* Villalobos, 1943							*		LC	–
13. *Faxonius virilis* (Hagen, 1870)	–	–	–	–	–	–	–	–	–	–
14. *Procambarus acanthophorus* Villalobos, 1948									LC	–
15. *Procambarus achilli* López, Mejía and Álvarez, 2003		•		•			*		VU	B1,D2
16. *Procambarus adani* Alvarez, Torres and Villalobos, 2021			?			•			CR	B1,D2
17. *Procambarus bouvieri* (Ortmann, 1909)		•		•		•	*		CR	B1
18. *Procambarus caballeroi* Villalobos, 1944			•						VU	B1,B2a, D2
19. *Procambarus catemacoensis* Rojas, Álvarez and Villalobos, 2000							*		EN	B1
20. *Procambarus cavernicola* Mejía-Ortiz, Hartnoll, and Viccon-Pale, 2003			?	•					EN	B1
21. *Procambarus chacalli* López-Mejía, Álvarez and Mejía-Ortiz, 2004	?	?	?	?	?	?	?		DD	–
22. *Procambarus citlaltepetl* Rojas, Álvarez and Villalobos, 1999		•		•		•			VU	B1
23. *Procambarus clarkii* (Girard, 1852)								•	LC	–
24. *Procambarus contrerasi* (Creaser, 1931)	?	?	?	?	?	?			DD	–
25. *Procambarus cuetzalanae* Hobbs, 1982	?	?	?	?	?	?			NT	–
26. *Procambarus cuevachicae* (Hobbs, 1941)		•		•		•			EN	B1
27. *Procambarus digueti* (Bouvier, 1897)			•	•	•	•	*	•	CR	B1
28. *Procambarus erichsoni* Villalobos, 1950	?	?	?	?	?	?			DD	–
29. *Procambarus gonopodocristatus* Villalobos, 1958	•	•	•	•		•	*		EN	B1

(continued)

Table 4.1 (continued)

	Threats								IUCN status and criteria	
Species	1	2	3	4	5	6	7	8	9	10
30. *Procambarus hidalgoensis* López-Mejía, Álvarez and Mejía-Ortiz, 2005	•		•			•			EN	B1
31. *Procambarus hoffmanni* (Villalobos, 1944)									LC	–
32. *Procambarus hortonhobbsi* Villalobos, 1950	?	?	?	?	?	•			DD	–
33. *Procambarus llamasi* Villalobos, 1954							*	•	LC	–
34. *Procambarus maya* Álvarez, López-Mejía and Villalobos, 2007						•			DD	–
35. *Procambarus mexicanus* (Erichson, 1846)									LC	–
36. *Procambarus mirandai* Villalobos, 1954	?					?			LC	–
37. *Procambarus oaxacae* Hobbs, 1973	?	?	?	•		•			EN	B1,B2a
38. *Procambarus olmecorum* Hobbs, 1987									DD	–
39. *Procambarus ortmannii* (Villalobos, 1949)	?	?	?	?	?	•			EN	B1
40. *Procambarus paradoxus* (Ortmann, 1906)	•		•			•			CR	B1
41. *Procambarus pilosimanus* (Ortmann, 1906)							*		LC	–
42. *Procambarus reddelli* Hobbs, 1973	?	?	?	•		•			VU	B1,B2a, D2
43. *Procambarus regiomontanus* (Villalobos, 1954)	•	•	•	•		•	•		CR	B1,B2a
44. *Procambarus riojai* (Villalobos, 1944)									LC	–
45. *Procambarus roberti* Villalobos and Hobbs, 1974	•	•	•	•		•	•		CR	B1
46. *Procambarus rodriguezi* Hobbs, 1943			?			•			VU	B1
47. *Procambarus ruthveni* (Pearse, 1911)		?	?	?	?	?			VU	B1
48. *Procambarus sbordonii* Hobbs, 1977	?	?	?		?	•			DD	–
49. *Procambarus strenthi* Hobbs, 1977		•	•			•			CR	B1
50. *Procambarus teziutlanensis* (Villalobos, 1947)					?				VU	B1
51. *Procambarus tlapacoyanensis* (Villalobos, 1947)					?				VU	B1
52. *Procambarus toltecae* Hobbs, 1943							*		LC	–
53. *Procambarus vazquezae* Villalobos, 1954							*		NT	B1
54. *Procambarus veracruzanus* Villalobos, 1954		?	?	?	?	?			DD	–
55. *Procambarus villalobosi* Hobbs, 1967	•	•	•	•	•	•			CR	B1,D
56. *Procambarus xihui* Pedraza-Lara, Gutiérrez-Yurita and De jesús-Bonilla, 2021	•	•	•			•	•		EN	B1
57. *Procambarus xilitlae* Hobbs and Grubbs, 1982	•		?			•			CR	B1,D
58. *Procambarus xochitlanae* Hobbs, 1975	?	?	?						VU	B1,D2
59. *Procambarus zapoapensis* Villalobos, 1954	?	?	?	?	?	?	?		NT	–
60. *Procambarus zihuateutlensis* Villalobos, 1950	?	?	?	?	?	?			DD	–

• means that the disturbance has been observed and is estimated to affect the conservation status of the species; ? indicates no data are available; *EX* extinct in the wild, *CR* critically endangered, *EN* endangered, *VU* vulnerable, *DD* data deficient (there is no data to evaluate the conservation status), (1) Increased rate of desiccation at regional scale (including possible impact of climate change), (2) freshwater extraction, (3) pollution, (4) habitat modification (dam, Channelization, dry up), (5) eutrophication, (6) fragmentation or isolation of populations, (7) impact by introduced species (* = introduced fish species co-occur and probably affect their populations, here, • = an introduced species of crayfish co-occur and represents a clear threat), (8) unregulated exploitation or culture of the species, (9) IUCN updated status, (10) IUCN fulfilled criteria individuals in previous sampling attempts made us suppose it is possibly extinct; however, this has to be confirmed by further sampling efforts. *C. prolixus* inhabits only very specific conditions at the Chapala Lagoon, in the Lerma basin, where the species is subject to severe changes in water regime, pollution and fishing.

The rest of epigean species assigned to a CR status also occur in one or a very reduced number of locations and their habitats face an increasing number of strong disturbances. That is the case of *P. bouvieri*, *P. digueti*, *P. paradoxus*, *P. regiomontanus*, *P. roberti*, *P. strenthi,* and *P. villalobosi*. For all of these, an increasing rate of habitat degradation, fragmentation, pollution, or local extinction has been observed in previous surveys. In addition, some species are under fishery pressure, such as *P. digueti*, which is intensively fished for human consumption without any regulation. If actual trends do not change, all these species are under great danger of extinction.

Nine species are assigned a status of endangered (EN): *P. catemacoensis*, *P. cavernicola*, *P. cuevachicae*, *P. gonopodocristatus*, *P. hidalgoensis*, *P. oaxacae*, *P. ortmanni, P. rodriguezi*, and *P. xihui*. This represents 13.8% of the native extant species in the country. These species have in common that they inhabit sensitive and reduced habitats; only one or a small number of populations have been recorded or these are fragmented or affected by different kinds of disturbances. Still, the habitat of these species is available, making their estimated distribution possibly larger than recorded, or its populations can probably reach each other eventually. These are, however, species with great risk of extinction in the middle term if no measures are taken to change the actual trends in local and regional disturbances affecting their habitats. Localities include headwater ecosystems or highly fragmented locations due to intensive agricultural practices which have isolated populations or for which there are records of locally extinct populations. That is the case of *P. gonopodocristatus*, recently recorded in a small well which fed a large citric culture zone in Veracruz, and *P. xihui*, for which three out of five recorded populations have become extinct in a period of nearly 20 years (Pedraza-Lara et al. 2021). Four cave-dwelling species are also considered as endangered: *P. cavernicola* from Oaxaca, *P. cuevachicae* from San Luis Potosí, *cP. oaxacae* also from Oaxaca and *P. rodriguezi* from Veracruz. Although some records exist from epigean populations for *P. cuevachicae*, they need posterior taxonomic confirmation because cave populations show some degree of morphological or genetic differentiation. Consequently, the only record confidently assigned to the species comes from the cave it was described from, and underground water is being extracted directly from the habitat. In the case of *P. cavernicola*, *P. oaxacae* and *P. rodriguezi*, they are only known from their cave type locality and they are among the six described species in Mexico showing morphological modifications to cave life, which similar to the rest of cave-adapted crayfish from Mexico, makes them especially vulnerable to disturbances, as it seems unlikely that they could sustain surface populations in the case of local disturbances are sustained inside or surrounding their cave habitats.

Twelve species are assigned the category of vulnerable (VU), representing 20.7% of the native extant species of cambarids. These species maintain a population assessed as relatively stable but occupy sensitive habitats or are surrounded by intermediate disturbances such as flood plains or suburban sewage discharge. In addition, it is believed that availability of its habitat can result in larger areas of occurrence than currently known, but they are already noticeably disturbed. That is the case of several epigean species occurring in headwaters or at intermediate altitudes. In addition, three species have been reported from relatively healthy cave ecosystems, such as *P. rodriguezi*, *P. teziutlanensis,* and *P. xochitlanae*, although they do not show morphological modifications to cave life or, as in the case of *P. reddelli*, are recorded in multiple cave localities, along a relatively large area.

Three species are assigned the category of near threatened (NT), by the proximity of the species to the criteria for the category vulnerable, especially regarding the estimates of population size or because there are no current threats, but there are plausible events that may cause the species to decline. Still, such events are unlikely to make the species extinct or critically endangered in the short term. This is the case of *P. cuetzalanae*, *P. zapoapensis* and *P. vazquezae*., which are only known from their type locality and a few sites nearby. Their populations in such sites, although subject to intermediate disturbances nowadays, could face habitat deterioration in the mean time, if trends are maintained. Assessed as least concern (LC) are species whose populations are stable in the long term and either threats are not detected in their habitats or they are apparently capable of tolerating such changing conditions. Thirteen species are classified in this category, which corresponds to 22.4% of the native, extant cambarids. That is the case of some species in *Cambarellus*, which are frequently observed in dammed conditions. Also included here are species of *Procambarus* which inhabit low-altitude water courses and could probably maintain stable populations in such habitats.

Finally, nine species could not be assessed because there is a lack of information and regarded as data deficient (DD). Most of them have only been collected one or a few times in the past from localities of difficult access. They probably occupy a small geographical area. Also, some of the regions from where they are reported are known to maintain the mentioned threats on aquatic habitats to some degree. Consequently, although the lack of information prevented their assessments, our expectations of the conservation status are not optimistic for most of them and it is possible that the numbers of species under any category will rise with the advancement in future surveys.

Together with the advance in surveys of crayfish populations, this fauna has been increasingly recognized as in need of ‘conservation attention’ (Taylor et al. 2007; Furse 2014). Approximately one-third of crayfish species worldwide are considered as threatened with extinction (Richman et al. 2015). Previous works have estimated that 48% of North American species and 25% of Australian species are threatened (Taylor et al. 2007; Furse 2014; Furse and Coughran 2011). In the near future, extinction rates for crayfish may increase by more than an order of magnitude exceeding those of freshwater fishes and amphibians (Ricciardi and Rasmussen 1999). This work shows that the situation of freshwater crayfish in Mexico is even more imperative, where more than half of the species are in danger of being lost if no measures are taken in order to revert current trends in habitats at local and regional scales. Future work should consider efforts to preserve this fauna through transdisciplinary studies to increase awareness on their ecological and cultural value and take steps to combine scientific knowledge with convenient public measures that will ensure that human needs will be resolved without the need to lose most of this unique component of the diversity. Furthermore, it is also important to promote the development of other lines of research to determine with certainty the population status of several species that have not been sampled in recent years. Recently, a significant number of crayfishes from different locations in Mexico have been deposited in the National Crustaceans Collection, at the Biology Institute, UNAM, particularly interesting are those from western and southeastern Chiapas, which probably represent several species complexes related to *P. mirandai* and *P. pilosimanus*, which are also being threatened by the development of the human communities. In such cases, we risk losing many species without ever knowing they existed.

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Chapter 5
The Freshwater Mollusks of Mexico: Can We Still Prevent Their Silent Extinction?

Alexander Czaja, Alan P. Covich, Jorge Luis Becerra-López, Diana Gabriela Cordero-Torres, and José Luis Estrada-Rodríguez

Contents

A. Czaja (✉) · J. L. Becerra-López · D. G. Cordero-Torres · J. L. Estrada-Rodríguez
Facultad de Ciencias Biológicas, Universidad Juárez del Estado de Durango,
Gómez Palacio, Durango, México
e-mail: drczaja@ujed.mx

A. P. Covich
Institute of Ecology, Odum School of Ecology, University of Georgia, Athens, GA, USA

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_5

5.1 Introduction

Freshwater mollusks, the second most diverse animal phylum, are among the most threatened animals worldwide and their habitats are highly impacted by many human activities (Modesto et al. 2017). Also, the number of documented extinctions of freshwater mollusks is the highest of all major taxonomic groups of animals (Lydeard et al. 2004). In Mexico, as in United States, both gastropods and bivalves are the most at risk of all aquatic biota, even more than fishes and crayfishes (Johnson et al. 2013; Czaja et al. 2020; Gladstone et al. 2021). Although current data on the distribution and conservation status of many Mexican gastropods are available in most regions, the ecological knowledge of the essential roles that mussels and clams play is very scarce. Entire states are completely unexplored for bivalves. To close this data gap, we present an updated and revised checklist, the first exclusively for Mexican bivalves. We also provide data on their general distribution, which, not surprisingly, corresponds mostly with that of the freshwater gastropods. We identify five hotspots as centers of diversity and endemism, where the most Mexican mollusks occur (Fig. 5.1).

Biogeographically, Mexico is complex because two ecoregions overlap. The Nearctic fauna occurs in the north and the Neotropical fauna occurs in the central and southern part of the country. Three large mountain ranges, the Sierra Madre Oriental, the Sierra Madre Occidental, and the Trans-Mexican Volcanic Belt along with the central plateau and the coastal plains, produce a great variety of different climates, landscapes, and ecosystems (Contreras-Balderas et al. 2008). These different geographic features and geological histories result in Mexico being a

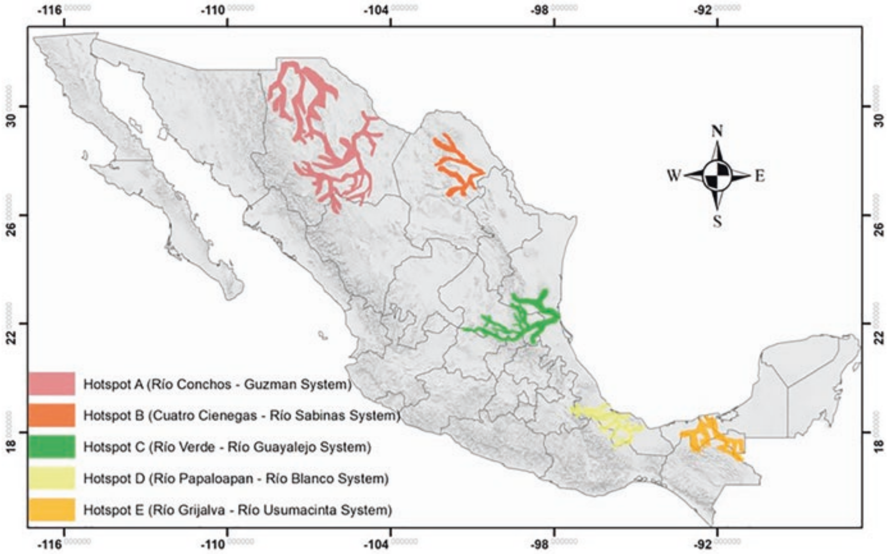

Fig. 5.1 Hotspots of Mexican freshwater mollusks (gastropods and bivalves)

megadiverse country that supports approximately 10% of the terrestrial diversity of the planet (Espinosa et al. 2008). This division in two biogeographic ecoregions is reflected by the distribution of most of the groups of the Mexican biota (Morrone 2005; Quiroz-Martínez et al. 2014). The malacofauna also conforms to this spatial pattern. According to Czaja et al. (2020), there is a similar division of two general types of biodiversity centers in particular drainage basins: The two Nearctic basins (Río Conchos - Guzman Basin System and Cuatro Ciénegas-Río Sabinas System) have dominant families with species that represent a present-day distribution mostly in the Nearctic. Three Neotropical basins (Río Verde-Río Guayalejo System, Río Papaloapan–Río Blanco System and Río Grijalva and Río Usumacinta System) contain families whose species have predominantly Neotropical distribution. Moreover, the northernmost Neotropical hotspot shows transitional communities as a dispersal corridor where both faunal elements occur together. The Mexican aquatic fauna is distributed in 37 major river basins and 70 major lakes with Lake Chapala (in Jalisco), along with Lake Cuitzeo and Lake Pátzcuaro (in Michoacan) being among the largest (Lyons et al. 2020). There are also several 100 small lentic environments such as pools and springs in the semi-arid north of the country, mainly in Cuatro Ciénegas (in Coahuila), and many cenotes (sinkholes) in the Yucatán Peninsula. There are few studies of molluscan species in subterranean habitats, although the stygobiont gastropod fauna was described recently by Gladstone et al. (2021).

The first checklist of Mexican freshwater gastropods and bivalves was reported by Contreras-Arquieta (2000) and contained 211 species, including 142 gastropod and 69 bivalve species, along with two invasive species in each class. Two decades later, Czaja et al. (2020) presented an updated checklist of native Mexican freshwater gastropods with data on their general distribution, hotspots of endemicity, threats, and, for the first time, their conservation status. This taxonomically revised checklist includes 193 species, representing 13 families and 61 genera. That revision was a first step for determining priority areas for conservation of imperiled Mexican freshwater gastropods. Recently, a new genus and two new species of freshwater gastropod was added to this list (Czaja et al. 2021, 2022). The main goal of this chapter is to provide a new revised checklist with Mexican bivalves to present the distribution and the main threats to the entire Mexican freshwater malacofauna. We discuss the necessary paradigm change to improve their conservation. We also provide an updated checklist of the freshwater mollusks of Mexico that includes systematic data of each species, information on endemicity, IUCN categories (assessed by IUCN), the affiliation to Nearctic or Neotropical Element, hotspot occurrence, and the general distribution (by state) in Mexico.

5.2 Mexican Freshwater Molluscan Fauna

Regarding gastropods, the present chapter is a compilation of our investigations on the diversity, distribution, and conservation status of living and fossil Mexican snails (Czaja et al. 2014, 2017a, b, 2019a, b, 2020, 2021, 2022). To create our new bivalve checklist, we used the only previously published list of Mexican mollusks published by Contreras-Arquieta (2000) as starting point. It contained 67 native bivalves. To update and revise this checklist, we conducted an extensive literature survey that included all available publications on Mexican freshwater bivalves. To establish the current taxonomic status of the species, we used the website MolluscaBase (MolluscaBase 2021). The World checklist of freshwater Bivalvia species, created by Bogan (2013), was also very useful in terms of the occurrence of certain mussel species in Mexico. Information on distributions we obtained, beside from the original descriptions, mainly from the MUSSEL Project Web Site (Graf and Cummings 2021). This source was also followed on some of the controversial issues of species ranges. This project is led by Daniel L. Graf and Kevin S. Cummings, two of the main authorities in the field of taxonomy of the North American freshwater bivalves. Subspecies are in our list not recognized. Species restricted to Mexico were defined as endemic.

The Mexican freshwater molluscan fauna is composed of 292 species (195 gastropods and 97 bivalves). However, our level of knowledge about the two groups is very different because most of the malacological investigations have focused almost exclusively on snails. For example, while the (NatureServe) conservation ranks are known for more than 80% of the gastropods (Czaja et al. 2020), so far only 3% of the bivalves have been assigned by the Mexican Secretary of Environment and Natural Resources list (SEMARNAT 2019). The IUCN's Red List included 40 freshwater mollusks that occur also in Mexico, but mostly without any information on their Mexican distributions and risks. For this reason, we consider it appropriate to present the diversity and distribution of the members of both classes separately.

5.2.1 Freshwater Gastropods

The Mexican native freshwater gastropod fauna contains 195 species, representing 14 families and 63 genera. Of these, 104 species and 14 genera are endemic to Mexico, and 76 of these endemics are considered local or microendemics because of their restricted distribution to extremely small areas. The Cochliopidae are the most diverse family with 62 species, followed by the Planorbidae (37) and Pachychilidae (31; Table 5.1). *Pachychilus* is the most species-rich genus (31), followed by *Tryonia* (20) and *Pyrgulopsis* (11). *Ladislavella elodes* (Say, 1821) (Lymnaeidae) is the most widely distributed native species, occurring in 14 states, from Baja California to the Yucatán Peninsula. Other widely represented species belong to the genera *Planorbella* Haldeman, 1843, *Biomphalaria* Preston, 1910 (both Planorbidae), and *Physella* Haldeman, 1842 (Physidae). However, the most extensively distributed Mexican freshwater species is the non-native, invasive snail *Melanoides tuberculata* (Müller, 1774) (Thiaridae), present in almost all water bodies in the country.

Table 5.1 Families, genera, and the number of imperiled (vulnerable, threatened, endangered, possibly extirpated, presumed extirpated) and endemic Mexican freshwater gastropods (updated after Czaja et al. 2020)

Family	Genera	Species	Imperiled species	Endemic
Amnicolidae	1	1	1	1
Ampullariidae	1	5	1	4
Assimineidae	2	2	2	1
Cochliopidae	22	62	43	44
Hydrobiidae	3	13	11	8
Lithoglyphidae	2	3	2	3
Lymnaeidae	4	9	0	0
Neritidae	3	4	0	0
Pachychilidae	2	31	14	20
Physidae	8	21	5	9
Planorbidae	12	37	11	8
Pleuroceridae	1	4	4	4
Valvatidae	1	2	1	1
Viviparidae	1	1	1	1
Total	63	195	96	104

5.2.2 *Freshwater Bivalves*

Table 5.2 shows the new checklist with Mexican bivalves and their general distribution based on the previous list of Contreras-Arquieta (2000) and an exhaustive search of all accessible sources. The number of bivalves in the new checklist increased by 31 species, which is a rise of 47%. However, of the 32 Mexican states we still do not have any record for freshwater bivalves from six states! (Aguascalientes, Baja California, Colima, Puebla, Quintana Roo, and Zacatecas).

The Mexican native freshwater bivalve fauna contains 97 species, representing 5 families and 32 genera (Table 5.3). Twenty-six (27%) species and one genus (*Actinonaias*) are endemic to the country. The Unionidae are the by far most diverse family with 76 species, followed by the Sphaeriidae (14) and Cyrenidae (5). *Nephronaias* is the most species-rich genus (11), followed by *Psoronaias* (8) and *Actinonaias* (7, all endemic). *Anodonta impura* Say, 1829 (Unionidae), is the most widely distributed native mussel, occurring in seven states. However, the most extensively distributed Mexican freshwater bivalve is the non-native, invasive clam *Corbicula fluminea* (Müller, 1774). The other two non-indigenous bivalves are *Corbicula largillierti* (Philippi, 1844), which has so far only been detected in Rio Conchos, in the state of Chihuahua (Tiemann et al. 2019), and *Dreissena polymorpha* (Pallas 1771), occurring in Río Coatzacoalcos in the state of Veracruz (Naranjo-García and Castillo-Rodríguez 2017).

Similar to the gastropods, of the 97 species of native bivalves that were reported from Mexico, at least 65 species live within the area of the defined five diversity hotspots. However, unlike the snails, where the diversity in the Nearctic hotspots A

Table 5.2 IUCN categories and assigned conservation status

Taxa	Endemic	UICN	NA/ NT	Hotspot	Distribution
Family UNIONIDAE Rafinesque, 1820					
Actinonaias computata (Crosse & Fischer, 1893)	E	–	NT	D	VER
Actinonaias coyensis (Pilsbry, 1910)	E	–	NT	C	SLP, TAMPS
Actinonaias medellina (Lea, 1838)	E	–	NT	C, D	HID, SLP, VER
Actinonaias moctezumensis (Pilsbry, 1910)	E	–	NT	C	SLP
Actinonaias sapotalensis (Lea, 1841)	E	–	NT	D	VER
Actinonaias signata (Pilsbry, 1910)	E	–	NT	C D	SLP, TAMPS, VER
Actinonaias undivaga (Pilsbry, 1910)	E	–	NT	C	SLP
Anodonta californiensis Lea, 1852	–	–	NA	A	CHIH
Anodonta impura Say, 1829	–	DD	NA		CDMX, DGO, GTO, HGO, JAL, QUE, SLP
Anodonta lurulenta (Morelet, 1849)	–	–	NT		YUC
Anodonta nuttalliana I. Lea, 1838	–	VU	NA		CHIH, SON
Anodontites cylindracea (I. Lea, 1838)	–	–	NT	D, E	CHIS, VER, SLP, TAB
Anodontites tehuantepecensis (Crosse & P. Fischer, 1893)	–	–	NT		OAX
Anodontites trapesialis (Lamarck, 1819)	–	–	NT		CHIS, GUER, JAL, SIN
Barynaias opacata (Crosse & Fischer, 1894)	E	–	NT	D	VER
Barynaias pigerrima (Crosse & P. Fischer, 1894)	E	–	NT		?
Barynaias plexus (Conrad, 1838)	E	–	NT	D	VER
Barynaias sallei (Crosse & Fischer, 1893)	–	–	NT	E	TAB
Cyrtonaias explicata (Morelet, 1849)	–	–	NT	E	CHIS, TAB
Cyrtonaias livida (Simpson, 1900)	–	–	NT	E	TAB
Cyrtonaias tampicoensis (I. Lea 1838)	–	–	NT	C, D, E	CAMP, COAH, NL, SLP, TAMPS
Cyrtonaias umbrosa (I. Lea, 1856)	E	–	NT	D	VER
Delphinonaias largillierti (Philippi, 1847)	–	–	NT	E	CHIS, TAB, YUC
Delphinonaias planivalvis (Morelet, 1851)	–	–	NT	E	CHIS

(continued)

Table 5.2 (continued)

Taxa	Endemic	UICN	NA/ NT	Hotspot	Distribution
Delphinonaias scutulata (Morelet, 1849)	–	–	NT		YUC
Disconaias conchos Taylor 1997	E	–	NA	A, B	CHIH, COAH
Disconaias discus (I. Lea, 1838)	E	–	NT	C	HGO, QUE, SLP, TAMPS, VER
Disconaias fimbriata (Frierson, 1907)	E	EN	NT	B, C	COAH, NL?, SLP, TAMPS, VER
Disconaias novileonis (Pilsbry, 1910)	E	–	NT	C	NL?, SLP
Disconaias panacoensis (Philippi, 1843)	E	–	NT	C	TAMPS
Disconaias purpuriata (Say, 1831)	E	–	NT		VER
Friersonia iridella (Frierson, 1907)	–	–	NT	C	SLP, TAMPS
Fusconaia mitchelli (Simpson in Dall, 1895)	–	CR	NA	C	COAH, NL, SLP, TAMPS
Lampsilis teres (Rafinesque, 1820)	–	LC	NA		TAMPS
Megalonaias nervosa (Rafinesque 1820)	–	LC	NA	B, C	NL, VER
Megalonaias nickliniana (I. Lea, 1834)	–	–	NT	C, E	TAB, TAMPS
Nephritica poeyana (I. Lea, 1857)	E	–	NT		MOR
Nephronaias aeruginosa (Morelet, 1849)	–	–	NT	E	CHIS
Nephronaias aztecorum (Philippi, 1847)	E	–	NT	C, D	JAL, SLP, TAMPS, VER
Nephronaias calamitarum (Morelet, 1849)	–	–	NT	E	CHIS
Nephronaias goascoranensis (Lea, 1858)	–	–	NT		OAX
Nephronaias hermanni (Haas, 1929)	?	–	NT	D	TAB
Nephronaias macnielii (I. Lea, 1869)			NT		TAB
Nephronaias mellea (Lea, 1859)	–	–	NT		?
Nephronaias plicatula (Küster, 1856)	–	–	NT		?
Nephronaias ravistella (Morelet, 1849)	–	–	NT		TAB
Nephronaias sphenorhyncha (Crosse y Fischer, 1893)	–	–	NT		?
Nephronaias tabascoensis (Küster, 1856)	–	–	NT		TAB
Pachynaias spheniopsis (Morelet, 1849)	–	–	NT	E	TAB

(continued)

Table 5.2 (continued)

Taxa	Endemic	UICN	NA/ NT	Hotspot	Distribution
Popenaias berezai Inoue et al. 2020	E	–	NT	C, D	SLP, TAMPS, VER
Popenaias ganina (Pilsbry, 1910)	–	–		C	SLP
Popenaias metallica (Say, 1831)	E	–	NT		CDMX
Popenaias popeii (Lea, 1857)	–	CR	NT	A, B	CHIH, COAH, NL, TAMP
Popenaias semirasa (Pilsbry, 1910)	E	–	NT	C	SLP
Popenaias tehuantepecensis (Crosse & Fischer, 1893)	–	–	NT		OAX
Potamilus alatus (Say, 1817)	–	LC	NA	E	TAB
Potamilus metnecktayi Johnson 1998	–	–	NA	B	COAH, TAMPS
Potamilus rovirosai (Pilsbry, 1900)	–	–	NT	E	TAB
Psoronaias distincta (Crosse & Fischer, 1893)	–	–	NT	D	VER
Psoronaias guatemalensis (Simpson, 1900)	–	–	NT	E	CHIS
Psoronaias herrerae (Marshall, 1923)	E	–	NT	E	TAMPS
Psoronaias ostreata (Morelet, 1849)	–	–	NT	E	TAB
Psoronaias percompressa (Martens, 1887)	–	–	NT	E	CHIS
Psoronaias profunda (Simpson, 1914)	–	–	NT	E	TAB
Psoronaias semigranosa (Philippi, 1843)	–	–	NT	C, E	CHIS, QRO, SLP, TAB, TAMPS, VER
Psoronaias usumasintae (Crosse & Fischer, 1892)	–	–	NT	E	TAB
Pyganodon grandis (Say, 1829)	–	LC	NA	D	VER
Quadrula couchiana (I. Lea, 1860)	–	CR	NA	B	COAH, NL
Sphenonaias colorata (Küster, 1856)				D	VER
Sphenonaias liebmanni (Philippi, 1847)	E	–	NT	D	VER
Sphenonaias mexicana (Philippi, 1847)	E	–	NT	E	TAB
Sphenonaias microdon (Martens, 1887)	–	–	NT	E	TAB
Sphenonaias taumilapana (Conrad, 1855)	–	–	NA	?	TAMPS
Truncilla cognata (Lea, 1860)	–	–	NA	B	NL
Uniomerus tetralasmus (Say, 1831)	–	LC	NA	A	CHIH
Utterbackia imbecillis (Say, 1829)	–	LC	NT	A	CHIH, TAMPS

(continued)

Table 5.2 (continued)

Taxa	Endemic	UICN	NA/ NT	Hotspot	Distribution
Family SPHAERIIDAE Deshayes, 1855 (1820)					
Euglesa casertana (Poli, 1791)	–	LC	–	D	EDOMEX, VER
Euglesa compressa (Prime, 1852)	–	–	–	B	COAH, NL
Eupera cubensis (Prime, 1865)	–	LC	–	B	COAH
Eupera insignis Pilsbry 1925	–	–	–	D	VER
Eupera singleyi (Pilsbry 1889)	–	–	–		YUC?
Musculium partumeium (Say, 1822)	–	LC	–	E	TAB
Musculium subtransversum (Prime, 1860)	E	–	–		TAB
Musculum transversum (Say 1829)	–	–	–		QRO, TLAX
Pisidium nitidum (Jenyns 1832)	–	LC	–	B	COAH
Pisidium punctiferum (Guppy, 1867)	–	–	–		SIN
Sphaerium martensi Pilsbry 1899	E	–	–		MICH
Sphaerium mexicanum Dall 1905	E	–	–		SLP
Sphaerium striatinum (Lamarck 1818)	–	LC	–	D	QRO, VER
Sphaerium triangulare (Say, 1829)	–	–	–		GTO, MICH
Family CYRENOIDIDAE H. Adams & A. Adams, 1857 (1853)					
Cyrenoida floridana Dall, 1896	–	–	–		VER
Family CYRENIDAE Gray, 1840					
Cyanocyclas paranacensis (d'Orbigny, 1835)	–	–	–		?
Polymesoda arctata (Deshayes, 1855)	–	–	–	E	TAB
Polymesoda caroliniana (Bosc, 1801)	–	–	–	D	VER
Polymesoda mexicana (Broderip & G. B. Sowerby I, 1829)	–	–	–		BCS, JAL, SIN
Polymesoda salmacida (Morelet 1851)	–	–	–		?
Family DREISSENIDAE Gray, 1840					
Mytilopsis leucophaeata (Conrad, 1831)	–	LC	–	D, E	TAB, TAMPS, VER

CR Critically endangered, *DD* Data deficiency, *EX* extinct, *EW* extinct in the wild, *LC* least concern, *NT* near threatened, *VU* vulnerable. State abbreviations: *BCS* Baja California Sur, *CDMX* Ciudad de México, *CHIH* Chihuahua, *CHIS* Chiapas, *COAH* Coahuila, *DGO* Durango, *EDOMEX* Estado de México, *GTO* Guanajuato, *GRO* Guerrero, *HGO* Hidalgo, *JAL* Jalisco, *MICH* Michoacán, *MOR* Morelos, *NAY* Nayarit, *NL* Nuevo León, *OAX* Oaxaca, *QR* Querétaro, *SLP* San Luis Potosí, *SIN* Sinaloa, *SON* Sonora, *TAB* Tabasco, *TAMPS* Tamaulipas, *VER* Veracruz, *YUC* Yucatán, *NA* Nearctic, *NT* Neotropical, *E* Endemic (Mexico), *A*, *B*, *C*, *D*, *E* = hotspots (Fig. 5.1)

Table 5.3 Families, genera, species, and the number of endemic Mexican freshwater bivalves

Family	Genera	Species	Endemic
Unionidae	23	76	26
Sphaeriidae	5	14	3
Cyrenidae	2	5	0
Cyrenoididae	1	1	0
Dreissenidae	1	1	0
Total	32	97	29

and B is the greatest, the species richness of the bivalves is in the Neotropical hotspots D and E. Their species richness is considerably larger than in the northern centers. The difference is particularly great between hotspot A, where only 5 species are reported, and the southern hotspot E, which contains 25 mussels. The dominance of the Neotropical malacofauna fauna becomes especially evident among the 76 unionid species where 57 (77%) species belong to the Neotropical element and only 13 (17%) mussels to the Nearctic (Table 5.2). Hotspot B shows clearly a transitional character where many species from both Nearctic and Neotropical elements occur. Except for *Disconaias conchos*, all other endemics are Neotropical species and are found mostly in the southern hotspots C, D, or E.

5.3 Diversity Hotspots

We define hotspots in this study as a concentration of native species, especially endemics, in a specifically defined region. To identify these hotspots, we used all available data on distribution based on a global map of biogeographic regionalization of the Earth's freshwater systems (Abell et al. 2008). These distributions were subsequently superimposed on the 1:8,000,000 ecoregions map of México. The resulting areas with concentrated spatial records within the respective basins were marked as hotspots using Arcmap 9.3.1 (for details, see Czaja et al. 2020).

Our analysis of species distributions shows that the most Mexican freshwater snails and bivalves occur in five diversity hotspots, denominated hotspot A, B, C, D, and E (Fig. 5.1), which are also the centers of endemicity (details see Czaja et al. 2020). Hotspot A (Fig. 5.2) contains 21 endemic species, most of them springsnails of the genera *Tryonia* and *Pyrgulopsis*. Many of the type localities are aquifer-fed springs in the Río Conchos region. Hershler et al. (2011) described 11 local-endemic springsnails from this region, but some species such as *Tryonia julimesensis* or *T. santarosae* were already at the time of their description possibly extinct. Because of their limited vagility and narrow environmental tolerances, springsnails are extremely vulnerable, not only in Mexico, but also worldwide and are the most endangered freshwater gastropods (Hershler et al. 2011, 2014; Burroughs et al. 2017; Czaja et al. 2020). Many areas of this hotspot are highly imperiled through human activities such as intensive agriculture, overexploitation of groundwater resources, and increased mining. We previously reported the urgent need for

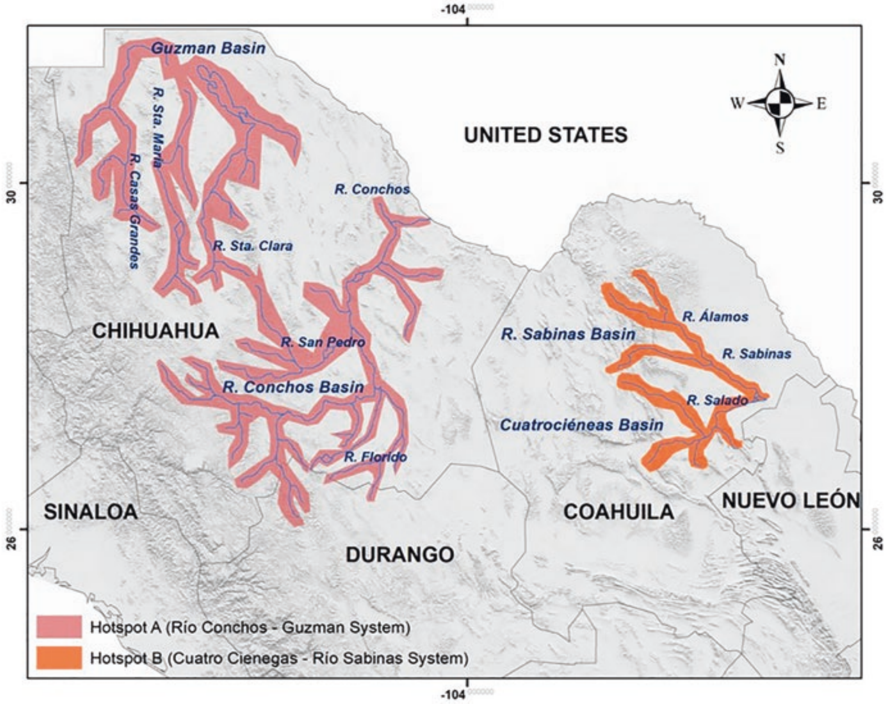

Fig. 5.2 Hotspots A (Río Conchos – Guzman Basin System) and B (Cuatro Ciénegas – Río Sabinas System)

restriction of groundwater extraction within hotspot A (Rio Conchos-Guzman system) and proposed that this region should have the highest priority for conservation in Mexico (Czaja et al. 2020). Other authors have made the same request to give to the highest status of conservation to the entire freshwater ecoregion of Río Conchos (Olson et al. 1998; Abell et al. 2000). However, none of these scientific appeals have so far had any positive effect on conservation measures in this region.

The hotspot B (Fig. 5.2) in the state of Coahuila includes the widely known Cuatro Ciénegas valley, a complex of more than 700 springs and marshes with several endemic genera and species of snails. All seven Mexican freshwater snails listed as endangered by the Mexican Secretary of Environment and Natural Resources (SEMARNAT 2019) occur in this small basin, including species of the emblematic Mexican endemic genera *Mexipyrgus* Taylor, 1966, *Mexithauma* Taylor, 1966, and *Paludiscala* Taylor, 1966. The other part of the hotspot B includes the Río Sabinas System, where streams such as Río Sabinas, Río Salado de los Nadadores, Río Álamos, and Río Monclova are the main habitats. Recently, a rich assemblage of freshwater gastropods was described from the Rio Sabinas (Czaja et al. 2019a, 2022). Unfortunately, hotspot B is also highly vulnerable and threatened by human activities, especially groundwater pumping, agriculture, and, like all hotspots, by the presence of non-native mollusks (*Melanoides* and *Corbicula*).

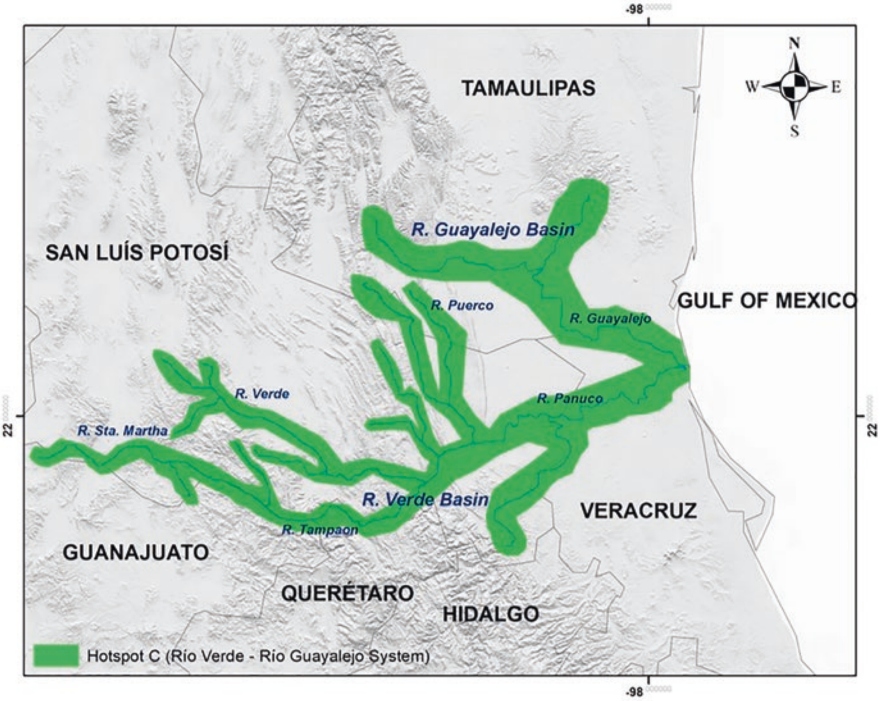

Fig. 5.3 Hotspot C (Río Verde – Río Guayalejo System)

The hotspot C (Fig. 5.3) is localized in eastern Mexican states of San Luis Potosí and Tamaulipas and includes the large Río Verde and Río Guayalejo basins. In contrast to the two previously mentioned hotspots, typical habitats in this transitional hotspot are large and small streams. The hotspot hosts a high number of endemic snails (21 species) and 11 *Pachychilus* (Pachychilidae) species are restricted to this system. Typical habitats are, besides the mentioned streams, also a few subterranean habitats which are type localities of the endemic stygobiont snail genera *Emmericiella* Pilsbry, 1909, and *Pterides* Pilsbry, 1909. Although less than hotspot A and B, hotspot C also is imperiled by human activities, especially agriculture and industry. Only the headwaters of the main rivers appear relatively undisturbed by human activities and their conservation statuses were assessed as "stable" by Abell et al. (2000). A current assessment of the situation in the region has not been carried out since then.

The hotspots D and E (Fig. 5.4) in southern Mexico were originally described as additional (potential) centers of freshwater snail diversity and endemism in Mexico (Czaja et al. 2020). Here, we present these potential centers as independent hotspots of mollusk diversity due to the large number of bivalves that occur in these two regions (see below). Contreras-MacBeath et al. (2014) reported that the rivers, marshes, and estuaries of this region are generally less contaminated and have a lower human population than hotspots A, B, and C. Hotspot D (Fig. 5.4) is found in

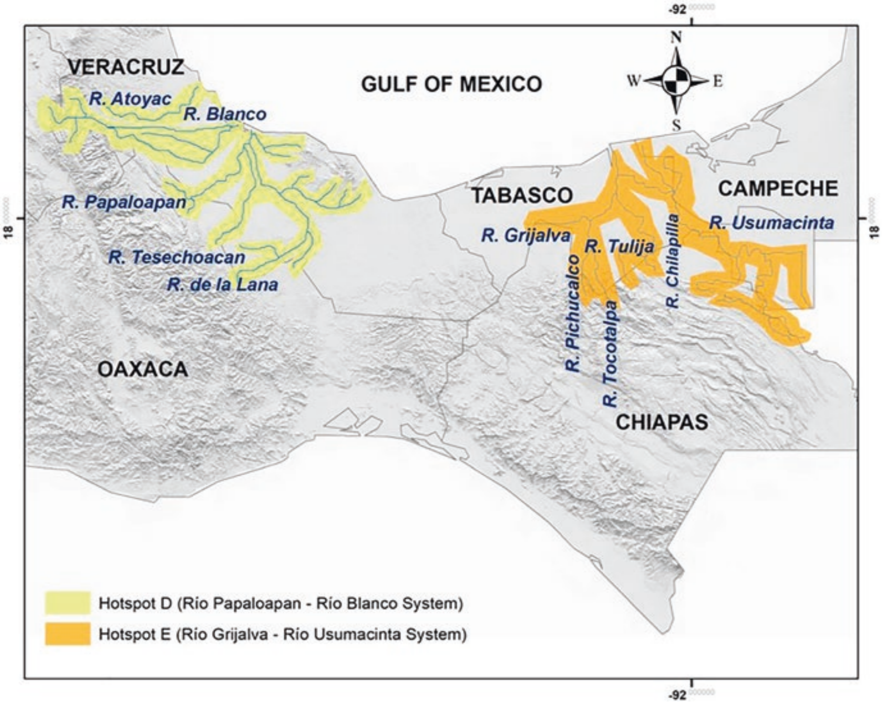

Fig. 5.4 Hotspots D (Río Papaloapan – Río Blanco System) and E (Río Grijalva and Río Usumacinta System)

the state of Veracruz along the southern part of the Gulf of Mexico and contain four large rivers (Río Papaloapan, Río Coatzacoalcos, Río Atoyac, and Río Blanco) with their tributaries which flow into the Gulf. Although the region is under sampled for mollusks, several rare endemic gastropod species such as *Pachychilus turati*, *P. schiedeanus*, *Mayabina bullula*, *Aroapyrgus orizabensis,* and *Pomacea catemacensis* were described from streams and lakes of this hotspot. The Río Grijalva-Río Usumacinta region in the state of Tabasco hosts the hotspot E (Fig. 5.4), where the diversity is relatively high and various local endemics such as *Pachychilus corvinus*, *P. glaphyrus*, *P. pilsbryi,* and *P. potomarchus* occur. However, like hotspot D, also this center is notably under sampled for mollusks and almost all species were described in the nineteenth century based only on morphological criteria of the shell without any anatomic or molecular genetic examination.

Of the entire Mexican freshwater snail fauna, almost half (48.7%) of the species are critically imperiled, imperiled, vulnerable, or possibly/presumably extirpated (Fig. 5.5). This seems at first glance lesser that in United States and Canada, where almost 3 quarters are imperiled, critically imperiled, or vulnerable (Johnson et al. 2013). However, this may be due to the fact that a large number (20%) of Mexican gastropods species are currently without a conservation rank. The family

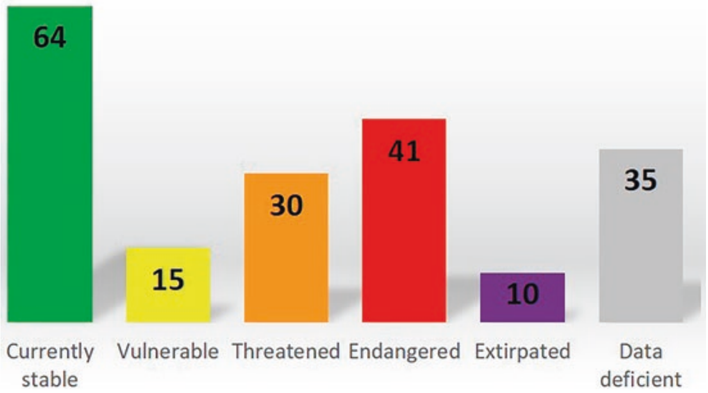

Fig. 5.5 Conservation statuses for Mexican freshwater gastropods based on the NatureServe conservation rank system (updated after Czaja et al. 2020)

Cochliopidae contains by far the highest number of endangered species of all Mexican gastropod families. Of all the 96 imperiled freshwater gastropods, 53 (55.2%) are hydrobioid species from the closely related families Cochliopidae and Hydrobiidae. This result is consistent with the data from the USA and Canada and the worldwide trend of hydrobioid families being the most imperiled of all gastropod families (Johnson et al. 2013; Miller et al. 2018).

5.4 Conservation

5.4.1 Status

The conservation status of almost all Mexican bivalves is completely unknown, and only three species (3.1%), *Cyrtonaias tampicoensis*, *Megalonaias nickliniana,* and *Polymesoda caroliniana*), are currently listed as endangered by the Mexican Secretariat of Environment and Natural Resources (SEMARNAT 2019). However, because mussels are frequently more vulnerable than snails, their situation is most likely even worse than that of the gastropods. The Red List contains three species (*Fusconaia mitchelli*, *Popenaias popeii,* and *Quadrula couchiana*) that have been assessed as endangered in United States (Table 5.2) (IUCN 2021). Recently, only two investigations dealing with conservation status of the Mexican bivalves were published. The first study was carried out by Tiemann et al. (2019) along the Conchos River, the core of the hotspot A, where the occurrence of unionid species was investigated. The authors conclude that "*…the Río Conchos is currently unsuitable for mussels in most, if not all, areas*" (Tiemann et al. 2019, p 184). One species, *Disconaias conchos,* just described in 1997 is now considered to be extinct in the Río Conchos as only dry shells were found. The other investigation was conducted at nine sites along the upper and middle part of the Río Sabinas in the state of Coahuila, the mainstream within the hotspot B (Czaja et al. 2022). Although several large unionid species have previously been described from this river (Johnson 1998), the authors could not find a single specimen of mussels from this family. Only small clams such as *Euglesa compressa*, *Eupera cubensis,* and *Pisidium nitidum* and massive occurrence of the invasive *Corbicula fluminea* were present.

5.4.2 Major Threats

Several studies confirm that freshwater mollusks belong to the most sensitive freshwater species to water pollution. Many species are used globally as bioindicators of water quality (e.g., Lopes-Lima et al. 2021). Almost all of the threats to their sustainability have worldwide anthropogenic causes (Dudgeon et al. 2006; Böhm et al. 2020; Tickner et al. 2020). In most countries, there are five main human activities which have severely impacted the malacofaunas (Köhler et al. 2012). Mexico is similar in that during the Anthropocene the most damage to molluscan communities has occurred because of (1) dam construction and other flow modifications; (2) water pollution mainly from inappropriate agricultural and industrial activities; (3) overexploitation of aquifers; (4) habitat degradation; and (5) the introduction of non-native species. In addition, there are the effects of climate change including seasonal and inter-annual shifts in the amount and timing of precipitation that are superimposed on the previous threats (Köhler et al. 2012). All five interacting threats affect the freshwater ecosystems of the five Mexican hotspots, but in varying degrees of intensity. Especially the rivers and springs of hotspots A and B of the Chihuahuan Desert, which generally have less water than those of the southern hotspots, are under increasingly strong anthropogenic and climatic pressure. Heat waves with maximum temperature of 50 °C have occurred in the last decade and the resulting increase in water temperatures affects species metabolism and ecosystem processes (Blunden et al. 2018). Dam constructions and flow modification during the past century caused great damage to the freshwater communities especially in the northern arid regions of the country. Although according to Martínez-Yrízar et al. (2012), Mexico had 840 major dams, there are no detailed studies on the impacts of dams on freshwater mollusks.

Other threats for both desert hotspots A and B are the natural or human-caused fluctuations of the water flow and groundwater pumping that impact directly critical environmental conditions (water temperature, pH, and dissolved oxygen) of the springs. According to Burroughs et al. (2017), these changes will be the main stressors in the future especially for cochliopid and hydrobiid springsnails. Hotspot A contains already the highest number of Mexican freshwater gastropods with the highest conservation rank; 15 species belonging to the family Cochliopidae are critically imperiled, two are possibly extinct. Hershler et al. (2011) even considered the entire endemic springsnail fauna of this hotspot to be at risk of extirpation. The situation with mussels is even more dramatic. Although the hotspot A occupies a large area including the Río Conchos (750 km in length) and its tributaries, only 2 living specimens of the native mussels *Utterbackia imbecillis* were found during the recent study of this river by Tiemann et al. (2019). All other mussels described from this river were found only as relict shells. Some of the bivalve species such as *Disconaias conchos* were just described at the end of the twentieth century. As causes for this decline, the authors suggest alterations in the physical habitat, water quantity and quality, organic pollution from agricultural activities, salinization, and gravel mining. The situation in Hotspot B, where all seven Mexican freshwater gastropod species listed as endangered live, is not much better. This alarming situation exists despite the wetlands of the Cuatro Ciénegas and Río Sabinas drainage basins being national protected areas and RAMSAR sites of international importance (Bezaury-Creel et al. 2017). Human activities such as groundwater pumping, agriculture, and non-native species continue to endanger the ecosystems of Cuatro Ciénegas. Endemic species, such as *Juturnia coahuilae*, *Paludiscala caramba,* and *Phreatoceras taylori,* although a few years ago were very abundant, now they have become rare in these springs (Czaja et al. 2020). De la Maza-Benignos (2017) considered that parts of the entire ecosystem of this site in the Chihuahuan Desert are at risk.

Within the three Neotropical hotspots C, D, and E, future threats may be less from groundwater depletion, but more from the impacts of agricultural, industrial, and human population growth. Effects of prolonged and more frequent dry periods will likely impact water quality even as more demand for clean freshwater increases for human consumption and navigation. The global effects of pollution, drought, water-level declines, and increased salinity are known to affect molluscan distribution in Mexico (e.g., Alcocer-Durand and Escobar-Briones 1992; Albarrán Mélzer et al. 2017). These impacts are especially evident in the Río Verde-Río-Guayalejo basin of hotspot C that is far more populated than the desert hotspots and therefore is more strongly imperiled by human activities and climatic extremes. Arriaga-Cabrera et al. (2000) considered that this basin has some of the most contaminated rivers in México. Aguilar et al. (2010) assigned one of the highest levels of conservation priority of all freshwater habitats in Mexico to the whole Pánuco ecoregion, the main part of the hotspot C. Given this situation and the fact that some of the molluscan species of this hotspot have not been recorded since the nineteenth or early twentieth centuries, it can be assumed that some species are already extirpated or extinct. Hotspots D and E with their rivers, marshes, estuaries, and lagoons are less contaminated and are among the Mexican regions with the lowest water pollution (Contreras-MacBeath et al. 2014). This difference would explain the relatively large diversity among the mussels compared to the desert hotspots in the north. However, we lack current studies of the conservation status of the mollusks that inhabit the streams of this hotspot.

Like many others taxonomic groups, native Mexican molluscan species suffer a severe negative impact from invasive species, especially *Melanoides tuberculata* (Müller, 1774) and *Corbicula fluminea*, which are distributed widely in freshwater sites in Mexico (Naranjo-García and Olivera-Carrasco 2014; Czaja et al. 2020). Although these impacts were never proven definitely and field experimental data are lacking, many authors consider that these species are able to displace native species and affect the integrity of native ecosystems (Burroughs et al. 2017). Our own observations since 2014 in rivers and springs of the hotspot A and B confirm that the presence of both invasive mollusks is always positively correlated with the absence of native species, especially of hydrobioid endemic snails and unionid mussels. In our recent study on the freshwater molluscan diversity of the hotspot B, we concluded that the sole presence of the invasive species is not the main problem for the native species, but rather the combination of their presence with the degree of pollution (eutrophication) of the sites is the limitation. In some regions, the mass die-offs of invasive species lead to deoxygenation and loss of native species. The less tolerant native forms are disadvantaged when these multiple factors act that can eventually lead to their final extirpation (Czaja et al. 2022). Similar observations were made by Dudgeon et al. (2006) in strongly impacted habitats. The presence of non-native species is a serious global challenge for conservation biology.

5.4.3 What Is the Real Situation of the Mexican Mollusks?

To obtain a complete picture of the situation of a taxonomic group or of an entire region or ecosystem, it is not enough to have information on the conservation status of the species and their current diversity. To understand the real situation of a particular taxonomic group, especially its possible rates of extinctions within a region, it is necessary to know the comparative values such as historic diversity and data on past species distributions. But such information is only available in very few cases and almost never if the taxonomic groups are freshwater invertebrates. In such cases, the application of a paleoecological approach, called Conservation Paleobiology, can be very helpful and is often the only way to obtain information on past distributions and local extirpation events (Dietl and Flessa 2011). This relatively new approach, which combines neobiological and paleobiological methods, provides important perspectives for conservation of modern ecosystems. For example, Neubauer et al. (2021) were able to show that the present extinction rates in European freshwater gastropods are three orders of magnitude higher than these estimates for the Cretaceous–Paleogene mass extinction.

We applied this paleobiological approach to investigate the human impact on freshwater gastropods in the transition area between hotspots A and B (Czaja et al. 2019b). The region, called Laguna District, contains one of the largest basins in Mexico (Nazas-Aguanaval Rivers) and was historically part of a large hotspot that included the currently separated desert hotspots A and B. Of the 32 species of freshwater snails present in the area of study through the Holocene, only four (12.5%) are still extant. Twenty-four (75.0%) species disappeared during the twentieth century due to dam construction and overexploitation of surface and ground waters and also probably the presence of invasive species. We called the region, which is about the size of Holland, a “ghost” center of endemism (in the sense of Contreras-MacBeath et al. 2014), where only a very impoverished molluscan fauna occurs. The dramatic extirpation event of the Laguna District happened “silently” and unrecognized only some 200 km away from one of the current greatest hotspots of gastropods diversity in North America, the Cuatro Ciénegas Basin. The same human activities, especially excessive groundwater pumping, that caused the loss of aquatic habitat in this "ghost" hotspot, continue to impact the similar aquatic ecosystems of the hotspot A and B. The families most affected by the extirpation were the Cochliopidae and Hydrobiidae, which are also currently among the most endangered families within the hotspots A and B. The bivalves were not integrated in the study, but our published and unpublished paleobiological studies from 2014 show that most of the pre-Anthropocene river sediments of the region contain many unionid and sphaerid shells of several species (Czaja et al. 2014 and unpublished data). Today, the unionid mussels and most of the sphaeriid clams are practically nonexistent in the large rivers of the "ghost" hotspot and, as already mentioned, also not in the large Río Conchos of the hotspots A and Río Sabinas in the hotspot B (Tiemann et al. 2019; Czaja et al. 2022). Thus, the impact on mussels was in the desert part of Mexico and probably even more dramatic than it was on gastropods. The fact that the hotspot A (at least in terms of mussels) is developing into another "ghost" hotspot is clearly shown by the results of the systematically studied mussels of the Río Conchos basin, where despite extensive research, almost no live mussels were found (Tiemann et al. 2019). The authors assume that, in addition to the anthropogenic causes, climatic factors also play a role in the impoverishment of the mussel fauna. The application of the described paleoecological approach could provide additional reliable knowledge. A typical characteristic of an impoverished malacofauna of such "ghost" hotspots is the lack of hydrobid snails and unionid mussels by simultaneous, massive presence of the invasive mollusks. Unfortunately, such assemblages can be observed more and more frequently in all five hotspots, but especially strong in the semi-arid hotspot A and B.

5.4.4 Conservation Efforts

Apart from the inclusion of seven gastropod and three bivalve species in the Mexican Secretariat of Environment and Natural Resources list (SEMARNAT 2019), very little effort has been made to protect the Mexican mollusks. This lack is mainly due to the fact that this taxonomic group has so far received very little scientific attention, and in the case of the bivalves, at least on national level, almost none at all. In Mexico, there is not a single biological monitoring program or conservation plan for sustaining freshwater mollusks diversity, not even in Cuatro Ciénegas basin. Already in our last paper (Czaja et al. 2020), we reported that we do not know the population structure, population size, or population trends of any species of Mexican freshwater snails or mussels. Unfortunately, nothing has changed. The few scientists who deal with the freshwater mollusks are in the unfortunate situation of recording the species occurrences (checklists) and at the same time documenting the current extirpation events.

The conservation of Mexican mollusks does benefit from their occurrence in a few protected areas and Ramsar sites. This strategy practiced by the Mexican government has proven to be quite successful. According to Lyons et al. (2020), the total area of protected terrestrial habitat in Mexico is of 25.3 million ha, an area larger than the entire United Kingdom, and corresponds to 11.1% of the nation's territory. In addition, many mollusks from hotspots A and B share their habitat with endemic fishes, for which there has long been a conservation focus (Contreras-MacBeath et al. 2014). This co-occurrence has benefited the endemic snails in these areas. Our experience over the last few years also indicates that protection of habitats and drainage basins is, especially for invertebrates, more efficient than other protection strategies such as focused on single rare species. However, the current results of the assessments of freshwater fishes and gastropods show that despite being protected areas, many species are still at risk of extinction (Lyons et al. 2020; Czaja et al. 2020). Translocation as a possible option to prevent impending extinction is probably not effective and not risk-free either in view of the scarce ecological data on the species life histories and vulnerability to predators and parasites.

5.5 Conclusion

5.5.1 Can We Still Stop the Silent Extinction of the Mexican Mollusks?

Freshwater mollusks have important functions in freshwater ecosystems and their importance in food webs cannot be overstated (Covich et al. 1999; Covich 2010). However, the current situation of freshwater mollusks leaves no doubt that the Mexican gastropods and bivalves, like most of the freshwater mollusks and many other invertebrates are globally vulnerable in the Anthropocene during this dramatic phase of extinctions. It is also more than likely that recent conservation efforts will not prevent of even slowdown these losses, especially in aquatic habitats in the semi-arid part of the planet. Moreover, research and recommendations based solely on the natural sciences clearly do not have sufficient social influence to resolve the global biodiversity crisis. The current environmental crisis has essentially socio-ethical dimensions and cannot be resolved with only scientific and technological approaches. Barthlott (2019) noted that "*Science only provides data and recommendations for action, but society, education, culture, politics, emotions and ideological attitudes decide.*" The reasons for the current environmental crisis, especially biodiversity loss, are manifold but have deeper causes, *causas primas* in a philosophical sense, that include how human think about short- and long-term problems and their reactions to changing behavior. Important factors include exaggerated narcissism, consumerism, and an excessive resource-intensive, materialistic lifestyle. We need a new collaboration between natural, philosophical, theological science, and society in general.

5.5.2 *Can We Change Our Philosophical Approach to be More Inclusive?*

That theology can contribute something to problem-solving of our environmental crisis was recognized more than 50 years ago (e.g., White 1967; Eckberg and Blocker 1989; Whitney 1993; Jenkins 2009). However, the major world religions paid little or no attention to environmental issues and it was not until the 1980s, inspired mainly by the reports of the Club of Rome (Meadows et al. 1972), that the five main religions finally signed the Nature Declarations (Barthlott 2019). For the western world, White (1967) pointed out that the anthropocentric Christianity had some responsibility for the environmental crisis and that environmental stewardship was needed (Sessions 1987). White himself recommended returning to the ecological egalitarianism of St. Francis whom he considered "the greatest spiritual revolutionary in Western history" (cited from Sessions 1987). Few Christian scholars today recognize that Saint Francis of Assisi (thirteenth century), with his still now revolutionary idea of the "*equality of all creatures, including man,*" is the "patron of ecology." The Assisi Declaration, signed jointly by the Buddhist, Christian, Hindu, Muslim, and Jewish religious representatives in 1986, begins with the famous sentence of Buddha: "*Because the cause was there the consequences followed; because the cause is there, the effects will follow.*" These words from the fifth century BCE are still confirmed today by the natural sciences, especially conservation biology. Although the subject of religion and the environment is now on the agenda of all world religions, the topic, similar to the natural sciences, is unfortunately restricted to small academic circles.

In the beginning of modern science (approx. 1620), Francis Bacon's idea of a "domination of nature" was already setting up a debate (Bacon 1949). Although he was one of the founding fathers of the modern empirical sciences, Bacon could not have foreseen the catastrophic extent of this human dominion over the nature. All sciences, the biological sciences too, will have to face such (self) critical debate. Are the hopes of an improvement in the situation justified in spite of the current precarious situation? We consider that the theological, philosophical, natural sciences and most of the society as a whole have a common goal: The preservation of nature. The rise of conservation biology in the 1980s was an important step within the biological science. Conservation biology is definitely part of the solution, but biology and an ecosystem approach are needed that strongly integrates human activities. In addition to the recognized necessary protection and conservation measures, the main priority must be to avoid further damage. If we do not eliminate the economic, legal, and political barriers to long-term regional and global ecosystem protection, the hope of resolution of our current crisis will remain an illusion (Piechocki 2002). We need to develop a scientific paradigm shift that comes with increasing knowledge and broad communication to counter a main cause of the current Anthropocene's current environmental crisis, the misdirected and irrational anthropocentrism (Moling 2019). Such self-destructive human behavior or *hubris* can only be avoided by improved understanding of the full value of biodiversity in the context of a socioeconomic and ecosystem context. We need a rapid change in the ways we communicate the necessity of a diverse molluscan biota to more people so that a contemplative change in thinking is based in a new ethic. There is no other sensible alternative.

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Chapter 6
Amphibians and Reptiles of Mexico: Diversity and Conservation

Ireri Suazo-Ortuño, Aurelio Ramírez-Bautista, and Javier Alvarado-Díaz

Contents

6.1 Introduction

Amphibians (frogs, salamanders, and caecilians) and nonvolant reptiles (snakes, lizards, turtles, crocodiles, and tuatara) are frequently considered as relevant examples of the current global biodiversity crisis, with amphibians receiving ample consideration after reports of population declines and species extinctions since the late 1980s (i.e., Blaustein and Wake 1990). Since amphibians are probably one of the most sensitive animals to react rapidly to substantial changes in their environments, they are frequently considered as indicators of ecosystem health (Saber et al. 2017). Currently, amphibians are considered as the most threatened vertebrate class, with about 41% of species at risk of extinction (IUCN 2021). Although receiving relatively less attention, various reports suggest that reptiles are experiencing similar rates of decline as those of amphibians (Gibbons et al. 2000; Reading et al. 2010; Todd et al. 2010). The critical importance of amphibians and reptiles in the broader

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I. Suazo-Ortuño (✉) · J. Alvarado-Díaz
Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, Mexico

A. Ramírez-Bautista
Centro de Investigaciones Biológicas (CIB), Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_6

context of biodiversity conservation is highlighted by the various ecosystem services provided by amphibians and reptiles. For example, both amphibians and reptiles contribute substantially to ecosystems' energy flow because, as ectotherms, consumed energy is efficiently transformed to biomass, which then becomes available to higher trophic levels (Vitt and Caldwell 2014), and in aquatic habitats amphibian larvae, which are mainly primary consumers, influence dynamics of primary production and organic matter (Flecker et al. 1999).

The highest rates of habitat loss and degradation occur in the 25 world's biodiversity hotspots (Sodhi et al. 2007) identified by Myers et al. (2000). The majority of Mesoamerica (Southern Mexico and Central America) correspond to one of these hotspots, and Mexico represents a region in which markedly high levels of diversity and endemism of amphibians and reptiles occur. According to Wilson et al. (2013), 64% of species of amphibians and reptiles registered in Mesoamerica occur in Mexico, and 60% of herpetofauna species found in Mexico are endemic to this country. Parallel to these high levels of herpetofauna diversity and endemism, amphibians and reptiles in Mexico are undergoing marked signs of population declines.

6.2 Diversity and Endemism

In Mesoamerica, Mexico stands out as the country with the highest levels of amphibian and reptile species richness and endemism. For this chapter, information on amphibian taxonomy, species numbers, and endemism proportions in Mexico was obtained from the data set of AmphibiaWeb (Amphibia Web 2021) and for reptiles, information on these subjects was obtained from the data set of Reptile Database (Uetz et al. 2021; for both, reptiles and amphibians, the sub-family taxonomic category was not considered). When information is drawn from other sources it is specified. The amphibian clade in Mexico consists of 411 species: 250 frogs (Order Anura), 158 salamanders (Order Caudata), and 3 caecilians (Order Gymnophiona). Reptiles in this country are composed of 1073 species: 58 turtles (Order Testudines), 572 lizards (including amphisbaenians; Order Squamata, Suborder Lacertilia sensu *lato*), 439 snakes (Order Squamata, Suborder Ophidia sensu *lato*), and 4 crocodiles (Order Crocodilia). Worldwide, Mexico occupies the fifth and second position of species richness of amphibians and reptiles, respectively. Additionally, the level of endemism is markedly high, with 69.8% of the amphibian and 52% of the reptile species occurring only in the country. Although as a country, Mexico is ranked as the number three in amphibian endemic species (Stuart et al. 2008), it is highly likely that these figures will shortly increase as the current rate of annual species description shows a steady increment (11.5 and 27.4% of Mexican anurans and salamanders, respectively, were described between 1992 and 2007; Frías-Alvarez et al. 2010). Of the endemic amphibian species, 152 are frogs, 134 are salamanders, and one is a caecilian, whereas for reptile species, 19 are turtles, 297 are lizards, and 242 are snakes. None of the four crocodile species occurring in Mexico are endemic to this country.

Mexican amphibian species are distributed in 11 families of frogs, four of salamanders, and one of caecilians (Wilson et al. 2013; Parra-Olea et al. 2014). Reptile species are distributed in 9 families of turtles, 15 of lizards, 7 of snakes, and 2 of crocodiles. The states in Mexico with higher reptile diversity are Oaxaca, Chiapas, and Veracruz, and those with the lowest diversity are Tlaxcala, Guanajuato, and Ciudad de Mexico (Flores-Villela and García-Vázquez 2014; Mata-Silva et al. 2015; Torres-Hernández et al. 2021). The states with higher amphibian diversity are Oaxaca, Chiapas, and Veracruz (Parra-Olea et al. 2014; Mata-Silva et al. 2015; Torres-Hernández et al. 2021).

The 250 frog species in Mexico are distributed in 11 of the 29 existent frog families, and of these 11 families, Centrolenidae, Pipidae, and Rhinophrynidae are represented by only one species each. *Xenopus laevis* (Pipidae), an exotic species from South Africa, occurs only in the northwest region of Baja California (Álvarez-Romero et al. 2008). The most speciose Mexican frog families are Hylidae (103 species, 40.1%), followed by Craugastoridae (36 species, 14.1%), Bufonidae and Eleutherodactylidae (34 species each, 13.5%), and Ranidae (27 species, 10.7%). The rest of the families are represented from three to six species (Table 6.1). The most speciose frog genera are *Craugastor* (36 species, 14.2%), *Eleutherodactylus* (34 species, 13.5%), *Rana* (*Lithobates*) (27 species, 10.7%), *Sarcohyla* (26 species, 10.3%), and *Incilius* (22 species, 8.7%). The remaining 29 genera are represented from 1 to 11 species (Table 6.1).

Salamander species in México are distributed in four of the nine existent salamander families. These four families are Ambystomatidae, Plethodontidae, Salamandridae, and Sirenidae. Salamandridae and Sirenidae are restricted to extreme northeastern Mexico and are represented by only one (Salamandridae; *Notophthalmus meridionalis*) or two species (Sirenidae; *Siren intermedia* and *S. lacertina*). Therefore, most Mexican salamanders belong to the families Ambystomatidae and Plethodontidae. Although only represented in four families, the 158 species of salamanders occurring in Mexico rank this country as the second highest in caudates species diversity. Of the 32 known ambystomatid species (all in the genus *Ambystoma*), 17 (53.1%) are found in Mexico north of the southern rim of the Mexican Plateau (Vitt and Caldwell 2014). Of the 17 species, 16 are only found in Mexico (Table 6.2). Of the 490 known plethodontids, 138 (28%) are distributed in Mexico, and of these, 116 (84.1%) are endemic to this country (Table 6.2). Six genera of plethodontid salamanders are endemic to Mexico: *Aquiloeurycea*, *Chiropterotrition*, *Isthmura*, *Ixalotrition*, *Parvimolge,* and *Thorius*. The endemism level of Mexican salamanders is markedly high (84.8%; García-Padilla et al. 2021).

The Mexican species of reptiles are distributed in 40 families, which correspond to 43.9% of the 91 world reptile families. Phrynosomatidae is the lizard family with the highest species richness (152 species, 26.7% of Mexican lizard species), for snakes is Colubridae (319 species, 72.7% of Mexican snake species), for crocodiles, the two families (Crocodylidae and Alligatoridae) share two species each, whereas for turtles the most diverse family is Kinosternidae (20 species, 35% of 58 Mexican turtle species; Table 6.3). The most diverse genus of lizards is *Sceloporus* (103 species, 18% of a total of 569 Mexican lizard species), for snakes it is the genus *Crotalus* (44 species, 10% of a total of 439 Mexican snake species), for crocodiles it is the genus *Crocodylus* (2 species, 50% of a total of 4 Mexican crocodile species; Table 6.3), whereas for turtles the most diverse genus is *Kinosternon* (16 species, 28% of a total of 58 Mexican turtles).

The only reptile family endemic to Mexico is Bipedidae, a natural group of fossorial forms without hind legs, nested within the lizard's clade (Flores-Villela and

Table 6.1 Number of species, number of endemic species, and number of species at global risk (CR, EN or VU) by family and genus of the frogs (Anura) of Mexico

Family	Genus	Species	Endemic species	Species at global risk
Bufonidae		34	14 (41.2)	7 (20.1)
	Anaxyrus	11	3 (27.3)	1 (9.1)
	Incilius	22	11 (50)	6 (27.3)
	Rhinella	1	0	0
Centrolenidae		1	0	0
	Hyalinobatrachium	1	0	0
Craugastoridae		36	24 (66.7)	16 (44.4)
	Craugastor	36	24 (66.7)	16 (44.4)
Eleutherodactylidae		34	28 (82.4)	11 (32.4)
	Eleutherodactylus	34	28 (82.4)	11 (32.4)
Hylidae		103	70 (68)	55 (53.4)
	Acris	1	0	0
	Bromeliohyla	1	1 (100)	1 (100)
	Charadrahyla	10	10 (100)	8 (80)
	Dendrosophus	5	1 (20)	0
	Duellmanohyla	3	2 (66.7)	1 (33.3)
	Ecnomiohyla	3	3 (100)	3 (100)
	Exerodonta	7	7 (100)	4 (57)
	Hyla	7	4 (57)	1 (14.3)
	Megastomatohyla	4	4 (100)	4 (100)
	Plectrohyla	11	4 (36.4)	9 (81.8)
	Pseudacris	3	0	0
	Ptycohyla	5	3 (60)	2 (40)
	Sarcohyla	26	26 (100)	21 (81)
	Scianix	1	0	0
	Smilisca	4	1 (25)	1 (25)
	Tlalocohyla	4	2 (50)	1 (25)
	Trachycephalus	1	0	0
	Triprion	3	1 (33.3)	0
	Agalychnis	4	1 (25)	0
Leptodactylidae		3	0	0
	Engystomops	1	0	0
	Leptodactylus	3	0	0
Microhylidae		6	0	0
	Gastrophryne	3	0	0
	Hypopachus	3	0	0
Pipidae		1	0	0
	Xenopus	1	0	0
Ranidae		27	16 (59.3)	10 (37)
	Rana	27	16 (59.3)	10 (37)
Rinophrynidae		1	0	0

(continued)

Table 6.1 (continued)

Family	Genus	Species	Endemic species	Species at global risk
	Rinophrynus	1	0	0
Scaphiopodidae		4	0	0
	Scaphiopus	1	0	0
	Spea	3	0	0

Percentages are presented in parenthesis

Table 6.2 Number of species, number of endemic species, and number of species at global risk (CR, EN or VU) by family and genus of salamanders (Caudata) and caecilians (Gymnophiona) of Mexico

Family	Genus	Species	Endemic species	Species at global risk
Caudata Ambystomatidae		17	16 (94)	12 (70.1)
	Ambystoma	17	16 (94)	12 (70.1)
Plethodontidae		138	118 (88.5)	117 (85)
	Aquiloeurycea	6	6 (100)	4 (66.7)
	Batrachoseps	1	0	0
	Bolitoglossa	21	11 (52.4)	12 (57.2)
	Bradytriton	1	0	1 (100)
	Chiropterotriton	23	23 (100)	21 (91.3)
	Cryptotriton	1	1 (100)	1 (100)
	Dendrotriton	2	2 (100)	2 (100)
	Isthmura	7	7 (100)	6 (86)
	Ixalotriton	2	2 (100)	2 (100)
	Nyctanolis	1	0	1 (100)
	Oedipina	1	0	0
	Parvimolge	1	(1 (100)	1 (100)
	Pseudoeurycea	39	36 (92.3)	38 (97.4)
	Thorius	29	29 (100)	27 (93.1)
	Aneides	1	0	0
	Ensatina	1	0	0
Salamandridae		1	0	1 (100)
	Notophthalmus	1	0	1 (100)
Sirenidae		1	0	0
	Siren	1	0	0
Gymnophiona				
Dermophiidae		3	1 (33.3)	0
	Dermophis	2	1 (50)	0
	Gymnopis	1	0	0

Percentages are presented in parenthesis

García-Vázquez 2014). Lizard species in Mexico present an endemicity of 52%. The lizard families with higher percentages of endemic species are Anguidae (80%), Xenosauridae (92%), Phyllodactylidae (81%), and Xantusiidae (79.3%; Table 6.4).

Table 6.3 Number of species, number of endemic species, and number of species at global risk (CR, EN or VU) by family and genus of the turtles (Testudines) and crocodiles (Crocodilia) of Mexico

Family	Genus	Species	Endemic species	Species at global risk
Testudines				
Emydidae		19	8 (42.0)	6 (32.0)
	Actynemis	1	1 (100)	0
	Chrysemys	1	0	0
	Deirochelys	1	0	0
	Pseudemys	2	0	0
	Terrapene	6	4 (66.7)	2 (33.3)
	Trachemys	8	4 (50)	4 (50)
Testudinidae		5	2 (40)	3 (60)
	Gopherus	5	2 (40)	3 (60)
Trionychidae		2	0	0
	Apalone	2	0	0
Chelydridae		2	0	1 (50)
	Chelydra	2	0	1 (50)
Kinosternidae		20	8 (42)	0
	Claudius	1	0	0
	Kinosternon	16	9 (56.3)	0
	Staurotypus	2	0	0
	Sternotherus	1	0	0
Dermatemydidae		1	0	1 (100)
	Dermatemys	1	0	1 (100)
Cheloniidae		5	0	5 (100)
	Caretta	1	0	1 (100)
	Chelonia	1	0	1 (100)
	Eretmochelys	1	0	1 (100)
	Lepidochelys	2	0	2 (100)
Dermochelyidae		1	0	1 (100)
	Dermochelys	1	0	1 (100)
Geoemydidae		3	1 (33.3)	0
	Rhinoclemmys	3	1 (33.3)	0
Crocodilia				
Crocodylidae		2	0	1 (50)
	Crocodilus	2	0	1 (50)
Alligatoridae		2	0	0
	Alligator	2	0	0

Percentages are presented in parenthesis

Three lizard genera present an endemicity of 100%: *Barisia* (7 species), *Bipes* (3 species), and *Ophisaurus* (2 species). Other lizard genus with high endemicity are *Xenosaurus* (92%, 11 species), *Uta* (86%, 6 species), *Lepidophyma* (85%, 17 species), *Phyllodactylus* (81%, 22 species), *Abronia* (81%, 21 species), and *Sauromalus*

(80%, 4 species; Table 6.4). The snake families with higher endemism proportion are Leptotyphlopidae (64.7%) and Viperidae and Colubridae (56% each). Several snake genera present an endemicity of 100%: *Conopsis* (6 species), *Mixcoatlus* and *Chersodromus* (4 species each), *Ophryacus* (3 species), *Sistrurus* and *Adelophis* (2 species each), and *Cenaspis*, *Manolepis*, *Sympholis,* and *Tantalophis* (1 species each; Table 6.5). Other snake genera with high endemicity are *Rhadinaea* (93.8%, 15 species), *Geophis* (88.2%, 30 species), and *Tropidodipsas* and *Epictia* (71.4%, 7 species each; Table 6.5).

Currently, 361 turtle species have been described worldwide (Uetz et al. 2021), and Mexico is the second richest country of turtle species (58), only after the United States. Additionally, Mexico also presents the highest proportion of species when compared to the rest of the world (19.9%; Legler and Vogt 2013). The turtle family with the highest percentage of endemic species in Mexico is Emydidae (42%), followed by Testudinidae and Kinosternidae (40% each). Turtle genera with high endemicity are *Terrapene* (67%, 4 species), *Trachemys* (50%, 4 species), *Kinosternon* (50%, 8 species), and *Gopherus* (40%, 2 species; Table 6.3).

6.3 Conservation Status of Mexican Amphibians and Reptiles

For the estimation of extinction risk of Mexican amphibian and reptile species, we used the threatened categories of the IUCN Red List of Threatened Species. The three categories of global extinction risk considered are: Critically Endangered (CR), Endangered (EN), and Vulnerable (VU) (IUCN 2021). Where appropriate we also used the data deficient (DD) and not evaluated (NE) categories. Amphibians and reptiles are crucial components of earth's ecosystems, influencing important ecological processes such as nutrient cycling, energy flow through trophic chains (as predators and prey), energy exchange between terrestrial and aquatic habitats, levels of primary productivity in aquatic habitat through bioturbation, pollination, and seed dispersal (Cortés-Gomez et al. 2015). Albeit their ecological relevance, amphibians are the most threatened vertebrate class, with 41% of species at risk of global extinction. Since the 1990s, various studies have registered declines of Mexican amphibians (Frías-Alvarez et al. 2008), such as salamanders and frogs that were frequently seen during the 1970s and 1980s, are now difficult to find (Rovito et al. 2009). In concordance with global estimations, Mexican amphibians are more threatened than other vertebrate groups as indicated by a larger proportion of amphibian species that are included in one of the three main categories of risk to extinction (58%) in comparison with Mexican birds (5%), mammals (19%) or reptiles (14%; Frías-Alvarez et al. 2010).

The Mexican frog families with highest proportion of threatened species are Hylidae (53.4%), Craugastoridae (44.4%), Ranidae (37%), Eleutherodactylidae (32.4%), and Bufonidae (29.4%). The remaining six frog families do not present

Table 6.4 Number of species, number of endemic species, and number of species at global risk (CR, EN or VU) by family and genus of lizards (Squamata: Lacertilia) of Mexico

Family	Genus	Species	Endemic species	Species at global risk
Dactyloidae		62	39 (63)	4 (5.6)
	Anolis	62	39 (63)	4 (5.6)
Phrynosomatidae		153	94 (62)	21 (14)
	Sceloporus	103	71 (68.9)	7 (6.8)
	Callisaurus	1	0	0
	Cophosaurus	1	0	0
	Holbrookia	6	1 (17)	0
	Petrosaurus	4	3 (75)	0
	Phrynosoma	20	6 (30)	0
	Uma	3	2 (67)	1 (33)
	Urosaurus	8	5 (63)	2 (25)
	Uta	7	6 (86)	4 (57)
Iguanidae		20	13 (65)	7 (35)
	Ctenosaura	10	7 (70)	4 (40)
	Cachryx	2	1 (50)	0
	Dipsosaurus	2	1 (50)	0
	Iguana	1	0	0
	Sauromalus	5	4 (80)	3 (60)
Phyllodactylidae		27	22 (81)	1 (4)
	Phyllodactylus	25	22 (88)	1 (4)
	Tarentola	2	0	0
Gekkonidae		6	0	0
	Gehyra	1	0	0
	Hemidactylus	4	0	0
	Lepidodactylus	1	0	0
Sphaerodactylidae		6	0	0
	Aristelliger	1	0	0
	Gonatodes	4	0	0
	Spaherodactylus	1	0	0
Scincidae		38	24 (63)	1 (2.7)
	Marisora	4	2 (50)	0
	Mesoscincus	2	1 (50)	0
	Plestiodon	23	16 (70)	1 (4.3)
	Scincella	9	5 (56)	0
Xantusiidae		29	23 (79.3)	3 (10.3)
	Lepidophyma	20	17 (85)	3 (15)
	Xantusia	9	6 (67)	0
Gymnophtalmidae		1	0	0
	Gymnophthalmus	1	0	0
Teiidae		50	26 (52)	2 (4)
	Aspidoscelis	41	22 (54)	2 (5)

(continued)

Table 6.4 (continued)

Family	Genus	Species	Endemic species	Species at global risk
	Holcosus	9	4 (44)	0
Anguidae		50	40 (80)	15 (30)
	Abronia	26	21 (81)	10 (38)
	Aniella	2	1 (50)	1 (50)
	Barisia	7	7 (100)	2 (29)
	Elgaria	5	3 (60)	0
	Gerronothus	8	6 (75%)	2 (25%)
	Ophisaurus	2	2 (100)	1 (50)
Diploglossidae		6	3 (50)	0
	Celestus	4	3	0
	Diploglossus	2	0	0
Xenosauridae		12	11 (92)	3 (25)
	Xenosaurus	12	11 (92)	3 (25)
Bipedidae		3	3 (100)	0
	Bipes	3	3 (100)	0
Helodermatidae		4	2 (50)	0
	Heloderma	4	2 (50)	0

Percentages are presented in parenthesis

species at global risk. The frog genera with the highest proportion of threatened species are all included in the Hylidae family. These genera are *Megastromatohyla* (4 species, 100%), *Plectrohyla* (9 species, 81.8%), *Sarcohyla* (21 species, 80.7%), *Charadrahyla* (8 species, 80%), *Ecnomiohyla* (= *Rheohyla* in part; 2 species, 66.7%), and *Exerodonta* (4 species, 57.1%). The remaining 28 frog genera include several species at risk from 0 to 27 (Table 6.1). Of the four Mexican salamander families, two present high levels of species at risk: Plethodontidae (84.1%) and Ambystomatidae (58.8%). The single species of Salamandridae (*Nophtophtalmus meridionalis*) occurring in Mexico is placed in the EN category.

Evidently, certain Mexican amphibian families are showing higher rates of risk. For example, in the case of frogs, in the family Hylidae, 55 species (53.4%) are listed as either VU, EN or CR. Additionally, Hylidae is the most speciose family (103 species) of Mexican frog families and presents a widespread distribution in the country. In the case of salamanders, 116 species (84.1%) of the family Plethodontidae are also listed in one of the three IUCN categories of risk. As in the case of the Hylidae family of frogs, Plethodontidae is the most speciose (138 species) family of Mexican salamanders, and as pointed out by Frías-Alvarez et al. (2010) most of the threatened species of this family have markedly restricted distributions and occupy specific microhabitats. Such is the case in species of the genera *Thorius*, *Chiropterotriton*, and *Pseudoeurycea*, which include 27 (93.1%), 21 (91.3%), and 38 (97.4%), respectively of threatened species. Ambystomatidae, the second most speciose family of salamanders in Mexico also presents high rates of risk. *Ambystoma* is the only genus in this family, and of the 17 species occurring in Mexico, 10

Table 6.5 Number of species, number of endemic species, and number of species at global risk (CR, EN or VU) by family and genus of snakes (Squamata: Ophidia) of Mexico

Family	Genus	Species	Endemic species	Species at global risk
Loxocemidae		1	0	0
	Loxocemus	1	0	0
Boidae		5	1 (20)	1 (20)
	Boa	2	0	0
	Exiloboa	1	1 (100)	1 (100)
	Lichanura	1	0	0
	Ungaliophis	1	0	0
Colubridae		319	178 (56)	17 (5.3)
	Adelophis	2	2 (100)	1 (50)
	Adelphicos	6	3 (50)	0
	Amastridium	1	0	0
	Arizona	2	1 (50)	0
	Bogertophis	2	0	0
	Cenaspis	1	1 (100)	0
	Chersodroumus	4	4 (100)	1 (25)
	Clelia	1	0	0
	Coluber	1	0	0
	Coniophanes	13	8 (61.5)	0
	Conophis	3	1 (33.3)	0
	Conopsis	6	6 (100)	0
	Cryophis	1	1	0
	Dendrophidion	1	0	0
	Diadophis	1	0	0
	Dipsas	3	2 (66.6)	0
	Drymarchon	1	0	0
	Drymobius	2	0	0
	Enulius	2	1 (50)	0
	Ficimia	7	5 (71.4)	1 (14.2)
	Gegras	1	1 (100)	0
	Geophis	34	30 (88.2)	1 (2.9)
	Gyalopion	2	0	0
	Heterodon	1	0	0
	Hypsiglena	9	6 (66.7)	0
	Imantodes	3	1 (33.3)	0
	Lampropeltis	15	8 (53.3)	0
	Leptodeira	8	4 (50)	0
	Leptophis	4	1 (25)	1 (25)
	Manolepis	1	1 (100)	0
	Masticophis	11	4 (36.4)	1 (9.1)
	Mastigodryas	2	1 (50)	0
	Nerodia	2	0	0

(continued)

Table 6.5 (continued)

Family	Genus	Species	Endemic species	Species at global risk
	Ninia	2	0	0
	Opheodrys	2	0	0
	Oxybelis	4	0	0
	Oxyrhopus	1	0	0
	Pantherophis	2	0	0
	Phrynonax	1	0	0
	Phyllorhynchus	2	0	0
	Pituophis	4	2 (50)	0
	Pliocercus	1	0	0
	Pseudelaphe	2	1 (50)	0
	Pseudoficimia	1	1 (100)	0
	Pseudoleptodeira	1	1 (100)	0
	Rhadinaea	16	15 (93.8)	3 (18.8)
	Rhadinella	9	4 (44.4)	1 (11.1)
	Rhadinophanes	1	1	0
	Rhinocheilus	3	2 (66.7)	0
	Salvadora	9	5 (55.6)	0
	Scaphiodontophis	1	0	0
	Senticolis	1	0	0
	Sibon	4	0	0
	Sonora	13	6 (46.2)	0
	Spilotes	1	0	0
	Stenorrhina	2	1 (50)	0
	Storeria	3	2 (66.7)	1 (33.3)
	Symphimus	2	1 (50)	0
	Sympholis	1	1 (100)	0
	Tantalophis	1	1 (100)	1 (100)
	Tantilla	30	17 (56.7)	2 (6.7)
	Tantillita	3	0	0
	Thamnophis	27	18 (66.7)	3 (11.1)
	Tretanorhinus	1	0	0
	Trimorphodon	6	2 (33.3)	0
	Tropidodipsas	7	5 (71.4)	0
	Xenodon	1	0	0
Elapidae		17	9 (52.9)	1 (5.9)
	Hydrophys	1	0	1 (6.7)
	Micruroides	1	0	1 (6.7)
	Micrurus	15	9 (60)	1 (6.7)
Typhlopidae		3	0	0
	Amerotyphlops	2	0	0
	Indotyphlops	1	0	0
Leptotyphlopidae		17	11 (64.7)	0

(continued)

Table 6.5 (continued)

Family	Genus	Species	Endemic species	Species at global risk
	Epictia	7	5	0
	Rena	10	6	0
Viperidae		76	43 (56.6)	8 (10.5)
	Agkistrodon	5	1 (20)	0
	Bothriechis	4	1 20)	2 (50)
	Bothrops	1	0	0
	Cerrophidion	3	2 (66.7)	0
	Crotalus	44	28 (63.7)	6 (13.7)
	Metlapilcoatlus	5	2	0
	Mixcoatlus	4	4	2 (50)
	Ophryacus	3	3	1
	Porthidium	5	2	0
	Sistrurus	2	0	0

Percentages are presented in parenthesis

(58.8%) are listed in one of the three categories of risk of the IUCN. Additionally, 16 (94.1%) of *Ambystoma* species are endemic to Mexico. Most of endemic species of *Ambystoma* exhibit markedly restricted areas of occurrence, and some of these, such as *Ambystoma mexicanum* in Xochimilco and Lake Chalco, as well as *A. dumerilii* in Patzcuaro lake are considered as emblematic of the Mexican culture and of the Mexican fauna (Frías-Alvarez et al. 2010).

Of the 246 amphibian species known by 2008 to be Mexican endemics, 171 (69.5%) are threatened by extinction: 27 categorized as VU, 67 as EN, and 77 as CR (Frías-Alvarez et al. 2010). The same authors point out that while a high percentage of Mexican amphibian species (64.3%) are declining, only 1.1% of species are showing signs of population increment and 19.8% are seemingly stable. Analyzing population tendencies by taxonomic order, they report that 71.1% of salamander species, 60.3% of frogs, and one of three of caecilians exhibited declining demographic tendencies.

Although there is marked variation in distributional range size among different groups, reptiles in general present narrower distributional ranges than other vertebrates such as birds and mammals (Anderson and Marcus 1992). The combination of these often-small ranges and their frequent association to specific microhabitats (Raxworthy et al. 2008) makes reptiles susceptible to threats associated with human activities, and therefore they are a group of conservation concern. Information about the global conservation status of reptiles as a whole is still incomplete and of 11,570 reptile species (Uetz et al. 2021), up to 2021, 8400 (86%) have been assessed by the IUCN Red List of Threatened Species (IUCN 2021). However, regional assessments in Europe (Temple and Cox 2009) and southern Africa (Bates et al. 2014) indicate that 20% and 10% of reptile species respectively are at risk of extinction. Additionally, it has been suggested that declines of reptile populations are similar in taxonomic extent, geographic terms, and severity to those presently registered in amphibians (Gibbons et al. 2000).

Information from Reptile Database (Uetz et al. 2021) and the Red List of the IUCN (IUCN 2021) indicates that turtles are the most endangered reptile group in Mexico, with 29% of species at risk, and 31% of turtle species are either not evaluated (NE) or placed in the category of deficiency of data (DD). The turtle families with higher proportion of species at risk are three families, two of sea turtles, Cheloniidae (5 species, 100%) and Dermochelyidae (1 species, 100%) and one of freshwater turtles, Dermatemydidae (1 species, 100%), followed by Testudinidae (3 of 5 species, 60%), Chelydridae (1 of 2 species, 50%), and Emydidae (6 of 19 species, 32%). Geoemydidae (3 species), Trionychidae (2 species), and Kinosternidae (20 species) do not have species at global risk in Mexico. It is noteworthy to point out that from the 20 species of the Kinosternidae family (the most speciose of the turtle families in Mexico), 40% (8 species) are either not evaluated or placed in the data-deficient (DD) category. *Chelonia*, *Eretmochelys*, *Caretta*, Dermatemys (one species each), and *Lepidochelys* (2 species) are the genera with 100% of their species at risk, whereas the genus *Gopherus* (5 species) presents 3 species at risk (60%). Other turtle genera in Mexico range from 0% to 50% of species at risk.

Of a total of 569 lizard species registered in Mexico, 57 (10%) are at risk. It is important to consider that 54 species (9.5%) are placed in the data deficiency (DD) category and an additional 116 species (20%) have not been evaluated (NE). The lizard family in Mexico with the highest proportion of species at risk is Iguanidae (7 species, 35%). The proportions of species at risk of the most speciose lizard families in Mexico, Phrynosomatidae, Teiidae, and Anguidae are 14%, 4%, and 30%, respectively. The Anguidae stands out as a speciose lizard family (50 species in Mexico) with high endemicity (80%), and 30% of species at risk. Additionally, 44% of its species are in the data-deficient (DD) or not evaluated (NE) categories. In the case of the Xenosauridae family, it is noteworthy to indicate that of 12 species in Mexico, 11 (92%) are endemic to the country. Although only 3 species (25%) are officially at risk, 58% (7 species) are either data-deficient (DD) or not evaluated (NE). The lizard genera with higher proportion of species at risk in Mexico are *Sauromalus* (60%, 3 species), *Uta* (57%, 4 species), *Ophisaurus* (50%, 1 species), *Ctenosaura* (40%, 4 species), *Abronia* (38%, 10 species), and *Barisia* (29%, 2 species; Table 6.3).

Of a total of 439 snake species registered in Mexico, 27 (6.2%) are included in one of the three categories of risk in the IUCN Red List of threatened species. It is noteworthy to consider that 65 species (14.1%) are placed in the data deficiency (DD) category and an additional 91 species (20.1%) have not been evaluated (NE). The snake family in Mexico with the highest proportion of species at risk is Boidae (20%). However, this family is represented by only five species in Mexico, and one of these is at risk. The most speciose snake family in Mexico is Colubridae (319 species) and 17 (5.3%) are considered at risk. Nonetheless, 58 species (18.1%) in this family are placed in the data deficiency (DD) category and an additional 51 species (16%) have not been evaluated (NE). Viperidae stands out as a speciose snake family (76 species in Mexico) with high endemicity (56.6%) and 8 species (10.5%) at risk. Additionally, 39.4% of its species are in the data deficiency (DD) or not evaluated (NE) categories. Snake genera in Mexico with a high proportion of species at risk are *Botriechis* and *Mixcoatlus* (50%, 2 of 4 species each), *Adelophis*

(50%, 1 of 2 species), *Storeria* (33.3%, 1 of 3 species). *Crotalus*, the most speciose snake genus in Mexico (44 species) presents only 6 species (13.7) in one of the three IUCN risk categories (Table 6.4). However, 27 of its species (61.4%) are placed in either the category of data deficiency (DD) or have not been evaluated (NE).

6.4 Main Threats for Mexican Amphibians and Reptiles

As occurs at a global scale, the main threats facing amphibians and reptiles in Mexico are habitat loss and degradation, environmental pollution, unsustainable use (for food and the pet trade), introduced invasive species, emergent diseases, and global climate change (Gibbons et al. 2000; Köhler 2011). In the case of amphibians, Frías-Alvarez et al. (2010) consider land use change as the most important threat to Mexican amphibians (86.6% of species affected), followed by emerging infectious diseases (23.3% actual or potential species affected). According to the same authors, additional threats are pollution (20.4% of species threatened by toxic chemicals), introduced species (11% of species threatened), global change and overexploitation (9.7% of species affected by each of these threats). The rate of natural habitats conversion to agricultural and urban land in México ranges from about 200,000 to 400,000 ha/yr (Wilson et al. 2013). Loss of vegetation cover by land use changes (i.e., urbanization, agricultural activities) often results in an increase of soil temperature, isolation of subpopulations, and decrease in availability of prey, refuges, and reproduction sites (Charruau et al. 2015).

As ectotherms, various aspects of the biology, physiology, and behavior of amphibians and reptiles are modulated by ambient temperatures (Vitt and Caldwell 2014). Therefore, climate change represents a major threat. One of the most significant documentations for the effect of global warming of amphibians and reptiles comes from studies of lizards in México. Among 48 lizard species at 200 Mexican sites that were monitored since 1975, 12% of local populations were extinct by 2010 (Sinervo et al. 2010). One might expect lowland tropical herpetofauna species to present higher temperature tolerances, and therefore be less susceptible to detrimental impacts of global warming. However, many lizard species inhabiting this vegetation type live near their critical thermal maximum, consequently a relatively small change in temperature in these forests can result in an extinction cascade in lizard species (Huey et al. 2009). In amphibians, global warming can affect them directly by causing drying up of breeding microhabitats, increment in the rate of body water loss, and a decrease in availability of adequate refuges, as well as indirectly through the increment in the vulnerability to pathogens due to physiological stress caused by temperature changes in the environment (Pounds 2001). One such pathogen is the fungus *Batrachochytrium dendrobatidis* (*Bd*) causing the disease known as chytridiomycosis, a worldwide primary driver of extinction of species and populations of amphibians (Pounds 2001). This fungus was first identified in 1998 and then described in 1999; by 2004 it was globally distributed and considered a major threat for amphibian populations. It has been hypothesized that *Bd* either originated in Africa, spreading out of this continent by international trade of the African clawed frog (*Xenopus laevis*; Weldon et al. 2004) or on the Korean Peninsula and spreading also through frog trade (O'Hanlon et al. 2018). The American bullfrog (*Lithobates catesbeianus*) is a *Bd* carrier that has been reported as an exotic species in at least six Mexican states: Coahuila, Hidalgo, Nayarit, Nuevo León, Puebla, and Tamaulipas (García-Padilla et al. 2021).

As for the rest of amphibians, the main threats for salamanders are habitat loss, water pollution, dam construction, acid rain, and overharvest. Important potential threats are climate change and emerging diseases (i.e., *Batrachochytrium salamandrivorans*, *Bsal*) (Vitt and Caldwell 2014). *Bsal* has been associated with recent declines in some European salamander species and Basanta et al. (2019) consider that wildlife trade is a potential risk for the introduction of Bsal into Mexican amphibian populations.

Of the approximately 361 turtle species (Uetz et al. 2021), 69% are either extinct or threatened with extinction (IUCN 2021), making turtles the most endangered order of vertebrates. Because turtles are long-lived and present delayed maturity, harvesting of adult individuals has a marked impact on their populations (Ernst and Barbour 1989).

An increasingly common phenomenon throughout different geographical regions of the word is the conversion of natural landscapes to semi-natural landscapes, with the subsequent decline in habitat quality, reduction in size of native habitat patches, and in the connectivity among them (Fischer and Lindenmayer 2007). These processes are resulting in defaunation (extinction of individual species and functional groups) that may provoke extinction cascades throughout the food web (Fischer and Lindenmayer 2007). Despite the potential role of habitat loss and fragmentation in the decline of herpetofauna populations, there is a markedly limited knowledge on the effects of anthropogenic effects and land use changes for herpetofauna in the neotropics (Gardner et al. 2007).

The role of natural protected areas (NPAs) as a relevant strategy for the spatial conservation of biodiversity is widely acknowledged (i.e., Greve et al. 2011), including the conservation of amphibians and reptiles in Mexico (Ochoa-Ochoa et al. 2014). However, these areas are frequently located in regions where there are numerous difficulties for an adequate functioning of ANPs (Vite-Silva et al. 2010). Frequently, these difficulties are associated with agricultural development, accelerated human population growth, as well as problematic social, cultural, economic, and political conditions (i.e., poverty, illiteracy, insecurity related to drug trafficking; Urbina-Cardona 2008).

A conservation approach that combines prioritization for conservation of species and sites they occupy is the Alliance for Zero Extinction (AZE). AZE is an alliance of 94 nongovernmental organizations (NGOs) whose goal is to protect species that are likely to go extinct without immediate conservation action (AZE 2010). The alliance criteria for choosing sites and species are: (a) Endangerment – An AZE site must contain at least one Endangered (EN) or Critically Endangered (CR) species, as listed on the IUCN Red List, (b) Irreplaceability – An AZE site should only be designated if it is the only area where an EN or CR species occurs, contains the most significant known population of the EN or CR species, or contains the most significant population for one life history segment (i.e., breeding or wintering) of the EN or CR species, and (c) Discreteness – The area of an AZE site must have a definable boundary within which the characteristics of habitats, biological communities, and/or management issues have more in common with each other than they do with those of adjacent areas. Increasingly, AZE sites are recognized as critical targets for conservation and as indicators of a country's commitment to biodiversity conservation. According to Ceballos et al. (2009), AZE serves as the basis for an efficient site-level prioritization for Mexican biodiversity, a complement to other conservation strategies. Amphibians represent about 55% of the global AZE list (AZE 2010). Although Mexico ranks second to Colombia in number of threatened amphibian species (Hilton-Taylor et al. 2009), it has the highest number of AZE sites (69) and species (151). Most of Mexico's AZE species are amphibians (65%). The states of Chiapas and Oaxaca in México contain about 33% of AZE species and sites (33.7% and 28.2% respectively). These states also present the highest level of amphibian species richness (Parra-Olea et al. 2014).

The Amphibian Conservation Plan launched in 2007 by the IUCN and other conservation organizations recommends among other strategies ex situ maintenance and reproduction of highly threatened amphibian species (Gascon et al. 2007). Ex situ initiatives are frequently regarded as the last line of defense against population and species extinction. There are several relevant considerations other than threat status to be examined when selecting if a species is suitable for a conservation breeding program (CBP). Some of these considerations include species biology, level of husbandry knowledge, possibilities to obtain enough founding stock to support genetically robust populations, public and political support (Tapley et al. 2017). The IUCN has established ex situ management guidelines, underlining that ex situ initiatives should only be undertaken when the expected positive results on the conservation of the focal species outweigh the potential negative impact to local populations, species, and ecosystems, and when it will be a reasonable use of resources (IUCN Species Survival Commission 2014). Key areas of research include the development and improvement of husbandry procedures, which are frequently highly specific (Tapley et al. 2017). Amphibian Ark (AArk), the international body established to coordinate the captive breeding components of the Amphibian Conservation Plan, encourages the establishment of CBPs within range countries (Wren et al. 2015).

In this contribution, we consider axolotls and sea turtles as conservation focal groups to exemplify the survival issues facing the Mexican herpetofauna as a whole. Both biological groups are markedly susceptible to anthropogenic environmental pressures and a large proportion of their species are at global extinction risk.

6.5 Axolotls

Of a total of 765 salamander species registered worldwide (Amphibia Web 2021), 158 occur in Mexico, ranking this country as the second highest in caudates species diversity (Basanta et al. 2019). Outside of Mexico, the term axolotl is usually assigned to the axolotl from Xochimilco (*Ambystoma mexicanum*), whereas in Mexico the term axolotl (or achoque for some species) is used to designate the 17 species of the genus *Ambystoma* (Ambystomatidae family) that occur in the country. Axolotls or ambystomatids are restricted to the Western Hemisphere, from southern Canada and Alaska to the Trans-Mexican Volcanic Belt in central Mexico. From 32 known species, 17 are found in Mexico (16 are endemic to the country). The axolotl has become a model for the study of numerous investigations in different fields, especially in regeneration research. In general, axolotls as other salamanders differ from other vertebrates in the capacity to regenerate lost body parts. Salamanders can not only regenerate tails, digits, and limbs, but also about everything else, including much of the brain and heart.

Various axolotl species have been important as both alimentary and mythology elements in several cultures. Such is the case of the Mexica civilization in the Valley of Mexico. In the Nahuatl language, axólotl (the word for *A. mexicanum*) means xólotl of water, in reference to the god Xólotl. In the Aztec mythology, Xólotl is the twin brother of the god Quetzalcoatl and to avoid being sacrificed so that the sun continued its movement across the sky it took refuge in the water taking the form of an amphibious animal, the axolotl (Bartra 2011). The axolotls have been an important nutritional element in the diet of ancient and present-day Mexicans in the Valley of Mexico and in other valleys and lakes of central Mexico, and in recent times it was frequent to find axolotls in markets of Xochimilco, Toluca, Patzcuaro, Zumpango, and other small localities of central Mexico. In these markets, axolotls were offered alive, roasted or prepared as tamales (Casas et al. 2004). In the 1700s, the naturalist Antonio Alzate registered the curative properties of the axolotl and mentioned that the beverage of axolotl was helpful to treat tuberculosis and malaria. This author considered that a syrup prepared from the skin of the axolotl was an important contribution of traditional indigenous medicine (Bartra 2011). The axolotl curative syrup is still offered for sale in several localities, including Patzcuaro in the state of Michoacan.

Axolotls (*Ambystoma* species) show large life history variations, especially those related to completion of metamorphosis. Some species are obligate pedomorphs, in which sexually mature adults retain a body plan associated to aquatic larvae, including the presence of external gills and an enlarged tail fin, whereas other species are obligate metamorphs, transforming from aquatic larvae to terrestrial juveniles that eventually return to the water to breed as adults (Vitt and Caldwell 2014). Populations are frequently facultative, transforming under certain ecological conditions, and obligate pedomorphosis is estimated to have evolved multiple times in the Trans-Mexican Volcanic Belt (Everson et al. 2021).

A potential risk to Mexican salamanders is the threat that represents the chytrid fungus *Batrachochytrium salamandrivorans* (*Bsal*), which has been the cause of recent decline in some European salamander populations (García-Padilla et al. 2021). Using ecological modeling to identify areas moderately to highly susceptible for the establishment of *Bsal* with high salamander diversity as potential hotspots for surveillance, Basanta et al. (2019) detected 13 potential hotspots (in which five or more salamander species occur) for *Bsal* monitoring, including the Trans-Mexican

Volcanic Belt. These authors stated that the wildlife trade has the potential of introducing *Bsal* to naive regions in Mexico. Amphibian trade restrictions are being set in place in some countries and regions (i.e., USA, Canada, and the European Union) to limit *Bsal* distribution and Mexico should follow these measures.

In addition to the potential threat of *Bsal*, Axolotl species face a number of threats. The threats evaluated by Zambrano et al. (2003) for the Xochimico axolotl (*A. mexicanum*) are likely shared by other axolotls, especially lacustrine species. These authors consider contamination of the aquatic habitat as an important threat for the survival of *A. mexicanum*. In Xochimilco, they found high concentrations of ammonium, chlorine, and nitrates. These contaminants in addition to heavy metals, the authors state, might be causing axolotl mortality, reducing the population size of the species. Aquatic organic contamination in Xochimilco includes coliform bacteria and other infectious bacteria such as *Streptococcus*, *Pseudomonas,* and *Aeromonas*. The authors state that various axolotl diseases are associated with these bacteria. The same authors consider that aquatic exotic species constitute an additional threat. Such is the case of the carp (*Cyprinus carpio*) that besides generating drastic changes in the trophic web, likely prey upon the axolotl eggs. Other introduced fish species such as the black bass (*Micropterus salmoides*) and the tilapia (*Oreochromis niloticus*) prey upon axolotl juveniles and or the eggs. The demand for axolotls, especially for *A. mexicanum* has fueled an illegal capture and trade that according to Zambrano et al. (2003) constitutes an additional pressure for wild axolotl populations. Besides a demand for research purposes, there is an international demand for axolotls as pets, and although there are breeding centers in Mexico City for *A. mexicanum* and in Patzcuaro, Michoacan for *A. dumerili*, these authors did not find an evident efficient trade supervision and control. As a result of the synergic effect of these and other threats, these authors registered a markedly population decrease for this axolotl and suggest that all these threats especially affect the population segment of less than 1 year old. Considering these threats, Zambrano et al. (2003) provide several actions to mitigate their negative effects. These actions include among others, the establishment of a plan for exotic species eradication, especially the carp and the tilapia, the maintenance of the prohibition of axolotls' extraction from the natural systems, a continuous monitoring of axolotl populations, especially in those areas of the aquatic habitat where they have been registered so that efficient actions of vigilance and protection can be implemented to stop the illegal extraction of wild individuals. It is also urgent that government agencies fund research projects that make it possible to assess the size and current state of populations of axolotl species, as well as the health status of the aquatic habitats where they occur.

6.6 Sea Turtles

Sea turtles are emblematic species of the world's oceans, since during their migrations they cross international borders and represent the delicate relationship between human actions and the health of marine environments. These environments include mangroves, estuaries, seagrass beds, beaches, and coral reefs that have made possible the existence of all species of sea turtles (except for the flat turtle, *Natator depressus*, endemic of Australia) in Mexican coasts. Sea turtles are a classic example of a broadly distributed group that has historically suffered population declines. Six of seven sea turtle species are currently considered at global risk (IUCN 2021): *Caretta caretta*, *Lepidochelys olivacea,* and *Dermochelys coriacea* as vulnerable (VU), *Chelonia mydas* as endangered (EN), and *Eretmochelys imbricata* and *Lepidochelys kempii* as critically endangered (CR). The seventh species, the flatback turtle (*Natator depressus*) is listed as data-deficient (DD). Populations of the six threatened sea turtle species have been registered in Mexico: the Kemp's Ridley (*Lepidochelys kempii*) in the Gulf of Mexico; the olive ridley (*Lepidochelys olivacea*) in the Pacific; the green (also known as black and as white turtle) (*Chelonia mydas*) in the Gulf of Mexico, the Caribbean, and the Pacific; the loggerhead (*Caretta caretta*) in the Pacific and the Caribbean, the leatherback (*Dermochelys coriacea*) in the Pacific, and the hawksbill (*Eretmochelys imbricata*) in the Caribbean and the Pacific. Although the reasons for the decline of sea turtle populations are numerous, and vary by species and by geographical region, the main global threat has historically been the demand for meat, skin, and eggs (Alvarado and Delgado 2004).

These reptiles are part of the culture of numerous human communities, especially coastal inhabitants, as relevant nutritional, cultural, and economic elements. Because they are relatively easy to catch and they have a high proportion of meat per individual, sea turtles have represented a source of animal protein for millennia, and for their legendary longevity and fecundity, different cultures have attributed them medicinal and religious properties. Because they can be maintained alive for a long time before being consumed – an important consideration when refrigeration facilities are not available – sea turtles have historically represented an important food source. In the American continent, the earliest written evidence about the relevance of sea turtles corresponds to Mayan glyphs of about 3000 years ago (Freidel et al. 1993). The importance of sea turtles for pre-Columbian cultures in Mexico extends beyond the coastal areas. Ancient documents indicated that part of the annual tribute that coastal inhabitants offered the Aztecs of the altiplano was a large variety of marine resources, including green and hawksbill turtle shells (Frazier 2003). In the Pacific Ocean, the Comcaac ("la gente", in their language), also known as the Seri, are an indigenous community that have inhabited the northwestern coast of Mexico along the Gulf of California for more than 2000 years and have used marine turtles, especially the green turtle (*Chelonia mydas*) for hundreds of years. Besides food, sea turtles or their parts were used by the Comcaac for dwelling construction and fabrication of fishing and home utensils (McGee 1898). In addition to the adult turtle, turtle eggs have been an important component in the diet of coastal communities since pre-Columbian times. Such is the case of the Nahuas in the coast of Michoacán and the Huave in the isthmus of Tehuantepec, where the predictable arrival of nesting sea turtles allowed coastal communities to alternate harvest of corn and other crops with gathering of turtle eggs (Cliffton et al. 1982).

In modern times, industrial sea turtle fishery in Mexico occurred on the Pacific coast, beginning in the 1960s of the last century, and concentrated on the olive ridley sea turtle (*Lepidochelys olivacea*). At the beginning of that decade, with the global decline in populations of crocodiles due to the demand for their skin for the manufacture of various luxury items, wildlife traders focused their interest on alternative sources, especially sea turtle skin. Because the olive ridley was abundant along the Pacific Mexican, especially during the breeding season, this species represented an attractive option. The process of the olive ridley turtle industry concentrated on a slaughterhouse in San Agustinillo on the coast of Oaxaca. By 1968, the number of olive ridley turtles processed at that location peaked at 300,000 and populations of this species markedly declined (Cliffton et al. 1982). In 1990, the capture and marketing of sea turtles and their products were banned in Mexico. However, the illegal capture continued, especially along the Pacific coastline. Consumption of eggs and turtles continued after the 1990 ban, albeit at lower rates.

Overall, the reduction in the illegal harvest at large scale is a reflection in the success of conservation actions in Mexican nesting beaches carried out by local communities, ONGs, universities, government agencies, and private initiative (Seminoff and Wallace 2012). These conservation programs resulted in a notorious increase in some sea turtle populations in Mexico by the 2000 decade. This is the case of olive ridley populations in the Mexican pacific. Contrastingly, nesting populations of leatherback turtles in the Pacific have diminished more than 90% within the last 25 years.

Globally it is estimated that from 100,000 to 250,000, sea turtles are consumed every year, and about one million people, at least periodically, consume sea turtle meat and eggs (Frazier et al. 2007). An additional important threat is incidental capture of sea turtles in fishing operations. Yearly, about 150,000 individuals of all species drown in the nets of shrimping fleets, whereas, about 200,000 loggerheads and 150,000 leatherbacks die in long-line fishing in high seas (Frazier et al. 2007). Plastic ingestion, especially bags are the cause of death of thousands of sea turtles, especially leatherbacks. Contamination, diseases, and climate change are additional threats (Aguirre et al. 2017). Conservation is a term that is frequently used to describe the protection and maintenance of nature's components and functions. One definition of conservation is "the management of the human use of organisms and ecosystems in a sustainable way. In addition to sustainable use, conservation includes protection, maintenance, rehabilitation, restoration, and improvement of populations and ecosystems" (IUCN 1980). The IUCN definition incorporates the sustainable use as a valid component in a conservation strategy. The component of sustainable harvest of sea turtles is not accepted by all sea turtle specialists, and the idea that sea turtles can be consumed in a sustainable way has been a controversial issue within the IUCN Group of Sea Turtle Specialists (Campbell 2002).

The lack of economic alternatives for the human communities that traditionally have used the eggs, especially of the olive ridley as an income source and the perception that nesting females of this species have shown a marked increase since the 2000 year in beaches such as Escobilla, Oaxaca has resulted in the existence of social pressures to lift, at least partially, the 1990 ban (Frazier et al. 2007).

Examples of sustainable harvest of sea turtles are markedly limited and the technical and social bases to achieve a sustainable harvest of sea turtles have not been clearly defined (Campbell 2002). But even if a sustainable harvest strategy was proposed with solid scientific bases to address the main concerns about the effects on turtle populations, science cannot justify the exploitation of wild species. Science can only predict results of the options of management strategies, but how human society behaves is finally decided on ethical values. Our perception on the harvest of sea turtles is that it is not in concordance with the moral compass of most of the segments of Mexican society. The harvesting of charismatic and helpless animals, such as sea turtles is nowadays not acceptable, especially when there are alternative strategies of economic benefit for local economies, such as ecotourism centered on the sea turtles.

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Chapter 7
Mexican Freshwater Fishes in the Anthropocene

Rosa Gabriela Beltrán-López, Ana Berenice García-Andrade, and C. Patricia Ornelas-García

Contents

R. G. Beltrán-López
Colección Nacional de Peces, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Colección Ictiológica del Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, Mexico

A. B. García-Andrade
Laboratorio de Macroecología Evolutiva, Red de Biología Evolutiva, Instituto de Ecología, Xalapa, Veracruz, Mexico

C. P. Ornelas-García (✉)
Colección Nacional de Peces, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: patricia.ornelas.g@ib.unam.mx

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_7

7.1 Introduction

7.1.1 Freshwater Fishes: Diversity and Conservation Status

Fishes are the most diverse group of vertebrates of the world with 36,179 valid species (Fricke et al. 2022), in 85 orders and 536 families (Nelson et al. 2016). They inhabit virtually all aquatic habitats with a conspicuous diversity in both form and function. Thus, fishes give a unique opportunity to explore the mechanisms that have given rise to this extraordinary diversity. They correspond to 55% of the vertebrate diversity, made up of 55% marine fishes, and 45% freshwater fishes. This freshwater fish diversity is extraordinary considering that they only occupy 0.02% of the aquatic habitat (Tedesco et al. 2017). Despite this diversity, freshwater fishes have received little attention for conservation purposes (Maitland 1995), with only preliminary studies at global scales (Abell et al. 2008).

In fact, recent studies have been focused on identifying hotspots (sites of high species richness and endemism) with the intent prioritizing these sites for conservation, but only at local scales and such diverse regions as the Amazon basin (Jézéquel et al. 2020).

Nearly 83% of the land surrounding freshwater systems has been impacted by the human footprint, and during the last five decades, intense pressure has been imposed on world freshwater ecosystems and on their associated species, which has result in a drastic decline in some fish species numbers and driving some species to extinction (Arthington et al. 2016).

Among the most important threats for the fish fauna globally are: (1) habitat loss or degradation, which includes the water pollution, caused by industrial and domestic effluents (Arthington et al. 2016), eutrophication as a result of land use (farming and forestry), mining, desiccation, and fragmentation (Lyons et al. 2020), (2) changes in the hydrological regime by industrial development, roads construction, dams, canalization, water extraction, and water reservoirs, (3) overexploitation of biological resources, that is, in some cases the resources exploitation is not regulated leading to a significant decrease or extinction of populations (Castello et al. 2015), and (4) introduction of non-native species (Maitland 1995; Dudgeon et al. 2006; Dudgeon 2019), have been considered the second greatest cause of extinctions worldwide after habitat loss (Clavero and García-Berthou 2005), these introductions could be intentional for aquaculture, recreational purposes, or biological control (e.g., mosquitofish *Gambusia spp.*). In some cases, these introductions are part of government programs, where deliberate releases have occurred (e.g., tilapia, *Oreochromis* spp.). Introduced fish species can generate a variety of problems such as competition with native species, habitat alteration, hybridization, and the transfer of parasites (Strayer 2010). These threats are not independent, for example, water extraction by humans and climate change reduce the capacity of rivers to dilute pollutants, etc. (Wen et al. 2017). Even changes in the land use, such as deforestation which increases sediment runoff, pose significant threats for the freshwater diversity (Benstead et al. 2003). Thus, freshwater biodiversity is in a global crisis with freshwater fish species among the most threatened of fauna in the Anthropocene (Dudgeon et al. 2006; Reid et al. 2019).

The conservation status for the fish fauna clearly reflects this problem, where from the 22,581 species analyzed by the IUCN (2021) nearly the 20% are threatened in some way, with 3.3% as categorized as Critically Endangered, 5% as Endangered, 6.4% as Vulnerable, and 3.4% as Near Threatened. The freshwater conservation problem is clear when we analyzed the threats by habitat, thus, 46% of freshwater fish species are threatened, 50% in marine species, and 4% for diadromous species (those that spend part of their life cycle in fresh and saltwater). In the North America region, the human-caused extinction rate has increased since the 1950s, and the status of fish fauna and their habitats continues to decline, especially in arid regions of western USA and northern Mexico (Maitland 1995).

7.1.2 Freshwater Ecosystems in Mexico

Mexico has 37 major river basins, and about 14,000 man-made reservoirs (Lyons et al. 2020). According to the National Water Commission (CONAGUA 2014), the Mexican organization in charge of national water management, the Rivers in Mexico form a 633,000 km-long hydrographic network. The seven most important rivers are Grijalva-Usumacinta, Papaloapan, Panuco, Coatzacoalcos, Balsas, Lerma-Santiago, and Tonala, which capture 65% of the total surface runoff (Miller et al. 2005; Lara-Lara et al. 2008). However, there is an unequal distribution of hydrological resources, thus, basins located at the northern part of the country comprise 45% of the territory but receive only 27% of the total precipitation. Whereas, basins located in the southern part comprise 28% of the territory but receive an average of 49% of the total rainfall. This inequality in precipitation, together with the reduction in rainfall due to climate change, has exacerbated the negative balance of hydrological resources in the arid zones, increasing the desertification processes in the northern part of the country (Sec. 4.1 in this volume).

The conservation status of freshwater systems in Mexico is critical, since there is strong pressure on water resources associated with human activity. It has been shown that by the year 2025, 55% of the territory will have significant water shortages. This combined with evidence that there is a clear human impact on the present water bodies since 73% show some degree of pollution (Balvanera et al. 2009). Present demand for water resources is: 75.7% agricultural, 14.6% public demand, 5.5% power generation, and 4.1% for industry (MEA 2005; Lira-Noriega et al. 2015; SEMARNAT 2016; CONAGUA 2018). Despite the relevance of this important resource, there are few examples of comprehensive analyses that allow the establishment of conservation and management strategies at the national level of freshwater ecosystems (Lira-Noriega et al. 2015).

Water availability represents an important challenge for our near future, considering both population growth rates and density in urban areas (He et al. 2021). Water extraction represents a major concern for Mexican hydrological systems, since in

2007 it was estimated that 79 cubic kilometers of water were extracted from rivers, lakes, and aquifers annually to supply the major human demands, this amount represents 17% of the total available water in Mexico (SEMARNAT 2008). Since 1970, the number of overexploited aquifers have been increasing, with 32 in 1975 to 104 in 2006. These overexploited aquifers are concentrated in Baja California, Sonora, Durango and Chihuahua basins, Bravo River, and Lerma-Santiago basin (CONAGUA 2007). Pollution is another factor affecting Mexican hydrological systems, particularly the discharge of domestic, industrial, agricultural, and livestock wastewater, generally directly discharged into rivers with no treatment, and whose main pollutants include nutrients (e.g., Nitrogen and Phosphorus), pathogens (bacteria and viruses), biodegradable organic matter, heavy metals, synthetic organic chemicals, hormones, and pharmaceutical products, among others (Silk and Ciruna 2004). For Mexico in 2012, the treated municipal flow was of 43.4%, while that the treated industrial flow was of 28.8% (CONAGUA 2014). The volume of urban wastewater has increased with the growth of the population and urbanization. Between 1998 and 2007, the human discharge increased from 239 to 243 cubic meters per second (SEMARNAT 2008). According to the surface water monitoring system, contamination by biological contaminants is found in areas with high population density, particularly in central Mexico (Mora et al. 2021). A total of 89% of the discharge of pollutants in the country impacts 20 basins, in which 93% of the population and 72% of industrial production are concentrated. The Bravo, Panuco, Lerma-Santiago, San Juan and Balsas basins receive 50% of the nation's wastewater discharges (CONAGUA 2016).

In summary, Mexico suffers from many of the globally common problems associated with unsustainable human development, including freshwater overexploitation, pollution, and habitat loss (OCDE 1998; Lira-Noriega et al. 2015; INEGI 2000). Natural system modification, including the development of hydraulic and hydropower infrastructure, and extraction of groundwater for domestic, industrial, and agricultural activities are some threats for freshwater fishes of Mexico (Lyons et al. 2020). Such changes often have profound consequences on freshwater habitat availability, sustainability, water quality, and on species conservation (Olden and Poff 2005).

7.1.3 Mexican Freshwater Fauna

Freshwater fishes distributed in Mexico show a high level of local and regional endemism due to the great physiographic and climatic diversity (Miller et al. 2005). With more than 600 species described of which 264 are endemic (43%) in 48 families, Mexico harbors half of the total freshwater diversity of North America (Contreras-MacBeath et al. 2014; Warren and Burr 2014). The 90% of these fish species are clustered in seven orders Cyprinodontiformes (193 species), Perciformes and Cichliformes (124), Cypriniformes (105), Atheriniformes (42), Siluriformes (34), and Characiformes (10; Miller et al. 2005).

Moreover, 124 species (23.3%) have a restricted distribution with 67% of these from only five families: Poeciliidae (19 species), Atherinopsidae (16), Cyprinodontidae (12), Leuciscidae (11), and Goodeidae (9; Contreras-MacBeath et al. 2014). At the species level, 57% of Mexican freshwater fish should be considered as rare based on the distribution of less than 50,000 km^2 criterion employed by International Union for Conservation of Nature (IUCN; Contreras-MacBeath et al. 2014).

Different criteria have been proposed to delimit the faunal regions according to the diversity of the ichthyofauna in Mexico (Miller et al. 2005; Abell et al. 2008; Lira-Noriega et al. 2015). One of the most used is the one proposed by Miller et al. (2005), who distinguishes eight provinces: Bravo River, Northwest Pacific, Baja California Peninsula, Tamesi-Panuco complex, Mesa Central, Balsas River, Chiapas-Nicaraguan province, and Usumacinta province. Accordingly with Contreras-MacBeath et al. (2014) and our richness map (Fig. 7.1a) reconstructed based on the species' ranges from Carvajal-Quintero et al. (2019) and García-Andrade et al. (2021), the regions of highest richness are: (1) the Usumacinta province in the south-eastern Mexico, (2) the Mesa Central in the highlands of Trans Mexican Volcanic Belt, and (3) the Bravo River in Northern Mexico along the border with the United States. (1) The Usumacinta province, which included Coatzacoalcos, Papaloapan, and Grijalva – Usumacinta basins, present 44 families and 249 species, of which Poeciliidae and Cichlidae families are the predominant (Contreras-MAcBeath et al. 2014). In this hotspot, there are two extinct species from the Manalapan River: *Atherinella callida* and *Priapella bonita* (Harrison and Stiassny 1999). (2) The Mesa Central, which includes the Lerma-Santiago basin, we can find 23 families and 103 species, which resulted from the confluence of Neotropical and Nearctic fauna (Miller et al. 2005; Contreras-MacBeath et al. 2014). Among the groups with the greatest diversity and endemism are the viviparous fishes of the Goodeidae family (Doadrio and Domínguez 2004; Webb et al. 2004), and the "silversides" from the Atherinopsidae, being an example of species flock (group of closely related species all living in the same ecosystem) as a result of trophic and habitat diversification (Barbour 1973; Betancourt-Resendes et al. 2018; Betancourt-Resendes et al. 2019). Finally, (3) the Bravo River, with 30 families and 119 species, of which the most diverse families are Cyprinidae, Poeciliidae, and Cyprinodontidae.

7.1.4 *Human Impacts and Conservation Status of Mexican Freshwater Fauna*

The human impact on the Mexican freshwater fish fauna and its environments has been latent since the first settlements in the territory. An example of this ancient effect was proposed by Corona-Santiago et al. 2015, which based on molecular evidence showed a translocation followed by a founder effect in the species *Allotoca catarinae*, by the pre-Hispanic settlements of the P'urhépecha culture around

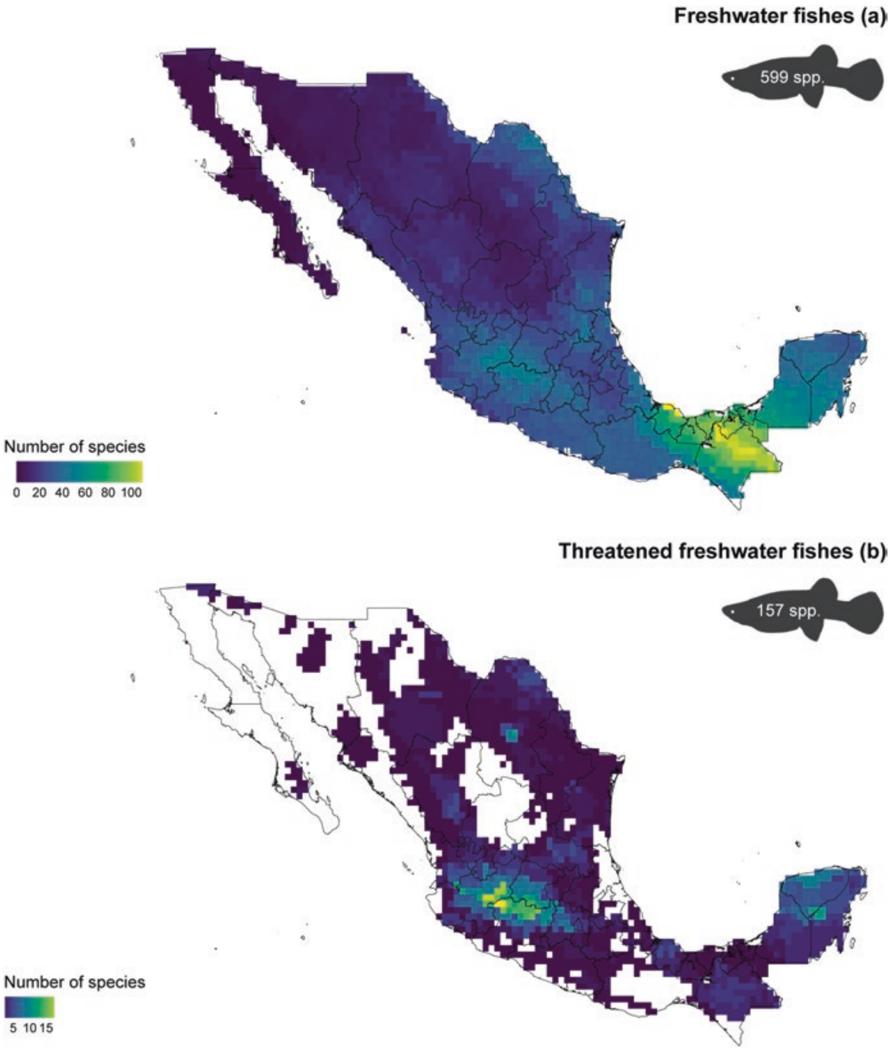

Fig. 7.1 Species richness of freshwater fishes in Mexico (**a**) as well as threatened species (**b**), both maps are in a grid cell resolution of 0.25 grades (~28 km at the Equator). Richness maps were reconstructed based on the species' ranges from Carvajal-Quintero et al. (2019) and García-Andrade et al. (2021), and the threatened status (vulnerable, endangered, critically endangered) from the IUCN (2021). Fish silhouettes represent *Gambusia* sp. from PhyloPic (phylopic.org)

1900 years ago. Currently, through the analysis of fish assemblages, we have been able to evaluate the effect of human impact in the freshwater species (e.g., Díaz-Pardo et al. 1993; Soto-Galera et al. 1998; Lyons et al. 1998; Lyons et al. 2020; Mercado-Silva et al. 2006), its distribution patterns (e.g., Contreras-MacBeath et al. 2014; Lyons et al. 2019), genetic diversity and structure (e.g., Bailey et al. 2007; Domínguez-Domínguez et al. 2008; Ornelas-García et al. 2012; Terán-Martínez et al. 2021; Beltrán-López et al. 2018, 2021), and through the evaluation of conservation status of the ichthyofauna (e.g., Ceballos et al. 2017; Lyons et al. 2020).

Recently 536 freshwater fish species were assessed for their conservation status (Lyons et al. 2020), where 165 were classified as some category of threat or extinct in the wild (Table 7.1; Figs. 7.1b and 7.2), representing 39.9% of all species assessed (Lyons et al. 2020). Of all assessed species, 12 were considered extinct in the wild, 44 critically endangered, 71 endangered, 50 vulnerable, 18 near threatened, and 234 as least concern according with the red list of the IUCN (IUCN 2021), while for the Mexican legislation (NOM-059-SEMARNAT; SEMARNAT 2010), 204 species are included under some category of risk, 13 species are considered as probably extinct, 81 threatened, 80 endangered, and 30 subject to special protection (Table 7.1; Fig. 7.2). Among the 48 Mexican freshwater fish families, the largest and most threatened are: Goodeidae (83%), Cyprinodontidae (48%), Atherinopsidae (45%), and Leuciscidae (40%; Contreras-MacBeath et al. 2014). The major threats identified by IUCN for these freshwater fishes were: (1) natural system modification by hydraulic and hydropower infrastructure, (2) groundwater extraction for domestic, industrial, and agricultural purposes, (3) pollution, by agriculture, forestry, domestic, and urban wastewater, and (4) the introduction, establishment, and spread of non-native species (Lyons et al. 2020). The latter represents an important threat for freshwater fauna, since five of the ten most widely distributed freshwater fishes of Mexico are exotics (Table 7.2; Gozlan et al. 2010; Contreras-MacBeath et al. 2014). Together, these impacts threaten nearly half (45%) of all freshwater fishes in Mexico (Lyons et al. 2020).

Table 7.1 Conservation status of the freshwater fauna in México based on the IUCN and the NOM-059-SEMARNAT evaluations

IUCN red list category	Number of species	NOM-059-SEMARNAT	Number of species
Extinct (EX)	12	Probably extinct (E)	13
Extinct in the wild (EW)	8	Threat (P)	81
Critically endangered (CR)	44		
Endangered (EN)	71	Endangered (A)	80
Vulnerable (VU)	50		
Near threatened (NT)	18	Subject to special protection (PR)	30
Least concern (LC)	234		
Data deficient (DD)	99		
Total species	536	**Total species**	204

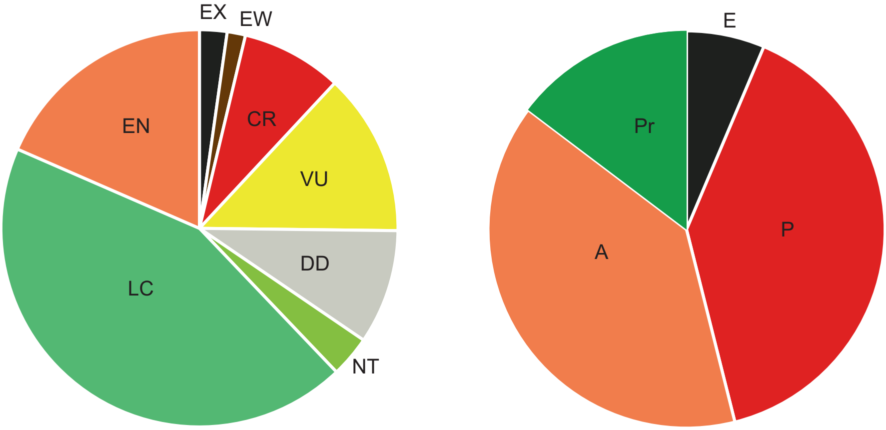

Fig. 7.2 Percentage (%) of each risk category for Mexican freshwater fishes, to the left risk categories according with the categories of the Red List of the IUCN; EX (Extinct), EW (Extinct in the wild), CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Near Threatened), LC (Least Concern), and DD (Data Deficient), to the right risk categories according to the NOM-059-SEMARNAT; E (Probably Extinct), A (Threat), P (Endangered), and Pr (Subject to Special Protection)

Table 7.2 Some introduced species reported in México

	Exotic species of Mexico	Family	Biogeographic origin	Origin
1	*Cyprinus carpio*	Cyprinidae	Eurasia	Exotic
2	*Carassius auratus*	Cyprinidae	Eurasia	Exotic
3	*Ctenopharyngodon idella*	Cyprinidae	China and Tailandia	Exotic
4	*Ictalurus punctatus*	Ictaluridae	Canada, United States of America and Mexico	Translocated
5	*Pterygoplichthys pardalis*	Loricariidae	South America	Exotic
6	*Pterygoplichthys disjunctivus*	Loricariidae	South America	Exotic
7	*Poeciliopsis gracilis*	Poeciliidae	Gulf of Mexico	Translocated
8	*Pseudoxiphophorus bimaculatus*	Poeciliidae	Gulf of Mexico	Translocated
9	*Poecilia reticulata*	Poeciliidae	Antillas and South America	Exotic
10	*Oreochromis aureus*	Cichlidae	Tropical, subtropical Africa, and Middle East	Exotic
11	*Oreochromis mossambicus*	Cichlidae	East Africa	Exotic
12	*Tilapia rendalli*	Cichlidae	Africa	Exotic
13	*Tilapia zillii*	Cichlidae	African and Middle East	Exotic
14	*Oreochromis niloticus*	Cichlidae	Africa	Exotic
15	*Amatitlania nigrofasciata*	Cichlidae	Central America	Exotic

Several endemic species are at some risk category according to the IUCN and/or NOM-059 (SEMARNAT 2010; Lyons et al. 2020) and are distributed in one of the three provinces with the highest species richness in Mexico: Usumacinta, Mesa Central, and Bravo River provinces (Fig. 7.1b). Indeed, these three provinces, are contrasting due to several factors of climate, precipitation, and anthropogenic activities, thus, threats for the ichthyofauna and the level of human impact could have distinct effects on the conservation status of freshwater fishes.

7.2 Case Study

7.2.1 *Evaluation of the Human Footprint in Three Freshwater Ecoregions*

In the present evaluation, we selected the three basins that are situated in the most diverse provinces of Mexico: (1) Cuatro Cienegas basin which is in the Bravo River province, (2) Lerma River basin which is in the Mesa Central province, and (3) Grijalva River basin which is in the Usumacinta province (Fig. 7.3). We provide a comprehensive analysis that included species richness and conservation status of freshwater fishes obtained in the last IUCN evaluation (IUCN 2021) for these ecoregions and used a recently developed layer of human footprint in Mexico (González-Abraham et al. 2015) to determine the percent of anthropogenic degradation in each basin as well as the vulnerability of fish species. These basins have representative climate and geographic conditions of the great variety of climates in our country. In addition, each of them is under a distinct level of impact of the human footprint.

7.2.2 *Case Study Ecoregions*

The Grijalva River immersed in the Usumacinta province includes all its tributaries in Mexico, from the upper headwaters until the lowlands in the Gulf of Mexico at the river's mouth, it is immersed in Central-southeastern hotspot proposed by Contreras-MacBeath et al. (2014), with the highest availability of water in Mexico and together with the Usumacinta basin present the highest species richness (Contreras-MacBeath et al. 2014; Lyons et al. 2020). Despite their diversity, this region represents one of the least studied in the country, which is evident in the latest IUCN report where several species have deficient data (Lyons et al. 2020). Despite this basin presents relatively low levels of pollution (Contreras-MacBeath et al. 2014), one of the major concerns is a large-scale conversion of forest to agriculture, that has intensified sediment runoff. In addition, the hydrological regime modifications have occurred due to the dam construction in this basin, including one of the largest dams in the Country, Falcon Dam (Miller et al. 2005). Further impacts

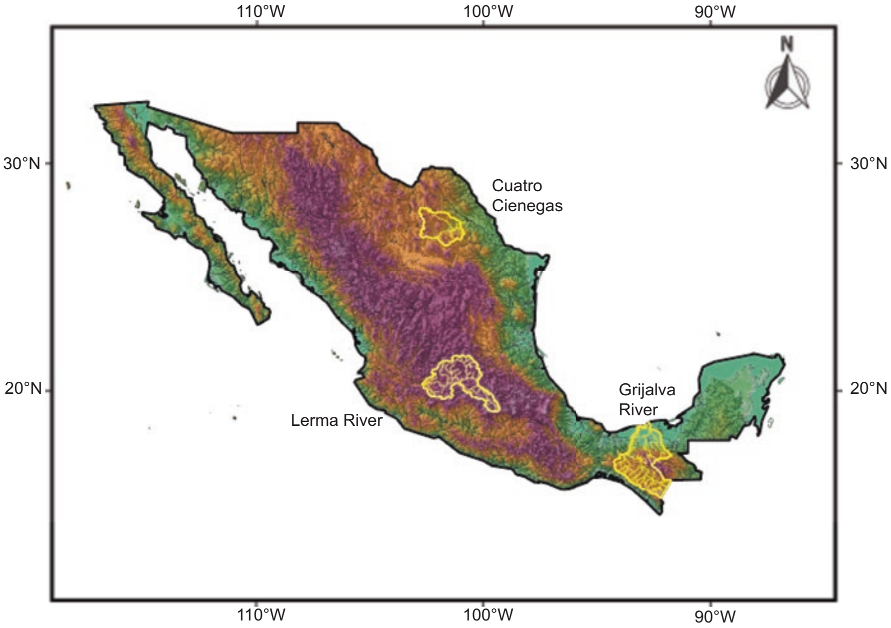

Fig. 7.3 Geographic position of ecoregions (basins) studied across Mexico

are derived from industry, particularly oil and natural gas extraction, evidence by the records of heavy metals identified along the Grijalva River, as arsenic (As) and mercury (Hg; Alvarado-Arcia et al. 2014; Musalem-Castillejos et al. 2018), which are threats to the freshwater fauna.

Within the Mesa Central, the Lerma-Santiago basin presents a great ichthyological diversity, being unique in the number of endemism present, with about 70% of its ichthyofauna classified as endemic (Lyons et al. 1998; Contreras-MacBeath et al. 2014). The Lerma River basin occupies an area of 53,500 km^2, and runs from Mexico City to Guadalajara (Fig. 7.3), this basin includes 700 km of the Lerma River basin that drains into Lake Chapala, and its tributaries, in addition to endorheic basins such as Lake Zirahuen, Lake Patzcuaro, and Cuitzeo Lake, later to join with the Morelia River (Lyons et al. 1998). However, for the present study the Lerma River basin was delimited as the Upper, Middle, and Lower Lerma regions (sensu Domínguez-Domínguez et al. 2006), but not included the endorheic basins of Cuitzeo, Patzcuaro, and Zirahuen. Along the course of this basin, we find the largest cities in Mexico, which makes the watershed with the highest population density in the country, and whose density continues to increase (Guzmán-Arroyo 1990; Lyons et al. 1998; González-Abraham et al. 2015) for which, unfortunately, the fish diversity of Lerma River basin has been strongly affected by pollution, which has led to the extinction of several species and a strong reduction of others (Lyons et al. 1998). In addition, there is a strong pressure on the Lerma-Santiago basin associated with the extraction of water for irrigation, industry, and human consumption. The most vulnerable of the freshwater ecosystems are the springs or small rivers which have been overexploited or have been transformed for exploitation for human development. Of the sites that have been evaluated in this River, about 50% no longer have fish and only 17% of the sites maintain sensitive species to environmental degradation (Lyons et al. 1998). In a long-term study (Mercado-Silva et al. 2006) in this River demonstrates that not only the native sensitive species have declined in the last 50 years but, carnivorous species have decreased, while exotic and tolerant species have increased, showing changes not only in composition but also in functional groups.

Finally, Cuatro Cienegas basin is immersed in the ichthyofaunistic province of North Mesa (Bravo River), which is an endorheic small basin of 1500 km^2 in the Coahuila desert that has the greatest number of endemic species of any plain in North America (Stein et al. 2000), also included the upper tributaries of the Salado River. This basin has about 70 endemic species, 25% of which are freshwater fishes (Espinosa-Pérez and Lambarri-Martínez 2019). This region was considered as a center of endemism for fishes of Mexico by Contreras-MacBeath et al. (2014). This biotic diversity is associated with a complex array of thousands of isolated geothermal springs, marshes, lakes, and streams (Souza et al. 2006), with fish fauna from both Neartic (e.g., Leuciscidae and Ictaluridae) and Neotropical regions (e.g., Characidae and Cichlidae). However, this exceptional biodiversity is critically endangered due to the desertification process which has been exacerbated by the human demands of the hydric resources. Particularly, the continuous extraction by artificial channels for agricultural purposes has directly affected the freshwater fauna of Cuatro Cienegas basin (WWF 2012; Carson et al. 2013). Additionally, it has been documented that since 1996, the introduction of the exotic species known as the jewelfish, *Hemichromis guttatus* (Contreras-Balderas and Ludlow 2003), has displaced native species such as *Cyprinodon bifasciatus* in some pools of Cuatro Cienegas basin (Espinosa-Pérez and Lambarri-Martínez 2019). Moreover, the artificial channels have put in contact species from outside of the valley, particularly from the Salado River, which has resulted in hybridization, an example of this has been reported between Minckley's cichlid *Herichthys minckleyi* and Texas cichlid *H. cyanoguttatus* (Magalhaes et al. 2015; Ornelas-García et al. 2018). The natural and human-induced desiccations of the system have affected not only the diversity but the species habits, migrating from ephemeral to permanent springs whose temperatures and conditions could act as environmental filters and limit species survival. These desiccation effects have been documented since 1984, where several studies have documented the deterioration and habitat loss in the area (Minckley 1984; WWF 2012; Carson et al. 2013; Espinosa-Pérez and Lambarri-Martínez 2019).

7.2.3 Freshwater Fish Diversity and Conservation Status

We delimited each region accordingly with the ecoregions' limits and considering the composition and distribution of the ichthyofauna. To characterize the species richness in each basin, we determined the species list according to the global database on freshwater fish species occurrence in drainage basins (Tedesco et al. 2017). This list was curated to keep the native and valid species, and we added missing species that were not reported in this initial list following data from published literature. Scientific names and synonyms were validated using "rfishbase" v.1904 (Boettiger et al. 2012). Then, species occurrences were downloaded from GBIF through the R package "rgbif" (Chamberlain et al. 2022). Occurrences were spatially filtered using basin polygons to determine the number of species distributed in the basin. Finally, species richness was determined as the number of species present in each basin. Then, detailed species richness was mapped across each onto a grid cells of 0.1°of resolution (~11.1 km at Equator), using the function lets.presab.points from the R package "letsR" (Vilela and Villalobos 2015) that generates a richness map and a presence-absence matrix.

We determined the number of species threatened and the knowledge gap about the species risk using the red list classification accessed through the R package "rredlist" (Chamberlain 2020). Accordingly, species are evaluated by experts who determine if the information about species is complete and assign a status based on it. So, species that have abundant populations are classified as least concern (LC) which means that they are not threatened, but if they could be at risk in the near future are classified as near threatened (NT). In addition, threatened species are classified into three categories depending on the level of risk in which they are: vulnerable (VU), endangered (EN), and critically endangered (CR). Species that are extinct in their natural habitats but survive in captivity are assigned as extinct in the wild (EW), and as extinct (EX) if they have not been seen in nature for a long time and neither have survived in captivity. Experts assigned species that have not been determined their threatened status because they do not have enough information as data deficient (DD). Species that have not been evaluated by the IUCN experts and have not appeared in the red list, were assigned as not evaluated (NE). We used these last two categories (DD and NE) to determine the number of species with an unknown risk status. Finally, to distinguish the vulnerability of fish assemblages, we mapped the threatened freshwater fishes (VU, EN, CR).

7.2.4 Human Footprint and Freshwater Fishes' Vulnerability

As a proxy of human impact, we used the human footprint layer that was recently developed for Mexico (González-Abraham et al. 2015), which is an index that covers from zero meaning no transformation changes, to ten that means full human modification. In short, to estimate this human footprint index the authors considered and scored variables related to anthropogenic modification such as population density, land use, and land cover. This index considers urban areas as the highest transformation level by intensity and extension. Human footprint layer was rasterized at a grid cell resolution of 0.1 grades to fit with species richness maps using the "sf" (Pebesma 2018) and "raster" (Hijmans 2015) R packages.

Then, we calculated the level of modification as the percent of human transformed area in each basin. In addition, we computed the percent of grid cells with fish occurrences and threatened fish occurrences that are in degraded sites. Thus, these estimations will provide an overview about the vulnerability and risk level of freshwater fish assemblages in Cuatro Cienegas, Lerma River and Grijalva River basins which are representative basins of Mexico.

7.2.5 Results and Discussion

7.2.5.1 Freshwater Fish Diversity

Grijalva River basin had the highest diversity with 92 freshwater fish species, 59 genera, and 26 families of freshwater fishes (Table 7.3). The most diverse families were Cichlidae and Poeciliidae with 24 and 21 species, respectively. Lerma River basin was the second most diverse with 33 species arranged in 18 genera and seven families, in which the pervasive family was Goodeidae with seven species. Finally, Cuatro Cienegas basin had the least diversity with 28 species, 15 genera, and 10 families, the most diverse was Leuciscidae with eight species (Table 7.3). Overall, Grijalva River basin had the highest number of species as well as the highest taxonomic diversity covering 17 orders of fishes, compared with the seven orders present in Cuatro Cienegas basin and the five of Lerma River basin.

7.2.5.2 Conservation Status and Extinction Risk of the Ecoregions

Regarding the species conservation status, in Cuatro Cienegas basin most of the species have a low risk of extinction classified as LC (11; 39.3%), whereas 12 species (42.9%) are in a threatened category such as VU, EN, and CR. Besides, in this

Table 7.3 Ichthyofauna diversity per basin, orders, families, genera, and species

Taxonomic level/drainage basin	Cuatro Cienegas basin	Grijalva River basin	Lerma River basin
Orders	7	17	5
Families	10	26	7
Genera	15	59	18
Species	28	92	33

region four species (14.3%) have not been evaluated or there is not enough data to be classified (Figs. 7.4a, b). Cuatro Cienegas basin has two cyprinids from the family Leuciscidae that have been reported as extinct (*Notropis orca* and *Nootropics saladonis*). The Grijalva River basin had the least number of threatened ichthyofauna as well as the greatest fish diversity (Fig. 7.4), with the highest number of species classified as LC and NT (56 spp., and 59.8% respectively), and only five species (5.4%) are considered as VU, EN or CR in the Grijalva River basin. However, this basin also had the highest level of uncertainty about the risk of extinction with the highest number of data-deficient species (22 spp., 23.9%) and species that were not evaluated (9 spp. 9.8%). In the Lerma River basin, most of the species (21 spp., 63.6%) are threatened, being classified as VU, EN, or CR. Only five species (15.2%) have a low risk of extinction (LC), while for seven species (21.2%), data are deficient or have not been evaluated, thus, their risk status is unknown (Fig. 7.4).

Species threatened within each basin belong to distinct or common fish orders and families according with the composition of the ichthyofauna, but each of these 38 species represent an endemism to at the species and/or genus level in their respective basin (Table 7.4). For instance, in Cuatro Cienegas the endemic Minckley's cichlid (*Herichthys minckleyi*) is endangered, similarly, in the Grijalva River basin the endemic Tailbar cichlid (*Vieja hartwegi*) is also endangered (Rodiles-Hernández and González-Díaz 2006). Although both species belong to the Cichlidae family, they are also members of a distinct genus, so they represent a distinct lineage.

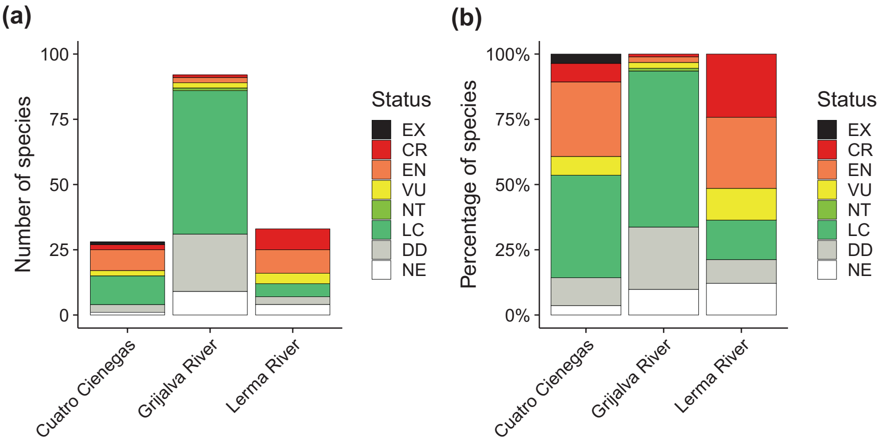

Fig. 7.4 Species' threatened status in each basin, according to the IUCN Red of threatened species. Number of species in each threatened category (**a**), and percentage of them per basin (**b**). Status, EX Extinct, CR Critically endangered, EN Endangered, VU Vulnerable, NT Near threatened, LC Least concern, DD Data deficient, NE Not evaluated

7.2.5.3 Fish Assemblage Vulnerability

Human modification included all changes in habitats, and ecosystems exploited to cover the human population's needs. Cuatro Cienegas was the smallest basin evaluated here and also the one with the lowest percentage of human modification. However, 46.88% percent of the occurrences of native fish occurrences and 18.75% of those for threatened fishes were in sites with a level of degradation (Table 7.5, Figs. 7.5a–c). For the Grijalva and Lerma River basins (Fig. 7.5), these had similar areas and percentages of area with human modification (Table 7.5). Nevertheless, fishes in Lerma River basin (Figs. 7.5g–i) had a higher level of vulnerability than Grijalva' fishes (Figs. 7.5d–f), because 92.0% of fish occurrences and 72.67% of the threatened fish occurrences are in human modified sites, versus 72.2% and 19.11% in the Grijalva River basin, respectively (Table 7.5). Finally, despite that the percent of modified area in Grijalva River and Lerma River basins was similar, in the Lerma River basin there were a greater number of observed grid-cells with high and very high human footprint than in the Grijalva, which indicates that the former has a greater human footprint.

Table 7.4 Threatened species and their taxonomic classification as well as their risk status by IUCN

Drainage basin	Order	Family	Species	Threatened status
Cuatro Cienegas Valley	Cichliformes	Cichlidae	*Herichthys minckleyi*	EN
	Cypriniformes	Leuciscidae	*Cyprinella xanthicara*	EN
			Dionda diaboli	EN
	Cyprinodontiformes	Cyprinodontidae	*Cyprinodon atrorus*	EN
			Cyprinodon bifasciatus	EN
		Fundulidae	*Lucania interioris*	EN
			Gambusia gaigei	VU
			Gambusia longispinis	EN
			Xiphophorus gordoni	EN
	Perciformes	Percidae	*Etheostoma grahami*	VU
			Etheostoma lugoi	CR
			Etheostoma segrex	CR
Grijalva River	Cichliformes	Cichlidae	*Chiapaheros grammodes*	VU
			Vieja hartwegi	EN
	Cyprinodontiformes	Poeciliidae	*Gambusia eurystoma*	CR
			Poecilia sulphuraria	EN
	Siluriformes	Heptapteridae	*Rhamdia laluchensis*	VU

(continued)

Table 7.4 (continued)

Drainage basin	Order	Family	Species	Threatened status
Lerma River	Atheriniformes	Atherinopsidae	*Chirostoma aculeatum*	CR
			Chirostoma bartoni	CR
			Chirostoma humboldtianum	VU
			Chirostoma lucius	EN
			Chirostoma riojai	CR
	Cypriniformes	Leuciscidae	*Algansea barbata*	CR
			Notropis calientis	CR
			Notropis grandis	EN
			Notropis marhabatiensis	CR
			Yuriria alta	EN
	Cyprinodontiformes	Goodeidae	*Alloophorus robustus*	VU
			Allotoca dugesii	EN
			Chapalichthys encaustus	VU
			Girardinichthys multiradiatus	EN
			Hubbsina turneri	CR
			Skiffia lermae	EN
			Skiffia multipunctata	EN
			Zoogoneticus purhepechus	VU
			Zoogoneticus quitzeoensis	EN
	Petromyzontiformes	Petromyzontidae	*Tetrapleurodon geminis*	EN
			Tetrapleurodon spadiceus	CR

Threatened status
EX extinct, *CR* critically endangered, *EN* endangered, *VU* vulnerable

7.2.5.4 Case Study Conclusions

In summary, the Mexican freshwater fishes during the last 50 years have been experienced an increased trend in the extinction risk (Lyons et al. 2020). For the three regions analyzed in the present evaluation, the percentage of human impact sensu (González-Abraham et al. 2015) is significant; however, we should consider that the human impact has increased over time, and currently these percentages should be even greater than those obtained several years ago. Moreover, the three regions analyzed in the present chapter, all showed high percentage of fish occurrence in sites with human modification, for Cuatro Cienegas basin the results are alarming considering the high levels of diversity and endemism for this region, even for Cuatro Cienegas basin which is considered as a Natural Protected Area, nearly 50% of fish-bearing sites have some level of human impact (Table 7.5; Fig. 7.5).

Our results agreed with previous studies that suggest that Lerma River basin is one of the most human impacted basins in Mexico and has the highest number of threatened species, but is also the region with highest endemism. Nevertheless, we have to point out that the data included in this study cover historical and current fish occurrences in these regions, thus, the scenery for the ichthyofauna in highly human modified regions such as the Lerma River basin could be worse than the findings presented here, if we considered only the current fish occurrences. The increase of human impact over time, specifically in the last years is worrying, strongly indicating that urgent actions are required to preserve the freshwater diversity of this basin (Lyons et al. 2020).

The Grijalva River basin showed the highest levels of biodiversity but also was the region with less available information, future actions for conservation require reinforcement of our knowledge of this basin, since we could lose much of this diversity before even knowing it.

Finally, the influence of introduced species was not included in this evaluation, but previous studies have confirmed the progressive decline of native freshwater fishes due to the detrimental impact of exotics (Gesundheit and Macías García 2018); therefore, further studies considering the interaction between habitat deterioration and exotic species could give a more realistic view about the threats for the freshwater fish fauna.

Table 7.5 Percentage of area with human modification (human footprint sensu González-Abraham et al. 2015) in the Cuatro Cienegas Basin, Grijalva River, and Lerma River basins, as well as the percentage of fish occurrences and threatened fishes (IUCN: Vulnerable, endangered, critically endangered) that are in sites with human modification

Drainage basin	Area (km^2)	Human modification (%)	Fish occurrences in sites with human modification (%)	Threatened fish occurrences in sites with human modification (%)
Cuatro Cienegas	~22,516.05	16.18	46.88	18.75
Grijalva River	~50,778.63	36.12	70.22	19.11
Lerma River	~42,308.23	36.00	92.00	72.67

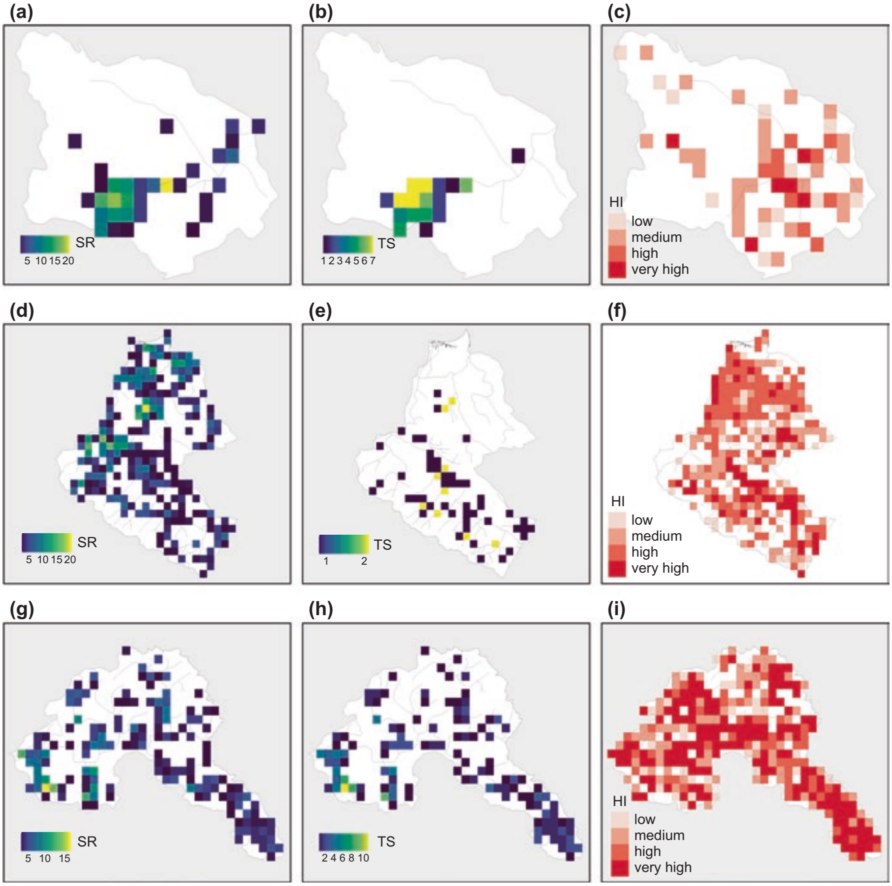

Fig. 7.5 Patterns of species richness (SR), threatened species (TS), as well as human footprint index (HI; González-Abraham et al. 2015) across the Cuatro Cienegas valley (**a–c**), the Grijalva River basin (**d–f**), and the Lerma River basin (**g–i**), respectively. Maps are at a resolution of 0.1 degrees (~11.1 km at Equator)

7.3 General Conclusions

7.3.1 Research Gaps of the Studied Regions

Approximately 18.5% of freshwater fishes of Mexico are data deficient (Lyons et al. 2020). In the above evaluation, it is important to note that for the comparisons among the three analyzed basins, the most diverse and least studied basin, the Grijalva River basin, revealed that most of its species were data deficient (Fig. 7.4). This is an example of the significant knowledge gap that exists for Mexican fishes that must be urgently addressed. We proposed that for future conservation efforts, a complete catalog of freshwater fishes of Mexico is needed with National and International cooperation. In addition, there is a need for the continuous monitoring of fish populations, at least in the most vulnerable regions. Before implementing a conservation program directed at freshwater fishes or aquatic habitats in general, it is necessary to fill the gap of diversity knowledge and species distribution, especially in those regions for which the studies are scarce, such as Grijalva River basin.

7.3.2 Conservation Recommendations

It has been recognized that the threat of freshwater fish extinction in Mexico is comparable to other biodiversity hotspots around the world (e.g., Madagascar and the Indian Ocean Islands; Máiz-Tomé et al. 2018). Based on our results, a challenge for a conservation strategy is our level of knowledge of the species diversity, and distribution, as well as its threatening factors, particularly at some regions where the many species have unknown conservation status. Moreover, we suggest establishing a continuous monitoring network, at those sites where there is a larger vulnerability due to significant human footprints that could threaten the continuity of fish communities. The proxy applied in this chapter could be used as one of many valuable criteria to prioritize those regions that present high species richness, high number of threatened species, and that may be more vulnerable due to human activities.

Moreover, we consider that strategies for the conservation of hydrological resources must contemplate an integral context (Moritz 2002) and the processes that allow their continuity, that is, they must preserve the variability in species life histories, their evolutionary history, and their connectivity (Cotler et al. 2004; Hand et al. 2015). This strategy includes the notion that the susceptibility of a species to human disturbance is dependent on its biological traits, including its life history, genetic structure, and ecological function, among others (Foden et al. 2009). Thus, it is desirable to propose conservation strategies from a multispecies-environment approach, to allow the integration of a complex system such as that presented by the problem of conservation of the diversity of freshwater fauna. We suggest following the recommendations of the IUCN for conserving biodiversity at three levels: ecosystems, species, and genetic diversity (McNeely et al. 1990).

At the national level, the Commission of National Protected Areas (CONANP) is in charge of establishing the National Protected Areas (NPAs) and Ramsar wetland sites. These conservation efforts have been effective in protecting many terrestrial species but few studies have evaluated the impact of these regions on the conservation of freshwater fishes, especially considering that even within these NPAs, freshwater fishes can still be at risk of extinction (Contreras-MacBeath 2006; De la Vega-Salazar 2006; Domínguez-Domínguez et al. 2006; Mercado-Silva et al. 2009). There are few cases in Mexico where NPAs and Ramsar sites have specific actions implemented to protect freshwater fishes (Lyons et al. 2020). Moreover, we need the application of the National Laws involving the freshwater ecosystems as the NMX-AA-159-SCFI-2012 (Secretaría de Economía 2012) that establishes the procedure for environmental flow determination in hydrological basins, or the NOM-001-SEMARNAT-2021 (SEMARNAT 2021) that establishes the maximum permissible limits of contaminants in the wastewater discharges in national water, among others, to reduce the current impact produced in freshwater fish diversity. We also recommend new strategies for water conservation due to rapid increase in population and water demand, such strategies should include a significant increase in the treatment and reuse of wastewater and the establishment of strict standards for the recovery and recycling of water. These will only be achieved through the enactment of effective and specific regulations and a strict enforcement regime (Valdivia-Alvarado et al. 2021).

Finally, there are examples of successful conservation initiatives in Mexico. One of these was for the endemic Leuscicidae *Notropis boucardi*, where a joint effort among the State University of Morelos, Government and local communities which established a RAMSAR site ("El Texcal") in 2010, where the genetic diversity of the species was evaluated for conservation purposes (Contreras-MacBeath et al. 2014). Another successful conservation program was the reintroduction of *Zoogoneticus tequila*, a species considered extinct in the wild. This initiative included the State University of Michoacan and many international institutions, integrating all steps suggested by the IUCN (Domínguez-Domínguez et al. 2018). The previous examples demonstrate that in order to have a successful conservation program, it is necessary to integrate different actors from various sectors of society (i.e., Universities, Government and local communities), which facilitate the implementation of an integrated management program. Providing the information that allows these conservation efforts to be prioritized will be a challenge for the coming years, but a crucial step to preserve freshwater biodiversity in the Anthropocene before reaching a point of no return.

Acknowledgments We thank the support of Fronteras de la Ciencia – CONACyT (Project No. 191986), and Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT), UNAM (Project No. IN212419). We would like to thank Pablo A. Tedesco and all the colleagues from the Laboratoire Evolution et Diversité Biologique (EDB) of the Université Paul Sabatier for facilitating the species' ranges that allowed us to reconstruct the species richness maps of freshwater fishes of Mexico. Also, we thank Charlotte González Abraham for allowing the shapefiles of the human footprint. Finally, R.G Beltrán López thanks CONACYT for the scholarship for postdoctoral stay.

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Chapter 8
Mexican Avifauna of the Anthropocene

David A. Prieto-Torres, Leopoldo D. Vázquez-Reyes, Lynna Marie Kiere, Luis A. Sánchez-González, Rubén Pineda-López, María del Coro Arizmendi, Alejandro Gordillo-Martínez, R. Carlos Almazán-Núñez, Octavio R. Rojas-Soto, Patricia Ramírez-Bastida, A. Townsend Peterson, and Adolfo G. Navarro-Sigüenza

Contents

David A. Prieto-Torres and Leopoldo D. Vázquez-Reyes contributed equally with all other contributors.

D. A. Prieto-Torres · L. D. Vázquez-Reyes · P. Ramírez-Bastida
Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

L. M. Kiere · L. A. Sánchez-González · A. Gordillo-Martínez · A. G. Navarro-Sigüenza (✉)
Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico
e-mail: adolfon@ciencias.unam.mx

R. Pineda-López
Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, Mexico

M. del Coro Arizmendi
Laboratorio de Ecología, UBIPRO, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

R. C. Almazán-Núñez
Laboratorio Integral de Fauna Silvestre, Facultad de Ciencias Químico-Biológicas, Universidad Autónoma de Guerrero, Chilpancingo, Guerrero, Mexico

O. R. Rojas-Soto
Red de Biología Evolutiva, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico

A. T. Peterson
Biodiversity Institute, University of Kansas, Lawrence, Kansas, USA

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_8

8.1 Introduction

"*Is biodiversity improving (going up) or worsening (going down)?*" is a question that many professional ecologists have asked to understand the impacts of the Anthropocene on biodiversity (Wiens and Donoghue 2004; Weir and Hey 2006; Rull and Carnaval 2020). This is an especially urgent question for biologists and conservationists today because biodiversity is dynamic in time and space and human impacts are multidimensional (e.g., Lenoir et al. 2008; López-Medellín et al. 2011; Golicher et al. 2012; Vázquez-Reyes et al. 2017; Prieto-Torres et al. 2020, 2021c). Currently, human activities are one of the main drivers of species extinctions (Ceballos et al. 2015). However, and despite increases in taxonomic, ecological, and biogeographical knowledge (e.g., Peterson et al. 2016), details of biodiversity trends and mechanisms in the face of urbanization, landscape transformation, and global warming remain poorly understood across most of Latin America (see Pearson et al. 2019).

This lack of information is critical in Mexico because the country has very high annual deforestation rates (over 1% nationwide), with more than 13.5 million ha of different ecosystems lost over the past 50 years (see FAO 2001; Mayani-Parás et al. 2020; Mendoza-Ponce et al. 2020). Moreover, there has been a spatially heterogeneous increase in mean annual temperature over the past century (see Cuervo-Robayo et al. 2020). Over the past two decades, several studies addressing the interactive effects of anthropogenic disturbances and global climate change (GCC) have suggested generalized modifications to the distribution of specialist species, a decrease in alpha diversity, and even species extinctions as the most likely consequence in the forthcoming decades (e.g., Peterson et al. 2002, 2015; Zamora-Gutierrez et al. 2018; Esperon-Rodriguez et al. 2019; Mayani-Parás et al. 2020; Prieto-Torres et al. 2020, 2021a). These modifications are relevant because the outcome of these range shifts may lead to significant biotic rearrangements, measured by the loss of biotic differences (i.e., homogenization) and the increase of differences (i.e., biotic heterogenization) among ecological communities over space and time (see Box 8.1). Such changes in beta diversity (i.e., biodiversity turnover) also alter ecosystem function and ecosystem services (Clavel et al. 2011).

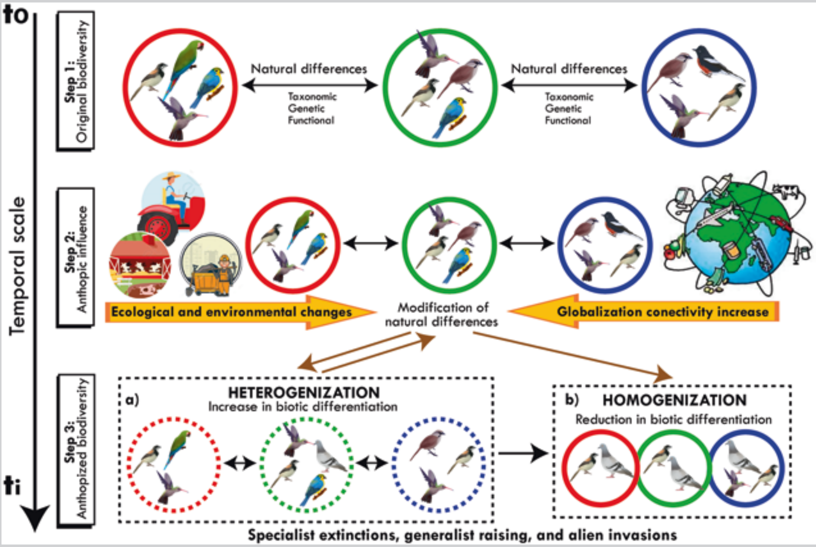
Mexico's megadiverse avifauna is not exempt from these critical scenarios. This avifauna includes many endemic elements, and it has experienced considerable losses as a consequence of intensive, long-term human activity across the landscape

Box 8.1. Conceptual Model of the Processes of Biodiversity Homogenization and Heterogenization in the Anthropocene

Because biodiversity loss patterns occur worldwide, beta diversity changes strongly characterize the Anthropocene (McGill et al. 2015). Here, we summarize two general and contradictory pictures of how anthropogenic modifications can impact biodiversity. The first, known as biotic homogenization, refers to the reduction of differences in biodiversity between sites (i.e., loss of beta diversity), which may lead to simplification. The second refers to the exact opposite process, known as biotic heterogenization, in which there is increased dissimilarity (i.e., increase of beta diversity) in ecological communities between sites (McGill et al. 2015).

How do these processes occur? First, consider two ecosystems that have contrasting ecological conditions (e.g., evergreen forests vs. scrublands), which lead to natural differences between their avifauna (step 1). The most immediately available measure of these differences is taxonomic turnover (species number), but the phenomenon also involves genetic and functional dimensions of biodiversity. These three dimensions reflect the historical and ecological processes that have shaped the identity of each avifauna (Olden et al. 2004). When humans alter the ecosystem (step 2) to make it more conducive to activities such as agricultural and livestock production, resource extraction, urban and industrial development, etc., the ecosystem conditions are changed in ways that can lead to major shifts in the biological components of the system (e.g., Kareiva et al. 2007; Hobbs et al. 2009; Corlett 2015). Climate change further alters the ecological conditions (Lovejoy and Hannah 2019), while the increase in connectivity worldwide due to the globalized economic system alters connectivity among natural habitats and the organisms that inhabit them (Rahel 2007).

Together, these human-induced changes can modify the degree of difference (in terms of presence or abundance of species) that defines the taxonomic, evolutionary, and functional identity of biotas (step 3). Initially, human alteration of ecosystems is expected to result in a widespread decline of populations and species, with a general decrease in alpha diversity (Root et al. 2003; Peterson et al. 2002, 2015; Golicher et al. 2012). However, not all species are necessarily affected in the same way. Human-induced environmental changes are expected to have particularly strong negative effects on organisms with specialist strategies (typically those with narrow ecological niches and small geographic distributions), resulting in population declines and potentially even local extinction. At the same time, species with generalist ecological traits (usually with broad ecological niches and large geographic distributions) may be favored by the prevailing ecological conditions in anthropized environments, increasing their representation in human-altered areas (Mckinney and Lockwood 1999; McGill et al. 2015). These dynamics lead to alterations to the natural patterns of co-occurrence patterns for biotas, resulting in a reorganization of species into novel assemblages across ecosystems and can set the stage for biological invasions (Hulme 2009; Baiser et al. 2012). Sketched birds within circles are species involved in an actual process of beta diversity loss driven by anthropization in central Mexico (see Vázquez-Reyes et al. 2017). Bird illustrations by Montserrat Serra Rojas de la Barrera.



Considering these species-specific responses, human-induced changes could be a potential driver of uneven modification of richness patterns of species assemblages for biotas among regions in both space and time. When the changes correspond mainly to local extinctions and/or reduction of most range sizes for most species, resulting in assemblages dominated by a greater proportion of specialists/restricted species, anthropic influence is likely a driver of differentiation across the three diversities for communities (Olden and Poff 2003). Therefore, the regions seem to be experiencing an ongoing biotic heterogenization process (step 3a), which is a result commonly identified across lowland ecosystems. Nevertheless, it is worth noting that this increase in biotic differentiation could be only the beginning of a future erosion of differences among places (i.e., homogenization process), because range contractions will increase the likelihood of complete extinction both locally and regionally in the medium- to long-term (step 3b; Olden and Poff 2003).

Considering that biotic homogenization is the most likely (worst) scenario in the global biodiversity crisis (Lewis and Maslin 2015; McGill et al. 2015), it is essential to implement both restoration and conservation strategies to recover, maintain, and protect natural ecosystems and their whole biotas (Koh and Gardner 2010; Rahel 2010; Melo et al. 2013). Actions must be implemented rapidly, for example, by changing current global economic models based on unlimited growth, unsustainable resource exploitation practices, extensive habitat anthropization, and global connectivity to satisfy transnational markets (Rozzi 2013; Moranta et al. 2021). The cost of not doing so is the ecological malfunctioning of the natural systems that sustain life, threatening the well-being of nature, and humanity in the future (Diaz et al. 2006), because as time passes, conservation possibilities will drastically decrease.

and the effects of GCC (Peterson et al. 2002, 2015; Vázquez-Reyes et al. 2017; Mendoza-Ponce et al. 2020; Prieto-Torres et al. 2020, 2021a, b; Kiere et al. 2021; Sierra-Morales et al. 2021). Several species have already become extinct, including the Guadalupe Storm-Petrel (*Hydrobates macrodactylus*), Guadalupe Caracara (*Caracara lutosus*), Imperial Woodpecker (*Campephilus imperialis*), and Slender-billed Grackle (*Quiscalus palustris*), to name just a few. In addition, almost 44% of bird species have been rated with some level of threat according to red lists at national and international levels (SEMARNAT 2019; IUCN 2021). More importantly, previous studies suggest that in most cases, the current network of Natural Protected Areas (NPAs) is not an effective safeguard of the whole array of species at present or into the future (e.g., Navarro-Sigüenza et al. 2011; Ramírez-Acosta et al. 2012; Arizmendi et al. 2016; Prieto-Torres et al. 2020, 2021a, c; Ramírez-Albores et al. 2021). As such, conservation efforts in Mexico are a crucial priority for global-scale bird conservation initiatives (Peterson and Navarro-Sigüenza 2016). More information and integrative studies considering both local and regional data are needed to understand the magnitude of Anthropocene threats to the Mexican avifauna, including the costs and consequences of inaction.

In this chapter, we review studies focused on the spatial and environmental consequences that characterize some of the effects of the Anthropocene on Mexican avifauna. Specifically, we present a general characterization of both ecological and geographic patterns on the bird taxa that have been confirmed across Mexico, as well as a general overview of avian studies addressing the following questions: (i) What is the current state of knowledge of factors that negatively impact biodiversity and species' responses to them?; (ii) are anthropogenic disturbances like urbanization, habitat loss, pollution, and GCC driving Mexican avifaunal rearrangements and biodiversity changes?; and (iii) how this knowledge has resulted (or not) in effective conservation policies to assure the long-term integrity of the avifauna? Based on this information, we discuss current challenges and future opportunities for these research topics across the country.

8.2 Mexico's Megadiverse Avifauna

Throughout its ~2,000,000 km^2 of surface area, Mexico's avifauna is highly diverse, both in terms of overall species richness and number of endemisms (Fig. 8.1). The country's complex geographic setting and topography have promoted the development of an ample variety of ecosystems throughout the national territory. Consequently, the Mexican avifauna comprises species with mixed biogeographic and ecological affinities (Escalante et al. 1998); Nearctic-related species are mainly found in arid regions and high mountain areas, while Neotropical-related species are primarily found in tropical lowland regions (Escalante et al. 1998; Navarro-Sigüenza et al. 2014a). The same pattern of heterogeneous diversity is also detected across altitudinal gradients in the main mountain ranges (distributed at middle and high elevation areas; Sánchez-González and Navarro-Sigüenza 2009; Ferro et al. 2017). Moreover, Mexico is considered a highly important wintering region for many migratory species (~23% of the entire avifauna of the continent), most of which arrive from breeding grounds in North America (Escalante et al. 1998; Navarro-Sigüenza et al. 2014a).

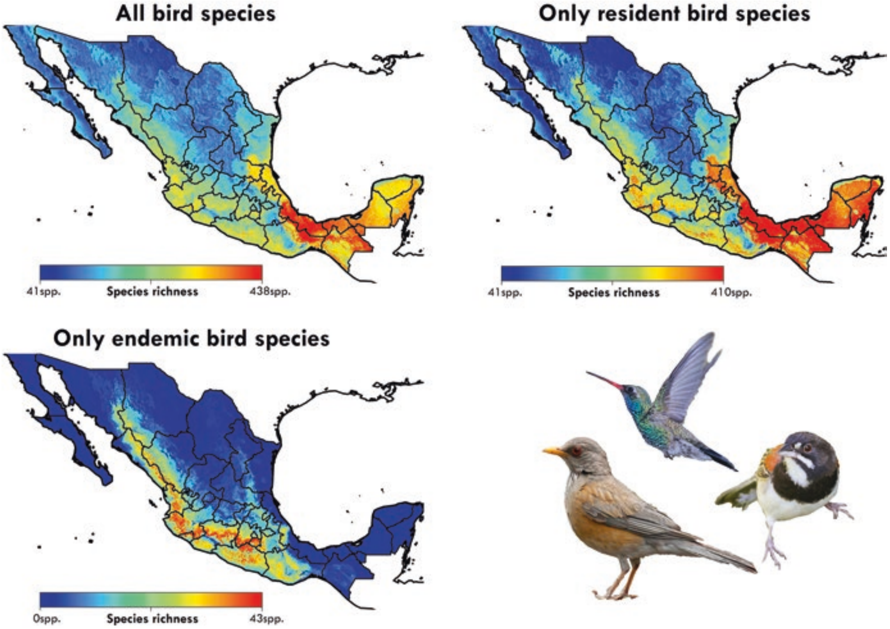


Fig. 8.1 Species richness patterns for avifauna across Mexico. The three geographical patterns were estimated based on the individual bird maps proposed by Navarro-Sigüenza and Peterson (2007). The birds shown in the figure are the Rufous-backed Thrush *Turdus rufopalliatus* (left), the Broad-billed Hummingbird *Cynanthus latirostris* and the Black-chested Sparrow *Peucaea humeralis* (right). Bird photos: Leopoldo D. Vázquez Reyes – Bio Pic

Although the total number of species varies depending on the taxonomic perspective, more than 1100 bird species (belonging to 26 orders, 95 families, and 493 genera) have been recorded in the country (see Navarro-Sigüenza et al. 2014a for a detailed discussion). This richness places Mexico eighth among the megadiverse countries of the world and fourth in the proportion of endemic species (~18%, >200 species). Nearly three quarters (74%) of the species in Mexico are terrestrial, 24% are aquatic, and only 2% of species inhabit both types of environments. The geographic pattern of species richness (Fig. 8.1) shows that the highest overall species richness is found in the coastal lowlands of the Gulf of Mexico, in the states of Oaxaca and Chiapas, and the Yucatan Peninsula. Meanwhile, the highest richness of endemic species is in western and central Mexico, mainly in the Upper Balsas Basin and mountains of the Trans-Mexican Volcanic Belt.

The ecosystems that have the highest bird species richness in Mexico are lowland rainforests (~29% of the total avifauna) and tropical deciduous forests (~24%). Several ecosystems have intermediate species richness values, including pine-oak forests (~20%), cloud forests (~18%), and arid scrubs (13%), while aquatic ecosystems have the lowest species richness values (<7%). When considering the richness of endemic species, the richest ecosystems are montane ecosystems such as pine-oak forests (~17%) and cloud forests (~11%) as well as tropical deciduous forests (~16%). In most ecosystems, the majority of species are year-round residents; however, in some aquatic environments there is a higher number of migratory species than resident species during the winter (Navarro-Sigüenza et al. 2014a).

The number of species that are included in some threat category vary among different international and national checklists, but the IUCN Red List includes 32–34% (369–390 spp.) of Mexican bird species (IUCN 2021), while 43–44% (486–507 spp.) are considered under the category of “Special Protection” by SEMARNAT (2019). According to the IUCN Red List, ~13% of species are highly threatened (Endangered, Critically Endangered or Extinct), ~14% are Vulnerable, and ~18% are Near Threatened. This includes species with extremely restricted distribution (e.g., the Short-crested Coquette *Lophornis brachylophus*, the Maroon-fronted Parrot *Rynchopsitta terrisi*, the Yellow Rail *Coturnicops noveboracensis*, and the Dwarf Jay *Cyanolyca nanus*) and those that have small population sizes and live in threatened habitats (e.g., Scarlet Macaw *Ara macao* and Resplendent Quetzal *Pharomachrus mocinno*), which are included on all of the extinction risk lists (Fig. 8.2).

8.3 Historical Implementation of Studies of Anthropogenic Disturbances

Human impacts on the Mexican avifauna started in pre-Hispanic times, increased during the colonial era, and reached the present level due to the growth of the human population and the associated economic activities in the country (Navarro-Sigüenza

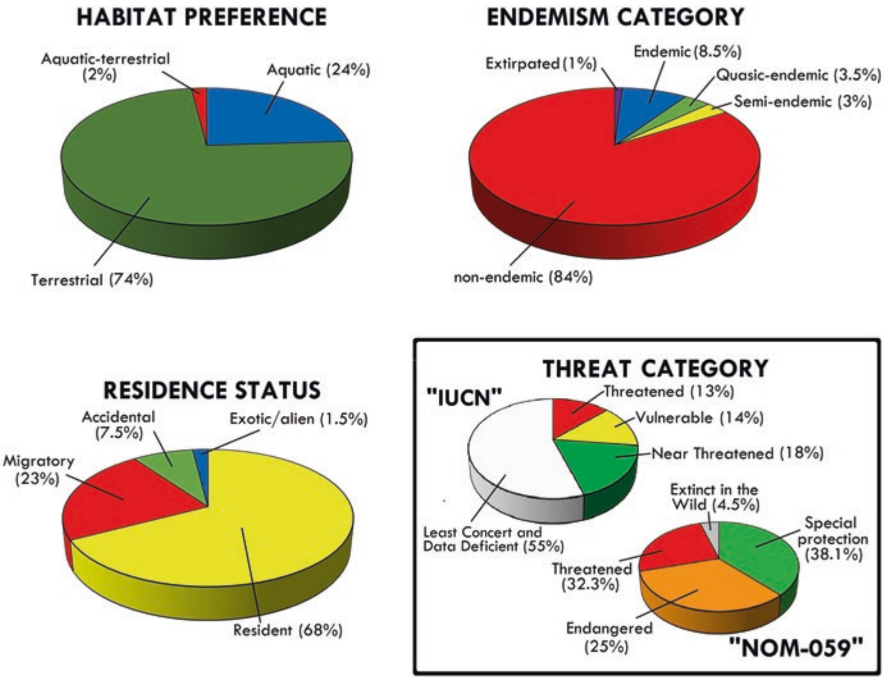


Fig. 8.2 The distribution of Mexico's ~1100 bird species among habits, endemism categories, residence status, and threat categories (based on inclusion in national or international threatened species listings)

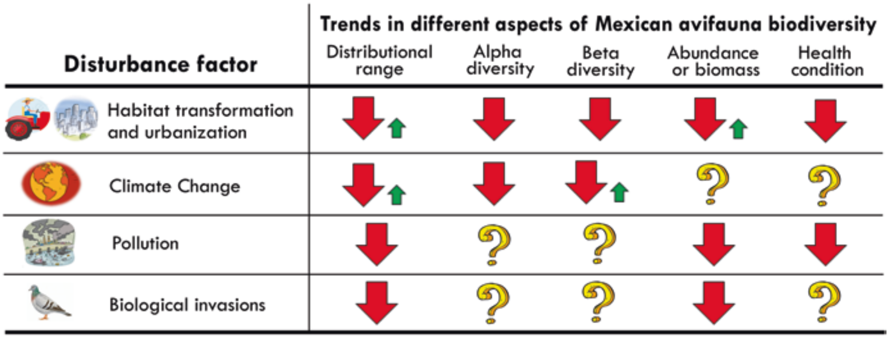
et al. 2008, 2015; López-Medellín et al. 2011). Many wild species in the region have long been exploited for food (Llamas 1935), sport hunting (Leopold 1959), feather art, and handcrafts (Navarijo Ornelas 2006), or have been domesticated (e.g., Wild Turkeys, *Meleagris gallopavo*, Manin et al. 2018; Corona-M 2020), raised in captivity for trade and commerce (e.g., *Ara macao*; Schwartz et al. 2021), or exhibited in zoos (Blanco et al. 2001). There is also evidence that the Aztec emperor Ahuizotl orchestrated the first recorded exotic introduction (Great-tailed Grackle, *Quiscalus mexicanus*; Haemig 2011).

To analyze the current state of knowledge of anthropogenic factors affecting Mexican bird diversity, we carried out a systematic search of the Web of Science Core Collection. Literature search criteria included combinations (in both English and Spanish) of keywords with search modifiers, including *"Mexico", "bird*", "avifauna", "globalization", "anthropization", "Anthropocene", "anthropic activities", "human activities", "perturbation", "habitat loss", "urbanization", "agriculture", "cattle", "pollution", "biological invasion", "extinction", "homogenization", "climate change", and "climate warming"*. Our review included only papers published in scientific journals and some of the references within articles found based on these keywords. We excluded unpublished graduate and undergraduate dissertations due to likely overlap with publications. We found 1845 articles published between 1950 and early 2021.

After gathering all of the available publications that met our search criteria, we manually selected those focused on investigating how bird assemblages have been impacted by long-term intensive human activity and environmental transformation of the landscape. We then compiled all of the information from these articles into a table including the following information: (a) entity of study (species, populations, communities, interactions); (b) geographical (i.e., local, regional, national or international) and temporal (short-, medium-, and long-term) scales; (c) theme addressed (habitat loss and fragmentation, pollution, climate change, invasions, etc.); (d) ecosystem type; (e) biodiversity level analyzed (taxonomic, phylogenetic, and/or functional); (f) biodiversity patterns included (alpha, beta, and/or gamma); (g) data sources (fieldwork, ornithological collections, online databases, etc.); (h) degree of anthropic intervention (intact vegetation, urban context, etc.); (i) effects recorded (positive, negative, null, mixed); (j) trend reported (e.g., local extinction, distributional shift, homogenization, etc.); and (k) conservation, management, and/or planning strategies and actions suggested.

Historically, most (ca. 75%) of the published articles about Mexican avifaunas correspond to new faunistic records that change species' ranges and local species lists. Notes reporting aberrant coloration (e.g., leucism) are also common in the literature. We excluded both of these types of publications from our review, since they do not report effects of human interventions on avian biodiversity. From our compilation of publications ($n = 467$) analyzing human factors that impacted avifaunas, we observed an increase in research over the past decade, with over a third of the contributions (38.9%) published over the past 5 years (2017–2021). These articles were primarily published in international journals (~80% of cases), and in 69.2% of cases the first or corresponding author was affiliated with a Mexican institution. Research assessing species' responses to anthropogenic disturbances was centered around landscape transformation (60.6%), GCC (19.3%), pollution (13.3%), and biological invasions (11.5%). Some articles (10.7%) were multidisciplinary, combining three or four of these topics. Most of the articles (~75%) used fieldwork as the main data source, 14.3% combined field data with information from ornithological collections and online databases, and 10.2% were based exclusively on data from specimens in collections' databases.

Of the total set of assessed publications, 39.0% focused primarily at the community level, of which 47.3% reported patterns of alpha diversity, 36.3% beta diversity, and 16.4% gamma diversity. Another 28.3% of the articles considered the species level as the entity of study, followed by those considering populations (15.4%), and a lower proportion considered ecological interactions (5.6%). Most of these publications addressed a single dimension of biodiversity information (taxonomic [44.1%] or functional [36.4%]), with a lower proportion (17.1%) of studies involving two or the three dimensions. The most frequent geographical and temporal scales were the local (61.9%) and short-term (71.5%), respectively. Regarding the ecosystem type, ~29% of the publications were carried out in temperate forests and rainforests, and ~22% were centered on the avifauna of tropical deciduous



Disturbance factor	Trends in different aspects of Mexican avifauna biodiversity				
	Distributional range	Alpha diversity	Beta diversity	Abundance or biomass	Health condition
Habitat transformation and urbanization	↓↑	↓	↓	↓↑	↓
Climate Change	↓↑	↓	↓↑	?	?
Pollution	↓	?	?	↓	↓
Biological invasions	↓	?	?	↓	?

Fig. 8.3 Schematic representation of main trends in studies examining the impact of anthropogenic factors on Mexican avifauna biodiversity. Arrows indicate the direction of described trends (red down arrows indicate negative effects, green up arrows indicate positive trends), and question marks indicate trends about which there is still little empirical evidence. In all categories where evidence was mixed (i.e., some studies reporting positive and others reporting negative trends), the bulk of the evidence was toward negative trends (represented by larger size of red arrows)

forests. Nearly three quarters of the papers (74.5%) were carried out in natural habitats, while 25.5% corresponded to urbanization gradients. In the following sections, we summarize the current knowledge on how each of the four main anthropogenic factors impact the biodiversity patterns of Mexican avifauna (Fig. 8.3).

8.3.1 Habitat Transformation and Urbanization

The replacement of natural habitat by anthropized landscapes due to agriculture, livestock grazing, and urbanization, is perhaps the most critical driver eroding bird biodiversity in Mexico. Many studies (~60%) have demonstrated negative trends in bird diversity due to habitat transformation, including losses of taxonomic richness, increased abundance of generalist species (commonly invasive alien species), and decreased abundance of species associated with natural forests (MacGregor-Fors and Schondube 2011a, b; Maya-Elizarrarás and Schondube 2015a, b). This pattern is consistent in many cities (MacGregor-Fors et al. 2020, 2021; Nava-Díaz et al. 2020). Conversely, several studies (~14%) have provided evidence that some native species such as the Rufous-backed Robin (*Turdus rufopalliatus*) and the Great-tailed Grackle (*Q. mexicanus*), can be successful in anthropized habitats, probably due to their remarkable adaptability to new environments (Christensen 2000; Martínez-Morales et al. 2010). There is also evidence of some birds (e.g., Harris's Hawks [*Parabuteo unicinctus*] and Spotted Wren [*Campylorhynchus gularis*]) using human-made resources opportunistically (Ortega-Álvarez and Calderón-Parra 2014; Vázquez-Reyes et al. 2020).

In Mexico, at least 24 bird species or subspecies have become extinct due to human landscape modification (Ríos-Muñoz 2002; Navarro-Sigüenza et al. 2014b;

Peterson et al. 2015). Probably one of the most sensitive changes are those documented by Peterson and Navarro-Sigüenza (2006), in which the transformation of wetland habitats and drainage of the lakes of the Valley of Mexico led to the local extinction of a large portion of the aquatic avifauna in the region. Hundreds of bird species lost most of their habitat within the basin, and today are relegated to a few relict areas. Furthermore, those habitats are currently imperiled by pollution and urban development because they have become part of the cities' drainage systems or even remain dry most of the year. Human modification in the swamps of Lerma, near Mexico City, led the global extinction of the Slender-billed Grackle (*Quiscalus palustris*; Haemig 2010), while logging and hunting led to the disappearance of the Guadalupe Caracara (*Caracara lutosa*; Abbott 1933) and the Imperial Woodpecker (*Campephilus imperialis*; Íñigo Elías and Enkerlin Hoeflich 2002). Unfortunately, these are not isolated cases in the country. Perhaps one of the most shocking cases of habitat loss is the "*Programa Nacional de Desmonte*" (PRONADE), which was coordinated by the Mexican government and funded by the World Bank and the Inter-American Development Bank. This program caused the loss of nearly 80% of Mexico's tropical rainforests between 1972 and 1983, transforming them into extensive pasture lands for the cattle industry (Corral Flores 2018). Unfortunately, almost all of the rainforests across the Gulf of Mexico and their astonishing biodiversity, which included Harpy Eagles (*Harpia harpyja*), Scarlet Macaws (*A. macao*), and hundreds of other tropical bird species (Howell and Webb 1995) faded away without even having complete biological inventories.

Recent works have also documented losses of taxonomic beta diversity leading to homogenization at the landscape scale across different ecosystems as a result of the development of human settlements in both rural (Ochoa-Ochoa et al. 2014; Hiley et al. 2016; Vázquez-Reyes et al. 2017) and urban settings (Puga-Caballero et al. 2014, 2020). Urbanization is a particularly severe type of habitat disturbance because in addition to the vast areas physically covered by buildings and paved streets, urbanization also involves the presence of large numbers of humans and automobiles, which generate noise, light, and chemical pollution. These conditions pose a whole new set of selective pressures that are strong enough to be of conservation concern for many species. For instance, there is high bird mortality due to collisions with automobiles on roadways as well as large buildings and other tall structures (González-Gallina et al. 2013; Hager et al. 2017; Gómez-Martínez et al. 2019; Uribe-Morfín et al. 2020). In addition, the increased predation by human-associated predators exerts strong pressure on both nestlings and adult birds within cities (Rivera-López and MacGregor-Fors 2016). In urban areas, predation by alien species such as black rats, and especially feral and domestic cats, is one of the main drivers of decreasing bird populations (Loss et al. 2013). It has also been suggested that the transformation of natural environments may contribute to increased avian morbidity due to haemosporidian infection (e.g., Santiago-Alarcon et al. 2019; Hernández-Lara et al. 2020), though more research is needed to determine the extent of this impact.

From a community ecology perspective, the best-known consequence of urbanization is the decrease of bird taxonomic diversity. Results suggest that specific traits of the urban landscape (like buildings and paved surfaces) negatively affect forest-dwelling bird species while favoring the ecological dominance of alien invaders and generalist species (Ortega-Álvarez and MacGregor-Fors 2009; MacGregor-Fors and Schondube 2011a, b; McDonell and MacGregor-Fors 2016; Puga-Caballero et al. 2020). The study of the effects of anthropization on bird diversity using trait-based approaches has just started in Mexico, but evidence suggests that habitat transformation is driving losses of phylogenetic and functional diversity in bird communities (Moreno-Contreras et al. 2019; Puga-Caballero et al. 2020). Directional shifts include favoring species with small (Nava-Díaz et al. 2020) or medium body sizes (Puga-Caballero et al. 2020), suggesting that urban landscapes may function as environmental filters. Habitat anthropization also drives the differential success of birds with "ruderal" evolutionary ecological strategies, defined by short life-cycles, high fecundity, and broad ecological niches (Vázquez-Reyes et al. 2022).

8.3.2 Climate Change

Mexican bird species are particularly vulnerable to rapid increases in temperature and variation in annual precipitation patterns (Peterson et al. 2002, 2015; Prieto-Torres et al. 2020, 2021c; Sierra-Morales et al. 2021). Such changes promote modifications in species' physiological responses and activity patterns, affecting their survival (Lawler et al. 2009; Şekercioğlu et al. 2012). The most common results in literature modeling shifts in species' ranges are changes in elevational ranges (including both the species disappearance and/or changes of its geographical ranges), migration patterns, and local abundance of avifauna (~88% of analyzed studies). Especially worrying is that extinction is plausible in the future for a number of range-restricted habitat specialists including the Horned Guan (*Oreophasis derbianus*), Yellow-lored Parrot (*Amazona xantholora*), and Cozumel Emerald (*Cynanthus forficatus*). Tropical sections of the Mexican mountains could be the most affected by GCC, where a loss of 25–38% of their endemic species is expected (Lawler et al. 2009; Peterson et al. 2015; Sierra-Morales et al. 2021). Although migratory species and seabirds have received less attention (~15% of studies), several of these species face unique challenges because they are exposed to multiple factors during their migrations, such as reduced body mass before migration and reduction of prey availability, among others (Ancona et al. 2011; Şekercioğlu et al. 2012). Furthermore, they face more frequent and severe meteorological phenomena such as hurricanes due to climate change (Ahola et al. 2007; Loarie et al. 2009; Şekercioğlu et al. 2012). For example, the analysis of 18-years of breeding data from a colony of the Blue-footed booby *Sula nebouxii* showed a delay in onset of breeding (including declines in clutch size, brood size, hatching success, and fledging success) when the global Southern Oscillation Index was negative (Ancona et al. 2011). These findings all reinforce the idea that climate warming is a major threat to both threatened and nonthreatened Mexican avifauna.

GCC is not expected to drastically decrease the distribution range of all species. For example, the distribution of the hummingbirds *Amazilia rutila* and *Leucolia viridifrons* is projected to remain stable or even have large habitat gains under future climate conditions (Prieto-Torres et al. 2021c). Consequently, the scenario of many "losers" and a few "winners" under new climate conditions supports the idea that a species' ecological generalization (including niche breadth and range size) is one of the critical attributes affecting their extinction risk (Şekercioğlu et al. 2012; Ortega et al. 2019; de Matos Sousa et al. 2021). However, given how difficult it is to accurately predict how species will respond to climates that do not exist at present, these general forecasts should be taken with caution. Most tropical bird species and their habitats will not be able to shift fast enough or far enough to track their preferred climate envelopes (Loarie et al. 2009; Şekercioğlu et al. 2012; Ortega et al. 2019). This is particularly important if we consider that only a small proportion of the existing studies (<5%) included factors such as each species' dispersal ability, reproductive rate, and degree of specialization in habitat requirements in Mexico (see Şekercioğlu et al. 2012).

Similar to habitat transformation, GCC could have effects beyond individual species' ranges to impact the overall taxonomic, functional, and phylogenetic composition and structure of ecological communities (Prieto-Torres et al. 2021b). Patterns of modification may even differ among regions, which could further alter ecosystem function and increase extinction risk (e.g., White et al. 2018; Lovejoy and Hannah 2019). Despite the relevance of these topics, few studies in Mexico (<20% of analyzed cases) have measured spatiotemporal species turnover and its contribution to biotic homogenization and/or heterogenization across different levels of biodiversity and temporal and geographic scales. Indeed, only ~7% of publications include information on populations and/or interactions. This is an important knowledge gap that restricts our understanding of the future consequences and threats to Mexican avifauna (and biodiversity in general) because changes in biotic associations can be as important as changes in temperature and precipitation, if not more so (see Araújo and Luoto 2007; Şekercioğlu et al. 2012; Atauchi et al. 2018).

8.3.3 Pollution

We found 62 empirical studies addressing a broad range of pollution types on Mexican avifauna. Most of these studies (76%) focused on chemical pollution. The remaining studies were divided among litter (8%), noise pollution (6%), light pollution (2%), or some combination of these categories (8%). Studies of chemical pollution addressed persistent organic pollutants (45% of chemical pollution studies), heavy metals/metalloids (e.g., lead, mercury, arsenic; 34%), hydrocarbons (13%), or both heavy metals and persistent organic pollutants (8%).

Studies of heavy metals/metalloids in Mexican avifauna considered several sources of exposure, including trophic bioaccumulation (55% of heavy metal studies), urban air pollution (18%), spent ammunition (14%), and metal mining (10%).

Two-thirds of these studies were limited to quantifying heavy metal levels in birds' tissues or reporting exposure itself (e.g., lead ammunition in gizzard contents). All of these studies found detectable levels of at least one heavy metal/metalloid (though it is important to note that most study species/locations were specifically chosen because there was some a priori expectation of heavy metal exposure). Although in 37% of heavy metal studies, the authors mentioned that the levels detected were below established harm thresholds or reported no relationship with fitness variables, it is generally recognized that there is no "safe" level of exposure (Mann et al. 2011). Elevated mercury and cadmium levels were reported in multiple studies, especially in aquatic species with generalist or piscivorous diets (Ceyca et al. 2016) and that forage close to shore (Soldatini et al. 2020). Only two studies addressed the accumulation of heavy metals in birds near mining activity, both of which found elevated arsenic and lead levels near mining sites (Chapa-Vargas et al. 2010; Monzalvo-Santos et al. 2016). Considering that nearly a third of Mexican territory, including 1.5 million ha of federal NPAs, was concessioned for mining by 2010 (Armendáriz-Villegas et al. 2015), the effect of Mexico's past and current mining activity on its flora and fauna is woefully understudied.

Urban pollution is another potentially widespread but still understudied source of pollution exposure in Mexican birds. Only two studies have measured heavy metal levels in urban birds (pigeons, *Columba livia*; Delgado et al. 1994 and Great-tailed grackles, *Quiscalus mexicanus*; Guzmán-Velasco et al. 2021), both of which found highly elevated levels of lead. Two additional studies in pigeons found higher genotoxicity in urban than rural birds, but did not measure heavy metal levels in tissues (González-Acevedo et al. 2016; Ceyca-Contreras et al. 2020). Lead exposure from spent ammunition is another geographically restricted but locally important driver of both acute (e.g., Schmitz et al. 1990) and chronic heavy metal exposure in aquatic birds in Mexico (even a decade after outlawing lead ammunition; Echeverría-García and Gold-Bouchot 2013). Together, these studies show that the Mexican avifauna is not exempt from the insidious nature of toxic heavy metals, whose long-distance dispersal, persistence in the environment, and bioaccumulative properties make them pollutants of major concern worldwide.

Research on persistent organic pollutants in Mexican avifauna has been heavily dominated by organochlorine pesticides, though several studies also included industrial compounds such as polychlorinated biphenyl compounds (PCBs) and polybrominated diphenyl ethers (PBDEs). The timing and taxa of these studies generally track with historical concern over DDT and eggshell thinning; the earliest study was published in 1973 (Gress et al. 1973), and 80% of the studies of persistent organic pollutants addressed waterbirds of birds of prey. Overall, 39% of these studies found elevated tissue concentrations of persistent organic pollutants in birds and/or negative physiological or fitness effects of exposure. Although the potentially devastating effects of exposure to organochlorine pesticides are irrefutable, the local scale, lack of long-term studies, and sometimes small sample sizes in this body of literature make it difficult to gain a broad view of the current status of the threat of organochlorine pesticides to Mexican avifauna. There are relatively few studies addressing the effects of oil contamination on Mexican avifauna (six studies, 13%

of all chemical pollution studies). Two-thirds of these studies specifically addressed effects of the 2010 Deepwater Horizon oil spill, and all of the studies found negative effects on birds, at levels ranging from individual mortality to community composition. Other chemical pollutants of emerging concern such as pharmaceuticals, surfactants, and per- and polyfluoroalkyl substances (Sauvé and Desrosiers 2014) have yet to be examined in Mexican birds.

Research on the effects of litter, artificial light, and noise on Mexican avifauna is currently limited to a small but rapidly growing group of studies (15 in total, 60% of which were published in 2016 or later). This is also a particularly integrative area of pollution research, with most of these studies considering multiple disturbance factors, complex response variables, and/or multiple levels of biodiversity. Several of these studies found effects of the pollution type they investigated. For example, noise pollution in Mexican cities affected the composition of songbird communities (González-Oreja et al. 2012; Manzanares Mena and Macías Garcia 2018), artificial light at night affected migration stopover patterns (Cabrera-Cruz et al. 2020), and the use of cigarette butts as nesting material decreased ectoparasite load, but increased genotoxicity (Suárez-Rodríguez et al. 2013, 2017; Suárez-Rodríguez and Macías Garcia 2014). These studies are just the tip of the iceberg in these more recent research topics. Given the ubiquity of artificial light, noise, and trash, especially in the context of urbanization, many more studies are needed to understand their effects on Mexican avifauna.

8.3.4 Biological Invasions

Alien species are a matter of concern in Mexico due to their current and future potential adverse effects on biodiversity (e.g., the spread of diseases, competitive exclusion, and eventual extirpation or extinction of native species; Keitt et al. 2002; Aguirre-Muñoz et al. 2008; CANSEI 2010; Koleff et al. 2021). At least 23 species of exotic birds have been documented across the country since the nineteenth century (e.g., Peterson and Navarro-Sigüenza 2006; Table 8.1), 21 of which are recognized as potential invaders. Some of these species have been established for more than 100 years, such as the Rock Pigeon (*Columba livia*) and the English Sparrow (*Passer domesticus*). However, most of the species have been introduced and have invaded more recently, like the Common Starling (*Sturnus vulgaris;* Brodkorb and Staebler 1939) and Old-World doves of the genus *Streptopelia* spp., among others (Álvarez Romero et al. 2008; CANSEI 2010).

Today, a few publications have focused on understanding the effect of invasive species on biodiversity and the specific mechanisms that favor successful invasions. Some studies in *P. domesticus* have documented its negative impact in displacing native species that have similar ecological requirements, such as siskins and finches (e.g., *Spinus psaltria* and *Haemorhous mexicanus*; MacGregor-Fors et al. 2010). Therefore, specific habitat management strategies have been proposed to reduce the incidence of these alien species in anthropized areas (Ramírez-Cruz and

Table 8.1 List of exotic-invasive bird species historically recorded in Mexico (CONABIO 2021)

Taxonomic family	Species	Common name
Phasianidae	*Phasianus colchicus*	Ring-necked Pheasant
Columbidae	*Columba livia*	Rock Pigeon
	Streptopelia decaocto	Eurasian Collared-Dove
	Streptopelia roseogrisea	African Collared-Dove
	Spilopelia chinensis	Spotted Dove
Ardeidae	*Bubulcus ibis*	Cattle Egret
Psittacidae	*Myiopsitta monachus*	Monk Parakeet
	Cyanoliseus patagonus	Burrowing Parakeet
Psittaculidae	*Psittacula alexandri*	Red-breasted Parakeet
	Psittacula eupatria	Alexandrine Parakeet
	Psittacula krameri	Rose-ringed Parakeet
	Agapornis fischeri	Fischer's Lovebird
Pycnonotidae	*Pycnonotus jocosus*	Red-whiskered Bulbul
	Pycnonotus cafer	Red-vented Bulbul
Sturnidae	*Acridotheres cristatellus*	Crested Myna
	Pastor roseus	Rosy Starling
	Sturnus vulgaris	European Starling
Passeridae	*Passer domesticus*	House Sparrow
Estrildidae	*Lonchura punctulata*	Scaly-breasted Munia
	Lonchura malacca	Tricolored Munia
	Amandava subflava	Zebra Waxbill
Icteridae	*Molothrus bonariensis*	Shiny Cowbird
	Quiscalus mexicanus	Great-tailed Grackle

Ortega-Álvarez 2021). Another recent important example is the introduction of the Monk Parakeet (*Myiopsitta monachus*). This species escaped from captivity and has spread rapidly, with high invasion potential and exponential population growth (MacGregor-Fors et al. 2011; Hobson et al. 2017). Although the Mexican government has invested in planning strategies for its control, the implementation is limited by people's affinity for a species they identify as charismatic, limiting the possibilities for its successful eradication (Ramírez-Bastida et al. 2017). The magnitude of the effects of the Monk Parakeet and other species with accelerated expansion remain unknown. Although a National Strategy for Invasive Species has already been published in Mexico, more studies and financial support from the government are urgently needed to define specific actions, based on scientific knowledge, that manage to stop the effects of invasive species on biodiversity (Álvarez Romero et al. 2008; Ochoa-Ochoa et al. 2017).

8.4 Are Natural Protected Areas the Best Conservation Strategy?

Overall, the protection of habitats and creation of new NPAs have been identified as fundamental to preserving biological diversity in Mexico (Jiménez Sierra et al. 2014). Detecting areas of importance for avifauna and proposing their protection is a common topic among the ornithological literature at local (e.g., Moreno-Contreras et al. 2019; Levey et al. 2021), regional (e.g., Ferro et al. 2017; Ramírez-Albores et al. 2021), national (e.g., Íñigo Elías and Enkerlin Hoeflich 2002; Prieto-Torres et al. 2021c), and international scales (e.g., Donald et al. 2018; Prieto-Torres et al. 2018). However, studies assessing the role of NPA across broad landscapes in the country have generally focused on individual species trends and alpha diversity patterns.

Despite the increase in the extent of terrestrial NPAs over the past few decades (CONANP 2021), important gaps for bird conservation have been detected across Mexico. Previous analyses have highlighted the importance of diverse regions in Mexico as important bird areas (Arizmendi and Marquez-Valdelamar 2000), highly endemic areas (Stattersfield et al. 1998), or areas that contain an attribute of evolutionary importance (Álvarez Mondragón and Morrone 2004). However, the current level of protection of bird faunas is still woefully inadequate (Navarro-Sigüenza et al. 2011, 2014a; Prieto-Torres et al. 2018, 2021b; Ramírez-Albores et al. 2021), and several globally threatened, ecologically restricted, and endemic species and community assemblages remain unprotected (e.g., Navarro-Sigüenza et al. 2014b; Arizmendi et al. 2016; Ortiz-Pulido 2018; Prieto-Torres et al. 2021b, c).

As the Anthropocene progresses, the ratio of species' ranges contained within NPAs will likely decrease substantially in the future due to GCC, especially considering the continued high annual deforestation rates in Mexico (see Mendoza-Ponce et al. 2020; Mayani-Parás et al. 2020). Moreover, most of the priority areas predicted to be highly resilient to GCC and land use change in the future are located outside of current NPAs (Rojas-Soto et al. 2012; Prieto-Torres et al. 2021a, c). This leaves the overall long-term conservation picture for birds relatively weak in Mexico.

Failure to protect this megadiverse avifauna would result in major losses of an evolutionary history that is unique in the world. For example, in the lowlands of northwestern Mexico, several sites have been identified as diversification hotspots and Pleistocene refugia for biota (e.g., Castillo-Chora et al. 2021), but those same areas are subject to high levels of habitat transformation and destruction by human activities (Prieto-Torres et al. 2016, 2018; Mendoza-Ponce et al. 2020). Therefore, planning to maximize the performance of the NPA network into the future must explicitly consider how the size and composition of the species pool are expected to change over time (see Hannah et al. (2007) and Carroll et al. (2010) for a complete discussion).

More studies describing a variety of spatiotemporal diversity patterns – including phylogenetic and functional trait diversity – will provide baseline information that is relevant for both in-depth ecological studies on ecosystem dynamics and conservation decision-making for long-term protection (Carvalho et al. 2010; MacGregor-Fors et al. 2020; Nori et al. 2020). To truly conserve biodiversity, it is not enough to protect a sufficient overall area of land. We must also ensure that NPAs are placed strategically in locations that will continue to be suitable for imperiled species into the future and assess the effectiveness of conservation efforts under different anthropogenic practices. Identifying places where high species richness and other biodiversity dimensions (e.g., endemism, functional, and phylogenetic diversity) coincide with areas where human-induced changes are not expected in the near future are of particular interest in this pursuit. It will be important to promote and financially support their long-term maintenance as well as restoration (Hannah et al. 2014; Naime et al. 2020; Sánchez-Romero et al. 2021), which has historically been rare in Mexico (Calva-Soto and Pavón 2018).

8.5 Challenges and Future Opportunities

As the title of this volume depicts, the Anthropocene is the current geological era, dominated by human activities and characterized by large-scale modifications of natural habitats that threaten the biodiversity at different levels: populations, species, and biological processes, resulting in alarming increases in extinction rates (Lewis and Maslin 2015; Turvey and Crees 2019). The recent ornithological literature is full of examples of how human perturbation factors impact Mexican avifauna. The relative risk of extinction and conservation gaps have been assessed for a number of important and emblematic species (Peterson and Navarro-Sigüenza 2016). With the historical and ecological perspectives explored in this chapter, we argue that it is time for a broader viewpoint that includes measurements and careful assessment of empirically quantified trends. Future research must go beyond simple descriptions of new avifaunal records, modeling predictions of individual species' distribution ranges, local/regional species lists, and examining contaminant levels in individuals' tissues. These are undoubtedly important questions, but they are not synonymous with researching the effects of human-induced environmental conditions on avifauna diversities, much less the degradation of ecosystem services and complex ecological systems in which birds interact.

Additional sources of variation, and their interactions, should be considered in future research to provide information about species' potential to adapt to future conditions (Araújo and Luoto 2007; Feeley et al. 2012; Silva et al. 2019). For example, the combined effects of GCC and human-modified areas could exacerbate the negative impact on tropical birds and increase extinction rates, especially endemic and range-restricted species (e.g., Jetz et al. 2007; Şekercioğlu 2011; Prieto-Torres et al. 2021b; Sierra-Morales et al. 2021). However, there is an important research gap in this area; certainly, species can be found in altered landscapes, but whether they successfully establish permanent reproductive populations in these transformed habitats is unknown for most species, especially in urban areas (Macgregor-Fors et al. 2021). Our understanding of the impacts of changing ecological conditions on natural and emerging disease systems (Peterson et al. 2004; Mendenhall et al. 2013) is similarly limited, especially considering that the risk of *Plasmodium* and *Haemoproteus* infection in birds is expected to increase with increasing temperatures on a global scale (Garamszegi 2011). Definitively, more research is needed on these topics, especially considering that these changes in species distribution may also affect the complex and dynamic networks of biotic interactions (Garamszegi et al. 2007; Şekercioğlu 2011). Future research should be focused on understanding the mechanisms behind birds' responses to anthropization and the consequences of changing bird diversity on ecosystem function (Salgado-Negret and Paz 2016). Moreover, the combined use of taxonomic, phylogenetic, and functional diversity maps could represent an essential step for mitigating the impacts of human activities (e.g., Devictor et al. 2010; Mazel et al. 2018; White et al. 2018) on Mexican birds and biota in general.

Finally, the unresolved question is whether, and to what extent, this information will make it possible to define management strategies to stop and reverse the negative effects of human influence on natural landscapes and their bird diversity. Therefore, there is an urgent need to review and assess the long-term implementation of restoration programs including habitat traits that favor native bird diversity such as natural vegetation coverage, the complexity of the vegetation, shrub and tree stratum density, resource availability, and habitat connectivity (Ortega-Álvarez and Lindig-Cisneros 2012; Zúñiga-Vega et al. 2019). In the case of aquatic environments, restoration efforts must consider the integrity of the littoral zone and microhabitats (see Ramírez-Bastida et al. 2018).

8.6 Conclusions

We hope that this analysis will spark the interest of biologists and conservationists to delve more deeply into the analysis of species diversity by incorporating multiple dimensions of diversity for avifauna across Mexico. Understanding the implications of environmental changes – on both evolutionary and ecological time scales – for biodiversity patterns is an essential step toward guiding effective conservation actions and management policies that protect both species and ecosystems in the long term.

We argue that the success of conservation strategies will depend on the explicit recognition and understanding of patterns and drivers of the biodiversity crisis. Therefore, we encourage researchers to perform studies that combine forecasts of both individual species range shifts and community-level taxonomic, phylogenetic, and functional biodiversity with systematic conservation planning tools. This integrative approach could inform new land-use planning and identification of priority groups and areas to avoid the loss of individual species and clades as well as community-level changes to species composition and loss of ecological traits. Ineffective execution of bird conservation in Mexico risks the loss of a major component of global bird diversity. Furthermorer, given their importance in tropical ecosystem functioning (Şekercioğlu 2006), an alteration in bird assemblages could also create a feedback loop with biodiversity loss and degradation of ecosystem services, threatening the well-being of nature and humanity in the future.

The ideas presented in this chapter are simply examples of a complex reality. In no case is a clear and detailed analysis available that crosses all the relevant scales and resolutions. We hope that more, better, and more integrative examples will emerge as this field further develops. Overall, we hope this review and conceptual essay will help provide the basic knowledge and guidance for future ecological and conservation studies and be considered by authorities in the decision-making processes for future projects (e.g., restoration, tourism, and environmental education).

Acknowledgments We thank the editors of the book for the useful comments and for inviting us to write this chapter; it has opened our eyes to the complexity of the biodiversity crisis and conservation across Mexico. Daniela Remolina-Figueroa, Jenifer Vargas, Giovani Medrano, Acis González, Ek Rodríguez, Luis Diego Martínez, Ilse Gutierrez, Alexis Mendoza, Oscar Brito, and Mónica Ramos, helped in surveying the literature used for analyses. We also thank the Dirección General de Asuntos del Personal Académico from Universidad Nacional Autónoma de México (DGAPA-UNAM; PAPIIT projects: IN215818; IN221920, IN214621; IA202822; IA210820), the Programa de Investigación en Cambio Climatico (PINCC-UNAM [grant to DAP-T and MCA]), the Rufford Foundation (DAP-T 16017-1; DAP-T 20284-2; DAP-T 28502B), the Consejo Nacional de Ciencia y Tecnología (CONACyT; project 152060), and the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO; project JM071) for the financial support that allowed us to perform the research and produce the illustrations that are included in this chapter. We thank BioPic (Biosphera Picture AC) for allowing the use of photos in Fig. 8.1.

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Chapter 9
Marine Birds

Yuri V. Albores-Barajas, Enriqueta Velarde, Cecilia Soldatini, Juan Esteban Martínez-Gómez, José Alfredo Castillo-Guerrero, Horacio de la Cueva, Reese Brand Phillips, Eduardo Palacios, and Dan Anderson

Contents

Y. V. Albores-Barajas
Consejo Nacional de Ciencia y Tecnología/Universidad Autónoma de Baja California Sur,
La Paz, B.C.S., Mexico

E. Velarde
Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana,
Boca del Río, Veracruz, Mexico

C. Soldatini (✉) · E. Palacios
CICESE Unidad La Paz, La Paz, B.C.S., Mexico
e-mail: csoldatini@cicese.mx

J. E. Martínez-Gómez
INECOL, Xalapa, Veracruz, Mexico

J. A. Castillo-Guerrero
Centro Universitario de la Costa Sur, Universidad de Guadalajara,
San Patricio-Melaque, Jalisco, Mexico

H. de la Cueva
CICESE, Ensenada, B.C., Mexico

R. B. Phillips
Invasive Species Biologists, Anchorage, Alaska, USA

D. Anderson
University of California, Davis, CA, USA

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_9

9.1 Introduction

Seabirds have evolved to take advantage of ocean resources. Winds, currents, food, oceanic islands, and marine environments in general are exploited by seabirds to complete their life cycles. Mexico has more than 11,000 km of coastline and more than 3000 islands, some as far as 700 km from the coast, providing the country with 3,269,386 km^2 of Economic Exclusive Zone (EEZ), and ranking it thirteenth in the world. Such an extensive EEZ serves as a vital refuge for marine life, making Mexico a critical country for the conservation of marine animals. The country ranks third for the number of species of seabirds and second for the number of endemic species (Croxall et al. 2012). Such high diversity reflects the heterogeneity in the environmental conditions across the country, from temperate waters of Mexico's northern Pacific to its warm tropical waters in the Caribbean.

The adaptation of seabirds to the marine environment has taken thousands of years. Unfortunately, most seabird species have not had time to adapt to the rapidly changing conditions that humans are creating. With human activities altering climate patterns, releasing pollutants into the environment, and warming waters, seabirds are struggling to meet their energetic requirements, particularly during adverse climatic conditions. For example, the frequency of El Niño events has increased, probably as a result of climate change; consequently, the oceanic thermocline is deeper, altering biological cycles and access to prey. Inevitably, all these changes will also alter the biological cycles of seabirds.

We summarize the information on seabirds in Mexico and try to forecast what is the future scenario for them. We start by defining the current status of seabirds. We then address the threats to seabirds, elucidate possible putative scenarios for specific species, where some populations may increase and decrease, and then close with possible actions to improve seabirds' conservation status.

9.1.1 Seabirds as Indicators

Since our early occupation of coastal and marine areas, humans have used seabirds' presence and behavior as indicators of the conditions in these environments. This is illustrated by the deep knowledge of extant hunter-gatherer-fishers' cultures such as the indigenous Comcaac (Seri), of the coastal region of central Sonora, Mexico, who name some seabirds according to their behavior (Morales-Vera and Velarde 2014). To name just a few examples of seabirds: Least Petrel (*Hydrobates microsoma*): “Xepe iti coquéht” = one that bounces on the sea, Brown Pelican (*Pelecanus occidentalis*): “Ziic cozáz” = bird that dives, Skua (*Stercorarius* spp.): “Ziic cacáataj” = bird that causes vomit, and “Ziic cöcaaitim” = bird that chases other birds, Skimmer (*Rynchops niger*): “Xepe czexe” = one that cuts the sea.

Seabirds have several characteristics that make them excellent bioindicators of environmental variability. They are conspicuous and generally breed in large aggregations and regularly occur in specific locations, thus are relatively easy to locate, observe, and study. This allows us to draw information from these habitats and, use them as indicators as many studies have demonstrated (Cairns 1987; Montevecchi 1993; Montevecchi and Myers 1995; Furness and Camphuysen 1997; Velarde et al. 2019).

During their life cycle, seabirds roam over vast areas in the ocean and are, therefore, excellent bioindicators of the health and status of the oceans (Furness and Camphuysen 1997). Their breeding success can be an indicator of food abundance. Analysis of feathers, blood or eggshells can provide information about the presence of pollutants. Alteration of the phenology may indicate a change in the climate patterns. Therefore, by studying different aspects of the seabirds, we can get a picture of the ecosystem’s health. Breeding success, chick growth, behavior, colony size can all be used as indicators of ecosystem health (Parsons et al. 2008). From the human perspective, seabirds can help to establish a fishing quota. A season with high breeding success indicates resource abundance, and potentially, less competition between fisheries and seabirds for food. On the other hand, a poor breeding season may indicate inadequate resources at sea, and as a consequence, competition with fisheries may have a more significant effect on seabirds and other marine fauna (Velarde et al. 2015a, b, c; Genovart et al. 2016; Oppel et al. 2018; Furness and Tasker 2000).

Recently, a meta-analysis involving many studies and seabird species, including some carried out in Mexico (Sydeman et al. 2021), showed that climate change and other impacts of human activities are causing profound effects on the productivity of marine ecosystems. Ocean warming has been shown to have different effects on the breeding success of seabirds in the Northern and Southern Hemispheres (Peterson et al. 2006; Sydeman et al. 2009). The most substantial effects can be found in fish-eating and surface-foraging seabirds in the Northern Hemisphere. This study shows how seabirds track these hemispheric differences and how this information can be used to suggest specific ocean management strategies in relation to the hemispheric differences: the Northern Hemisphere, needs tactical, climate-based recovery plans for forage fish resources, which are depleted or very close to. The protection of large marine ecosystems is long overdue to sustain marine food webs and maintain predator productivity. Seabirds, as marine predators, enable us to identify ecosystem changes in remote areas and help us identify and comprehend the impacts occurring in the ocean and their scales.

9.2 Current Status

Despite a large number of seabird species, little effort has been directed at obtaining information and updating their conservation status in Mexican oceans. So far, most of the studies concentrate on the northwest, where also the largest biodiversity and abundance occurs (Albores-Barajas et al. 2020), with the southern Pacific areas of Mexico largely neglected and very few studies focusing on the Gulf of Mexico (GoM) and Mexican Caribbean (MC) where, also due to historically greater human impact, very few nesting colonies remain. These studies mostly comprise offshore censuses in the Veracruz Reef System, and some coastal surveys close to the Tuxpan Reef System, both reef areas off the western coast of the GoM (Velarde et al. 2015a, b, c; Arguelles et al. 2015; Arguelles-Jimenez et al. 2019). Information on seabird nesting colonies is scarce and mainly comprise Alacranes Reef, North of the Yucatan Peninsula and other reefs such as Cayo Arcas and Cayo Arenas in the Sonda de Campeche (Arenas 2012; Morales-Vera et al. 2017; Tunnel and Chapman 2000). The most recently updated species list for the GoM is compiled by Gallardo et al. (2004), and population trends are unknown. Other risks such as oil spills have been documented for other large marine vertebrates, with negative effects. Similar impacts could be expected for seabirds.

Most of the studies focused on Mexican seabirds are centered on a single colony (See Albores-Barajas et al. 2020) or single species. For instance, the Blue-footed Booby (*Sula nebouxi*) colony from Isla Isabel is well known (Drummond et al. 2008, 2011; Ancona et al. 2018), or the seabird on Isla Rasa (Velarde and Anderson 1994; Velarde and Ezcurra 2002; Velarde et al. 2005), but there is no information on the whereabouts of other colonies in the Gulf of California (GoC).

9.3 Threats and Conservation Actions

Human population growth in the last centuries with consequent expansion of urban areas and increasing human activities linked either to urban development or tourism is having direct and indirect impacts on breeding populations of seabirds (Nisbet 1981; Culik and Wilson 1991; Carney and Sydeman 1999). Below, these impacts are discussed.

9.3.1 Climate Change

In addition to habitat loss, pollution, and introduced predators or competitors, climate change is considered one the primary threats to the persistence of many avian populations (Møller et al. 2004; Halpern et al. 2007, Hoegh-Guldberg and Bruno 2010; Maxwell et al. 2013). It may affect seabirds at different scales, such as distribution, phenology, population dynamics, and demographic traits (Trenberth and

Hoar 1997; Perriman et al. 2000; Walther et al. 2002; Moe et al. 2009; Sydeman et al. 2012). Population resilience to climate change (Jenouvrier 2013), i.e., the species ability to cope with new environmental conditions, is the result of adaptation, phenotypic plasticity, and homeostasis, which are essential defenses against extinction (Moller 2008).

Seabirds are sentinels of changes occurring at large scales because they are directly affected by environmental variability (Wolf et al. 2009; Barbraud et al. 2012; Watanuki and Ito 2012; Meier et al. 2017). Their at-sea distribution is influenced by environmental and trophic conditions, which reflect optimal ecological niches (Furness and Camphuysen 1997; Moreno et al. 2016). Oceanographic conditions affecting prey availability directly influence seabird population dynamics (Furness and Tasker 2000; Frederiksen et al. 2004, 2008). A few abundant mid-trophic species, such as small pelagic schooling fish, dominate pelagic ecosystems (Rice 1995; Batten et al. 2006), playing an important role in ecosystem dynamics regulation. In fact, small pelagic schooling fish function as key prey of predatory fish, marine mammals, and seabirds by channeling energy and nutrients from planktonic primary and secondary producers to top predators (Høines and Bergstad 1999; Furness 2002; Gende and Sigler 2006). For this reason, bottom-up climatic forces may be influential for a variety of marine taxa. Global warming may induce oscillatory environmental conditions with the consequence of a temporal mismatch between life-history strategies at different trophic levels (Jenouvrier et al. 2008; Ainley and Hyrenbach 2010; Barbraud et al. 2011; Sydeman et al. 2012).

Although seabirds evolved in marine systems characterized by cyclic climatic events, they have shown to be negatively affected by the rapid increase of environmental stochasticity. The effects of extreme climatic events are not well understood, some cases remain unexplained with contradictory results (Croxall et al. 2002; Forcada and Trathan 2009; Jenouvrier et al. 2015). Regarding breeding performance, it is documented that sea surface temperature (SST) may have a direct effect by changing the distribution or abundance of important prey species of seabirds (Frederiksen et al. 2008). Unfavorable climate conditions, such as warm SSTs, may induce seabirds to skip breeding altogether (Jenouvrier et al. 2005; Olivier et al. 2005; Cubaynes et al. 2011; Soldatini et al. 2016), or it may affect nest-site conditions (Chambers et al. 2011; Moreno and Møller 2011; Soldatini et al. 2014).

Seabirds are central-place foragers (Quintana et al. 2011); as such, during breeding, they are strongly influenced by environmental stochasticity affecting their foraging areas. In times of limited food availability, parental foraging strategies are likely influenced to some degree by inter- and intraspecies competition and may be mediated by spatial segregation at sea (Hyrenbach et al. 2002; Fernandez-Juricic et al. 2002; Phalan et al. 2007; Kappes et al. 2010; Hedd et al. 2014; Paiva et al. 2017, Soldatini et al. 2019). Another strategy, consistent with "the prudent parent hypothesis" (Le Bohec et al. 2007; Drent and Daan 1980; Cam et al. 1998), is to skip breeding during years with unfavorable environmental conditions to have better chances in subsequent years (Cubaynes et al. 2011; Shoji et al. 2015; Soldatini et al. 2016).

In Mexico, the effects of climate variability have been studied in a few species, mainly those that depend on the upwelling system of the GoC. In general, such species exhibit high sensitivity to variations in ocean conditions. For example, with slight increases in SST, Blue-footed Boobies modify their foraging behavior and diet (Castillo-Guerrero and Mellink 2011; Ancona et al. 2012; Gilmour et al. 2018), delay breeding onset, decrease their clutch size and breeding success, and offspring grow slower (Ancona et al. 2011). The sex ratio of offspring is also sensitive to ocean warming as during warm years, the cohorts are male-biased (Torres and Drummond 1999). Also, the demography of this species is influenced by climatic variations. Warm water winters increase mortality slightly in adults, but notably in the young (Oro et al. 2010), and the probability of recruitment is affected by the temperature before and during the reproductive season, in interaction with age and sex (Oro et al. 2010). However, Ancona and Drummond (2013), who studied a Blue-footed Booby colony on Isla Isabel in the southern GoC, found a transgenerational effect in females who were daughters of females who experienced ENSO conditions in their natal year. These second-generation females showed improved breeding success, which they interpreted as developmental plasticity of the species. This enabled it to neutralize potential long-term impacts of harsh climatic conditions experienced early in life by individuals of specific cohorts.

Similarly, in the Black-vented Shearwater (*Puffinus opisthomelas*), whose main colony is on Isla Natividad, in the southern part of the California Current System, West from the coast of central Baja California Peninsula, the onset of breeding may be delayed up to 1 month in years with unfavorable conditions, namely El Niño years (Soldatini et al. 2021). The at-sea distribution of the species is also affected by food scarcity with sexual segregation during warmer SST years (Soldatini et al. 2019), and the carry-over effect is reflected by reduced feather growth, mainly in females due to higher metabolic costs (Soldatini et al. 2021).

It has been shown that climate change has an increasingly negative effect on breeding success and changes the breeding distribution in seabird species worldwide (Humphries et al. 2015). These effects have been documented in some seabird species that consume small-pelagic fish in the GoC, such as Elegant Tern (*Thalasseus elegans*), Heermann's Gull (*Larus heermanni*), and California Brown Pelican (Anderson et al. 2013, 2017). In some of these studies, the effect of climate change has also been compounded by overfishing of forage fish species (Velarde et al. 2015a, b, c; Velarde and Ezcurra 2018). Elegant Terns have slowly shifted their breeding distribution to the Pacific coast, with ever smaller numbers nesting in their main breeding colony of Isla Rasa in the Midriff Island Region of the GoC. Because forage fish sustain a large component of the food web, the negative effect is not restricted only to the breeding and distribution of seabirds but also reverberates throughout the whole food web (Botsford et al. 1997; Mellink 2003; Sydeman et al. 2013; Velarde et al. 2013). The so-called BLOB, a regional but extreme environmental fluctuation, has affected some eastern boundary current systems and had profound effects at all levels of the trophic web (Varela et al. 2021; Weber et al. 2021).

Species with tropical affinity have been less studied; however, they seem less sensitive to the effects of variations in sea temperature than upwelling specialists.

For the Red-billed Tropicbird (*Phaeton aethereus*), although foraging behavior, parental attendance, and diet adjustments are made in warm years, they can maintain their reproductive activity and some reproductive success even in El Niño years (Castillo-Guerrero et al. 2011). In specific locations, such as Isla Clarion, it seems that local conditions remain relatively homogeneous between years, and effects related to larger-scale warm events such as El Niño are not evident in foraging behavior and areas used at sea for Masked Boobies (Lerma et al. 2020). In these cases, there are no studies evaluating the demographic consequences or carry-over effects.

9.3.2 Contaminants

Seabirds and other marine wildlife are potentially affected by various pollutants. In many ways, pollutants may interact with other factors to bring about unwanted ecological effects on marine wildlife through synergism, antagonism, and additive effects (Eeva et al. 2006; Erikstad et al. 2011; Tanaka et al. 2020). Due to the mobility of most seabirds, contaminant sources for widespread patterns are likely to be mostly from nonpoint-source origins, such as aerial fallout. Ocean discharges are more likely to affect local populations. Both sources of contaminants, either local or widely distributed, must be considered important. Regional locales and surrounding terrestrial lands are also important in the determination of pollutant patterns observed in Mexican seabirds, and we can envision at least three areas of consideration, the GoC, the GoM -MC, and open coastal areas. The coastline in northwestern Baja California is an area where extensive pollution research has been done; in the North, associated with the Southern California Bight (SCB) region and the southern California Current area. There are many publications concerning different contaminants. Because of the extensive nature of the published work, few of those studies are mentioned here.

Ocean pollution is a global concern. Many pollutants from urban, industrial, and agricultural use are transported by rivers and runoff reaching marine ecosystems (Cravo et al. 2012). Some due to their high persistence and affinity for organic compounds are accumulated and transferred through the trophic chain (Wu et al. 2009). This transfer often causes biomagnification in tissues of top predators (including seabirds), which depending on the magnitude, can affect their behavior, physiology, reproductive performance, and demography (Anderson et al. 1975; Thompson and Hamer 2000; Burger and Gochfeld 2001; Goutte et al. 2014; Oudi et al. 2019).

The potential of seabirds as biomonitors of pollutants is clear (Furness and Camphuysen 1997; Elliott and Elliott 2013; Gilmour et al. 2019), and in some countries, long-term monitoring programs have been established as a tool in decision-making on environmental and public health. In Mexico, information about pollutants and their effects on seabirds is very scarce. The concentrations of some organochlorines and heavy metals have been characterized for a few species and only in specific locations and years. There are no historical data or long-term studies to assess the current state and trends.

9.3.2.1 Organochlorines

In Mexico, there are few studies on the dynamics and effects of this group of pollutants on seabirds. In northwestern Baja California, the concentration of DDT and DDE in Western Gull (*Larus occidentalis*) eggs during 1991 was lower than in southern California during the 1970s, and no effect on eggshell thickness was detected (Jimenez-Castro et al. 1995). In the GoC and central Pacific, low concentrations of three organochlorines (from 13 analyzed) were detected in Brown Booby eggs from nine colonies, without a relationship between DDE concentration and eggshell thickness (Mellink et al. 2009). In central-north Sinaloa, relatively low concentrations of 19 organochlorines were reported in plasma from breeding Blue-footed Boobies, with no apparent relationship to body condition, heterophil/lymphocyte ratio, and micronucleated erythrocytes (Piña-Ortiz et al. 2021). These studies indicate that seabirds remain exposed to a vast diversity of OCPs but in low concentrations, reflecting a historical exposure followed by a subsequent reduction and disuse. Although the aforementioned studies did not report adverse effects, chronic interactive effects between different groups of pollutants (including organochlorines) cannot be ruled out.

In the Mexican portion of the GoM, there is only one study that analyzed the persistent organic pollutants and polycyclic aromatic hydrocarbons. This was conducted in eggs of the Least Tern (*Sternula antillarum*) and Sooty Tern (*Onychoprion fuscatus*) in Terminos Lagoon and Arrecife Alacranes. In Least Tern eggs, high concentrations of DDE (>12 ppm) were detected, which exceeded the values considered detrimental for reproduction (low hatchability, reduced shell thickness, and low reproductive success) of other species of aquatic birds. However, the OCP's values in general were lower than those reported for the northern part of the GoM (US portion). The study included 2 years of data in which there were notable inter-annual variations (up to two orders of magnitude; Vallarino and Von Osten 2017).

9.3.2.2 Heavy Metals (Mercury, Cadmium, and Lead)

As for other groups of pollutants, studies on heavy metals and their effects on seabirds in Mexico are few. Mercury concentrations have been characterized in a few species, at specific sites and with a temporal coverage of only one or 2 years (e.g., Ceyca et al. 2016; Lerma et al. 2016; Soldatini et al. 2020).

In a study that included eight species and several colonies along the coast of Sinaloa, interspecies differences were detected in the concentration of Hg and Cd in eggs. Such differences were related to foraging ecology and diet. Piscivorous species had the highest concentrations of Hg (Ceyca et al. 2016). There were variations between study years and between sampling sites indicating that sources at the local scale, as well as changes either in oceanographic conditions or in continental runoff influence the concentrations of these pollutants (Ceyca et al. 2016).

In the Blue-footed Booby, blood mercury concentrations varied within the breeding season at Isla El Ranchod, Sinaloa. A higher concentration of mercury was found in the early stages of breeding, decreasing gradually as breeding advanced, indicating a gradual decrease in the environmental availability of mercury. Males and adults had higher mercury concentrations than females and chicks. Although Hg concentrations in the blood of Blue-footed Booby adults were among the levels known to cause adverse effects in other bird species, no evident effects on breeding performance (hatching and fledging success) were detected (Lerma et al. 2016).

A couple of studies in Mexico have focused on heavy metals. The first in which an adverse effect of mercury exposure has been detected was in Black-vented Shearwater nesting on Isla Natividad, in the southern portion of the California Current System. Males and females had similar Hg concentrations. Mercury exposure was related to habitat use at an individual scale. Shearwaters that predominantly forage in coastal areas (reflected by δ13C) exhibited higher Hg concentration than those using offshore areas. Higher concentrations of Hg were related to lower activity of the antioxidant enzyme glutathione peroxidase and lower nonenzymatic antioxidant capacity (Soldatini et al. 2020). These adverse effects could have implications for the conservation of this species because 95% of the global population breeds in this colony. The other study focused on Ospreys (*Pandion haliaetus*), where they found low levels of mercury in the GoC (Henny and Anderson 1979).

9.3.2.3 Oil Spills

Oil drilling activities are widespread in the GoM (Haney et al. 2019). Pemex (Petróleos Mexicanos), the state-owned Mexican oil monopoly either drills or leases drill concessions in the Sonda de Campeche waters. Oil is then moved to the mainland in tankers for export or refinement.

In June 1979, Mexico experienced its major marine oil spill with the explosion of the platform Ixtoc I that caused the first massive oil spill in a tropical marine environment. More than 3.4 million barrels of crude oil were spilled in an ecosystem formerly renowned for its pristine conditions (Soto et al. 2014), affecting seabirds and all other marine life. No major oil spill has been reported in Mexican waters since that time. However, given the large oil reserves and activities in the Sonda de Campeche, combined with budget constraints that compromise equipment maintenance, the possibility of another oil spill remains. Three decades later, in April 2010, the Bristish Petroleum Deepwater Horizon oil spill surpassed the effects of Ixtoc I. releasing into the ocean approximately 4.9 million barrels and killing about 200,000 seabirds in the southern coast of United States (Haney et al. 2014; Makocha et al. 2019).

After the Ixtoc I oil spill in the northern GoM, PEMEX became concerned with the legal and monetary costs of a major oil spill in Mexican waters that could move through the GoM toward USA waters. PEMEX and the Secretaría de Energía funded a program on the order of 75 million dollars, CIGOM (Consorcio de Investigación del Golfo de México), to model the effects of such an oil spill. Unfortunately, seabirds were left out of the study, but the studies were done on other large air-breathing vertebrates, marine mammals, and sea turtles (Liceaga Correa 2021; García Aguilar

2021) on cetaceans and can foresee the future of any seabird that is touched by the oil spill while feeding or resting. Nonetheless, it is essential to create and train response groups to cope and clean the oil contaminated ocean, beaches, plants, and fauna, including birds, if a major oil spill occurs.

9.3.2.4 Emerging Pollutants

During the last decades, the presence of plastics in the marine environment has increased, but only recently has a large amount of research focused on the issue. It has been less than 30 years, since first detection of plastic pieces in seabirds' guts. However, the effects are enormous, and evidence is mounting every day about the adverse effects of plastics present in the marine food web. In Mexico, there are no published studies about the presence of plastics on seabirds' diets, but there is an indication that they might, so further studies are needed.

Further regarding POPs (Persistent Organic Pollutants), and other contaminants in the GoC, the surrounding desert environment and lack of riverine inflow from the Colorado River system (e.g., Brusca et al. 2016) probably help "protect" the northern part of the GoC from many forms of contamination. Farther south, however, residue levels of many pollutants have been shown to be of more concern, as has been demonstrated for toxic blooms (Beman et al. 2005). Yet, increasing human activities on lands adjacent to coastal areas, expanding agriculture, and greater human inhabitants and their potential negative effects, are expected to increase their pollutant contributions in the future (Lluch-Cota et al. 2007).

Pollutant-induced eggshell thinning is often measured as a critical biomarker tool in birds, it is especially useful in determining levels of DDE, a persistent metabolite of the insecticide DDT, but also suggests through its dose-response, other contaminant levels that "travel" with DDE due to similar pharmacodynamics. In other geographical areas, for example, Arctic-dwelling Ivory Gulls (*Pagophilia eburnea*) containing low levels of POPs have been associated even with vitamin deficiency levels, as biomarkers (Miljeteig et al. 2012). These few examples illustrate just how subtle and complex small amounts of pollutants might affect seabirds and other marine wildlife, making it difficult to specifically identify single causes of physiological damage or to have the ability to measure minuscule effects. For example, endocrine disruptors are both very widespread (mostly as nonpoint-source contaminants) and act at very low concentrations (e.g., Tanabe 2002).

Mellink et al. (2009) demonstrated encouraging recoveries of POP effects in the GoC from a previous period of more intense organochlorine contamination. Similar recoveries were found in the Southern California Bight by Anderson et al. (1976) for the California Brown Pelican, along with many other species worldwide. Thus, regarding POPs in general, there has likely been a significant decrease in most areas, worldwide, brought about by environmental regulation and management backed by extensive scientific research. Yet the persistence worldwide of many POPs, such as DDE, has resulted in many of these compounds being termed by many ecotoxicologists as “Legacy Toxicants” (Clatterbuck et al. 2018), and represent continuing threats to marine life (ex. Jepson and Law 2016).

Vander Pol et al. (2012) first reported bromated flame retardants in pelican eggs from the GoC, along with a large spectrum of POPs, but at very low levels. Anderson et al. (in prep.) have shown many of these classes of pollutants in the GoC to be very low in comparison to other areas of North America (ex. regarding Hg as a pollutant and sulfur as a nutrient).

9.4 Fisheries, Overfishing, and Bycatch

There are two main interactions of seabirds and fisheries: (1) Overfishing of the seabird’s food resources and (2) Seabird’s bycatch-related mortality. These two factors, together with the introduction of exotic species in their nesting habitat (treated separately in this work), are arguably the main causes of seabird conservation concerns worldwide, as well as in Mexico.

Forage fish are one of the most important food sources for seabirds, as well as for other marine vertebrates (García-Rodríguez and Aurioles-Gamboa 2004). Due to a constantly developing industry, overfishing of these resources has increased through time reaching an over exploiting fishing effort with negative effects to the ecosystems (Cisneros-Mata et al. 1996; Gutierrez-Benitez et al. 2019; Girón-Nava et al. 2021). These effects are just now beginning to be detected and quantified, particularly in those processes that are driven by bottom-up trophic mechanisms (Lluch-Cota et al. 2007; Velarde et al. 2015a, b, c).

There is a general and growing consensus that overfishing of marine species that seabirds feed on, and particularly forage fish, is one of the main threats to seabird populations. This has had an increasingly negative effect on seabird populations through a reduction of breeding success and increased mortality of independent immatures and adult seabirds (Ainley et al. 1994; Furness and Tasker 2000; Croxall et al. 2012; Paleczny et al. 2015). Additionally, the negative impact of overfishing exacerbates the effects of low productivity of the ocean due to oceanographic conditions, both naturally occurring ones such as El Niño Southern Oscillation (ENSO), and the more recently observed due to climate change, such as The “BLOB” (Varela et al. 2021; Weber et al. 2021). Examples in Mexico importantly include the GoC where the forage fish fishing industry has developed and grown considerably since the late 1960s, resulting in overfishing of the food resources of seabirds and other marine species.

Failure to establish colonies, nest abandonment, high chick mortality, and shifting of breeding areas, mainly along the GoC, Pacific coast of NW Mexico, and the southern California coast, have been observed for the Elegant Tern, Heermann’s Gull and Brown Pelican (DWA field observations). These reports occur where the effect of overfishing in the GoC is compounded with the occurrence of years of anomalously warm sea surface temperature (SST), which further reduces forage fish availability (Velarde et al. 2015a, b, c). In recent decades, most importantly in the 2000s, climate change has added to the negative effects of overfishing and warming SST, resulting in an increased frequency of anomalously warm SST years. For example, in the Midriff Island Region (MIR) of the GoC, the average frequency of anomalously warm years, mainly due to ENSO, was about one every decade. However, in the last decades, the frequency of ENSO years plus years of regional positive anomalies has increased to about five every decade (Velarde and Ezcurra 2018). This combination of SST anomalously warm years and overfishing of the seabird's prey base results in an almost continuous lack of adequate food supply, negatively impacting breeding success and survival of young and adult individuals in the area.

Bycatch is presently one of the most important mortality factors for seabirds (Ellis et al. 2013). Most fishing gear, whether artisanal or industrial, generates some type of seabird bycatch, but industrial fishery is the one that generates the highest death toll (Lewison et al. 2014). However, due to the methods used to document bycatch, it is estimated that the death toll is generally underestimated (Brothers et al. 2010), while indirect mortality due to interaction with fisheries is seldom included in the seabird death estimates (Huin and Croxall 1996). Seabird bycatch impact in Mexico has been poorly evaluated (Suazo et al. 2017) and the few studies that are underway are in their initial phase. However, there is evidence of high seabird bycatch during the fishing operations of the sardine fishing fleet that operates in the GoC, off the ports of Guaymas and Yavaros in the State of Sonora (Velarde et al. 2018). Bycatch has been found to affect up to 17 species, but mainly the California Brown Pelican, followed by Blue-footed Booby and Brown Booby (*S. leucogaster*), the first two listed in the Mexican protected species list (NOM-059-SEMARNAT-2010). For example: during the fishing operations of the Sonora fish fishery in the GoC, it is estimated that an average of about 1000 pelicans die, victims of bycatch, every month, most of which are birds with oiled plumage from oil residues from caught fish. Oiled birds are unable to fly, thermoregulate, and become waterlogged (Morandin and O'hara 2014), and the effect of fish oil on the plumage is considered to be worse than petroleum oil. This mortality rate has been estimated to be three times higher than the estimated natural mortality and so quadruples the mortality rate of the species in the central GoC. Evidence of population decline has been observed in the pelican nesting population in breeding colonies monitored in the area. For example, the nesting population of Brown Pelican on Isla San Pedro Martir has been observed to show a significant declining trend between 1970 and 2015, particularly after about 1990, dropping from 6000 to 2000 nests (Anderson et al. 2017) and this decline could be attributed to the high mortality of individuals in the bycatch. There are other similar fleets operating off the coast of the states of Baja California Sur and Sinaloa in the GoC, and off the states of Baja California and Baja California Sur along the Pacific side, but there is no public data available from these fleets yet. Therefore, it would be important to encourage the managers of these fleets to implement observers' programs that could produce information on this problem for each one of them. Besides, it will be important to estimate the overlap between fisheries and seabirds' feeding areas.

9.4.1 Bycatch Reduction

There is an urgent need to document and evaluate seabird's (as well as other species) bycatch generated by all fishing gear and operations, but mainly the industrial fishing operations. Although efforts already exist in different parts of the world, Mexico is not evaluating these or, if some evaluations of fishing operations have been conducted, no information is available. Actions needed are: (1) To evaluate bycatch by independent observer programs in all fisheries (mainly industrial) using all types of fishing gear, and (2) That the generated information is available and open. This will generate valuable information for a better understanding of this problem trust in the sustainability of the fishing operations, and the veracity of the information. Also, mitigation measures need to be established according to the results of the observers' programs, to reduce bycatch. Independent observer's programs to evaluate bycatch are a must if complete and unbiased records are to be obtained.

The certification of fishery products has been created to provide the consumers with an incentive to ideally choose the best environmentally-responsible sound product. This is one which has been obtained in a sustainable fashion, such as following evaluation of the species' population status, avoiding ecosystem negative effects, avoiding bycatch of other species, and using the best fishery methods. However, many certifications have been given to fisheries that many scientists or other stakeholders do not consider to be following the standards that would allow them to be certified (Christian et al. 2013; and references therein). These and other authors have identified loopholes in the certification standards and weak interpretation of the principles by third-party certifiers. This has caused fisheries that are considered controversial to be certified, but without informing the consumer about the controversy. This has caused some conservation organizations and/or other stakeholders such as other fishermen or even academics, to file formal objections to the certification of these controversial fisheries, or to provide evidence of undeserved eco-labeling, or lenient interpretation of the certification standards. Furthermore, most objections filed are not upheld, worsening the disputes between parties and causing distrust of the certified fishery and misleading consumers.

9.5 Invasive Species

9.5.1 Threats

Globally, invasive species are the principal cause of island extinctions (Reaser et al. 2007) and are considered the primary threat to threatened seabird populations (Croxall et al. 2012; Szabo et al. 2012; Dias et al. 2019). Most notable are predatory mammals, such as dogs (*Canis lupus familiaris*), cats (*Felis catus*), rats (*Rattus* spp.), and mice (*Mus musculus*), which prey on seabird adults, chicks, and eggs

(Bonnaud et al. 2012). Invasive ungulates (e.g., goats [*Capra hircus*], sheep [*Ovis aries*], donkeys [*Equus asinus*]) have a detrimental effect on seabirds via destruction of habitat and burrows, the latter potentially killing chicks or eggs (McChesney and Tershy 1998). Similarly, invasive European rabbits (*Oryctolagus cuniculus*) destroy vegetation, resulting in increased erosion and impacts to burrowing substrate (in Brodier et al. 2011) and can compete with seabirds for nest burrows. Not only invasive mammals have detrimental impacts on seabirds. In Hawaii, invasive Barn Owls (*Tyto alba*) are known to prey on eight species of seabirds, including the U.S. federally listed Newell's Shearwater (*Puffinus newelli*) and Hawaiian Petrel (*Pterodroma sandwichensis*; Raine et al. 2019). On Ascension Island and in Hawaii, Indian Mynas (*Acridotheres tristis*) preyed heavily on Sooty Tern (*P. griseus*) and Wedge-tailed Shearwater (*P. pacificus*) eggs, respectively (Hughes et al. 2008; Byrd 1979). Although more insidious than invasive vertebrates, invasive invertebrates (e.g., ants) have been introduced to islands worldwide and are recently being recognized as a major threat to nesting seabirds (Plentovich et al. 2008). Lastly, invasive plants may pose a threat to their reproductive habitat (e.g., Schirmel et al. 2015).

9.5.2 Impacts

Overall impacts on Mexico's insular populations mirror those of global populations (Croxall et al. 2012), with most of the insular extinctions and extirpations attributable to invasive mammals (Wood et al. 2017). In Mexico, islands comprise 0.2% of the total land mass, yet 50% of the nation's historic extinctions are from islands, which currently harbor 18% of the endangered mammals and birds (Aguirre-Muñoz et al. 2011). Although seabirds have suffered only a single extinction, the Guadalupe Petrel (*Oceonodroma macrodactyla*; Jehl and Everett 1985), at least 28 seabird populations have been extirpated (Aguirre-Muñoz et al. 2009) and many more impacted by invasive mammals, as well as human disturbance and contaminants (Aguirre-Muñoz et al. 2018). Feral cats were implicated in the decline and extirpation of Xantus's Murrelets (*Synthliboramphus hypoleucus*) on multiple Pacific islands off Baja California (Jehl and Bond 1975). On Natividad, cats are thought to have extirpated Xantus's Murrelets and Cassin's Auklet (*Ptychoramphus aleuticus*) and greatly impacted the Black-vented Shearwater (*Puffinus opisthomelas*; Keitt and Tershy 2003). On Isla Isabel, feral cats were killing 23–33% of nesting Sooty Terns (*Onychoprio*n *fuscatus*) each year and between 1991 and 2004 the tern population declined from 150,000 to roughly 1000 individuals (Osorio and Torres 1991). Following the eradication of cats in 1998, sooty tern nest mortality dropped below 2% (Rodríguez et al. 2006). In the Revillagigedo Archipelago, Townsends's Shearwaters (*Puffinus aruicularis auricularis*) currently breed on Socorro and Clarion islands (Martínez-Gómez et al. 2015, Ortiz-Pulido et al. 2016). On Isla Clarion, predation from feral pigs and habitat destruction induced by European rabbits decimated its population (Martínez-Gómez and Jacobsen 2004; Howell and Webb 1989). On Isla Socorro, their main colony survives despite extensive habitat degradation caused by feral sheep (*Ovis aries*), which were eradicated in 2012 (Ortiz-Alcaraz et al. 2019); however, predation from feral cats continues to threaten this shearwater population on Isla Socorro (Martínez-Gómez and Jacobsen 2004; Ortiz-Pulido et al. 2016).

Although invasive rodents are widely distributed on Mexico's islands, documentation of their impacts on seabirds is difficult to confirm, thus evidence is often minimal and anecdotal. Despite the lack of causal evidence, managers have often adopted the "precautionary principle" and proceeded with invasive rodent eradication because of the documented evidence of impacts to native species elsewhere. Ironically, some of the strongest evidence of invasive rodents' impacts on Mexican seabirds arises from population recoveries post eradication. Following rodent eradication on Farallon de San Ignacio, Red-billed Tropicbirds (*Phaethon aethereus*) showed a 60% increase in nests post eradication, as well as an increase in hatching success (Samaniego-Herrera et al. 2011). On San Pedro de Martir, Craveri's Murrelet (*Synthliboramphus craveri*) began nesting on the island again after rodent removal. On Isla Rasa, Heerman's Gull (*Larus heermanni*) increased breeding success fivefold and Elegant Terns (*Thalasseus elegans*) had a significant increase in the number of nests post eradication. On Isla San Roque, Brandt's Cormorant (*Phalacrocorax penicillatus*) and Cassin's Auklet (*Ptychoramphus aleuticus*) are both nesting again after years of extirpation (Samaniego-Herrera et al. 2011, references therein). Despite these success stories, recovery for some species requires further restoration efforts to attract birds to the islands from which they were extirpated (Aguirre-Muñoz et al. 2011).

9.5.3 Eradication and Monitoring

Eradication of invasive mammals and monitoring of invasive species and threatened species are of utmost importance to secure viable seabird populations (Campbell et al. 2011; Nogales et al. 2013). Eradication efforts have yielded important conservation gains for Mexican seabirds. In total, 60 populations of invasive mammals have been removed from 39 islands, with 30 of these islands now completely free of invasive mammals (Aguirre-Muñoz et al. 2018). However, these efforts have not entirely averted the extinction of endangered seabirds since 83 eradications on 34 islands await (McChesney and Tershy 1998; Aguirre-Muñoz et al. 2011; Koleff et al. 2021). Recent efforts have identified and ranked Mexican islands or archipelagos that warrant immediate conservation action (Latofski et al. 2014; Albores-Barajas et al. 2020, 2021). Albores-Barajas et al. (2020, 2021) specifically prioritized islands or archipelagos based on importance to seabirds and identified 91 islands or archipelagos that are important to seabird conservation. Ten islands or archipelagos received a "high conservation priority" ranking, all of which have seabird populations threatened by invasive mammals. Four of these high priority islands are among Mexico's largest islands: Ángel de la Guarda (936 km^2), Cedros (357 km^2), Guadalupe (242 km^2), and Socorro (132 km^2).

Several erradication campaigns in Mexico have not been successful or have been in place for many years. For instance, on Isla Espíritu Santo (80 km^2), feral goats still remain despite almost 20 years of efforts to remove them (Aguirre-Muñoz et al. 2004; Aguirre-Muñoz et al. 2011; Koleff et al. 2021). There are two unsuccessful campaigns in the Revillagigedo Archipelago, an effort to eradicate European rabbits from Isla Clarion (20 km^2) was declared a failure in 2003 and the eradication of feral cats from Isla Socorro has not been completed after 10 years despite of repeated declarations of “confirmation of abscence” (Ortíz-Alcaraz et al. 2017; CONANP 2018; Koleff et al. 2021). On Isla Guadalupe goat eradication was completed but a cat control program is still running after 10 years (Luna-Mendoza et al. 2011). In Islas Tres Marías, cat control was conducted for a short time (Ortiz-Alcaraz et al. 2008). Given the difficulty demonstrated in removing cats from larger islands, it is noteworthy that cats are present on eleven large islands ranging in size from 112 to 936 km^2, all of which are designated important areas for seabird reproduction and nesting (Albores-Barajas 2020, 2021). In fact, predator eradications have not been entirely successful on large islands concentrating most of some species’ breeding population. Such is the case of the critically endangered Townsend’s Shearwater on Isla Socorro, the presumably extinct endemic petrel of Guadalupe, or the largest breeding population of Magnificent Frigatebirds (*Fregata magnificens*) on Isla Margarita that was entirely decimated by predators (Marrón et al. 2021). On small islands like Isla Natividad (ca. 7 km^2), which hosts 95% of the breeding population of Black-vented Shearwater, cats were eradicated but invasive chipmunks remain (Keitt and Tershy 2003). Cat control has benefited Laysan Albatrosses on Isla Guadalupe; however, control efforts require continuous human intervention (Hernández-Montoya et al. 2014). Only on Isla Rasa (ca. 0.6 km^2), where 90% of the Elegant Tern and Heermann’s Gull breeding populations are located, predators were completely eradicated (Velarde et al. 2011, 2015b).

As target species, cats, mice, and goats represent a challenge on large islands while rabbits represent a challenge on small islands, like Isla Clarion (Wanless et al. 2009). Perhaps the greatest invasive species challenge remaining on Mexican islands is the eradication of invasive rodents, which are present on all of the high seabird priority islands identified above. As island size increases, removing rats via trapping or use of bait stations becomes increasingly challenging and aerial broadcast of rodenticide becomes essential. While this method is highly effective, it comes with a greater risk of impacts, such as primary poisoning, to non-target native species.

Eradication success requires highly trained personnel, that incorporate a comprehensive suite of removal techniques, and methods to evaluate eradication efficacy that are independent of those used for the removal of animals; it is unlikely that the method that achieves the initial knockdown will also remove the last few individuals (Phillips et al. 2005). Although not critical for achieving eradication, maintaining genetic samples of the population removed from the island will be informative if the invasive species is “rediscovered” after eradication and it is necessary to determine whether eradication failed or if re-introduction occurred. Furthermore, successful eradication campaigns require a consistent, scale-appropriate effort (Bester et al. 2002), making it critical to secure long-term funding proportional to the erradication effort so that the campaign is maintained without significant pause. Otherwise, because of invasive species inherently high reproductive rates, any prolonged cessation of removal efforts leaves a potential for the invasive species to recover and reoccupy cleared areas. Additionally, an independent entity should be involved in the evaluation of the eradication campaign to ensure an objective assessment of the effort.

Field crews conducting the removal and monitoring efforts should take the appropriate steps to avoid impacting sensitive native species (e.g., Carney and Sydeman 1999; Martínez-Abraín et al. 2008); for instance, reduced reproductive success of Townsend's Shearwater coincident with intense monitoring of breeding grounds has been observed (Ortiz-Pulido et al. 2016; Hernández-Mendoza 2019; Albores-Barajas et al. 2021). Seabird conservationists must always keep in mind historical researcher impacts, such as the extensive collection of Guadalupe Petrels at a time when their population was known to be declining (Thayer and Bangs 1908). Conservation efforts must focus on prioritary native and endemic species, before investing in nonthreatened species.

9.5.4 Future Threats

Invasive species arrive either as intentional introductions or as hitchhikers, i.e., accidental introductions. Fortunately, intentional introductions have become much less of a risk because authorities have or are beginning to recognize the threat invasive species pose not only to the environment but also to human health and the economy. Accidental introductions remain a risk and must be addressed by implementing biosecurity measures to prevent potentially invasive species from arriving and establishing (Scientific Committee of the GEF 2017). While Mexico's islands have been invaded by many species of plants and animals, many other species are potential threats. They may pose even greater risks and challenges than the current suite of invasive species. Future threats will likely arise from invasive invertebrates (e.g., Yellow Crazy Ants (*Anoplolepis gracilipes*)) or diseases such as avian malaria. The best approach to addressing these concerns is with a rigorous biosecurity system.

9.6 Harvesting

Harvesting of seabird eggs for human consumption has been a common practice in many coastal communities in Mexico. Some well-known examples are from the GoC, where locals, most famously from Santa Rosalía, traditionally collected eggs from Rasa and San Pedro Martir islands. There are reports of some 50,000 eggs collected in Isla Rasa (Danemann et al. 2008). However, this phenomenon is not new. In 1856, the naturalist and explorer Federico Craveri visited the island and reported on their team collecting pelican and gull's eggs and witnessing the nesting birds abandon the island after their egg collection and wandering on the island for eight continuous days to do their surveys (Bowen et al. 2015). California Brown Pelicans used to nest in Isla Rasa for likely hundreds of years, and until at least 1856, as attested by this island being known to the Comcaac as “Tosni iti ihiiquet” (where the pelicans have their offspring). In the GoM, locals also practiced seabird egg collection at the nesting colonies on the islands of Arrecife Alacranes (Morales-Vera et al. 2017). These activities may generate severe depletion of nesting colonies, as attested by Craveri’s chronicle, as well as by the recovery of the nesting populations of most of the seabird species nesting in Alacranes Reef since it was declared a protected area (Morales-Vera et al. 2017).

9.7 Light Attraction

It has been a long time since light attraction to land facilities and vessels has been identified as a serious risk to marine birds (Jones and Francis 2003; Merkel 2010; Rodríguez et al. 2014; Guilford et al. 2019; Friswold et al. 2020). A Leach’s Storm Petrel attracted to navigation lights of a scientific boat in the vicinity of Isla Guadalupe is among the first records of light attraction in México (McLellan 1926). This phenomenom has been observed several times in the Revillagigedo Islands (J.E. Martínez-Gómez unpublished field notes). On Isla Socorro, Townsend’s shearwaters have been attracted at least on two occasions (1994, 2006), one shearwater died and the other one was helped to return to the sea. One Wedge-tailed Shearwater collided with a radio antenna on Isla Socorro and died (2012). A Laughing Gull was attracted to the naval base on Isla Socorro (2014) and a Leach’s Storm Petrel to the lights of an anchored Navy Patrol (2016); both were assisted to go back to the seas. On Isla Clarion, a Wedge-tailed Shearwater landed next to the naval garrison and was moved to a dark area nearby (2013). Near Isla San Benedicto, one Wedge-tailed Shearwater landed on the deck of a diving boat and was returned to sea (2012). With the support of the crowdfunding platform experiment.com and the Mexican Navy, streetlights on Isla Socorro were changed to minimize light radiation being directed toward the night sky hoping to reduce the numer of birds being lured to land. These examples show how even in a remote, minimally developed and preserved ecosystem, like the Revillagigedo National Park, light attration still can be a cause of endangerment for seabirds. They also show that modest conservation actions can save stranded seabirds. Once marine birds have landed, it is necessary to implement rescue efforts to collect them and to relocate them at sea or in nearby colonies (e.g., Reed et al. 1985; Raine et al. 2020). Light attraction, can be reduced by turning off streetlights or changing their wavelength (Rodríguez et al. 2017). All insular, marine and coastal natural protected areas must include in their management programs specific measures to prevent and miniminze the impacts of light attraction. Further study is required to determine which species are affected and to assess the extent of seabird mortality caused by light attraction.

9.8 Other Sources of Disturbance

9.8.1 Hormones and Sleep

Anthropogenic effects on animal populations have been described since ancient times (i.e., the extinction of dodos; Hume 2012; Meijer et al. 2012), nevertheless, physiologically mediated mechanisms underlying individuals' response to disturbance have only recently obtained researchers' attention. Together, welfare and conservation issues concerning seabird species are receiving particular attention (Carney and Sydeman 1999).

Most seabirds are ground-nesting species and being vulnerable to predation, have developed specialized behavioral strategies to breed in inaccessible areas such as cliffs or remote islands (Schreiber and Burger 2002). Some species have also adopted nocturnal behavior to access the colony at night, thus avoiding contact with predators (Miles et al. 2013). These strategies have prevented contact with humans to the point that the presence of seabird colonies is often unknown even to the people living close by (Albores-Barajas et al. 2008, 2012; Massa 2009).

Human presence and activities can induce disturbance acting as a generic stress factor leading to a physiological stress response which in turn results in an increase of glucocorticoids circulation (in birds: Corticosterone, CORT hereafter (Romero and Romero 2002; Hau et al. 2010). A stress response is essential for survival because it suppresses all "unnecessary" ongoing activities and allocates energetic resources to functions essential for immediate survival (Sapolsky 1992, 2000; Rodrigues et al. 2009). Animals will react differently to different stressors (Vos et al. 1985; Canoine et al. 2002) because the physiological stress response will coordinate physiological and behavioral reactions according to sudden environmental changes (Gross and Siegel 1988; Wingfield and Ramenofsky 2011; Cohen et al. 2012). Stress may become chronic (i.e., a stress condition that lasts for a long time, or that is repetitive) with negative consequences on the metabolic system such as the disruption of breeding-related activities (Silverin 1986; Ouyang and Hau 2013). Increased baseline CORT levels indicate chronic stress and result in the inhibition of many essential functions such as the immune system, reproductive activity, and a reduction of body condition with a strong impact on the individual physiology and ultimately on its survival (Creel 2001; Tarlow and Blumstein 2007). On the other hand, several studies have shown that in some cases, animal populations can habituate to repetitive stress (Blanchard et al. 1998), such as tourism (Romero and Wikelski 2002; Mullner et al. 2004; Soldatini et al. 2015). Recently CORT measurement is used more and more frequently in conservation biology as biomarkers of individuals and/or populations under stress conditions and their response to specific stressors such as anthropogenic disturbances, environmental/climatic changes, or diseases (Hau et al. 2010; Wingfield 2008).

Another important factor, usually overlooked in terms of seabird conservation research topics is their need for rest, namely, to sleep. Sleep is an important component of an animal's daily life. Sleep has many important functions that outweigh the costs of the reduction in environmental awareness. Experimental research has demonstrated that sleep is involved in many processes, including conserving, or managing energy (Ferretti et al. 2019), maintaining the immune system (and as such balancing eventual damage due to chronic stress), brain development recovery, and protection, modulating synaptic strength and number with direct effects on memories, and information acquisition.

Some animals during the migration or for breeding activities engage in prolonged periods of constant activity. There are several examples of birds flying nonstop for periods of many days to many months (Rattenborg 2017). Some mammal species, such as dolphins, can sleep with only one cerebral hemisphere at a time (i.e., unihemispherically, Lyamin et al. 2008) and Mallard Ducks (*Anas platyrhynchos*) can switch between sleeping deeply with both hemispheres to sleeping deeply with only one (i.e., asymmetrically) in response to changes in perceived predation risk (Rattenborg et al. 1999). Among seabirds, Great Frigatebirds (*Fregata minor*) fly for up to 2 months without ever perching (Weimerskirch et al. 2016). Recently, sleep in flight was confirmed for the first time with electroencephalogram (EEG) recordings in Great Frigatebirds flying over the Pacific Ocean (Rattenborg et al. 2016) and occurred unihemispherically or asymmetrically. This means that once at the colony or roosting site, seabirds strongly need to rest to recover from reduced sleep periods due to the foraging activities. Therefore, sleep is an important element to be considered when managing areas important for seabird species. Tourist boats or terrestrial trails approaching colonies or roosting sites should maintain a safe distance (experimentally determined) ensuring not to induce behavioral or stress reactions in birds. Those reactions may be seen as a plus on the tourists' side as giving the opportunity of seeing and taking pictures of flying individuals. Nevertheless, the effect on the seabird side may go from simply disrupting resting behavior to physiological consequences induced by the stress response, chronic stress, and ultimately the exposure of the nest/nestling to interspecific or intraspecific predation risk.

9.8.2 Tourism

With the increase of the human population, more people will be traveling around, visiting places where their presence will increase pressure on the environment, more people visiting the protected areas, national parks, etc. More human presence means more disturbance to wildlife, and seabirds are no exception. A person walking close to a colony may flush the incubating adults, leaving the eggs and chicks exposed to predation or adverse climatic conditions.

Even for burrowing species, human presence can have a negative effect on breeding success and on the body condition of the chicks, perhaps compromising their survival (Albores-Barajas et al. 2009; Watson et al. 2014). Also, chronic stress leads to a decrease in body condition due to an increase in metabolic rate (Nimon et al. 1996). This extra energy expenditure, coupled with a lower food intake due to higher alertness and lower food searching can also lead to low body condition (Riou et al. 2010).

9.9 Conservation Policy

9.9.1 Marine Important Bird and Biodiversity Areas (IBAs)

Mexico has recently designated large portions (22.05%) of its Exclusive Economic Zone (EEZ) as marine protected areas (MPAs; REDPARQUES and Pronatura-México 2018). This originates from the country's commitment to protect and improve the conservation status of its marine biodiversity as a signatory member of the Convention on Biological Diversity (CBD) and the Convention on Fishing and Conservation of Living Resources of the High Seas of 1958 (ONU 1967). Designated areas coincide with or include marine priority regions for biodiversity (Arriaga-Cabrera et al. 2009), which are based on information on the presence of marine species although not considering seabirds (Arriaga-Cabrera et al. 2009). More in detail, the current network of MPAs does not consider at-sea distribution data of seabirds due to a lack of information and an appropriate analytical approach. Given that there are few published data and detailed analyses for the identification and protection of core use areas of seabirds in Mexican waters (Block et al. 2011; Soldatini et al. 2019), it is likely that the current Important Bird and Biodiversity Areas, IBA (BirdLife-International 2010), network for seabirds is incomplete. IBAs are sites of importance for focal species identified using standardized and internationally agreed-upon criteria (Donald et al. 2019; Waliczky et al. 2019).

Current Marine IBAs (mIBAs; those covering the marine component of seabird distributions) in Mexican waters are primarily centered on the islands with large seabird colonies (BirdLife_International 2015). In fact, they are based on a buffering approach which may not capture all the important core at-sea areas used for foraging by pelagic species, which are also the ones at a higher risk of extinction (Dias et al. 2019). To provide an enhanced understanding of where some of the most important marine areas are for seabirds, it is critical to consider detailed distribution data. A first attempt was recently made to identify core use areas of the Black-vented Shearwater (*Puffinus opisthomelas)*, analyzing four breeding seasons' tracking data against IBA criteria and detailed segment tracking behavioral analysis using the expectation-maximization binary clustering. Through stakeholder appropriation of results, the aim of this kind of studies is to serve as the evidence to support any appropriate extension of Area Based Management Tools (such as protected areas or fisheries restriction zones) from the breeding grounds to at-sea core use areas of species where implementation of effective protection measures may be required.

Seabird research is a relatively new science in Mexico and therefore only a few research groups are established. Long-term studies have focused on a single site and mostly one species. An example is the Blue-footed Boobies studied since 1981 at Isla Isabel (Drummond et al. 1986; Ancona et al. 2011). Distinguishing between basic and applied research makes little sense for seabird research in Mexico. The group involved in the Blue-footed Booby studies has also been involved in eradication programs at Isla Isabel (Rodríguez et al. 2006), and basic research findings have turned to fisheries predictors (e.g., Meraz et al. 2013; Velarde et al. 2013).

Future basic and applied research in the Mexican Exclusive Economic Zone must include basic biology, species richness in islands, including reproductive censuses, island as stopovers in migration routes, food base, fisheries interactions, and oil spill risks (Herzka et al. 2021). Climate change effects on food sources, reproduction, and food distribution and density also need to be studied. Besides our efforts, the Sonoran Joint Venture has developed a Bird Conservation plan (Sonoran Joint Venture Technical Committee 2006) for all birds in the Mexican NE Pacific and the GoC.

9.9.1.1 Endangered and Priority Species Lists and Legislation Reform

Effective conservation action requires constant revision of conservation policy and its instruments to achieve long-term conservation goals. Concerted efforts are required to strengthen official instruments such as the NOM- 059-SEMARNAT-2010 (SEMARNAT 2010) and the national list of priority species for conservation (SEMARNAT 2014) which have been criticized for being incomplete, biased, and outdated (De Grammont and Cuarón 2006; Cuarón and De Grammont 2007; García-Aguilar et al. 2017; Albores-Barajas et al. 2021). Basically, the rules for incorporation and endangerment levels in the NOM-059 for threatened species must be revised, while a thorough revision of the list of priority species for conservation must be carried out to delete species that are neither threatened nor endangered. To accomplish these objectives, it is necessary to assemble a representative panel of experts to avoid biases, and conflicts of interest and to follow recognized good practices. All criteria must be critically pondered to redefine conservation priorities in Mexican seas (e.g., Albores-Barajas et al. 2020, 2021). Additionally, intensive and coordinated work with legislators is necessary to make critical reforms to laws – fisheries and aquaculture, wildlife, and environment, related to the conservation of marine conservation and sustainable management of land and sea required for the reproduction and foraging of marine birds.

Acknowledgments This chapter synthesizes countless seasons in the field and hours in the lab. We thank students, technicians, and volunteers who helped in the lab and during fieldwork. We recognize the financial support of CONACYT, The Island Endemics Foundation, CICESE, INECOL, Mohamed Bin Zayed Species Conservation Fund, American Bird Conservancy, Experiment.com, and other funders. We are grateful for the logistic support provided by the Mexican Navy through patrol vessels and naval stations throughout the study area and that of the diving boats Rocio del Mar and Southern Sport – Grupo Cantamar. We sincerely appreciate the support provided by SEGOB, SEMARNAT, CONANP, and other government agencies responsible for granting permits. We appreciate the comments provided by the editors, Stefan Stadler, Helen Horblit and Noemí Matías-Ferrer to earlier versions of this manuscript.

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Chapter 10
Mexican Terrestrial Mammals in the Anthropocene

Nalleli E. Lara Díaz, Jorge L. Reyes Díaz, Mircea G. Hidalgo Mihart, and Carlos A. López González

Contents

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/978-3-031-17277-9_10.

N. E. Lara Díaz · J. L. Reyes Díaz · C. A. López González (✉)
Laboratorio de Zoología, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, Mexico
e-mail: carlos.lopez@uaq.mx

M. G. Hidalgo Mihart
División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco, Villahermosa, Tabasco, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_10

10.1 Introduction

The Anthropocene is a concept whose use has increased in recent decades in various areas of knowledge and human development, although there is no consensus that defines its meaning or starting period (Lundgren et al. 2017; Malhi 2017). Despite this, in the Natural Sciences, it is a useful concept, and it has become relevant to refer to the period when human activities have caused profound negative effects on the planet, including climate change, loss of biodiversity, and the impact on ecological processes, among others (Dirzo et al. 2014; De Vos et al. 2015; Malhi 2017; Harfoot et al. 2021). In the Anthropocene, land mammals have played a central role in recognizing human impact.

10.1.1 Terrestrial Mammals in the Anthropocene

Many species of fauna have disappeared in a relatively recent period of time in connection with anthropic activities. For terrestrial mammals, it is estimated that around 103 species have become extinct since 1500 (MDD 2021). Mammals as a group experience medium levels of susceptibility to human impact compared to other groups of terrestrial vertebrates, especially in tropical regions worldwide, where there is a combination of high species richness, high level of endemism, and high human pressure (Schipper et al. 2008; Harfoot et al. 2021). Other types of effects such as changes in their abundance, the reduction, or disappearance of populations, and their consequences on the structure and functioning of the ecosystem are difficult to quantify (Dirzo et al. 2014; Ripple et al. 2015), reflecting that a considerable proportion of terrestrial mammals have insufficient data to assess their level of risk (Schipper et al. 2008; Harfoot et al. 2021).

As with other wild species, terrestrial mammals have different capacities to survive in modified environments (Dirzo et al. 2014). Factors inherent to their biology and ecology have been recognized that, together with human impacts, enhance their risk and can produce selective patterns of extinction. Among them, body size and size of the geographic range have been frequently used as significant predictors of extinction risk (Verde Arregoitia 2015). The body size of mammals, in addition to being notable for their frequency of use in research, also stands out for their bias toward extinction throughout their history of coexistence with humans (Dirzo et al. 2014; Ripple et al. 2015, 2019).

The role of human activities and rapid population growth in the megafauna extinction has been widely debated as early as the late Pleistocene (Smith et al. 2018a). The probability of extinction of terrestrial mammals since then has reflected a significant positive association with their size. Despite this, within the Anthropocene, the threats have changed, leading to an increase in the probabilities of impacting terrestrial mammals of all sizes worldwide. Within these threats, we find invasive species, hunting, and trapping leading to overexploitation, added to urbanization, agricultural expansion, pollution, and climate change (Smith et al. 2018a; Ripple et al. 2019; Harfoot et al. 2021). Additionally, it has been estimated that the biomass of terrestrial mammals has decreased approximately seven times to date; with an important replacement in its dominance, whereas humans together with livestock exceed the biomass of the rest of the mammalian species, and in general, of all terrestrial vertebrates (Bar-On et al. 2018). Changes in the patterns of richness and diversity of mammalian species also bring additional consequences on human communities, such as the decrease or lack of primary resources for their subsistence (Dirzo et al. 2014).

On the other hand, there are species tolerant to different degrees of disturbances in the Anthropocene. In terrestrial mammal species, this is mainly associated with opportunistic and generalist feeding habits, high reproductive potential, high dispersal abilities, and plasticity in the selection of habitat and reproduction sites. Mammals with all or some of these combined characteristics are classified as resilient species (Cabello 2006; Beasley et al. 2011; Ramírez-Albores and León-Paniagua 2015; Begon and Townsend 2021; Magioli et al. 2021). Tolerance to anthropized environments implies more interactions between wild species and human populations, with results that can range from positive to negative, to neutral such as increasing the risk of mortality and/or modifying their behavior to avoid encounters with humans, which may in turn reduce the species niche (Baker et al. 2007; Bennie et al. 2014; Dirzo et al. 2014; Smith et al. 2018b; Soulsbury and White 2019; Penjor et al. 2021). Additionally, mammals have been identified as the group from which originate the most emerging or re-emerging diseases, where anthropogenic activities are the underlying factors for the increase in their transmission between wildlife, domestic animals (i.e., livestock), and humans (Keesing et al. 2010; Han et al. 2016; Wang et al. 2021). These transmission processes threaten public health, food security, and economics worldwide (Allen et al. 2017).

10.2 Diversity and Extinction Risk of Mexican Mammals in the Anthropocene

Currently, about 25% of the world's mammalian species are in danger of extinction (Schipper et al. 2008). The order Rodentia is the most diverse group within mammals and also the one that includes the largest number of threatened and extinct species. Although they are underrepresented in the assessment and in the research of their extinction risks, the order Eulipotyphla (which includes moles and shrews, among others) stands out because it is practically absent from taxon-specific literature despite its diversity and record of extinctions (Verde Arregoitia 2015).

At a global level, Mexico‘s mammalian richness places it in third place, with more than 564 species (Sánchez-Cordero et al. 2014; MDD 2021). Among them, there are currently 396 species of land mammals (non-flying) belonging to 10 orders, 25 families, and 102 genera (Carleton and Arroyo-Cabrales 2009; Spradling et al. 2016; Álvarez-Castañeda and González-Ruiz 2017; McDonough et al. 2022; MDD 2021; Supplementary Material 10.1). Similarly, to the world, in Mexico, the order Rodentia is the most diverse, representing 50% of the genera and 67.42% of the species. In number of species, it is followed by the orders Eulipotyphla, Carnivora, Lagomorpha, and Didelphimorphia; the orders Cetartiodactyla, Primates, Cingulata, Pilosa, and Perissodactyla have 10 species or less represented in the country (Table 10.1).

About 27.52% of the land mammals in Mexico are under some category of risk, and about 15% of the total are endemic species according to the Mexican List of Species at Risk (NOM-059; DOF 2019). The orders with the highest number of species at risk are also the three most diverse (Rodentia, Eulipotyphla, Carnivora). These three orders, and Lagomorpha, represent the endemic species at risk (Table 10.1; Supplementary Material 10.1). On the other hand, the red list of the International Union for Conservation of Nature (IUCN) considers 93 species within seven orders of terrestrial mammals in one of the four risk categories (Near Threatened, Vulnerable, Endangered, Critically Endangered) and 230 species as Least Concern (IUCN 2021). Fifteen species are considered with insufficient data, including five endemics (Eulipotyphla: *Cryptotis alticola* Merriam 1985 and *C. peregrinus* Merriam 1985; Rodentia: *Neotoma insularis* Townsend 1912 and *Orthogeomys cuniculus*; Lagomorpha: *Sylvilagus insonus* Nelson 1904). Finally, 58 species do not appear on the IUCN red list (Table 10.1; Supplementary Material 10.1); this may be due to recent taxonomical changes that resulted in additional species or a lack of assessment by IUCN.

Table 10.1 Orders and number of species of terrestrial mammals in Mexico

Order	Total species	Species at risk		Endemic species (NOM-059)	LC	DD	Not listed
		NOM-059	IUCN		(IUCN)		
Carnivora	33	12	5	2	25		3
Cetartiodactyla	10	4	3		6	1	
Cingulata	2	1			1	1	
Didelphimorphia	12	3			8		4
Eulipotyphla	48	20	9	13	23	5	11
Lagomorpha	18	4	8	4	7	1	2
Perissodactyla	1	1	1				
Pilosa	2	1			2		
Primates	3	3	3				
Rodentia	267	60	64	39	158	7	38
Total	**396**	**109**	**93**	**396**	**230**	**15**	**58**

The number of species under some risk category of NOM-059 (Special Protection, Threatened, and Endangered; DOF 2019) and the red list of the International Union for Conservation of Nature (Near Threatened, Vulnerable, Endangered, Critically Endangered; IUCN 2021), in addition to the number of Endemic Species (DOF 2019), *LC* least concern, *DD* data deficient, and Not listed according to the red list (IUCN 2021)

The list of terrestrial mammals in Mexico includes species that have not been recorded for more than 100 years, belonging to the orders Rodentia (*Peromyscus mekisturus* Merriam 1898, *Tylomys bullaris* Merriam 1901, *T. tumbalensis* Merriam 1901) and Eulipotyphla (*Sorex stizodon* Merriam 1895, *S. sclateri* Merriam 1897). The species of the genus *Tylomys* may be misidentifications, but *P. makisturus* and both species of the genus *Sorex* have a high probability of being currently extinct (Monroy-Gamboa 2021).

10.3 Tolerance to Human Environments

Within the diversity of terrestrial mammals recognized in Mexico, we find different degrees of tolerance of species to anthropized environments, as well as species with very specific requirements that need conserved areas to survive and need to avoid anthropized environments. We selected some representatives of both tolerant and avoider species and characterized them as follows (Fig. 10.1).

10.3.1 Virginia Opossum

In the order Didelphimorphia, we find the Northern opossum (*Didelphis virginiana* Kerr, 1792), one of the 12 species of the Didelphidae family that inhabits Mexico (MDD 2021). The Virginia opossum (Fig. 10.1a) is of medium size with a robust body, elongated and conical face, long and rough coat of whitish to gray color in various shades, and a long, prehensile tail, hairy at the base and scaly at the rest (Reid 1997; Gardner and Sunquist 2003). They are active mainly at night, with variations depending on the season, and having an omnivorous diet that let them take advantage of food such as fruits, grains, arthropods, vertebrates, and carrion (Gardner and Sunquist 2003). They are distributed from southern Canada through the United States and Mexico, into northern Costa Rica (Ramírez-Pulido et al. 2005). In Mexico, they are widely distributed throughout the country, except for Baja California Sur and certain areas of the Central Highlands (Cervantes et al. 2010; Zarza and Medellín 2014). It is the marsupial with the widest distribution in the American continent, due to its habitat plasticity and flexibility in diet, which allow it to use large areas with diverse vegetation, including areas with anthropic disturbance (Sunquist et al. 1987; Cabello 2006). In Mexico, they have a population density of up to 100 individuals/km^2, four times higher than that registered in the United States (Ceballos and Galindo 1984; Zarza and Medellín 2014). A range extension in its North American distribution appears to be facilitated by anthropogenic activities, and it is likely that an increase in population sizes is taking place (Pérez-Hernandez et al. 2016; Walsh and Tucker 2018). Despite how successful the species is, even in disturbed environments, individuals commonly are killed from collision with vehicles on roads and highways, attack by domestic animals (dogs

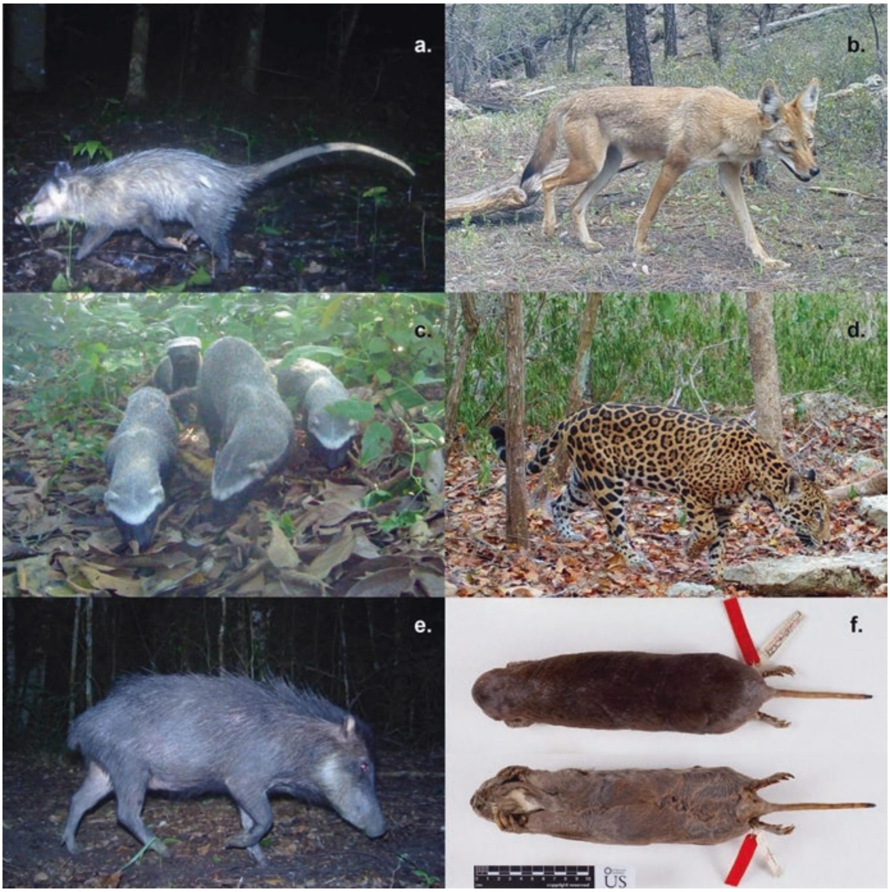

Fig. 10.1 Representative mammals of both tolerant and avoider species to human environments. (**a**) * Virginia opossum (*Didelphis virginiana* Kerr, 1792), (**b**) ** Coyote (*Canis latrans* Say, 1823, (**c**) * Grison (*Galictis vittata* Schreber, 1776), (**d**) ** Jaguar (*Panthera onca* Linnaeus, 1758), (**e**) * White-lipped peccary (*Tayassu pecari* Link, 1795), (**f**) *** Holotype of Michoacan gopher (*Zygogeomys trichopus* Merriam, 1895). (Photographs by: * Laboratorio de Mamíferos/UJAT, ** Laboratorio de Zoología/UAQ, *** Division of Mammals, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution)

and cats), conflicts with the agricultural sector due to damage provoked with plantations and poultry, as well as conflicts with the general human population, who perceive them as large rodents (Flórez-Oliveros and Vivas-Serna 2020). Also, due to their wide interaction in anthropized environments, they are commonly associated with zoonotic diseases (e.g., Haro et al. 2021). Under these characteristics, we consider it as a tolerant species to anthropic environments and disturbance, favored by changes in land use, so it will continue to thrive during the Anthropocene, and play an important role in interactions with other organisms within urban and semi-urban areas.

10.3.2 Coyote

The most successful generalist predator in anthropized environments, as well as the one with the greatest distribution in the American continent, is the Coyote (*Canis latrans* Say, 1823; Fig. 10.1b), a species of the Canidae family (Order: Carnivora). Its size is similar to that of a medium-sized dog, with an elongated muzzle, large pointed ears, and a coat that can vary between shades of gray, brown, and red (Bekoff and Gese 2003). They are social animals with mainly twilight habits, but they can be active throughout the day, and in areas of increased anthropization, they tend to be nocturnal (Gifford et al. 2017; Serna-Lagunes et al. 2019; Franckowiak et al. 2019). They thrive in a great diversity of habitats, from sea level to elevations above 3000 m, preferring within this range, open landscapes such as grasslands and arid scrubland, as well as open forested areas (Bekoff and Gese 2003). They have high reproductive rates, a wide dispersal capacity, and a high potential as opportunistic and generalist predators, which, together with their habitat plasticity, contributes to their success and has allowed them to use habitats with different degrees of human disturbances, including urban and suburban developments where they avoid human encounters (Monge-Nájera and Morera-Brenes 1986; Cove et al. 2012; Franckowiak et al. 2019; Drake et al. 2020). Due to these traits, as well as the extension of the agricultural landscape, an increase in forestry management, and the consequent fragmentation and loss of native vegetation during the twentieth century, coyotes have colonized a large part of the continent, with a current distribution from Alaska to Panama, including most of the Mexican territory, and maintaining an upward population trend (Hidalgo-Mihart et al. 2004; Ramírez-Albores and León-Paniagua 2015; Hody and Kays 2018; Kays 2018). Additionally, it is possible that coyotes benefited from the decline or absence of large carnivores during the twentieth century (e.g., wolves [*Canis lupus*], bears [*Ursus americanus* and *U. arctos*], jaguars [*Panthera onca*], and pumas [*Puma concolor*]; Leopold 1959; Ripple et al. 2013; Hernández and Laundré 2014). Even though coyotes have not been affected as other large carnivores, they have a history of conflict with humans, including a variety of aspects ranging from taking advantage of food waste in urbanized areas (usually not considered a negative interaction), to becoming the most harmful predator for livestock (Hidalgo-Mihart et al. 2004; Franckowiak et al. 2019; Drake et al. 2020; Flores-Armillas et al. 2020). Under such conditions, different management strategies are carried out to reduce and control problematic individuals to regional populations throughout their distribution area (e.g., Bergstrom 2017; Breck et al. 2017). In Mexico, the strategies to control coyotes are poorly documented; however, the prevalence of poison and poaching through spotlighting are common in livestock producing areas. Despite these actions, coyotes are a clear example of a tolerant and favored species during the Anthropocene.

10.3.3 Greater Grison

The grison (*Galictis vittata* Schreber, 1776; Fig. 10.1c) is a species of the Mustelidae family (Order: Carnivora) and the only representative of the *Galictis* genus in Mexico (Ramírez-Pulido et al. 2014). It has a medium size, a weasel-like, elongated body, and short legs, with grayish fur on the back reaching up to the head, and black on the rest of the body (Álvarez del Toro 1991). They are solitary and mainly diurnal, although they can be active at night (García-Morales and Diez de Bonilla-Cervantes 2021). They have a carnivorous diet, which includes rodents, birds, amphibians, reptiles, and fish (Bisbal 1986; Sunquist et al. 1989; Roemer et al. 2009; Hidalgo-Mihart et al. 2018a). The species is distributed in tropical and subtropical areas of low elevation in America, although it can be found from sea level to 1790 m in elevation. Grisons range from the central-eastern and southeastern Mexico, extending through Central America, to southern Brazil and Bolivia and northern Argentina (Yensen and Tarifa 2003; Cuarón et al. 2016; Jiménez-Alvarado et al. 2016; Contreras-Díaz et al. 2020). In Mexico, they are found in the eastern slopes of the states of Tamaulipas, San Luis Potosí, Hidalgo, Veracruz, Tlaxcala, Puebla, Oaxaca, Chiapas, Tabasco, and throughout the Yucatan Peninsula (Campeche, Yucatán and Quintana Roo states; Contreras-Díaz et al. 2020; Lucas-Juárez et al. 2021). This species can occupy localities with secondary or modified vegetation, and even urban and suburban sites (Contreras-Díaz et al. 2020; García-Morales and Diez de Bonilla-Cervantes 2021). *Galictis vittata* are considered a low-density species with stable populations (Arita et al. 1990; Cuarón et al. 2016). In Mexico, it considered a threatened species, although its actual conservation status is uncertain due to the scarcity of information on its ecology and abundance (de la Torre et al. 2009; Hernández-Sánchez et al. 2017; DOF 2019). Anthropic factors such as illegal hunting for a trade market (i.e., pets), destruction of their habitat, collision with vehicles, conflicts due to the attack on poultry, and zoonoses (e.g., canine distemper) can affect their populations (Escobar-Lasso et al. 2013; Salcedo-Rivera et al. 2020; García-Morales and Diez de Bonilla-Cervantes 2021). Studies that include few records of grisons or that were hoping to detect them without success have been carried out in conserved areas (Hernández-Sánchez et al. 2017; Ortiz-Lozada et al. 2017; Hidalgo-Mihart et al. 2018a; Hernández-Hernández and Chávez 2021; Ríos-Solís et al. 2021). However, it seems that the species is highly adaptable to modified environments and has the potential to maintain reproductive populations in urban areas. It is important to direct monitoring efforts to these environments, acknowledging that citizen science portals have contributed a significant and important number of recent records (García-Morales and Diez de Bonilla-Cervantes 2021). We consider this to be a species that rather than declining has found the mechanisms to survive the effects of the Anthropocene.

10.3.4 Jaguar

The jaguar (*Panthera onca* Linnaeus, 1758; Fig. 10.1d) is a species of the Felidae family (Order: Carnivora), the only representative of the *Panthera* genus and the largest feline in America (Seymour 1989). Its fur is from pale yellow to reddish brown, lighter on the chin, chest, and internal parts of the limbs; they have black rosettes all over the body (Seymour 1989). This is a very plastic species, capable of living in a variety of environments including tropical forests, temperate oak forests, and arid thorn scrub (López-González 2006). Jaguars feed on large and medium mammals such as deer (*Odocoileus virginianus* and *Mazama sp.*), peccaries (*Tayassu pecari* and *Dicotyles tajacu*), coatis (*Nasua narica*), armadillos (*Dasypus novemcinctus*), and tepezcuintles (*Cuniculus paca*), as well as reptiles and birds (Miranda et al. 2016). It was distributed from the southwestern United States to southern Argentina, but has now lost 49% of its range and is extinct from Uruguay, El Salvador, and possibly the United States (Guggisberg 1975; de la Torre et al. 2018; WWF 2020). In Mexico, jaguars are found along the slopes of the Pacific coasts, and the coastal plain of the Gulf of Mexico, including the Yucatán Peninsula (Brown and López-González 2001; Chávez et al. 2016). Their populations are considered to be declining, particularly outside the Amazon Basin, as a result of their low abundance, degree of isolation, human impacts, and lack of protection, placing jaguars as Near Threatened on the IUCN red list (Quigley et al. 2017). In Mexico, they are considered endangered (DOF 2019), with a population estimate of 4800 individuals (de la Torre et al. 2018; Jedrzejewski et al. 2018; Ceballos et al. 2021a). Threats to jaguars are diverse. The predation of domestic animals provokes reprisals such as hunting and poisoning. The fragmentation of their habitat due to the change in land use, and illegal hunting for trade worldwide, has also affected their populations (Azuara and Pallares 2011; Álvarez et al. 2015; Guerrero-Rodríguez et al. 2020; Khan et al. 2018, 2020). It is possible that jaguars are the endangered species that receives the most attention for research, recovery, and conservation efforts. In Mexico, progress has been made in studies on ecological aspects (Cruz et al. 2021), population abundance, and density (Ávila-Nájera et al. 2015; Carrera-Treviño et al. 2016; Coronel-Arellano et al. 2017; Ceballos et al. 2021a), as well as connectivity (Rodríguez-Soto et al. 2013; Hidalgo-Mihart et al. 2018b; Ceballos et al. 2021b). As it is considered a priority species for conservation in Mexico, it has been included in several conservation programs by federal agencies (CONANP 2009, 2021a). Various non-governmental organizations, both national and foreign, use the jaguar as a flag species and implement outreach, monitoring, and protection activities (e.g., Panthera México, Northern Jaguar Project, WWF, Pronatura Peninsula de Yucatán, Alianza Nacional para la Conservación del Jaguar).

Despite the plasticity of the species in habitat and food, its populations are considered to be declining throughout its distribution (Quigley et al. 2017), although the latest estimates consider that the population in Mexico increased by 20% in the last 8 years (Ceballos et al. 2021a). In the Anthropocene, jaguars are on the borderline between the risk of being a large declining carnivore, or having a substantial population increase that resulted from the resources and efforts provided for its conservation. Thus, a reassessment of its risk category in Mexico may be required, as well as an assessment of its effects on species and ecosystems related to the reported increase of an apex predator.

10.3.5 White-Lipped Peccaries

The white-lipped peccary (*Tayassu pecari* Link, 1795; Fig. 10.1e) is a species of the Tayassuidae family (Order: Artiodactyla), whose genus is monospecific (MDD 2021). It is an ungulate with a pig body shape that can weigh between 25 and 40 kg, with toes covered with hooves; it has a vestigial tail and a musk gland in the posterior medial-dorsal region (Mayer and Wetzel 1987; Reyna-Hurtado and March 2014). Their fur is coarse and thick, completely black in adults, except for a white line around the lips that extends toward the cheeks (Mayer and Wetzel 1987).

They are mainly diurnal animals, with a decrease in activity in the warm hours of the day (Sowls 1997; Pérez-Irineo and Santos-Moreno 2016). Of a social nature, it is one of the few ungulates in America that forms united and large groups in tropical environments, even reaching 100 individuals (Reyna-Hurtado et al. 2016; Thornton et al. 2020). White-lipped peccaries are considered habitat specialists, selecting conserved tropical areas, with movements strongly influenced by the availability of water (Sowls 1997; Reyna-Hurtado and Sánchez-Pinzón 2019). They feed mainly on fruits (80%) and invertebrates (Pérez-Cortez and Reyna-Hurtado 2008).

The white-lipped peccary has a Neotropical distribution, from southeastern Mexico, where it extends through the humid tropical forests and cloud forests of the Gulf of Mexico, the Caribbean Sea, and the South Pacific, to the north of Argentina (Keuroghlian et al. 2013; Reyna-Hurtado et al. 2014). Currently, this corresponds to about 74% of its historical distribution on the continent, with greater losses occurring in Mesoamerica. In Mexico, between 84% and 87% of its range has disappeared, particularly in dry tropical forests, an environment in which populations have little chance of survival (Altrichter et al. 2011; Reyna-Hurtado and Sánchez-Pinzón 2019; Thornton et al. 2020). There are only six small and highly isolated populations located in the country, five that appear to be declining, and three with less than a thousand individuals; the most stable population in Mexico is shared with Belize and Guatemala (Thornton et al. 2020). It is a species endangered with extinction according to Mexican laws (DOF 2019), and vulnerable in the IUCN red list, with its populations in decline (Keuroghlian et al. 2013). The main threats for white-lipped peccaries are deforestation, habitat transformation, and human population growth (Altrichter et al. 2011). Additionally, overexploitation has strongly impacted their populations, as they are among the favorite prey for subsistence and recreational hunting, and their meat is highly appreciated (March 1993; Reyna-Hurtado and Sánchez-Pinzón 2019). Given that range assessments continue to show a rapid reduction in recent decades (Altrichter et al. 2011; Thornton et al. 2020), white-lipped peccaries are the largest mammal species in Mexico with the most restricted and accelerated distribution loss, requiring additional attention and efforts.

10.3.6 Michoacan Gopher

The Michoacan gopher (*Zygogeomys trichopus* Merriam, 1895; Fig. 10.1e) is a Mexican endemic species that belongs to the Geomyidae family (Order: Rodentia), and a monospecific genus (Ramírez-Pulido et al. 2014). It is a medium-sized gopher with males larger than females (Calede and Brown 2021), very small eyes, a pad on the nose lacking hair, and a bare tail; their fur is short, fine, and shiny in appearance (Hafner and Hafner 1982). The Michoacan gopher feeds on plant matter such as roots, tubers, stems, or branches, which it consumes during its foraging activity below the surface; it is possible that it is not active aboveground, because it is very rare to observe and the unique mounds it builds lack an opening at the top (Hafner and Hafner 1982; Hafner and Barkley 1984). The Michoacan gopher lives in regions with friable soils, in conserved and cultivated areas, in pine, oyamel, and oak forests above 2200 masl (Hafner and Hafner 1982; Hafner and Barkley 1984; Fernández et al. 2014; Álvarez-Castañeda et al. 2018). Its distribution is quite limited and fragmented, since it is currently only found in three of the four localities where it used to live in the mountains of Michoacan state, and it has been extirpated from its type locality (Nahuatzén; Allen 1895; Hafner and Barkley 1984; Fernández et al. 2014; Álvarez-Castañeda et al. 2018). Their populations were considered remnants of a more widespread population in the past, but in recent decades they are small and have low genetic variability, high inbreeding, and lack of gene flow (Hafner and Barkley 1984). Although they can inhabit disturbed environments such as various crops, increasing agricultural frontiers may facilitate the spread of the genus *Pappogeomys* to higher elevation areas, putting *Z. trichopus* at a competitive disadvantage (Hafner and Barkley 1984). The populations of the Michoacan gopher continue to decline and are in danger of extinction within NOM-059 and on the IUCN red list (Álvarez-Castañeda et al. 2018; DOF 2019). Despite the fact that it is an endemic and at-risk species, it has been little studied. It has been included in nonspecific studies (e.g., Escalante et al. 2005), but there are no ecological studies on this species after the mid-1980s (Hafner and Barkley 1984). Moreover, it has even been mentioned that there is no current confirmation of its presence (Monterrubio-Rico et al. 2014). Records for the species in zoological collections are scarce, and the latest is from two decades ago, for the year 2001 (GBIF 2021). Despite this, the Michoacan gopher is assumed to be responsible for an important proportion of the herbivory of the legume *Lupinus elegans*, as well as the *Pinus pseudostrobus* and *P. montezumae* pines within its potential distribution area (Díaz-Rodríguez et al. 2013; Barrera Ramírez et al. 2018). However, this was concluded without any reliability in the identification of the species or herbivory produced by similar species (e.g., *Pappogeomys*). Their small populations are difficult to locate and their individuals are secretive (Hafner and Barkley 1984), limiting studies on the species and increasing uncertainty about its status. It is an example of the situation in which many small non-charismatic mammals with restricted distributions may be facing in Mexico, including the lack of interest and resources for their research, nor any conservation effort. Such species are not coping well during the Anthropocene.

10.4 Perspectives

At the beginning of the twentieth century, the Mexican government began efforts to manage and regulate the sustainable use of its wildlife resources in the territory through the creation of the Central Board of Forests and Groves, which became the current Ministry of the Environment and Natural Resources (SEMARNAT; INE 2007). Among other tools developed by the institution for this purpose are the Mexican list of species at risk (DOF 2019), Natural Protected Areas (CONANP 2021b), and Management Units for the Conservation of Wildlife (UMAs; CONABIO 2020).

The Mexican list of species at risk is a normative instrument that was established in 1994 and integrates a list of species, subspecies, or populations under different risk categories in Mexico (INE 1994; DOF 2019). In its most recent versions (2001, 2010, and 2019), the inclusion or change of category within the list is regulated based on the Method of Evaluation of the Risk of Extinction of Wild Species in Mexico (MER), which uses a hierarchical assessment based on four categories, referring to the amplitude of its distribution, habitat status, biological vulnerability, and anthropogenic impacts (Tambutti et al. 2001; DOF 2019). Prior to the existence of this list, species at risk could be found listed in temporary or permanent ban for their use, through different formats within the wildlife harvest calendars, which continue to be published regularly (e.g., DOF 1992; DGVS 2021). Since its existence, the Mexican list of species at risk has been taken as a reference to assess the conservation status and the development of public (and recently private) policies of multiple taxa, including terrestrial mammals (García-Aguilar et al. 2017). However, scientific inclusion, classification, or re-classification criteria are lacking for numerous taxa, and only an approximate proportion of 10% has been evaluated through the MER; there is no concordance of the degree of risk in the national (NOM-059) and international lists (e. g. IUCN), either due to a lack of information or potentially due to greater deterioration in Mexico (more species at risk) than globally. Also, the status of endemic species may be underestimated, and there may even be a pervasive particular interest for the inclusion of certain species (García-Aguilar et al. 2017). This requires a profound modification of the Mexican list of species at risk to transform it into a solid baseline for the evaluation, and a proposal to lead management actions, including the conservation of terrestrial mammals, among other taxa, within the country.

In 1917, the first National Park in Mexico was established, but it was until 1988 that the Natural Protected Area Commission (CONANP) was established as an instrument, encompassing those Natural Protected Areas (NPAs) decreed up to that moment ($n = 93$; DOF 1988; CONANP 2021b). The NPAs are considered a portion of the Mexican territory that has not been significantly altered by anthropogenic activities and that requires to be conserved and sometimes restored (DOF 2000). Among its objectives is the conservation of biodiversity in a broad context, ensuring the sustainable use of biodiversity, promoting scientific research and dissemination of knowledge that contribute to its objectives, as well as protecting its cultural heritage (DOF 2000). Currently, there are 182 NPAs under six management categories, with a cumulative area of 90,830,963 hectares. In addition, there are 363 Voluntary Designated Conservation Areas (596,867.34 ha), a recently created category (CONANP 2021b). This makes NPAs the most widespread conservation instrument in the country, and one of the most successful, probably related to more than a century of history. The polygons of the NPAs are drawn mainly on areas of private, ejidal or communal property, that is, practically the entire surface has human populations that carry out different productive activities within them, making the social component a fundamental basis for their operation (Álvarez-Gordillo et al. 2017; Zamora Lomelí 2020).

The structure and operation of the NPAs is undoubtedly related to the Sustainable Development Goals (SDG), framed in the 2030 Agenda on Sustainable Development (Rodríguez Soto and Martínez Reynoso 2019; Agenda 2030 2020). The SDG include ending poverty, ending hunger by ensuring the sustainability of production systems, adopting measures to counteract climate change and its effects, as well as stopping the loss of biodiversity and conserving, restoring, and using ecosystems sustainably (United Nations 2015). But NPAs face different challenges, such as overexploitation, poaching and looting of species, fires, loss of habitat, and biodiversity, in addition to impacts related to climate change (Rodríguez Soto and Martínez Reynoso 2019; Álvarez-Gordillo et al. 2017). Undoubtedly, this tool has a wide potential to contribute in the long term to the maintenance of the diversity of terrestrial mammals, as well as of biodiversity in general, as well as strengthening sustainable development, as long as public policies ensure the interest of maintain and provide resources for its operation, improvement, and development on a constant basis.

The Management Units for the Conservation of Wildlife (UMAs) are environmental policy instruments created in 1997, whose purpose is to regulate the sustainable use of wildlife, contributing to the conservation of biodiversity and providing socioeconomic alternatives to the inhabitants (Juárez Mondragón et al. 2015). UMAs can have different specific objectives, including restoration, maintenance, reproduction, reintroduction, research, exhibition, environmental education, and, mainly, sustainable use (Masés-García et al. 2016). The species which are the focus of the UMAs and depending on the objective can be extracted (through collection, capture, and hunting), non-extracted (there is no removal of individuals) and mixed use (SEMARNAT 2009). Likewise, they can be classified into intensive, where the specimens are held under human care (ex situ), and extensive, where the specimens occur free and wild in nature (in situ; Juárez Mondragón et al. 2015; Masés-García et al. 2016).

Currently, 52 species of terrestrial mammals are used in Mexico, 33 of which are native, highlighting animals such as white-tailed deer (*Odocoileus virginianus*

Zimmermann 1780), collared peccary (*Dicotyles tajacu* Linnaeus 1758), pacas (*Cuniculus paca* Linnaeus 1766), and coyote; in addition to several species of lagomorphs (CONABIO 2020; SEMARNAT 2021). To date, Mexico has 134 registered UMAs that cover a total area of 79,710 ha (SEMARNAT 2021). Although UMAs are one of the main instruments for the sustainable use and conservation of wildlife, there are several concerns. For example, there is a negative trend to establish new UMAs since the inception of the program, both in number and in their area (SEMARNAT 2021). In addition, there are deficient management plans, few evaluations on the impact on biodiversity conservation and the benefits to the people who implement them, with a potential bias toward greater economic profitability in the north of the country, dependence on government subsidies, scarcity of access roads to UMAs, little value added to wildlife in the market, among other problems (Gallina-Tessaro et al. 2009; Álvarez-Peredo et al. 2018; Pineda-Vázquez et al. 2019). Such factors reduce the continued economic profitability of UMAs, despite the fact that some have benefits in habitat conservation (particularly extensive UMAs) or in the valuation of biodiversity by communities (Pineda-Vázquez et al. 2019). The proper functioning of the UMAs still has a long way to go to reach the objective of this instrument. Improvement depends on the integration of multiple actors, management plans, public and market policies, among other variables, accompanied by the reduction of the inequality and poverty gaps that affect Mexican rural areas.

Despite its biodiversity in terms of mammals, Mexico is also classified as one of the countries with great habitat loss, leading the nation to occupy the first place worldwide in likely decline in the richness of mammalian species projected by 2050 (Visconti et al. 2011). It has also been detected as an extinction "hotspot" for terrestrial mammals, with an overwhelming lack of studies in this regard (Verde Arregoitia 2015). Mexico's southeast stands out as an area where land mammals face a larger number of threats, coinciding with most of the Neotropical ecoregion; although other areas of future species' loss for this group include the pine-oak forests of the Madrean archipelago, in the Sierra Madre Occidental (Visconti et al. 2011; Harfoot et al. 2021). Additionally, defaunation affects many ecological processes such as pollination, trophic cascades, pest control, human health, nutrient cycles, among others (Dirzo et al. 2014; Ripple et al. 2015), which are not being systematically studied in the country.

The aforementioned environmental instruments must contribute to the knowledge, protection, and sustainable use of wild species hand in hand with the well-being of human populations immersed in their habitat. Any such program must comply with current environmental legislation, seeking an increase in productivity with better capabilities and technologies, and fewer losses to producers (Visconti et al. 2011). It is also necessary to increase and correct the lack of technical, economic, and managerial capacities to optimize the environmental tools in the country. In addition to the loss of biodiversity, we are facing a climate change crisis. Without a comprehensive address of environmental issues that includes the well-being of local communities, many species of terrestrial mammals will continue their trend toward disappearance during the Anthropocene.

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Chapter 11
Mexican Bats: Threats in the Anthropocene

Romeo A. Saldaña-Vázquez, María Cristina MacSwiney G., Beatriz Bolivar-Cimé, Rafael Ávila-Flores, Emma P. Gómez-Ruiz, and Issachar L. López-Cuamatzi

Contents

R. A. Saldaña-Vázquez (✉)
Instituto de Investigaciones en Medio Ambiente Xabier Gorostiaga, S.J. Universidad Iberoamericana Puebla, San Andrés Cholula, Puebla, Mexico
e-mail: romeoalberto.saldana@iberopuebla.mx

M. C. MacSwiney G. · I. L. López-Cuamatzi
Centro de Investigaciones Tropicales (CITRO), Universidad Veracruzana, Xalapa, Veracruz, Mexico

B. Bolivar-Cimé
Instituto de Investigaciones Forestales, Universidad Veracruzana, Parque Ecológico "El Haya", Xalapa, Veracruz, Mexico

R. Ávila-Flores
División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco, Villahermosa, Tabasco, Mexico

E. P. Gómez-Ruiz
Parque Ecológico Chipinque, A.B.P, San Pedro Garza García, Nuevo León, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_11

11.1 Introduction

Bats are one of the most diverse groups of mammals in the world. This diversity is, likewise, accompanied by a wide number of trophic guilds, varied morphologies, behaviors, and use of specific habitats and a great variety of ecosystems (Fig. 11.1). Due to their capacity of using different habitats, they have a plethora of reported biotic interactions, such as pollination, seed dispersion, parasitism, and predation (Jones et al. 2009; Fleming et al. 2020). These biotic interactions are related to ecosystem functions resulting in the provision of important ecosystem services (Díaz

Fig. 11.1 Some species of common bats in Mexico's cities. (**a**) *Molossus nigricans* (insectivorous), (**b**) *Myotis velifer* (insectivorous), (**c**) *Artibeus jamaicensis* (frugivorous), (**d**) *Pteronotus fulvus* (insectivorous), (**e**) *Leptonycteris yerbabuenae* (nectarivorous), (**f**) *Glossophaga mutica* (phytophagous). (Photos by: Juan Cruzado Cortés (**a**, **b**, **d**, **e**, **f**) and Cristina Mac Swiney (**c**))

Fig. 11.2 Bat species of Mexico categorized in extinction risk by Mexican government. (**a**) *Musonycteris harrisoni*, (**b**) *Myotis vivesi*, (**c**) *Myotis planiceps* and (**d**) *Vampyrum spectrum*. (Photo by Romeo A. Saldaña-Vázquez (**a**), Edgar G. Gutierrez (**b**), Juan Cruzado (**c**), y Frank Clarke (**d**))

et al. 2018). Some of the most important bat contributions to humans are plant pollination, insect population control, and seed dispersal (Maas et al. 2016; Ratto et al. 2018; Saldaña-Vázquez et al. 2019). For this reason, the well-being of many human populations is highly related with the stability of bat species populations.

Mexico holds the world's fifth place in bat species richness, with nearly 140 bat species in 8 families (Wilson and Mittermeier 2019). With this high richness, it is not surprising that an important number of Mexican species are threatened. According to the Mexican Official Standard for Threatened Species NOM-059-SEMARNAT-2010, there are four bat species in extinction risk; these are

Musonycteris harrisoni, *Vampyrum spectrum*, *Myotis planiceps*, and *Myotis vivesi*. This risk category is related to their reduced distribution size and their specific ecological demands such as specialized diet or specialized habitat. For example, *Musonycteris harrisoni* is a hyper-specialized nectarivore that has a small distribution and only occurs in six out of the 32 states of Mexico (Fig. 11.2). This species is highly sensitive to anthropogenic changes and found to have reduced feeding activities in fragmented forests when compared to continuous forests (Tellez and Ortega 1999; Stoner et al. 2002). Moreover, there are 34 more species with some degree of risk, as the result of low population densities or the susceptibility to rapid population declines due to human activities. The origin of risks to the species of Mexican bats is related to the geologic epoch that we are now experiencing, the Anthropocene. The Anthropocene is defined as the geological moment that humanity is currently experiencing on planet Earth (Crutzen 2006). This is characterized by the global environmental change of human origin which began with the industrial activities, and which has left a chemical signature in the deep sediments of the soil and the environment. The main indicators of the beginning of this epoch are found in the increase in global temperature of more than one degree and in the increase in atmospheric carbon dioxide above 300 parts per million (Zalasiewicz et al. 2008).

Previous studies have discussed the principal threats derived from the Anthropocene that affect bat populations (Table 11.1). However, there is no present research that examines the prevalence of these threats in Mexico, and how the country's bats will respond within the unique and complex environmental characteristics of the territory. Therefore, the objective of this chapter was to conduct a revision of the knowledge of the effects of human activities of the Anthropocene epoch on Mexican bat diversity and ecology. In addition, we predict some responses that are expected based on previous studies and our knowledge about Mexican bat ecology (Table 11.1). To achieve this goal, we designed a literature review protocol (see below) that may be used in future revisions of these topics for Mexican bats.

11.2 Material and Methods

We made 11 literature searches (Table 11.2) based on the 11 bat threats (see Table 11.1) related to the Anthropocene. We used Google Scholar (GS) and Web of Science (WoS) as literature research engine and literature repository, respectively. Searches were carried out in March of 2021, and they were not limited by year or publication type. In Table 11.2, we summarize the number of documents found by search, keywords, search engine, or repository. Additionally, we made secondary searches in documents resulting from the searches and in our personal literature libraries.

The document screening was carried out by one or two of the authors; the study eligibility criteria were as follows: (1) study was done with bats; (2) study has been done in Mexico; (3) the studies are related to bat Anthropocene treats. Documents that accomplished the eligibility criteria were then selected for this narrative review.

Table 11.1 Anthropocene bat threats reported in the literature and the expected response of Mexican bats

Threat	General response	Response expected for Mexico	References
Habitat fragmentation	Differences in species richness, evenness, abundance, and assemblage composition between interior, edge, and matrix habitats would decrease with fragment size.	Differences in phyllostomid species richness, evenness, abundance, and assemblage composition between continuous forest and fragments decrease with fragment size, unknown response for other families.	18
Agriculture	Species richness, functional and taxonomic diversity decrease with increasing land use intensity, and disturbance. Frugivore, nectarivore, and omnivore bats are positively associated with agroforestry crops. In contrast, monocultures retain only sanguivores and omnivores bats.	Frugivorous and nectarivorous bats are positively associated with agroforestry crops or agroecosystems.	19, 20, 24
Cattle ranching	Species richness, functional, and taxonomic diversity increase with decreasing land use intensity and disturbance. Large size frugivores, aerial insectivores, and omnivores are more frequently recorded in cattle-ranching areas than carnivores, gleaning insectivores, nectarivores, small size frugivores, sanguivores.	Frugivorous and sanguivorous bats are the most frequent in cattle-ranching areas.	19, 21, 26
Urbanization	Species richness, functional, and taxonomic diversity increase with decreasing land use intensity and disturbance. Bat species that forage in open and edge space and have flexible roosting strategies are more frequently recorded in urban areas.	Species of the Molossidae family and some vespertilionids that feed near lights have higher activity in urban sites than other insectivore's families, but unknown response for other families and guilds.	19, 22, 27
Air pollution	Reduction of insectivorous bat activity in sites with higher air pollution, there is not a mechanism.	Reduction of insectivorous bat activity, unknown response for other guilds.	1, 2
Water pollution	Insectivorous bats are little affected by water pollution because insects that bats consume tolerate water pollution.	Insectivorous bats do not reduce their activity with water pollution, unknown response for other guilds.	3

(continued)

Table 11.1 (continued)

Threat	General response	Response expected for Mexico	References
Sound pollution	Reduction of insectivorous bat activity in higher sound polluted sites, because sound pollution interferes with echolocation behavior of bats.	Reduction of insectivorous bat activity of bats that catch flying insects, neutral response for other guilds.	4
Light pollution	Bats with low flight speed reduce their activity in light-polluted sites, due to the increase of predation risk and low prey capture success.	Reduction of activity of low flight speed bats and bats that forage in highly cluttered space, neutral response for other guilds.	4, 5, 6
Climate change	Changes in precipitation and increasing temperatures due to climate change will affect global water availability, especially in arid regions. Species that use climatic cues to dictate the timing of foraging, breeding, hibernation, parturition, or migration are expected to respond more immediately to climate change.	Increased drought in arid regions of Mexico due to climate change may affect insectivorous bats‘reproductive success as lactating females require a significant water intake. Migratory nectar-feeding bats in Mexico rely on seasonality of flowering plants to complete their annual migratory and reproductive cycle and are vulnerable to potential effects of climate change on plant phenology and distribution.	7, 8, 28
Human–bat conflicts	Intentional killing of bats is higher in locations where (1) large bats are used for food or medicine, (2) people have negative perceptions of bats due to cultural beliefs, (3) bats live near humans, (4) bats are believed to consume fruits crops, and (5) bats are linked to endemic zoonotic diseases.	Intentional killing of bats is more common in small- to medium-size urban locations and in tropical cattle-ranching areas.	23, 25

(continued)

Table 11.1 (continued)

Threat	General response	Response expected for Mexico	References
Human infrastructure	Wind energy facilities represent a threat to bat populations, especially, but not exclusively, for migratory and open-space foraging species, due to the high rate of mortality caused by direct collision or barotrauma.	Wind energy facilities are a considerable threat for Mexican bats species, due to the high number of migratory genera (*Lasiurus*, *Tadarida*, *Leptonycteris*) and open-space foraging species present in the country.	9, 10, 11
	Road and railway networks may affect bat population stability because they can affect the interpopulation connectivity and can cause a high number of fatal collisions with motor vehicles.	Mexican bat populations are affected by road and railway networks, especially in tropical region where large colonies are present and urban development is higher.	12, 13
	Buildings may be both beneficial and detrimental for bat species. Beneficial when building offers foraging sites, diurnal and/or maternity roosts, hibernacula, and opportunity for geographic expansion. Detrimental when smooth surfaces of buildings (i.e., glass windows) interfere with the echo-sound pathway of bat echolocation calls (acoustic mirror) and increase the risk of collision.	Bridges and other buildings are used for bats such as foraging sites, diurnal, and/or maternity roost and hibernacula. Skyscrapers in cities and other buildings with many smooth surfaces represent a threat for bats. In order of urbanization degree, skyscrapers are more abundant in bigger cities; therefore, suburban areas and urban-transition zones are more susceptible to holding more beneficial human-made structures for bats.	14, 15, 16, 17

The general response was based on the following references: (1) Rachwald et al. (2004); (2) Rachwald (2019); (3) Salvarina (2016); (4) Moretto and Francis (2017); (5) Lewanzik and Voigt (2014) (6) Rowse et al. (2016); (7) Adams and Hayes (2021); (8) Sherwin et al. (2013); (9) Arnett et al. (2016); (10) Grodsky et al. (2011); (11) Wang and Wang (2015); (12) Altringham and Kerth (2016); (13) Fensome and Mathews (2016); (14) Ancillotto et al. (2016); (15) Greif et al. (2017); (16) Russo and Ancillotto (2015); (17) Voigt et al. (2016); (18) Rocha et al. (2017); (19) Farneda et al. (2020); (20) García-Morales et al. (2013); (21) Gonçalves et al. (2017); (22) Jung and Threlfall (2018); (23) Frick et al. (2020) (24) Castro-Luna and Galindo-González (2012); (25) O'Shea et al. (2016); (26) MacSwiney et al. (2007); (27) Rodríguez-Aguilar et al. (2017); (28) Gómez-Ruiz and Lacher Jr (2019)

Table 11.2 Number of documents found by search, keywords, search engine, or repository

ID	Keywords	Spanish	English	WoS	GS
1	Habitat fragmentation	Topic: (Chiroptera OR murciélagos) AND Topic: (bosque continuo OR fragmentos OR matriz OR paisaje) AND Topic: (diversidad OR dieta OR gremios OR abundancia) AND Topic: (México OR Norteamérica OR Neotrópico)	Topic: (Chiroptera OR Bats) AND Topic: (continuous forest OR fragments OR patches OR matrix OR landscape) AND Topic: (diversity OR diet OR guild OR abundance) AND Topic: (Mexico OR North America OR Neotropics)	91	200
2	Agriculture	Topic: (Chiroptera OR murciélagos) AND Topic: (agroecosistemas OR monocultivos) AND Topic: (gremios OR riqueza OR diversidad OR dieta OR abundancia) AND Topic: (México OR Norteamérica OR Neotrópico)	Topic: (Chiroptera OR bats) AND Topic: (agroecosystems OR monocultures) AND Topic: (diet OR guild OR richness OR diversity OR abundance) AND Topic: (Mexico OR North America OR Neotropics)	9	199
3	Cattle ranching	Topic: (Chiroptera OR murciélagos) AND Topic: (pastizales inducidos OR ganadería) AND Topic: (riqueza OR diversidad OR dieta OR gremios OR abundancia) AND Topic: (México OR Norteamérica OR Neotrópico)	Topic: (Chiroptera OR Bats) AND Topic: (induced pasturelands OR grasslands OR cattle ranching) AND Topic: (richness OR diversity OR diet OR guild OR abundance) AND Topic: (Mexico OR North America OR Neotropics)	7	199

4	Urbanization	Topic: (Chiroptera OR murciélagos) AND Topic: (Urbanización OR ciudades) AND Topic: (actividad OR riqueza OR diversidad OR abundancia) AND Topic: (México OR Norteamérica OR Neotrópico)	Topic: (Chiroptera OR Bats) AND Topic: (urbanization OR cities) AND Topic: (activity OR richness OR abundance) AND Topic: (Mexico OR North America OR Neotropics)	15	200
5	Air pollution	Topic: (Chiropteta OR murciélagos) AND Topic: (contaminación del aire OR OR metales pesados OR polvo) AND Topic: (actividad OR diversidad OR riqueza OR abundancia) AND Topic: (México OR Norte América OR Neotrópico)	Topic: (Chiroptera OR bats) AND Topic: (air pollution OR heavy metals OR dust) AND Topic: (activity OR richness OR diversity OR abundance) AND Topic: (Mexico OR North America OR Neotropics)	2	200
6	Water pollution	Topic: (Chiroptera OR murciélagos) AND Topic: (eutroficación OR drenaje OR nitrógeno OR toxinas OR basura) AND Topic: (diversidad OR riqueza OR actividad Or abundancia) AND Topic: (México OR Norteamerica OR Neotrópico)	Topic: (Chiroptera OR bats) AND Topic: (eutrophication OR sewer system OR nitrogen levels OR toxines OR waste OR sewage) AND Topic: (diversity OR richness OR activity OR abundance) AND Topic: (Mexico OR North America OR Neotropics)	3	200

(continued)

Table 11.2 (continued)

ID	Keywords	Spanish	English	WoS	GS
7	Sound pollution	Topic: (Chiroptera OR murciélagos) AND Topic: (contaminación por ruido OR ruido urbano) AND Topic: (diversidad OR riqueza OR actividad OR abundancia) AND Topic: (México OR Norteamerica OR Neotrópico)	Topic: (Chiroptera OR bats) AND Topic: (noise pollution OR urban noise) AND Topic: (diversity OR richness OR activity OR abundance) AND Topic: (Mexico OR North America OR Neotropics)	0	200
8	Light pollution	Topic: (Chiroptera OR murciélagos) AND Topic: (luz de noche OR luz antropogén* OR contaminación lumínica OR lámpar*, bruma de cielo OR alumbrado público) AND Topic: (diversidad, riqueza, actividad OR abundancia) AND Topic: (México, Norteamérica, Neotrópico)	Topic (Chiroptera OR bats) AND Topic: (light at nigh* OR anthropogen* ligh OR urban light* OR light pollution* OR night-light* OR streetlight* OR streetlamp* OR skyglow*) AND Topic: (diversity OR richness OR abundance OR activity) AND Topic: (Mexico OR Neotropics OR North America)	5	100
9	Climate change	Topic: (Chiroptera OR murciélagos) AND Topic: (sequía OR fenología OR agua OR OR cambio climático) AND Topic (reproducción OR planta-polinizador) AND Topic: (México OR Norteamérica OR Neotrópico)	Topic: (Chiroptera OR bats) AND Topic: (drought OR climate change OR water OR phenology) AND Topic: (lactation OR reproduction OR plant-pollinator) AND Topic: (Mexico OR North America OR Neotropics)	33	200

10	Human–bat conflicts	Topic: (Chiroptera OR murciélagos) AND Topic: (sacrificio OR control poblacional OR erradicación OR exclusión OR guano OR histoplasm* OR rabia) AND Topic: (México OR Norteamérica OR Neotrópicos)	Topic: (Chiroptera OR bats) AND Topic: (culling OR population control OR eradication OR exclusion OR guano OR histoplasm* OR rabies) AND Topic: (Mexico OR North America OR Neotropics)	240	200
11	Human infrastructure	Topic: (Chiroptera OR murciélago) AND Topic: (puente* OR carretera* OR aerogenerador* OR colisión*) AND Topic (México OR Norteamérica OR Neotrópico)	Topic: (Chiroptera OR bats) AND Topic: (bridge* OR road* OR wind turbine* OR collision*) AND Topic (Mexico OR North America OR Neotropics)	69	199

The Google Scholar (GS) and Web of Science (WoS) search engine and repository were used. The parentheses in the keywords section indicate the group of words used in the WoS search engine. From GS results, we only revised the first 30 pages, where more documents related with the topic appeared (Haddaway et al. 2015). The search period in WoS repository was 1980–2021. ID is the identification number of the search

11.3 Results and Discussion

We revised 2571 documents, of which only 68 studies contained empirical data about the effect of anthropic activities on bat ecology. The Anthropocene threat of bats most studied in Mexico was the effect of habitat fragmentation and deforestation on bat diversity, followed by human infrastructure and effects of agriculture on bat diversity and ecology (Table 11.3). These human activities are related to land use change and potential reduction of bat habitat. Other interesting and important phenomena related with human activities such as pollution, or climate change were less studied for Mexican bats.

11.3.1 Effect of Land Use Change on Mexican Bats

Many investigations have been carried out in Mexico to evaluate the response of bats to land use change. These studies compare some attributes of the bat community present in continuous forest or forest fragments with other types of land use. Coffee plantations with different management intensity have been widely studied in different parts of the country, especially in the states of Veracruz and Chiapas (Sosa et al. 2008; Saldaña-Vázquez et al. 2010; Williams-Guillén and Perfecto 2010). Other types of land use studied were citrus plantations (Estrada et al. 2004), mango plantations (Madrid-López et al. 2020), agricultural lands (Briones-Salas et al. 2019), pastures (Estrada et al. 2004; MacSwiney et al. 2007), and urban areas (Avila-Flores and Fenton 2005; Rodríguez-Aguilar et al. 2017). Most of the studies have been carried out in the tropical zone of the country, still leaving gaps of information for temperate and arid zones. Furthermore, a large part of the research performed has a bias toward the Phyllostomidae family, since only mist-nets at ground

Table 11.3 Number of studies selected to make the narrative review of the effects of Anthropocene over bat ecology

Human activity or Anthropocene phenomena	No. of studies selected
Habitat fragmentation or deforestation	21
Agriculture	11
Cattle ranching	4
Urbanization	5
Air pollution	1
Water pollution	0
Sound pollution	2
Light pollution	2
Climate change	2
Human–bat conflicts	7
Human infrastructure	13

level were used to monitor the bat community, which limits the knowledge about the response of other bat families to land use change. In urban areas, acoustic or mist-net monitoring has been used separately (Avila-Flores and Fenton 2005; García-Méndez et al. 2014); few studies utilized both methods (Medina-Cruz 2019), emphasizing the need of use complementary sampling methods to better understand the response of bat community to their habitat modification.

Mexican bat species richness and composition of different guilds, such as frugivores or insectivores, were statistically similar between forest and polycultures (coffee, mango), monocultures, pastures, or urban areas of the same region (Pineda et al. 2005; MacSwiney et al. 2007; Rodríguez-Aguilar et al. 2017; Briones-Salas et al. 2019; Madrid-López et al. 2020). Although a greater reduction of species richness in urban areas or in highly managed plantations woud be expected than in less managed ones, this trend was observed in very few cases (Avila-Flores and Fenton 2005; Estrada et al. 2006). On the other hand, there is not a clear pattern about the effect of land use change on the relative abundance of Mexican bats. Some studies report a higher abundance or bat activity in forests compared to urban or agriculture land use (Sosa et al. 2008; Saldaña-Vázquez et al. 2010; Briones-Salas et al. 2019), but others report a higher relative abundance in plantations with high or low management intensity, especially for phyllostomids frugivorous bats (Williams-Guillén and Perfecto 2010, 2011; Mendoza-Saénz and Horváth 2013; Madrid-López et al. 2020). These contradictory results are related to the high vagility of bats and the ability for some species to use well-preserved habitats immersed in a mosaic of various types of land use (Moreno and Halffter 2001), or which they could obtain important resources (food, shelter, corridors) in some plantations with high vegetation complexity such as shaded coffee or mango (Cortés-Delgado and Sosa 2014; Hernández-Montero et al. 2015; Lavariega and Briones-Salas 2016; Vleut et al. 2019).

Landscape ecology studies of Mexican bat diversity have clarified these contradictory results of the effects of land use change over Mexican bat relative abundance. It has been documented that some landscape elements such as riparian corridors, in forest or pasture landscape matrices, maintain higher diversity of bat guilds and species (de la Peña-Cuéllar et al. 2015). Even isolated trees may have a role similar to that of riparian corridors in maintaining bat diversity in Mexican-modified landscapes (Galindo-González and Sosa 2003). In addition, it has been found that bat species richness and diversity are positively associated with the amount of forest cover or the amount of mature vegetation in the landscape (Vleut et al. 2012; Arroyo-Rodríguez et al. 2016; García-Morales et al. 2016; Kraker-Castañeda et al. 2017), although other studies only found a positive relation with bat relative abundance and forest cover at landscape scale (García-García and Santos-Moreno 2014). Relative bat abundance does not have a clear relationship with forest cover, as studies have reported a greater abundance in forest fragments than in continuous vegetation (Bolívar-Cimé et al. 2013) or have found no differences (Barragán et al. 2010; Vleut et al. 2012). This contradictory pattern is related to two characteristics of the study sites: (1) the type of ecosystem and (2) the vegetation structure of edge forest fragments. In Mexico, dry forest are sites with low diversity and abundance of phyllostomids bats. In these ecosystems, the forest fragments with sources of water such as rivers or cenotes (water sinkholes) had higher vegetation diversity. Therefore, phyllostomids bats, especially frugivores and nectarivores, can be abundant in forest fragments. In ecosystems, such as tropical rainforests, forest fragments can have "soft" edges that contain great diversity of plants consumed by understory frugivorous bats, resulting in an increase of abundance of this species in forest fragments.

At the guild level, frugivorous and nectarivorous bats are one of the most common phyllostomids bats in Mexico. Their diversity responds positively to the proximity and the mean distance between forest fragments and negatively to the fragments mean size (Avila-Cabadilla et al. 2012; García-García and Santos-Moreno 2014). The abundance of canopy frugivores decreases when secondary vegetation increases and mature vegetation decreases in landscapes, while understory frugivores show the opposite pattern (Arroyo-Rodríguez et al. 2016). Whereas sanguivores fly close to linear elements of the landscape to avoid open areas, thus requiring landscape connectivity (Ávila-Flores et al. 2019; Bolívar-Cimé et al. 2019; Mendoza-Sáenz et al. 2021). However, to better understand the use of landscape elements at the guild or species level, further studies with GPS or radio tracking are needed.

In general, the effects of land use change on bat diversity reported in studies of other parts of the world are in accordance with the results reported for Mexico. Relative abundance was the only diversity parameter that does not correspond with the effects reported in other parts of the world possibly because Mexico contains dry ecosystems (deserts, dry forest, savannas, etc.) with some superficial water availability that promotes that forest fragments maintain similar major bat abundance compared with non-fragmented forests, especially of phytophagous phyllostomid bats. In addition, the effects of urbanization and cattle ranching over Mexican bat diversity are not conclusive yet, and probably the trends are like other parts of the world.

11.3.2 Effect of Pollution on Mexican Bat Diversity

Noise pollution is an invisible threat that affects the health and many other functions in humans and other animals. One of the most common sources of this pollution is the human-generated noise, particularly from transportation in terrestrial environments (Shannon et al. 2016). Traffic noise is mainly generated by the combination of the noises produced by commercial (aircrafts, trains, buses) and private transportation (cars and motorcycles). Traffic noise may affect the echolocation calls of bats. However, until now, this aspect has been poorly investigated in Mexico (see Table 11.3). A recent review found only 12 published papers have dealt with this issue and these investigations were mainly carried out in North America and Europe (Bednarz 2021). As a general finding, bats tended to be negatively affected by traffic noise, decreasing the ability to forage and their foraging intensity (Siemers and

Schaub 2011; Luo et al. 2015), although certain species demonstrated a considerable degree of tolerance to this disturbance (Bednarz 2021).

In Mexico, we found that in recent years four undergraduate and graduate projects have investigated the effect of noise on bat activity or in the echolocation characteristics of some species or guilds. In the first study, Lara-Nuñez (2018) investigated the effect of anthropogenic noise on the echolocation pulses of the aerial insectivorous bats *Molossus sinaloae* and *Mormoops megalophylla* within an urban site (city of Cuernavaca, Morelos) and compared it with a natural habitat (Sierra de Huautla Biosphere Reserve). The results showed that, under the background noise at an intensity of 75 dB in the urban environment, *M. sinaloae* echolocation calls were higher in frequencies on an average of 5.8 kHz. For *M. megalophylla*, statistically significant changes were only observed in the start and end frequencies of the pulses, as well as in the middle of these. The author concluded that the increase in the maximum amplitude frequency for *M. sinaloae* could be a response to the Lombard effect, which is the increase in vocal amplitude in response to the increase in background noise (Lara-Nuñez 2018).

In a second study, Medina-Cruz (2019) characterized the bat assemblages in urban sites in Oaxaca, Mexico, registering bats species with mist-nets and with acoustic monitoring. She found that the site with the highest noise pollution (mainly emitted by cars) showed the lowest species richness of insectivorous bats that hunt at ground level. The third study, Pérez-Pérez (2020) related the structure of echolocation calls of *Molossus rufus* emerging from different urban roosting sites with the environmental noise. The author did not detect an effect on the structure of calls at the emergence of *M. rufus*. However, the effect of urban noise during foraging needs to be investigated, as the traffic noise reduces the effectiveness and efficiency of the foraging in other species such as *Myotis daubentonii* and *Myotis myotis* (Schaub et al. 2009; Luo et al. 2015). Finally, a study by Ferreyra-García (2020) in the Morelia city evaluated the effect of noise pollution, light pollution and vegetation cover over insectivorous bats activity. They found that vegetation cover was the most important variable to explain the bat activity, especially of bats that forage in near to the ground.

Air pollution is a mixture of solid particles and gasses in the air that include several chemicals, factory and car emissions, pollen, and dust. Air pollution particles have devastating consequences for human and other organisms' health, in the form of lung cancer, brain diseases, neurodegenerative diseases, respiratory infections, heart diseases, among others (Herndon and Whiteside 2019). Despite large amounts of combustion-type pollution particles released into the atmosphere appear to harm the specialized respiratory organs and high metabolism of foraging bats (Voigt et al. 2018), research in this subject has been poorly conducted until now.

One of the few studies investigating different degrees of air pollution and bat activity has been carried out in West Poland, the area of highest impact of heavy industry, where authors found that the largest bat diversity was found at the less polluted forests (Rachwald et al. 2004). In a review, Herndon and Whiteside (2019) highlighted the importance of coal fly ash (CFA), the toxic waste product of coal burning, that can directly enter bat bodies through respiration or trans-dermally. These authors found in their study that CFA is the origin of pollutants on bat tissue and guano, urging authorities to reduce the harmful combustion-type nanoparticle emissions and the implementation of international programs to quantify, monitor, and regulate ultrafine particulate air pollution.

In the Megalopolis of Mexico, one of the largest cities in the world, Ramos-H et al. (2020) investigated the associations between metal exposure and the accumulation patterns in the insectivorous bat, *Tadarida brasiliensis*. They found that higher concentrations of copper (Cu) and zinc (Zn) in bats at two localities were associated with vehicular traffic, whereas higher concentrations of vanadium (V) were attributable in one of the sites where fossil fuel combustion was generated by the Industrial Complex in Tula, in the state of Hidalgo. These results highlight the need for more investigations to uncover the exposure that bats are facing to air pollutants in the human-dominated ecosystems.

Finally, light and water pollution are also poorly studied in Mexico, according to our literature search, although there are some studies that have investigated the effects of water pollution, light pollution, and vegetation cover effects on bat activities. Research results found that contaminated rivers can maintain insectivorous bat activity despite light and noise pollution and that the vegetation cover of the rivers was the principal factor that explained the bat activity in the rivers (Ferreyra-García 2020). On the other hand, it has been documented that light pollution reduces the visitation rate of frugivorous bats to *Ceiba pentandra* flowers in the city of Merida (Dzul-Cauich and Munguía-Rosas 2022). However, this reduction of visit rate does not affect the reproductive success of the plant. With such limited present evidence of the effects of pollution on Mexican bat diversity and ecology, we cannot affirm that the trends are as predicted by literature for other countries.

11.3.3 Climate Change

Anthropogenic climate change is causing multiple effects on fauna, such as the reduction of suitable conditions and changing distributions, changes in phenology, loss or changes in migratory behaviors that are threatening species coexistence and the maintenance of ecological processes affecting the healthy functioning of ecosystems (Blois et al. 2013; Urban 2015). The speed of these changes is also a concern especially for species with limited mobility and dispersal capacity, which although might not be the case for bats directly, but does affect their foraging resources and species assemblages as well as trophic relationships (Harrington et al. 1999; Loarie et al. 2009). Mexico is highly vulnerable to the effects of climate change due to its social, economic, and geographical characteristics. Its location between two oceans along with its latitude and topography exposes the country to extreme hydrometeorological phenomena. About 90% of the country's territory has been affected either by cyclones or by severe drought (INECC 2018).

Studies report different effects of global warming on bats, for example, latitudinal and altitudinal movements, effects on reproductive success due to changes in water availability especially in arid regions, mismatches between foraging resources availability and migratory bats, prey detection ability in echolocating bats, disruption of hibernation and migration patterns, increased vulnerability to disease (Jones and Rebelo 2013; Sherwin et al. 2013; Luo et al. 2015; Hall et al. 2016; Hayes and Adams 2017; Adams 2018; Chattopadhyay et al. 2019; Adams and Hayes 2021). Studies directly addressing impacts of future climate change scenarios on bats in Mexico are scarce and focused on changes in environmental suitability of bat species (Zamora-Gutierrez et al. 2018) and their foraging resources (Gómez-Ruiz and Lacher Jr 2019). Projections in these studies indicate, overall, that bats will be affected by unfavorable conditions in at least 80% of their range and will have to migrate more than 100 km to reach suitable environments in distant regions by the 2050s. Moreover, future climate change scenarios predict severe humidity decrease especially in the arid and semi-arid regions affecting endemic Mexican bat species occurring in the arid regions of Baja California and the Mexican Plateau (Zamora-Gutierrez et al. 2018). Surface water availability is important during lactation in bats and its reduction due to climate change will impact reproduction success and population numbers (Adams and Hayes 2008; Adams 2010; Hayes and Adams 2017). For insectivorous bats, surface water availability offers opportunities for finding insect prey (Korine et al. 2016). Severe drought events due to climate change will decrease surface water area and reduce foraging habitat for insectivorous bats that will need to spend more energy in finding prey.

Climate change affecting bat distributions might result in dispersal of zoonotic diseases (Mills et al. 2010). Hayes and Piaggio (2018) assessed the potential impacts of climate change on the distribution of common vampire bats (*Desmodus rotundus*). Their models indicate range expansion to northern Mexico and southern Texas in the United States where cattle-ranching activities are widespread, and that cattle could be more exposed to rabies virus transmitted by vampire bats.

Migratory bats are exposed to high rates of evaporative water loss; therefore, they need to access drinking water along the way (Popa-Lisseanu and Voigt 2009). Bats have been proposed as indicator species for the effects of climate change on migratory animals. The Mexican free-tailed bat (*Tadarida brasiliensis*) is one of the species suggested as a proxy for cave-dwelling bats in the Tropics because there is a large and long-term population data that correlate the impact of changes in temperature and other regional weather patterns on population size at maternity roost sites (Newson et al. 2009). Migratory nectar-feeding bats are especially vulnerable since they rely on nectar resources and plant phenology, particularly flower availability, which is linked to precipitation and will likely be modified due to climate change resulting in plant–pollinator asynchrony (Gómez-Ruiz and Lacher Jr 2019). Humphries et al. (2002) show evidence that global warming might constrain the suitable habitat for successful hibernation in mammals. Bats hibernation duration may be reduced because of climate change, and insect abundance might not be sufficient to offset the increased energetic costs associated with more frequent arousal by bats (Jones and Rebelo 2013).

Current knowledge on the effects of climate change and bat physiology, lactation, and reproduction is the result of long-term studies (Adams 2010, 2018; Lučan et al. 2013). To better understand how climate change will impact Mexican bats, we need to start collecting data in a systematic manner. Furthermore, bats are bioindicators for monitoring climate change, so it is urgent to implement a global network for monitoring their populations (Jones et al. 2009). At present, the information available concerning Mexican bats is insufficient to conclude that they are responding as global predictions postulate (Table 11.1).

11.3.4 Human–Bat Conflicts

Conflicts between humans and bats in Mexico have been rarely documented in the scientific literature. In a recent review of human-wildlife conflicts in Mexico, not a single study included bats as a source of conflict with people (Flores-Armillas et al. 2019). However, information in gray literature and anecdotal reports suggests that intentional killings may represent a primary force behind human-driven mortality of bats in Mexico. For North America, including Mexico, it has been estimated that intentional killing of bats represents the third cause of multiple mortality events (≥10 individuals found dead), just behind white-nose syndrome and wind turbine collisions (O'Shea et al. 2016). The impact of direct killing on bat populations may be particularly severe, at least at the local scale, for those species living in large colonies. Destruction or entrance blocking of natural and artificial day roosts may result in the death of many resident bats, whereas surviving individuals may abandon the roost with uncertain fate. In urban settings, civil protection offices and pest control companies are regularly called to kill or exclude bats roosting in residential buildings. In Mexico City, for example, 57% of bat roosts were recently vacated after intentional destruction, entrance blocking, or fumigation (García-Bermúdez 2018). Almost as a rule, bat control in Mexico is implemented without previous approval and supervision of environmental agencies. Unfortunately, no data on the actual death rates due to direct killing are available for any bat species in any Mexican location. The exception is for the vampire bat *Desmodus rotundus*, whose culling campaigns for bovine rabies control killed about 90,000 individuals in 2020, assuming a conservative rate of 5 deaths per each individual treated with vampiricide (SENASICA 2020).

In Mexico, direct interventions on bat colonies and their roosts are strongly motivated by negative ideas, perceptions, and emotions toward bats. For example, in the Volcanic Complex of Colima, nearly 40% of local caves were intentionally collapsed by local people due to the fear inspired by bats (Segura-Trujillo and Navarro-Pérez 2010). As occurs globally, negative attitudes toward bats among Mexican people result from two main factors: the cultural links of bats with witchery and evil-oriented mythological stories, and the strong association that people make between bats and infectious diseases (Flores-Monter et al. 2017). In addition, the physiognomy of bats appears repulsive to most Mexicans across the country (Torres

Romero and Fernández-Crispín 2012; Aguilar-Rodríguez et al. 2016; Flores-Monter et al. 2017), which makes it difficult to create empathetic links with bats. Aversion to bats is often enhanced when bat colonies roost inside or adjacent to inhabited houses and buildings, either in urban or in rural settings. In many cases, the presence of odors, moisture, and insects associated with bat guano stimulates rejection, repugnance, or even hatred toward bats (Aguilar-Rodríguez et al. 2016). Negative attitudes may intensify when bat feces and urine fall into home interiors or damage structural components of buildings.

Transmission of infectious diseases is probably the most important factor promoting fear or rejection to bats among Mexican people. Surveys conducted in rural and urban locations of the country indicate that most people believe that bats transmit rabies and other infectious diseases (Aguilar-Rodríguez et al. 2016; Flores-Monter et al. 2017; Hernández-Sánchez 2019). Although human rabies seems to be present in the mind of many Mexican people when thinking about bats, bloodsucking by itself (and secondarily, the death of domestic animals) may cause the greatest fear among people in some rural locations (Torres Romero and Fernández-Crispín 2012; Flores-Monter et al. 2017). A small proportion of Mexican respondents associate bats or bat guano to some kind of fungal disease (i.e., histoplasmosis), but only in urban locations (Aguilar-Rodríguez et al. 2016). Anecdotal observations and informal social networking suggest that the COVID-19 pandemics has strengthened the negative public image of bats, particularly because they are often misidentified as the origin of SARS-CoV-2. However, no study to date has evaluated the changes in perceptions, attitudes, and actions toward bats during the COVID-19 pandemics among Mexican people.

Habituation to the presence of bats in human spaces (urban or rural buildings) and local cultural values may determine more positive bat–human interactions in Mexico (Retana-Guiascón and Navarijo-Ornelas 2012). For example, in the Mixteca Poblana region, bats tend to be more appreciated in towns located near caves harboring large amounts of guano, which is then collected, used, and sold as a fertilizer by local people. In Nahuatl-influenced locations of the same region, symbolic values linked to ancient cultures may result in more respect to bats (Flores-Monter et al. 2017). Appreciation of ecosystem services provided by bats may play a central role in local strategies that promote bat conservation both in urban and in rural locations (Torres Romero and Fernández-Crispín 2012). Knowledge of ecosystem services provided by bats may be prominent both in urban (Flores-Monter et al. 2017) and in rural (Hernández-Sánchez 2019) locations, especially among young people, depending on the way residents interact with bats. In Mexico City, knowledge on ecosystem services of bats is more precise among people with higher education living in proximity to bat roosts (Mendieta-Vázquez 2017). In the latter study, urban residents were willing to donate for conservation of bats (on average, 10.00 USD/year per person) once they were informed that a local colony of insectivorous bats consumed about 500 g of dipterans every night. Clearly, science communication and environmental education may be effective tools to reduce threats to bats in Mexico.

Contrary to other Anthropocene threats, human–bat conflicts in Mexico are like international observations about human–bat conflicts. In addition, the presence of the vampire bats in Mexico promotes that human–bat conflicts being a constant threat to other bat species populations.

11.3.5 Human Infrastructure and Their Impact on the Mexican Bats

The continuous growth of human population implies a proportional growth of human-made infrastructures and the subsequent affections on native fauna. Under the Anthropocene, wind farms, roads or highways, and buildings are the most notorious human-made infrastructures to affect bat fauna worldwide, and Mexico is not the exception. For wind farms, we found seven published articles that met the selection criteria. The topics of these studies were (i) the mortality of bats caused by wind turbines (Torres-Morales et al. 2014; Bolívar-Cimé et al. 2016; Cabrera-Cruz et al. 2020); (ii) the temporal dynamics of scavengers' community in wind farms (Villegas-Patraca et al. 2012); (iii) changes of bat community and activity patterns (Briones-Salas et al. 2017), (iv) detection of physiological stress in bats (Medina-Cruz et al. 2020), and (v) a global synthesis of wind energy impacts on bats (Arnett et al. 2016). Except for the latter, which is a global review, the rest of the studies were done within one of the largest wind farms of Mexico located in the Isthmus of Tehuantepec (IT), in Oaxaca, México. Yet in 2021, Mexico had 68 operating wind farms in 14 states (AMDEE n.d.), which therefore supposes a considerable geographic bias on the knowledge of the effect of wind farms on Mexican bat fauna. The carcasses recovered in the wind farms placed in the IT wind farm corresponded to 28 species and seven indeterminate taxa (Fig. 11.3). These victim species, as was found, in other wind farms in the temperate zone, are adapted to forage and echolocate in open areas (Arnett et al. 2016). However, while the migratory species are the most vulnerable in temperate zones, the resident species too, are highly vulnerable in the IT. Similar results have been observed in other studies of the Neotropics (Rodriguez-Duran and Feliciano-Robles 2015) and may indicate that the impact of wind farms on bat fauna is higher for tropical regions. This supposes an important issue for the development of the Eolic industry in tropical countries such as Mexico as relates to the conservation of the bat fauna. These findings may also apply to the more sub-tropical regions of northern Mexico. On a wind farm in Texas, close to the United States-Mexican border, Weaver et al. (2020) reported bat mortality and that *Tadarida brasiliensis* was the most threatened species. This species has an agriculture-economic relevance due to its role in insect pest control (Cleveland et al. 2006). The authors suggest that due to the similar species composition, the wind farms placed in the more arid subtropics of northeast Mexico may show similar impacts to those in tropical regions.

Fig. 11.3 A Northern Yellow Bat (*Lasiurus intermedius*) killed by collision with a wind turbine. (Photo by Juan Cruzado)

Several challenges exist for the bat researchers and wildlife managers dedicated to the study of the impact of wind turbines on Mexican bat fauna. The lack of knowledge for the rest of the wind farms that are operating in Mexico and the unresolved scientific questions are some of these challenges. However, bat researchers face social and political challenges that are not always considered. For example, most of the wind turbines are placed in crop fields (Bolívar-Cimé et al. 2016; Cabrera-Cruz et al. 2020) where conducting ecological studies requires interaction among bat researchers and landowners. On the other hand, the diffusion of data associated with the measurements of the impact of wind farms is urgently needed; however, this information is not always available to researchers due to strict data use policies. With this panorama, we recommend enhancing the collaboration among landowners, farmers, bat researchers, ecologists, engineers, and windfarm administrations.

With respect to roads, we found only six studies that report bat casualties by roadkill (Grosselet et al. 2004; Escobedo-Cabrera and Calmé 2005; González-Gallina and Benítez-Badillo 2013; Nahuat-Cervera et al. 2021; Sánchez-Acuña and Benítez 2021; Vargas-Contreras et al. 2021). These studies were done on highways located in the states of Yucatan, Campeche, Oaxaca, Puebla, and Veracruz. From these studies, only two reported a detailed list of road-killed bat species (González-Gallina et al. 2013; Nahuat-Cervera et al. 2021; Vargas-Contreras et al. 2021). Third research (González-Gallina et al. 2013) mentioned *Lasiurus borealis*, and "Chiroptera sp." and the rest of studies did not identify at the level of species and just referred such as "Chiroptera" or "bats."

Despite a variety of studies that report mammal roadkill, bat species are not always reported. Why do some Mexican highways result in being more dangerous for bats? Ecological traits, presence and location of roosts, and highways characteristics may answer this question but further studies are needed (Altringham and Kerth 2016). For example, bat refuges close to the roads look like a perfect catastrophic scenario. In Campeche, El Volcán de los Murciélagos (VM) located in the Balam-kú reserve is the largest cave in the neotropics and houses 2.2 millions of bats of eight species (Vargas-Contreras et al. 2021). The 186th highway is located 400 meters from the VM and the roadkill rate is relatively high as showed Vargas-Contreras et al. (2021) who analyzed a 2000 m transect of the highway divided into subsections of 50 m. They estimated a mortality rate of 23.3 individuals/year-1 per each 50 m subsection. Despite this number do not seem high, the study of Vargas-Contreras et al. (2021) just focused on a section of 2000 m of the ~150 km length of the Escarcega-Xpujil 186th highway placed along the Mayan jungle. Other larger colonies refuges such as El Sótano de Cerro Colorado in Apazapan, Veracruz, and La Cueva de los Murciélagos in Mavirí, Sinaloa are located close to roads, but we found no roadkill data for bats at these sites.

Worldwide, those bat species that fly near the ground are the most threatened by roads (Altringham and Kerth 2016). This same pattern is shown in the VM, where the low flying species, *Natalus mexicanus* and *Pteronotus mesoamericanus,* have the highest reported mortality (Vargas-Contreras et al. 2021). In addition, other species that do not fly at low altitude are also killed and it is presumed that collision occurs when they move among roosts, or they are searching for water or food resources (Altringham and Kerth 2016; Vargas-Contreras et al. 2021). What other factors could increase the risk of roadkill in bat species not typically threatened by roads? This is an open area for future research. In Mexico, "Road Ecology" is a research field with a recent development and with several gaps of information in particular taxa such as bats. Many unresolved questions remain, and this highlights the need for further studies related to roadkill of bat fauna and how we can mitigate this negative impact.

Finally, human-made buildings (HMB) may positively affect bats when these serve as daily roost sites (Russo and Ancillotto 2015). However, some structures may have negative effects exposing bats to: (i) collision risk, (ii) native or exotic predators, (iii) diseases or infection agents, or (iv) persecution by humans (Voigt et al. 2016). In Mexico, positive outcomes have been reported where bats use HMB as daily roosts (Borges-Jesús et al. 2021), hibernating refuges (López-González and Torres-Morales 2004), and reproduction sites (León-Galván et al. 2015). However, to our knowledge, no studies report negative effects in Mexico. Urban bat ecology and particularly the interaction among bats and HMB is a research field with many gaps of knowledge and unresolved questions. Further studies are needed to understand how species are responding to changes imposed by urban growth and particularly, determination of the main threats that bats are facing in this new "ecosystem."

11.4 Conclusion and Perspectives

We conclude that, in general, the responses expected by each threat of human activities on Mexican bats were fulfilled. This was particularly true for topics such as land use change, human–bat conflicts, and human infrastructure. To reduce the impact of these threats in Mexican bat populations, it is necessary to promote public policies that preserve their habitats, as well as the conservation of forest fragments, regardless of their vegetation successional stage. Avoiding intentional killing or roost disturbance is essential, but to achieve this it is important to recover and promote the cultural values that link human life with bats. Agriculture with low environmental impact, agroecology, and conservation agriculture also needs to be promoted. These challenges demand the use of interdisciplinary science, with co-construction knowledge from local people. These actions will promote changes in human infrastructure and the use of new technologies to reduce the impact of Mexican bat populations. Finally, there are important issues related with the Anthropocene such as pollution and climate change that need scientific data to assess the potential impact and make decisions. Both are the result of human activities, and they demand the use of new technology and long-term research given the limitations of the scientific information of Mexican bats, and the effects of these phenomena on Mexican bats populations could be slowly or cryptic.

Acknowledgments The authors thank Robert W. Jones, Patricia Ornelas García, Rubén Pineda-López, and Fernando Álvarez García for their invitation to write this chapter, and the anonymous reviewers that improved the content of the manuscript.

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Part III
Ecosystems

Chapter 12
Impacts of Land Use and Cover Change on Land Mammal Distribution Ranges Across Mexican Ecosystems

Eduardo Mendoza, Roger Guevara, and Rodolfo Dirzo

Contents

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/978-3-031-17277-9_12.

E. Mendoza
Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michocana de San Nicolás de Hidalgo, Morelia, Mexico

R. Guevara (✉)
Biología Evolutiva, Instituto de Ecología, A.C. (INECOL), Xalapa, Mexico
e-mail: roger.guevara@inecol.mx

R. Dirzo
Department of Biology, Stanford University, California, CA, USA

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_12

12.1 Introduction

The phenomenon of defaunation, defined as the decline or outright loss of wildlife populations and species caused by anthropogenic activities and the cascading effects this produces, has fortunately started to gain greater visibility in the scientific arena, as well as in the popular literature (Dirzo et al. 2014; Galetti and Dirzo 2013; Benítez-López et al. 2017; Dirzo 2019). For a long time, defaunation had remained eclipsed by the more publicized anthropogenic global impacts such as tropical deforestation and climate change. Indeed, a visible publication on the changing ecology of tropical forests labeled defaunation as "the invisible threat" (Phillips 1997). Undoubtedly, land use change and anthropogenic climate disruption are two major threats to Earth's biodiversity. However, growing evidence provides a compelling view of the magnitude and variety of impacts brought about by defaunation –at the local and global levels– revealing this phenomenon as one of the greatest disruptions to the structure and functioning of the planet's natural ecosystems (Young et al. 2016).

The magnitude of vertebrate global extinctions, though seemingly low (estimated to be around 340 species since the year 1500; Ceballos et al. 2015), is nevertheless deceiving, unless they are put in the context of background extinction rates. For example, recent research by Andermann et al. (2020) has documented that historical extinction rates are 1700 faster than those observed over the 120,000 years of the Late Pleistocene, and the authors' modeling exercise strongly suggests that human population size predicts past mammal extinctions with 96% accuracy. Clearly, the loss of the evolutionary legacy caused by the global extinction of mammal species is an issue of concern for society at large. However, global species extinction is not the only facet of defaunation. In addition, the escalation of the rate at which the local abundance of a myriad vertebrate species is declining, and wildlife populations are being lost, is equally alarming (Dirzo et al. 2014). For example, in the case of mammals, an analysis of the changes in the geographic range of a sample of 177 species showed that slightly less than 50% of the species examined had suffered a range contraction of 80% or more in the period 1990–2015, signaling a mass population extinction (Ceballos et al. 2015). Such trends of population extinctions represent a prelude to global extinction as the loss of local populations eventually occurs throughout the entire species' ranges. The significance of these defaunation metrics is that, in contrast with other manifestations of global change (e.g., pollution, overexploitation, and even climate change), species extinction is an irreversible anthropogenic impact.

Beyond the numerical metrics of defaunation, it is critical to consider the multifaceted ecological consequences of the loss of animal species, as this causes cascading effects at several trophic levels, thus affecting the entire ecosystem's functioning (Dirzo et al. 2014; Valiente-Banuet et al. 2015). However, the systematic study of such cascading effects is in its infancy. Some attention has been paid to those cases where species interactions and associated ecosystem services such as pest control and crop pollination are affected (Cleveland et al. 2006; Trejo-Salazar et al. 2016).

In contrast, other consequences of defaunation are poorly documented. This includes the alteration in herbivory, seed predation, and dispersal interactions, and the cascading consequences on the community, as has been shown in the case of plant diversity changes in the understory of tropical forests (Dirzo and Miranda 1991; Camargo-Sanabria et al. 2015; Martínez-Ramos et al. 2016). This in turn may affect regeneration and major biogeochemical processes of the ecosystem. For example, recent evidence indicates that the absence of large vertebrates, and the subsequent cancelation of their seed dispersal services in tropical forests, will likely cause a reduction in the occurrence of large trees. The limited or absent recruitment of such trees, with their typical high-density wood, in turn, may result in a reduction in the capacity of forest ecosystems to store carbon (Bello et al. 2015). More recently, defaunation has been in the spotlight due to its relationship with emerging infectious diseases. A study of experimental defaunation in African savanna showed that the loss of large mammalian wildlife favors the proliferation of small-bodied species, particularly rodents, many of which are hosts to a variety of zoonotic pathogens (Young et al. 2014, 2017). Human perturbation and encroachment of natural habitats of mammals, overexploitation, and the negligent handling of bushmeat represent latent triggers of emerging infectious disease (Johnson et al. 2020) and have the potential to unleash a variety of zoonotic spillovers (Glidden et al. 2021) and, potentially, pandemics such as COVID-19 (Watsa et al. 2020).

The complexity of the defaunation process generates a need to address the study of its magnitude, mechanisms, and consequences from various perspectives. Given the current pace of mammalian defaunation in terms of the local decline in abundance across a myriad of species (Dirzo et al. 2014), and the loss of populations signaled by the contraction of the range of species across their geography (Ceballos et al. 2015), in this chapter we examine tropical land mammal defaunation in Mexico from the perspective of changes in the natural land cover that represents the distribution range of a large sample ($N = 252$) of mammalian species from this country.

12.2 Species Richness and Overall Conservation Status of Land Mammals in Mexico

As a preamble to our analysis, we first provide a brief overview of the richness and conservation status of the country's mammalian fauna across the country's major ecosystems. Mexico supports a rich land mammalian fauna comprising about 496 species distributed in 11 orders, with Rodentia and Chiroptera at the top of the list (Ramírez-Pulido et al. 2014). Out of this faunal contingent, approximately 50% of the species predominantly inhabit tropical rain and dry forests, making these ecosystems a great concern for mammalian conservation (Ceballos and Oliva 2005). Unfortunately, a significant proportion of the overall diversity of Mexican land mammals is under great human pressure leading to their endangerment. An

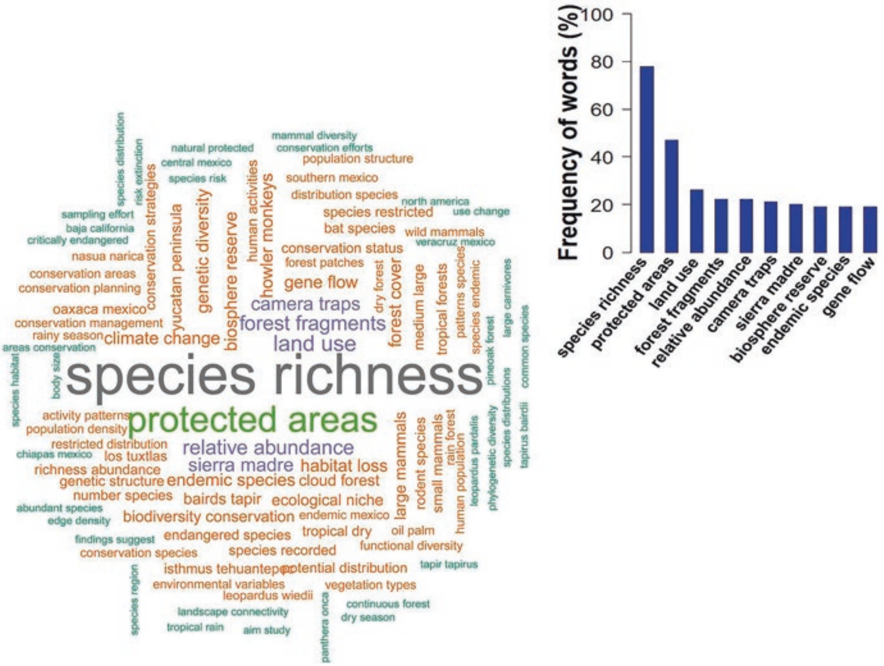

Fig. 12.1 The most commonly used two-word phrases in published papers (1993–2021) addressing the conservation of land mammals in Mexico

examination of the Red List of the International Union for the Conservation of Nature (IUCN 2021) reveals that as much as 18% of these species are globally threatened (categories: critically endangered, endangered, and vulnerable). Moreover, about 27% of these species are classified as seriously endangered (categories: "probably extinct in the wild," "threatened," "in danger of extinction," and "under special protection") in the Mexican List of Threatened Species (Norma Oficial Mexicana-059; SEMARNAT 2019). Additionally, 8% of the country's total number of species are classified as threatened at both the national and global levels.

There is a rich body of literature addressing a wide variety of topics related to the conservation of the mammalian fauna of Mexico. To identify the main topics that have been addressed concerning the conservation of terrestrial mammals in the country, we interrogated the ISI Web of Knowledge © platform with the text strings "TS = mammal* and TS = conservation and TS = Mexico." After discarding studies dealing with non-land mammals and those conducted outside Mexico (e.g., New Mexico), we obtained 267 studies published between 1993 and 2021. The most common term of these studies was, by far, species richness, which reflects the wide use of this metric as a response variable to characterize the country's mammalian communities (Fig. 12.1). Also, the prevalence of this term indicated that we should place special emphasis on tropical mammals, given the well-known biological richness of these ecosystems. This term is followed by that of “protected areas,” emphasizing the researchers’ interest in the role of reserves for mammalian conservation. A closer look at the papers included in this review reveals that very few attempts have been made to evaluate changes in mammal distribution ranges due to anthropogenic impact. This, and the fact that habitat loss due to land use change, together with overexploitation is regarded as the major drivers of defaunation (Young et al. 2017), triggered our motivation for the present analysis.

12.3 Distribution Range of Land Mammals and Changes in Vegetation Cover

One of the principal challenges to characterize the conservation status of wild mammals is the lack, in most cases, of consistent information on the original distribution of the species—the distribution before undergoing significant anthropogenic impact leading to the loss of local populations. Nonetheless, the advances in the accumulation of species’ presence data and their systematization provide a valuable resource that, in combination with spatially explicit climatic data and the species’ currently known climatic envelopes, open the possibility to approximate the species’ original distribution. Thus, with sufficient records of a given species across its distribution, it is possible to develop climatic niche models whose outputs may serve as estimates of the original distribution of the species, even beyond the areas where it has been recorded. Naturally, given the spatial distribution of the available records, the climatic models of the distribution of the species may overestimate or underestimate the potential distribution area. Restricting the predictions to those regions where the species are known to occur (the accessibility area) minimizes the overestimation effect (Cooper and Soberón 2017). On the other hand, to address underestimates, the only option is to have access to as much data (and as widely geographically distributed) as possible.

For the present analysis, we emphasize species whose distributional range overlaps, at least partially, with that of the country’s tropical forests. We used the available records of mammals (CONABIO 2021) to model their potential distribution based on MaxEnt models fed with climatic variables from the Worldclim 2 project (Fick and Hijmans 2017). We discarded duplicate records of mammals, and thus, we considered a single record within each cell of the worldclim raster. We modeled the occurrence area only for those species with at least 30 records after discarding duplicates. Consequently, we modeled the distribution of 252 mammal species.

The climatic variables used to model the distribution of each species were selected by a Monte Carlo classification of presence/(pseudo)absence data—a forest of classification tree (De’ath and Fabricius 2000; Cutler et al. 2007; Fox et al.

2017). For this procedure, we ran 1000 iterations, each based on 80% of the available presence/(pseudo)absence data.

It is worth mentioning that (pseudo)absence data were generated considering the species accessibility area (i.e., the area where the species would have had historic occurrence, similar to the notion of fundamental niche). To do this, we overlayed rasters of the biogeographic provinces of Mexico (Morrone et al. 2017) and the potential vegetation cover (CONABIO 1990), which led to 84 unique combinations. Then, based on the actual records of each species, we determined the accessibility area as all those unique combinations (biogeographic provinces-potential vegetation cover) for taxa with three or more records. Unique combinations with only one or two records were disregarded to avoid the risk of introducing inaccuracies in species occurrence (geographic coordinates) and identification. Afterward, (pseudo) absence data were randomly extracted from those combinations outside the accessibility area.

Predictions of MaxEnt models were binarized based on a threshold of 0.1 suitability. Then, for each species' predicted distribution area, we overlayed the potential vegetation cover and the current land use and vegetation cover (INEGI 2002) to characterize the distribution range before and after the extensive transformation of landscapes by humans. Thus, for each species, we have two matrices describing the land use in the predicted distribution range. One matrix accounts for the historical vegetation cover (before transformation), and the second matrix reflects the current status of the vegetation coverage and the different land uses therein. Based on these two matrices, we conducted a co-inertia analysis (Dolédec and Chessel 1994) to (i) establish multivariate correlations and (ii) ordinate the species across multidimensional space. For those readers interested in the details of such analysis, here we provide a short account. Other readers can refer to the citations indicated here. Briefly, each matrix is PCA-ordinated and rescaled, such that both ordinations are at the same scale. Then, the ordinations are superimposed and rotated until the distance between the corresponding pairs (the same species in each ordination) is minimized (Dray et al. 2003). Thus, if significant correlations existed between the two matrices, species with similar historic vegetation cover in their distribution ranges should also share similar configurations of the current land use. Such relationships can be represented as vectors originating in one zone of the ordination space (i.e., historic vegetation cover) and ending in a different zone (current land use). The closeness between both sets of observations is established through the RV coefficient (a generalization of the squared Pearson correlation coefficient; Robert and Escoufier 1976). Then, the significance of such correlations was tested with a 10,000-permutation Monte Carlo procedure in which the identity of the samples in both matrices was swapped and the co-inertia metric recalculated to establish a null probabilistic distribution against which the observed value was compared (Heo and Gabriel 1997).

Based on the co-inertia analysis, we identified eight clusters of species that, overall, yielded a multivariate correlation coefficient of RV = 0.84 between the configuration of the vegetation cover in the distribution ranges of mammals before and after the anthropogenic transformation of the corresponding ecosystems (Fig. 12.2).

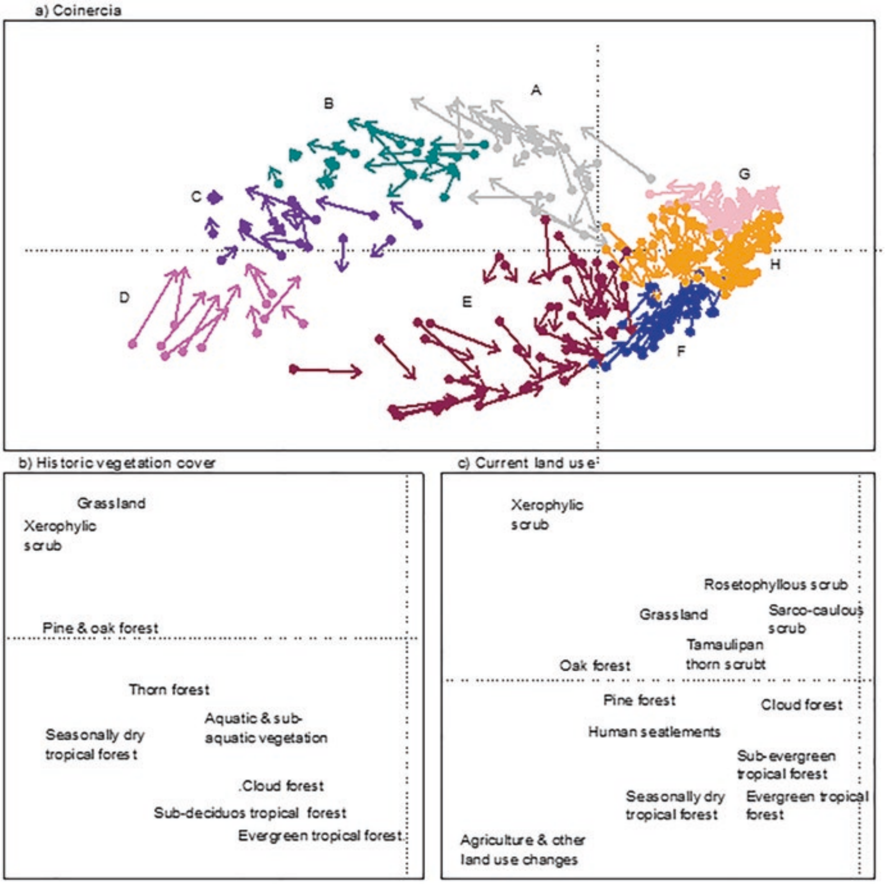

Fig. 12.2 Co-inertia analysis representing the multivariate correlation of the land cover change configuration (historic vegetation cover and current land use) and the distributional ranges of 252 species of mammals of Mexico

Regarding the historic vegetation cover, oak, pine, and thorn forests, together with bushland, grasslands, and seasonally dry tropical forests, predominated along the first axis. Semideciduous and evergreen tropical forests, along with cloud forests and aquatic vegetation dominated the second axis. On the other hand, regarding the current vegetation cover status across the multivariate space, we observe that the first axis was characterized by transformed vegetation (agriculture, urban centers, bare soil), oak and pine forests, as well as seasonally dry forests, and arid and semi-arid vegetation. In contrast, evergreen and semi-evergreen forests predominated along the second axis.

Next, we describe the main characteristics of the eight species' clusters identified in our analysis (Fig. 12.2). We provide examples of the current land use cover in each group (Supplementary Material 12.1), and land use cover maps of other species are available upon request.

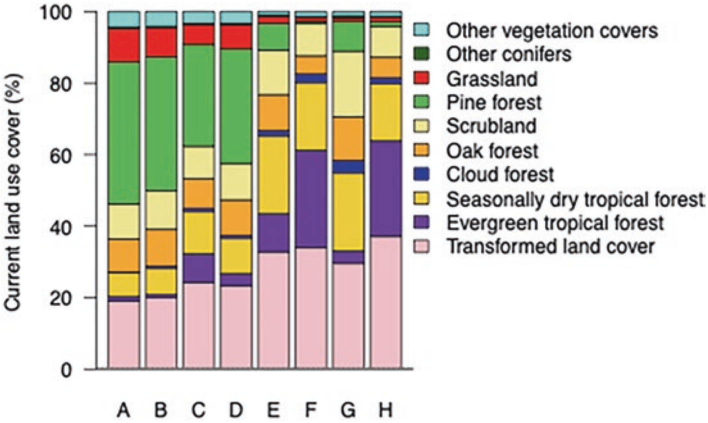

Fig. 12.3 Proportional distribution of land cover vegetation types and uses in the eight mammal species clusters (A-H) identified in this study

12.3.1 Limited Distribution with Low Habitat Transformation and Low Representation in Tropical Forests

The species in this cluster (*n* = 22) had limited distribution occupying predominantly arid and semiarid environments (scrub vegetation, 40% ± 12%, mean ± standard deviation; grasslands 9.5% ± 3%), followed by forest with marked seasonality (pine forest, 9.8% ± 5.8%; oak forest 9.3% ± 4.6%), but with species poorly represented in tropical forests (seasonally dry, 6.7% ± 5.3%; evergreen, 1.2% ± 2.4%). On average (derived from the percentage of transformation within each distribution range), land cover transformation constitutes 19% ± 4.2% of the potential distribution ranges of the species in this group (Fig. 12.3).

Rodentia (*n* = 10) and Chiroptera (*n* = 8) were the best-represented orders, accounting for 47.6% and 38% of the species in this group. In Rodentia, Cricetidae was the best-represented family (*n* = 6), followed by Heteromyidae and Sciuridae with two species each. In Chiroptera, the Vespertilionidae included four species: three of Molossidae, and one species of Phyllostomidae. Also, this group had one species of Carnivora (*Spilogale gracilis*), and one species in Artiodactyla (*Dicotyles angulatus*) and Soricomorpha (*Notiosorex crawfordi*). All but one species in this group were classified as least concern by the IUCN, and *Corynorhinus mexicanus* (Vespertilionidae) was classified as near-threatened (Solari 2019). For details, see Supplementary Material 12.1.

12.3.2 Wide Distribution, Low Habitat Transformation, and Low Representation in Tropical Forests

As found in group A, species in this group ($n = 19$) had low representation in tropical forests (evergreen, 0.7% ± 0.4% and seasonally dry, 7.5% ± 2.6%) but are widely distributed in scrubland (37.4% ± 4.8%.), pine (10.8% ± 2.8%), and oak (10.4% ± 2.1%) forests, and grasslands (8.2% ± 1.0%). On average, land cover transformation comprises 20.1% ± 1.5% of the potential distribution ranges of the species in this group (Fig. 12.3).

Chiroptera ($n = 9$, or 47.4%) was the predominant order in this group followed by Rodentia ($n = 6$, or 31.6%). Vespertilionidae ($n = 7$; or 77.8%) was the best-represented family in Chiroptera, while Phyllostomidae had only two species (22.2%). Also, Rodentia included only two families, Cricetidae ($n = 5$, 83.3%) and Sciuridae ($n = 17.7\%$). Carnivora included three species (*Bassariscus astutus*, *Lynx rufus,* and *Spilogale putorius*) and Lagomorpha one species (*Lepus callotis*). About 78% of the species in this group were classified as least concern, but *Choeronycteris mexicana* (Phyllostomidae), *Spilogale putorius* (Mephitidae), and *Leptonycteris nivalis* (Phyllostomidae) were classified as near-threatened, vulnerable, and endangered, respectively (Solari 2018; Gompper and Jachowski 2016; Medellín 2016a). For details, see Supplementary Material 12.1.

12.3.3 Wide Distribution, Moderate Habitat Transformation, and Moderate Representation in the Seasonally Dry Tropical Forests

This cluster included species ($n = 16$) of wide distribution across many vegetation types with moderate representation in tropical forests (scrubs, 32.0% ± 4.1%; pine and oak forests with 10.1% ± 1.7% each; and 10% ± 1.5% and 3.3% ± 1.7% of seasonally dry and evergreen tropical forest, respectively). Land cover transformation in the species' distribution ranges in this group averaged 23.4% ± 1.9% (Fig. 12.3).

Rodentia and Chiroptera were equally represented in this group with six species each representing 75% of the species. Cricetidae accounted for 83% of all rodents in this group ($n = 5$), while Heteromyidae included only one species (17%). Vespertilionidae ($n = 4$) represented 67% of all bats in this group, while Phyllostomidae and Molossidae had one species each (16.5%). The other order represented in this group was Carnivora with three species (25% of all species in the group): *Canis latrans*, *Puma concolor,* and *Conepatus leuconotus*. All but one species (i.e., 15, 94%) were classified as least concern. Only the bat *Leptonycteris yerbabuenae* (Phyllostomidae) was classified as near-threatened (Medellín 2016b). For details, see Supplementary Material 12.1.

12.3.4 Species with the Widest Distribution, Moderate Habitat Transformation, and Moderate Representation in Tropical Forests

This group includes only 10 species of wide distribution that occupied mostly scrublands (28.5% ± 2.7%) and seasonally dry tropical forests (11.9% ± 1.0%), followed by pine (9.1% ± 0.8%), oak (8.3% ± 0.9%) and evergreen tropical (8.0% ± 0.8%) forests. On average, 24.3% ± 1.0% of the potential distribution ranges have been transformed into productive activities (Fig. 12.3).

Carnivora was the best-represented order with three species (*Urocyon cinereoargenteus*, *Mustela frenata,* and *Procyon lotor*). Rodentia (*Peromyscus leucopus* and *Sigmodon hispidus*) and Chiroptera (*Mormoops megalophylla* and *Natalus mexicanus*) included two species each. Both rodent species were in the Cricetidae, while bats were in Mormoopidae and Natalidae, respectively. Artiodactyla was represented by *Odocoileus virginianus,* Didelphimorphia by *Didelphis virginiana,* and Lagomorpha by *Sylvilagus floridanus*. All species in the group are considered as least concern by IUCN (2021). For details, see Supplementary Material 12.1.

12.3.5 Widely Distributed, Well Represented in the Seasonally Dry Tropical Forest

Species of wide distribution are well represented in seasonally dry (21.5% ± 3.3%) and evergreen (10.6% ± 4.2%) tropical forests, followed by pine (12.4% ± 3.1%) and oak forests (9.9% ± 2.2%). Habitat transformation in the distribution ranges of the species in this group averages 33.6% ± 2.6% (Fig. 12.3).

This group includes 41 species, of which 56% (*n* = 23) were bats primarily in Phyllostomidae (*n* = 15), while Mormoopidae and Vespertilionidae had three species each. Also, there was only one species of Molossidae and Emballonurida. Six species represented Carnivora, notoriously the Felidae, with four species (*Herpailurus yagouaroundi*, *Leopardus pardalis*, *Leopardus wiedii,* and *Panthera onca*) and Mustelidae and Procyonidae, each with one species (*Lontra longicaudis* and *Nasua narica*, respectively). Rodentia included nine species, seven of them in the Cricetidae and one in each of Heteromyidae and Sciuridae. Other orders represented in this group were Cingulata (*Dasypus novemcinctus*) and Didelphimorphia (*Didelphis marsupialis* and *Tlacuatzin canescens*). The conservation status of 88% of the species in this group was least concern. Nonetheless, the Carnivora *Leopardus wiedii* (de Oliveira et al. 2015), *Panthera onca* (Quigley et al. 2017), and *Lontra longicaudis* (Rheingantz and Trinca 2015) are considered near-threatened and the rodent *Peromyscus melanocarpus* (Cricetidae) is classified as endangered (Álvarez-Castañeda et al. 2018c). For details, see Supplementary Material 12.1.

12.3.6 Primarily Distributed in Tropical Forests with Major Habitat Transformation

Species in this group are distributed chiefly in evergreen (27%) and seasonally dry (19%) tropical forests with modest penetration into pine (9%) and oak (5%) forests. Transformation of the distribution ranges of the species reaches up to 34% (Fig. 12.3).

The group included 29 species, with bats representing 41.4% of the species in the group (n = 14), while rodents accounted for 24% of the species (n = 7). Carnivora included three species (*Bassariscus sumichrasti*, *Eira Barbara,* and *Potos flavus*). In comparison, Primates (*Alouatta villosa* and *Ateles geoffroyi*) and Didelphimorphia (*Philander opossum* and *Marmosa mexicana*) were represented by two species each. Artiodactyla, Pilosa, and Soricomorpha included only one species each (*Mazama temama*, *Tamandua mexicana,* and *Cryptotis mexicanus*, respectively). Almost 90% of the species in this group are considered of least concern, but the two Primates in this group, *Alouatta villosa* (Cuarón et al. 2020) and *Ateles geoffroyi* (Cortes-Ortíz et al. 2021b), are regarded as endangered. For details, see Supplementary Material 12.1.

12.3.7 Restricted Distribution, Mainly in the Seasonally Dry Tropical Forest and High Habitat Transformation

The species of this group are of restricted distribution, predominantly in the seasonally dry tropical forest (22%) and have low representation in evergreen tropical forests (3.5%) but are distributed in pine (18%) and oak (12%) forests, as well. The transformation of the vegetation cover is on average of 30% (Fig. 12.3).

The group included 39 species, mostly of Rodentia, with 27 species (67.5%), while Chiroptera (n = 5) and Soricomorpha (n = 5) each accounted for 12% of the species in the group. Lagomorpha included two species (*Lepus alleni* and *L. flavigularis*) while there was only one species of Carnivora (*Spilogale pygmaea*). Only about 53% of the species in this group are considered of least concern. Within this group, the Rodents *Chaetodipus goldmani* (Lacher and Álvarez-Castañeda 2019) and *Callospermophilus madrensis* (Álvarez-Castañeda et al. 2016a) are considered near-threatened. Also, five species are considered vulnerable: the Carnivore, *Spilogale pygmaea* (Helgen et al. 2016), the Phyllostomid bat *Musonycteris harrisoni* (Arroyo-Cabrales and Ospina-Garces 2015), and the rodents *Peromyscus simulus* (Álvarez-Castañeda et al. 2018b) and *Peromyscus zarhynchus* (Álvarez-Castañeda et al. 2018d) in the Cricetidae, and *Neotamias bulleri* in the Sciuridae (Álvarez-Castañeda et al. 2016b). Further, five species of cricetid rodents (*Megadontomys thomasi*, *Microtus oaxacensis*, *Peromyscus melanurus*, *Peromyscus ochraventer,* and *Megadontomys cryophilus*) and the Lagomorph *Lepus flavigularis* are considered endangered (Álvarez-Castañeda and Castro-Arellano 2019; Álvarez-Castañeda

2018, 2019; Álvarez-Castañeda et al. 2019b; de Grammont and Cuarón 2018a; Lorenzo and Smith 2019). Likewise, *Habromys lepturus* (Rodentia: Cricetidae) is considered as critically endangered (Álvarez-Castañeda et al. 2018a). For details, see Supplementary Material 12.1.

12.3.8 Restricted Distribution, Mostly in Tropical Forests and High Habitat Transformation

Species in this group are mostly restricted to evergreen (27%) and seasonally (16%) tropical forests with low occurrence on pine (9%) and oak (6%) forests. Of all groups, this was the one for which we observed the highest habitat transformation, reaching on average 37%.

The group included 77 species, of which 32 and 27 corresponded to rodents (41.6%) and bats (35.1%). Within the Rodentia, Cricetidae accounted for 59% of the species ($n = 19$) while Heteromyidae ($n = 4$) and Sciuridae ($n = 4$) represented each 12.5% of all rodents, and Geomyidae ($n = 3$) represented 9.4% of the rodent species in this group. Also, two of the largest rodents of the Mexican tropical forest forests (Dasyproctidae: *Dasyprocta mexicana* and *D. punctata*) are included in this group. Among bats, Phyllostomidae ($n = 15$) represented 55.6% of the Chiroptera in this group. Emballonuridae (18.5%) included five species, Molossidae (11%) and Vespertilionidae (11%) contributed with three species each, and Noctilionidae included only one species. Soricomorpha ($n = 6$) represented 8% of all species in the group. In contrast, Artiodactyla ($n = 3$, *Mazama pandora*, *Dicotyles crassus,* and *Tayassu pecari*) and Carnivora ($n = 3$: *Conepatus semistriatus*, *Spilogale angustifrons,* and *Galictis vittata*) represented each 4% of all species in the group. Lagomorpha included two species (*Sylvilagus brasiliensis* and *S. cunicularius*), while Didelphimorphia (*Caluromis derbianus*) and Pilosa (*Cyclopes didactylus*) included one species each. The group also included *Tapirella bairdii* (Perissodactyla) and *Alouatta palliata* (Primates). A high fraction (86%) of the species in this group are considered of least concern, and the Cricetid mouse *Microtus quasiater* is considered near-threatened (Álvarez-Castañeda et al. 2019a), as are the Artiodactyls *Mazama pandora* and *Tayassu pecari*, and the Primate *Alouatta palliata*. The Cricetid mice *Oryzomys chapmani* and *Sigmodon alleni*, the Emballonurid bat *Balantiopteryx io,* and the shrew *Cryptotis magnus* are all considered vulnerable (Keuroghlian et al. 2013; Lim 2015; Weber et al. 2016; Cuarón and de Grammont 2018; de Grammont and Cuarón 2018b; Vázquez 2018; Cortes-Ortíz et al. 2021a). Also, the largest wild Mexican herbivore, *Tapirella bairdii,* is endangered (García et al. 2016), while the large rodent, *Dasyprocta mexicana,* is critically endangered (Vázquez et al. 2008). For details, see Supplementary Material 12.1.

12.4 Discussion

The reviewed literature reveals a great effort directed to document the composition of mammalian communities across Mexico, but few attempts have been made to assess the overall conservation status of tropical land mammals considering the trends of anthropogenic impact. Although our analysis examines the situation of mammals distributed in all forested ecosystems, as well as grasslands and scrublands, it was our initial attempt to examine the status of tropical mammals in detail, given the disproportionate species richness of tropical ecosystems. However, one of the obvious but still necessary caveats to highlight in this analysis is that the definition of tropical forests mammals is not straightforward. While some species were indeed restricted to tropical forests, many others also occurred in a wide variety of ecosystems. Here, we analyzed the conservation status based on the land use change across the ranges of 252 species, that were distributed, at least partially, in tropical forests. Our analytical findings indicated that species with distribution predominantly in tropical forests (clusters E-H) are more endangered because transformation of their habitat reaches up to 37%. In comparison, species that chiefly inhabit other ecosystems, mainly arid and semiarid vegetation (clusters A-B), occur in areas where habitat transformation is around 20% (Fig. 12.3).

As expected, rodents and bats predominated in most clusters as these groups account for 50% and 28%, respectively, of all mammals known to occur in Mexico (Ramírez-Pulido et al. 2014). The exception was in group D, which included the species of broadest distribution. In this group, rodents and bats combined (36%) barely surpassed the Carnivora (27%), while in the other seven clusters, rodents and bats together represented over 70% of the species. Furthermore, rodents were over 5 times more represented in group G (restricted distribution mainly in the seasonally dry tropical forest) than bats. Similarly, in group E, rodents exceeded the number of bat species. In group F, which clustered species primarily distributed in tropical forests, bats ($n = 12$) were represented by 70% more species than rodents ($n = 7$).

We found considerable variation in the degree to which natural vegetation has been replaced by other land cover types and uses in the eight species' clusters. However, in most of the cases, the area converted to agricultural lands surpasses 20% on average. This situation underscores the generalized anthropogenic impact on the mammal's natural habitats that has occurred to a considerable degree throughout the country. This is particularly worrisome in those clusters of species of restricted distributions, predominantly within tropical forests (Groups G and H). The consequences of such an impact will likely depend on the mammal's life-history traits and the occurrence of other sources of anthropogenic perturbation. As a general principle, however, we can forecast that species with large body sizes, which generally require a large area of habitat to maintain viable populations, will be the most impacted (Young et al. 2016). Thus, species such as *Tapirella bairdii*, *Alouatta palliata*, *Mazama pandora*, *Dicotyles crassus,* and *Tayassu pecari* (group H) are at high risk, very likely due to their large body size, which demands large tracts of suitable habitat and combined with restricted distributions. Nonetheless, there are other species that, albeit of smaller size, are microhabitat specialists (e.g., Soricomorpha) and therefore are also at risk. Groups G and H, characterized by the reduced distribution of the species, included 85% ($n = 11$) of all shrews analyzed in this study ($n = 13$).

Species distributed mainly in non-tropical forests (Groups A-D) had the lowest values of habitat transformation to "productive" land. Still, about one-fifth of their distribution ranges has been converted to agricultural and farming lands. Because of the wide variety of habitats used by these species and their relatively wide distribution ranges, they can be deemed of low concern for the conservation of their populations. However, the populations of some species in group A, such as *Eumops perotis* (Barquez and Diaz 2015) and *Spilogale gracilis* (Cuarón et al. 2016), are known to be declining.

For species whose distribution ranges cover large extents of tropical forests (Groups E-H), the extensive transformation of their habitat reaches up to 37%. Although the conservation status for species of wide distribution (Groups E and F) is least concern (per IUCN's Red List), the status is near-threatened for habitat specialists such as the freshwater-dependent *Lontra longicaudis* (Rheingantz and Trinca 2015), and large predators such as *Panthera onca* (Quigley et al. 2017). In general, species whose distributional ranges are largely limited to tropical forests (Groups F and H) face the most extensive habitat transformation. On the other hand, the conservation status for some tropical species (e.g., *Mazama temama*, *Conepatus semistriatus*) is unknown due to the lack of data. In contrast, for other species such as *Tayassu pecari*, and *Alouatta palliata,* the conservation status is deemed vulnerable, while *Ateles geoffroyi* and *Alouatta villosa* are considered endangered. A particularly noticeable case is that of *Tapirella bairdii*, a mammal that in Mexico ranked highest (No. 28) in the EDGE score. [The EDGE score classifies mammals (among other vertebrates) based on two criteria: (1) their degree of evolutionary distinctiveness and (2) their level of threat according to the IUCN Red List (https://www.edgeofexistence.org/species/species-category/mammals/)]. All that said, however, the occurrence of highly threatened species in tropical forests is not exclusive to large-bodied mammals, as exemplified by the bat *Balantiopteryx io* (Lim 2015).

Two clusters (G and H) stand out for having the most significant number of species globally threatened (IUCN Red list categories: critically endangered, endangered, and vulnerable). Together (considering the species included in this study), those two clusters harbor 100%, 63.6%, and 83.3% of the species categorized as critically endangered, endangered, and vulnerable, respectively. From these clusters, H stands out for supporting species whose distribution is closely linked to the tropical forest (evenly distributed between evergreen and dry) subjected to marked human-driven transformation.

A similar situation occurs when considering the threatened species at the country level: again, clusters G and H make, in general, the most outstanding contribution to the categories endangered (A), at risk of extinction (P), and subjected to special protection (Pr). Together, these two clusters account for 59.3%, 38.5%, and 78.3% of the mammal species classified as endangered, at risk of extinction, and subjected to special protection, respectively.

It is worth pointing out the factors that can affect our estimations of habitat transformation within the distribution range of mammals. Such factors may lead to underestimations and overestimations of the impacts on the fauna. For example, for species that are actively persecuted by humans (of game value, pets, or perceived as threats), estimation of human impact based solely on assessments of habitat transformation may represent a gross underestimation. Indeed, a recent global assessment of the magnitude of hunting-induced changes in mammal populations across the tropics uncovered that mammal abundances declined, on average, by 83% due to hunting and that mammal populations located up to 40 km from hunters' access points were severely depleted (Benítez-López et al. 2017). Inclusion of these effects in our study would undoubtedly have resulted in more drastic reductions in the distribution ranges of several species. Clearly, this is an aspect that warrants further research.

In stark contrast, for some species the transformation of their natural habitats, rather than engendering a disadvantageous situation can open the possibility to increase their abundance and distribution range. For example, species such as the coyote (*Canis latrans*) have undergone a recent increase in their distribution range, likely favored by habitat transformation (Hidalgo-Mihart et al. 2004). This situation has favored the appearance of this species in habitats where it did not occur before, such as tropical rain forests (Zamora-Espinoza et al. 2021). Likewise, it has been found that some small rodents in the Cricetidae family (e.g., *Sigmodon toltecus*) increase their abundance in tropical areas where forest cover is reduced due to human impact (Barriga-Carbajal 2021). This contrast of effects is consistent with the frequently argued dichotomy of species as "losers" and "winners" in the context of anthropogenic impact (e.g., Young et al. 2016). A deeper understanding of the life history and differential resilience/susceptibility of species in the face of habitat transformation (and its synergy with other anthropogenic impacts) is an aspect that warrants further research. Such research may guide the implementation of effective conservation efforts if we are to prevent a furthering of the country's mammalian defaunation we have sketched in this analysis.

Acknowledgments We thank Norma Tolama for helping to compile the information on the distribution of land mammals. Francelli Macedo helped to conduct a literature search and to summarize the information in a word cloud. E. M. had support from Mexico's National Research System-CONACyT while conducting this research. R.D. was supported by Stanford's School of Humanities and Sciences.

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Chapter 13
Anchialine Fauna of the Yucatan Peninsula: Diversity and Conservation Challenges

Fernando Álvarez, Brenda Durán, and Samuel Meacham

Contents

13.1 Introduction

The term “anchialine” was first proposed by Holthuis (1973) to describe the habitat of caridean shrimps found in land-locked pools near the coast in a series of Pacific islands and the Sinai Peninsula. The original definition “pools with no surface connection with the sea, containing salt or brackish water, which fluctuates with the tides” has now evolved to better describe this unique environment. The first revision of the term was done by Stock et al. (1986) in which they broadened the definition

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F. Álvarez (✉) · B. Durán
Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico
e-mail: falvarez@ib.unam.mx

S. Meacham
Centro Investigador del Sistema Acuífero de Quintana Roo A.C. (CINDAQ), Solidaridad, Quintana Roo, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_13

to include flooded caves in addition to pools that had "restricted exposure to open air under terrestrial and marine influences." A second revision of the term by Bishop et al. (2015) provided a more comprehensive definition: "a tidally-influenced subterranean estuary located within crevicular and cavernous karst and volcanic terrains that extends inland to the limit of seawater penetration." Although the latter definition is more precise and incorporates important elements, there are still flooded caves with anchialine species that do not completely agree with it. One example are caves and wells in southern Campeche, at the geological southern limit of the Yucatan Peninsula where species of the crustacean *Typhlatya* occur and no salt or brackish water has been reported. In any case, an anchialine habitat can be recognized as it harbors a particular fauna that is exclusive to this environment. In fact, anchialine caves around the world often have related species that have a Tethyan origin and thus are present in distant areas, for example the remipedes, present in the Greater Caribbean, Canary Islands, and Australia, or atyid shrimps of the genera *Antecaridina*, *Halocaridina*, *Stygiocaris,* and *Typhlatya* distributed in Japan, the Philippines, Hawaii, the south Pacific, Australia, and around the Caribbean and Mediterranean basins (Iliffe and Álvarez 2018).

13.1.1 The Yucatan Peninsula

In this review, we consider the island of Cozumel as part of the YP based on the similarities of the flooded caves and because both areas share several species. The YP has been intensely studied and many published accounts describe its geology and biota (e.g., Bauer-Gottwein et al. 2011; Mercado-Salas et al. 2013).

Regarding the distribution of the anchialine species in the YP, here we recognize four main patterns, although there are also some departures that are pointed out in Table 13.1. As mentioned, most species distributions conform to one of these patterns: (1) the Ring of Cenotes (RC), in the State of Yucatan, an area in the northwestern corner of the peninsula representing the outermost border of the impact crater that formed by the impact of a meteorite at the end of the Cretaceous; (2) the Caribbean Cave Area (CCA), which corresponds to a 12 km wide band of coastline from Puerto Morelos to Tulum, Quintana Roo; (3) Cozumel (COZ), the island separated by a 16 km wide and 400 m deep channel from the peninsula; and (4) a widespread distribution throughout the whole peninsula (Fig. 13.1).

Table 13.1 List of anchialine species registered in the Yucatán Peninsula, including Cozumel Island

Species	Distribution	Water mass	Depth	Number of sites	References
Porifera					
Demospongiae					
Calyx maya	COZ	MW	5–6	1–5	Gómez and Calderón-Gutiérrez (2020)
Haliclona (Reniera) stygobia	COZ	MW	4–8	1–5	Gómez and Calderón-Gutiérrez (2020)
Haliclona (Halichoclona) chankanaabiis	COZ	MW	4–8	1–5	Gómez and Calderón-Gutiérrez (2020)
Svenzea germanyanezi	COZ	MW	5–6	1–5	Gómez and Calderón-Gutiérrez (2020)
Siphonidium ramosum	COZ	MW	4–6	1–5	Gómez and Calderón-Gutiérrez (2020)
Cinachyrella kuekenthali	COZ	MW	4–6	1–5	Gómez and Calderón-Gutiérrez (2020)
Discodermia adhaerens	COZ	MW	4–11	1–5	Gómez and Calderón-Gutiérrez (2020)
Neosiphonia microtriaeneae	COZ	MW	4–8	1–5	Gómez and Calderón-Gutiérrez (2020)
Diplastrella cozumella	COZ	MW	4–8	1–5	Gómez and Calderón-Gutiérrez (2020)
Homoscleromorpha					
Plakinastrella onkodes	COZ	MW	5–6	1–5	Gómez and Calderón-Gutiérrez (2020)
Annelida					
Nerillidae					
Speleonerilla sp.	CCA	MW	NA	1–5	Worsaae et al. (2018)
Crustacea					
Remipedia					
Xibalbanus cozumelensis	COZ	MW	9–10	1–5	Olesen et al. (2017)
Xibalbanus fuchscockburni	CCA	MW	16–19	1–5	Neiber et al. (2012)
Xibalbanus tulumensis	CCA	MW	>20 m	6–15	Yager (1987)
Copepoda					
Calanoida					
Balinella yucatanensis	CCA	MW	12–15	1–5	Suárez-Morales et al. (2006)
Exumella tsonot	CCA	MW	10–16	1–5	Suárez-Morales and Iliffe (2005)
Diacyclops chakan	P	FW	10–16	6–15	Fiers et al. (1996)
Diacyclops puuc	RC	FW	5–15	1–5	Fiers et al. (1996)
Halicyclops cenoticola	P	MW	5–30	6–15	Rocha et al. (1998)
Mesocyclops chaci	RC	FW	5–8	1–5	Fiers et al. (1996)
Mesocyclops yutsil	P	FW	5–30	1–5	Fiers et al. (1996)

(continued)

Table 13.1 (continued)

Species	Distribution	Water mass	Depth	Number of sites	References
Prehendocyclops abbreviatus	RC	FW	0–8	1–5	Rocha et al. (2000)
Prehendocyclops boxshalli	RC	MW	0–15	1–5	Rocha et al. (2000)
Prehendocyclops monchenkoi	P	MW	0–8	6–15	Rocha et al. (2000)
Mexicophria cenoticola	CCA	MW	19–23	1–5	Boxshall et al. (2014)
Speleophria germanyanezi	COZ	MW	11	1–5	Suárez-Morales et al. (2017b)
Stephos fernandoi	COZ	MW	11	1–5	Suárez-Morales et al. (2017a)
Ostracoda *Humphreysella mexicana*	CCA	MW	>20	6–15	Kornicker and Iliffe (1989)
Spelaeoecia mayan	CCA	MW	>20	1–5	Kornicker and Iliffe (1998)
Pseudopolycope (Pseudopolycope) helix	COZ	MW	18	1–5	Kornicker et al. (2007)
Malacostraca					
Thermosbaenacea *Tulumella unidens*	CCA	FW	4.6–25	>15	Bowman and Iliffe (1988)
Mysida					
Antromysis cenotensis	P	FW	0–16	>15	Creaser (1936)
Stygiomysida					
Stygiomysis cokei	P	FW	4.6–25	6–15	Kallmeyer and Carpenter (1996)
Stygiomysis cf. *holthuisi*	P	FW	7–15	>15	Álvarez et al. (2015)
Amphipoda					
Bahadzia bozanici	P, COZ	MW	2–23	1–5	Holsinger (1992)
Bahadzia setodactylus	COZ	MW	12	1–5	Holsinger (1992)
Mayaweckelia cenoticola	P	FW	5–7	6–15	Holsinger (1977), Iliffe (1992)
Mayaweckelia yucatanensis	RC	FW	5–8	1–5	Holsinger (1977)
Mayaweckelia troglomorpha	RC	FW	20–33	1–5	Angyal et al. (2018)
Tuluweckelia cernua	P	FW	?–16	>15	Holsinger (1990)
Isopoda					
Metacirolana mayana	P, COZ	MW	17–20	6–15	Bowman (1987)
Cirolana yucatana	P	FW	10–40	1–5	Botosaneanu and Iliffe (2000)
Cirolana yunca	P	FW	10–60	1–5	Botosaneanu and Iliffe (2000)
Creaseriella anops	P	FW	1–>50	>15	Creaser (1936), Durán and Álvarez (2021)

(continued)

Table 13.1 (continued)

Species	Distribution	Water mass	Depth	Number of sites	References
Haptolana bowmani	RC	FW	NA	1–5	Botosaneanu and Iliffe (1997), Botosaneanu and Iliffe (1999)
Yucatalana robustispina	RC	FW	4–50	1–5	Botosaneanu and Iliffe (1999)
Curassanthura yucatanensis	P	FW	10–15	1–5	Álvarez et al. (2019)
Decapoda					
Procaris mexicana	COZ	MW	7–9	1–5	von Sternberg and Schotte (2004)
Typhlatya mitchelli	P	FW	0–18	>15	Hobbs and Hobbs (1976)
Typhlatya pearsei	P	FW	1–15	>15	Creaser (1936)
Typhlatya dzilamensis	P	MW	10–25	1–5	Alvarez et al. (2005)
Typhlatya campecheae	RC	FW	NA	1–5	Hobbs and Hobbs (1976)
Jonga serrei	CCA	FW	0–5	1–5	Álvarez et al. (2015)
Yagerocaris cozumel	COZ, CCA	MW	9–12	1–5	Kensley (1988)
Triacanthoneus akumalensis	CCA	MW	25–40	1–5	Álvarez et al. (2012)
Anchialocaris paulini	COZ	MW	25–50	1–5	Mejía-Ortiz et al. (2017)
Creaseria morleyi	P	FW	0–16	>15	Creaser (1936)
Calliasmata nohochi	CCA	MW	18	1–5	Álvarez et al. (2015), Escobar-Briones et al. (1997)
Agostocaris bozanici	COZ	MW	18–31	1–5	Iliffe (1992)
Agostocaris zabaletai	COZ	MW	25–50	1–5	Mejía-Ortiz et al. (2017)
Barbouria cubensis	CCA	MW	>15	1–5	Bishop and Iliffe (2012)
Parhippolyte antiguensis	COZ	MW	NA	1–5	Chace (1972), d'Udekem d'Acoz (2000)
Parhippolyte sterreri	COZ	MW	NA	1–5	Hart and Manning (1981)
Mollusca					
Gastropoda					
Teinostoma brankovitsi	CCA	MW	17–20	1–5	Rubio et al. (2016)
Echinodermata					
Copidaster cavernicola	COZ	MW	6–18	1–5	Solis-Marín and Laguarda-Figueras (2010)
Chordata					
Typhlias pearsei	P	FW	1–>15	>15	Møller et al. (2004)
Ophisternon infernale	P	FW	1–24	6–15	Schmitter-Soto (1996)

Each species distribution is classified according to four patterns: Caribbean Cave Area (CCA), Ring of Cenotes (RC), Cozumel (COZ), and throughout the Peninsula not including Cozumel (P). The water masses in which each species has been recorded are broadly classified as marine water (MW) and freshwater (FW). The depth range of the species occurrences is presented in meters, *NA* not available. The number of sites column corresponds to the number of localities where each species has been recorded; it is presented in three intervals: 1–5, 6–15, and over 15. The source of each record is in the column "References"

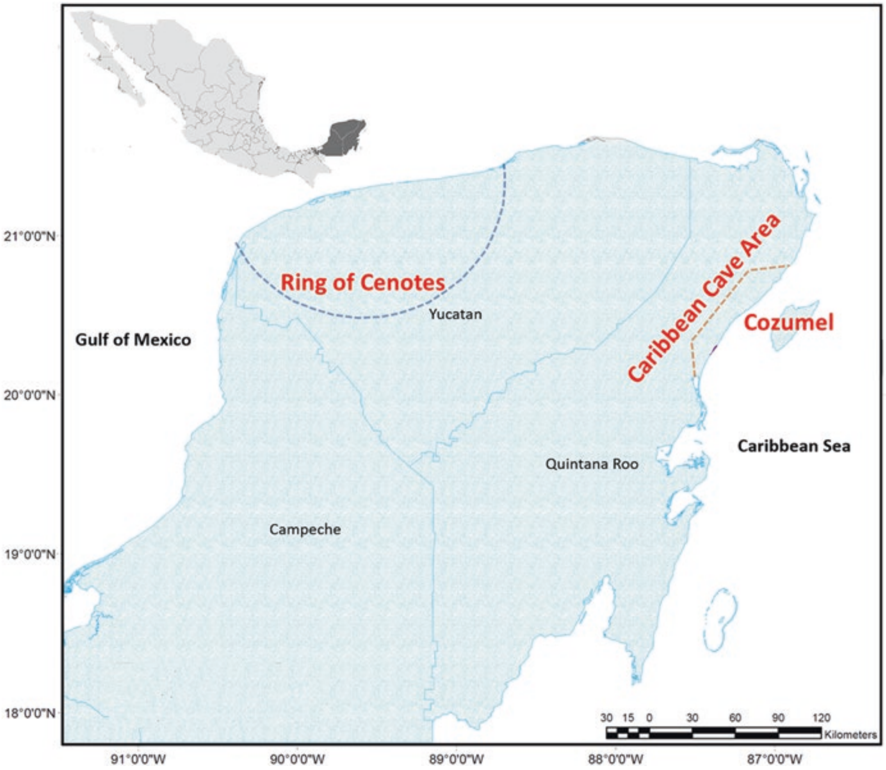

Fig. 13.1 Map of the Yucatan Peninsula showing in red the three main areas where anchialine caves have formed: Ring of Cenotes (RC), Caribbean Cave Area (CCA) and Cozumel Island (COZ).

13.2 Faunal Account

13.2.1 Species List

Several accounts have recorded the diversity of species in the anchialine caves of the Yucatan (Iliffe 1993; Álvarez and Iliffe 2008; Álvarez et al. 2015; Calderón-Gutiérrez et al. 2017); however, new species are being constantly described making periodic updates necessary. Up to now, a total of 67 anchialine species have been recorded in the flooded caves of the YP (Table 13.1), including organisms belonging to six phyla: Porifera, Annelida, Crustacea, Mollusca, Echinodermata, and Chordata.

The 10 species of anchialine sponges are all from Cozumel Island occurring, so far, in only two caves: La Quebrada and Aerolito (Gómez and Calderón-Gutiérrez 2020). What is remarkable is that they belong to two classes, 9 families and 9 genera, showing a high taxonomic diversity (Table 13.1). Furthermore, La Quebrada Cave is unique in the whole YP as the 10 known species of sponges occur there.

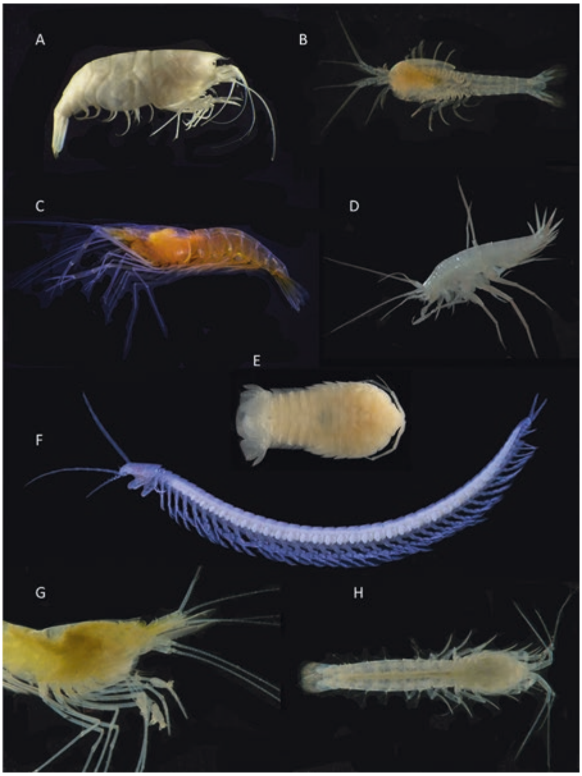

Fig. 13.2 Examples of anchialine species from the Yucatan Peninsula: (**a**) *Yagerocaris cozumel*; (**b**) *Tulumella unidens*; (**c**), *Creaseria morleyi*; (**d**) *Tuluweckelia cernua*; (**e**), *Metacirolana mayana*; (**f**) *Xibalbanus tulumensis*; (**g**) *Typhlatya mitchelli*; (**h**) *Stygiomysis holthuisi*

Worsaae et al. (2018) reported on the presence of an undescribed species of annelid of the genus *Speleonerilla* from two cenotes in the CCA: Taj Mahal and 27 Steps. However, they did not describe a new species due to the limited number of individuals available. This genus belongs to the family Nerillidae which includes meiofaunal forms, several of which occur in marine and anchialine caves (Worsaae et al. 2018).

Crustaceans represent the most diverse group in the anchialine caves of the YP (Table 13.1; Fig. 13.2), with 51 species that belong to 4 classes, 9 orders, 23 families, and 36 genera. This group shows a high level of endemism in the YP with two families (Anchialocarididae, Tulumellidae), 9 genera (*Mexicophria*, *Tulumella*, *Mayaweckelia*, *Tuluweckelia*, *Creaseriella*, *Yucatalana*, *Yagerocaris*, *Anchialocaris*, *Creaseria*), and 44 species occurring only in the YP. It is interesting to note that the endemism is present at different taxonomic levels, from families to species, and that it occurs in very distant, unrelated lineages suggesting that they are the result of large-scale isolation processes. By group, the decapods are the most diverse (16 spp.), followed by the copepods (12 spp.), isopods (7 spp.), amphipods (6 spp.), remipedes, ostracods and mysids (3 spp.), and the thermosbaenaceans (1 sp.). The number of anchialine crustacean species from the YP has been steadily increasing suggesting that more species are going to be described in the following years, especially in the copepods and peracarids.

Up to now, one species of anchialine mollusk has been described from the YP, the gastropod *Teinostoma brankovitsi* (Rubio et al. 2016). This is a minute species with a width of 1.49 mm and a height of 0.85 mm that belongs to the family Tornidae which includes interstitial species (Rubio et al. 2016). *T. brankovitsi* has no eyes and lacks pigmentation, two characters common in other interstitial gastropod species present in marine environments. However, due to the finding of live specimens of this species restricted to anchialine environmenst confirm that they are not a marine accidental occurrence (Rubio et al. 2016). Grego et al. (2019) described two stygobiont species of snails from cenotes in the YP from the cavern area at 46 m depths. Since these species were described from empty shells and no living organisms have been recorded from inside anchialine caves, more data are needed to correctly classify their habitat.

The echinoderm anchialine fauna of the YP is underestimated as only one species of sea star, *Copidaster cavernicola*, has been recorded so far from cenote Aerolito in Cozumel (Solis-Marín and Laguarda-Figueras 2010). Bribiesca-Contreras et al. (2013) using DNA barcoding detected up to six undescribed species of asteroids and ophiuroids, all from cenote Aerolito that await formal description. As all echinoderms are strictly marine, their presence in anchialine caves is always in sections next to connections to the sea.

Two species of fish, the blind cusk eel *Typhlias pearsei* (Dinematichthydae), and the blind eel *Ophisternon infernale* (Synbranchidae) occur in the anchialine caves of the YP, always in the freshwater layer. The former was described originally as *Typhlias pearsei*; however, it has changed names several times creating some confusion. It initially belonged to the genus *Ogilbia*, then *Typhliasina* and finally returning to *Typhlias* (Hubbs 1938; Scharpf 2017). Very little is known about the ecology of the two species, with *T. pearsei* being much more common throughout the YP than *O. infernale* which is considered very rare.

13.2.2 Distribution Patterns

As expected, the distribution of anchialine species in the YP is not homogeneous and not all species occur in all regions. Several factors may be shaping the species' distribution, such as the number of cenotes and their associated caves in each area, the geologic age of the region, the type of cenote and the length and depth of the caves, the degree of connectivity among cave systems, the distance, and thus the influence, from the sea, among others. It is interesting that in the YP, due to its calcareous conformation, cenotes and caves have formed not only along the coastlines but also far inland, for example the southern section of the Ring of Cenotes is 80–90 km from the coastline, or cenotes around the town of Valladolid can be more than 100 km from the sea.

The YP is a low and flat carbonate platform that has been affected by sea level changes through geologic time. The presence of speleothems in the now flooded cave passages is proof of the significant sea level changes that have occurred modifying the extent and characteristics of the anchialine habitat. These changes, seen here simplified as low and high-water level events, have shaped the distribution of the stygobitic fauna. Few studies have explored the distribution patterns of anchialine species in the YP and fewer have used geological or historical approaches to explain them. Botello and Álvarez (2010) studying the palaemonid shrimp *Creaseria morleyi,* proposed that sea level changes have produced contractions in the distribution of the species and subsequent reinvasions, producing genetic bottlenecks that are supported by widely distributed haplotypes throughout the PY.

The data gathered here (Table 13.1) show that 25 species occur in COZ, including sponges, crustaceans, and echinoderms; all of them restricted to the marine water layer. A total of 35 species occurs in the CCA, also considering those with ample distribution throughout the peninsula, including annelids, crustaceans, mollusks, and fishes; of these, 18 species are present in the marine water layer, whereas the remaining 17 occur in the freshwater lens. In the RC occur 30 species, including those with wide distribution throughout the peninsula, 24 of which are freshwater species; the groups represented in this area are crustaceans and fishes. Overall, species restricted to marine water predominate with 41 representatives, while 25 species occur exclusively in the freshwater lens. Sixteen of the 21 widely distributed species occur in freshwater.

As a measure of rarity, we recorded the number of localities where each species has been found using three intervals (Table 13.1). The results show that 48 (74%) species are known from 1 to 5 sites, 8 (12%) are known from 6 to 15 sites, and 9 (14%) have an ample distribution in the peninsula excluding COZ, occurring in more than 15 sites. The most common and widely distributed species are 8 crustaceans: one thermosbaenacean (*T. unidens*), two mysid shrimps (*A. cenotensis*, *S. holthuisi*), one amphipod (*T cernua*), one isopod (*C. anops*), three shrimps (*T. mitchelli*, *T. pearsei*, *C. morleyi*); and one fish (*T. pearsei*). Interestingly, all of them are freshwater species distributed throughout the northern section of the YP and are also the most abundant ones.

In this chapter, we distinguish between fresh and marine water species. We are aware that in several cases this classification is too broad and lacks precision, since there are species that occur at the halocline, or just above it in brackish water and there could be a salinity gradient in the water column instead of discrete water masses. However, with this classification we can draw some general distributional patterns.

Further, several of the groups present in the YP have what has been defined as a "Tethyan distribution pattern," with related species occurring on both sides of the Atlantic, the Mediterranean Basin, and even Australia (Iliffe and Álvarez 2018). Examples of this are members of the genera *Speleophria*, *Curassanthura,* and, *Typhlatya* that have species on both sides of the Atlantic (Jurado-Rivera et al. 2017; Álvarez et al. 2019) and the remipedes with representatives in the Greater Caribbean, Canary Islands, and Australia (Iliffe and Álvarez 2018).

13.3 Importance of the Anchialine Fauna of the YP

Several anchialine species from the YP have received special attention due to their taxonomic importance or ecological role. Undoubtedly, the remipede *Xibalbanus tulumensis* is the most relevant species known from the YP. *Xibalbanus tulumensis* is considered one of the top predators in the anchialine ecosystem; it has robust and prehensile maxillipeds, which suggests that it has developed a carnivorous habit. This species represents the first record of a poisonous crustacean in the world, it has venom glands which produce a cocktail of enzymes and toxins capable of immobilizing and degrading prey for later consumption, and this behavior places it in the highest part of the trophic web (von Reumont et al. 2013). It has been seen preying on *Typhlatya* shrimp. Interestingly, the composition of the remipede venom is very different from that of other venomous arthropods such as spiders, centipedes, and scorpions (von Reumont et al. 2013). One possible explanation, partly supported by phylogenetic studies, supposes a long evolutionary history of remipedes as an independent isolated lineage (von Reumont et al. 2013).

Further, *X. tulumensis* has been used in several phylogenetic studies of the higher taxonomy of the Arthropoda, becoming a key element to propose the “Pancrustacea” and link the crustaceans to the hexapods (e.g., Lozano-Fernandez et al. 2019). Studies on the organization of the nervous system, blood respiratory pigments, and structure of some neuropeptides closely link remipedes to hexapods (Ertas et al. 2009; Christie 2014; Stemme et al. 2013).

The atyid shrimps of the genus *Typhlatya* have been the subject of several studies, taxonomic and phylogenetic, upon which several biogeographical hypotheses have been put forward. Their wide distribution in the Western Atlantic, Galápagos Islands, and Mediterranean Basin has allowed to make biogeographical inferences on the origin and distribution patterns of the world’s anchialine fauna (Botello et al. 2013; Jurado-Rivera et al. 2017). Their disjunct distribution pattern, shared with other anchialine groups of species (e.g., isopods, amphipods, and thermosbaenaceans), points to an ancient relict Tethyan origin. Both the isolation and dispersal of these organisms are linked to the movement of plate tectonics including the opening of the Atlantic Ocean, the rupture of Gondwana, and the closure of the Tethys seaway (Iliffe and Álvarez 2018).

Typhlatya shrimps are also important due to their relative high abundance in anchialine caves and to their specialized feeding habits. Atyid shrimps have modified chelae of the first and second pereiopods, with tufts of setae used primarily, in epigean species, to filter out suspended particles. In the case of *Typhlatya*, they scrape the biofilm that develops on the rocks inside the caves or can also filter out other particles from the water column, although typically anchialine caves are ultra-oligotrophic. The evidence suggests that *Typhlatya* shrimps may feed on nitrifying and methanotrophic bacteria (Brankovits et al. 2017), thus acting as the primary consumers and the main link to introduce organic nutrients into higher trophic levels. Their central role in the anchialine trophic web is based on their abundance and their ability to feed on bacteria.

13.4 The Future Conservation of the Anchialine Fauna of the YP

Paradoxically, the high diversity areas for anchialine fauna are those where the more intense development in the YP is occurring. The karst nature of the peninsula allows for a rapid infiltration of contaminants into the aquifer. This condition combined with a growing population that demands services, housing, food and energy, and a booming tourist industry pose important challenges for the long-term preservation of these ecosystems and ultimately the health of the human populations in the region.

Some of the main pollutants are agrochemicals including organochlorine pesticides (Polanco-Rodríguez et al. 2018) used in agricultural practices, wastes from animal farming, wastewater from human settlements (with stimulants, pharmaceuticals and a variety of other drugs; Metcalfe et al. 2011), fecal contamination (Hoogesteijn-Reul et al. 2015), and urban and road runoff containing hydrocarbons (Medina-Moreno et al. 2014). For example, the RC around the city of Merida holds important freshwater reserves that are compromised with animal farming, and urban and agricultural development in the area. As in other areas, the aquifer is now exhibiting high levels of pollution that combined with overexploitation produces a critical situation.

The presence of fecal coliforms, fertilizers, pesticides, drugs, and narcotics has been found in different cenotes, as well as in the caves associated with these bodies of water, mainly in the freshwater layer. This fact is believed to be related to the presence of a halocline which functions as a density trap which does not allow the passage of the bacterial community and other materials into the saltwater layer (Alcocer et al. 1999).

13.5 Conclusions

Rampant development continues to threaten one of Mexico's largest, most pristine, and significant aquifers. The coast of Mexico's Riviera Maya faces unprecedented growth that ranks it among the fastest growing regions of the world. Out of sight and mind, the flooded cave systems of the region play a crucial role as the conduits for freshwater moving from the jungle interior out to the Mesoamerican Barrier Reef. To date, close to 2000 km of cave, passageways have been mapped, including Sistema's Sac Actun and Ox Bel Ha which rank as the second and third longest caves on Earth. The flooded caves are the connective tissue that hold the many ecosystems of the region together. Within them is contained an incredible web of biological life that we are only beginning to understand with paleontological remains that are helping us to understand the origins of human migration into the Americas. Other archeological evidence here helps us better explain the rise and fall of the ancient Maya Civilization, and sediment records that help tie the climate change to it all. The need to explore and better understand the aquifer of northern Quintana

Roo is important as it directly influences the health and economic well-being of the human population above it and the many ecosystems it nourishes from below. Due to the aquifer's extreme fragility and vulnerability to contamination, the development at the surface poses a significant threat to not only the stability of this valuable natural and cultural resource, but also to the economic and social welfare of the region. Since this region contributes approximately 10% of Mexico's Gross Domestic Product, the impact of a contaminated aquifer and associated ecosystems has far-reaching and potentially disastrous results not only for the region's tourist-based economy but for Mexico as a whole. Cave diving explorers provide a critical knowledge base by mapping and documenting the subterranean waterways, providing a foundation for scientific work that ultimately can help understand and protect the aquifer and the many ecosystems that it supports. Legislation at the municipal, state, and federal levels is urgently needed to ensure the protection of this irreplaceable resource.

Acknowledgments The first author gratefully acknowledges the funding received through grants PAPIIT IN208519 (DGAPA-UNAM) and CONACYT Ciencia Básica A1-S-32846.

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Chapter 14
Mezcal Boom and Extinction Debts

Alfonso Valiente-Banuet

Contents

14.1 Introduction

During the nineteenth century, ecology emerged as a scientific discipline, being Alexander von Humboldt one of the central figures who recognized the dominant role of climate in governing plant geography and vegetation zonation (Jackson 2009). Thus, histories of ecology and biogeography are indissolubly tied as they emerged at the same time with overlapping explanations for species richness patterns from local to global scales.

Humboldt's expeditions, which occurred mainly within the American tropics, were decisive to relate the intrinsic relationships between nature and climate disturbances, as well as societal issues. In a century characterized by wars and worldwide

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A. Valiente-Banuet (✉)
Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, México City, México
e-mail: avalient@ecologia.unam.mx

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_14

colonialism, Humboldt noticed the profound environmental transformations in the colonized territories. Large-scale deforestation preceded monoculture plantations for exportation purposes, which replaced the typical food crops grown by local inhabitants (Norder 2019). Humboldt pointed out the disastrous effects of deforestation, not only on nature and on climate, but also on societal issues such as poverty and marginalization of the original inhabitants (Norder 2019).

In fact, he provided important evidence about the reciprocal effects of vegetation and the physical and chemical properties of the atmosphere with potential effects on climate. Consequently, he was one of the first worldwide to propose human-induced climate change, which, up to now, is one of the most important risks for humanity (Jackson et al. 2001; Norder 2019).

Surprisingly, and despite the prevalent mechanistic reductionistic paradigm by which phenomena is understood (through the analysis of the intrinsic properties of its components) (Levins and Lewontin 1985), Humboldt envisioned the world as an interconnected web of life (Norder 2019). Accordingly, animal and plant species depend on each other through their interactions for their survival (Norder 2019). Humboldt's holistic view of nature that sets the beginning of ecology and biogeography contrasts with the reductionistic philosophical view coined during the sixteenth and seventeenth centuries during the named "Scientific Revolution," which marked at the same time the beginning of the Industrial Revolution (Fritjof 1996). Under industrialism, "development" was based on accelerated exploitation of resources in the colonies, characterized by the generation of surpluses and the accumulation of capital. This form of "development" was accompanied and validated by the preponderant reductionistic science through technological proposals focused on specific species. Thus, Humboldt's holistic view of nature did not echo in subsequent ecological research (Shiva 1988). On the contrary, further scientific research grew under an unlimited short-term desire for natural resources exploitation focusing on individual species and as an almost the unique way to understand the structure and dynamics of populations, communities, and ecosystems (Brown et al. 2001). In fact, more than 60% of studies published in the journal *Ecology* in the eighties, dealing with diversity and biotic interactions dealt at most with two species (Kareiva 1994).

However, since the eighties, ecology has slowly and differentially transited from the reductionistic approach to the study of systems ecology, in which the properties of the whole emerge from the interactions between the parts and therefore the whole is more than the sum of their parts (Levins and Lewontin 1985). This means that in an ecosystem, animals, plants, as well as microorganisms depend on each other for their maintenance through their interactions. This interdependence among species and their maintenance occurs within and across trophic levels not only locally, but also regionally, affecting species distribution, speciation, and extinction or persistence of species during past climate changes (Valiente-Banuet et al. 2006; Brooker et al. 2009; Wisz et al. 2013), as well as future ones (Davis et al. 1998). Consequently, any disturbance directed to one or a group of species may have concomitant effects on others, as well as on higher levels such as ecosystem processes.

At present, fast-paced rates of habitat loss and fragmentation, as well as species overexploitation, are some of the most important anthropogenic drivers of species extinctions and the present environmental crisis (Valiente-Banuet et al. 2015).

Therefore, and under the environmental crisis, forecasting plays a preponderant role to assess the effect of human activities on Earth and its ability to sustain biodiversity at local and global scales as a paramount for human subsistence (Barnosky et al. 2012). On this vein and under a systems ecology approach, different authors have demonstrated that critical transitions caused by threshold effects lead to state shifts producing unanticipated biotic effects (Scheffer et al. 2009; Wisz et al. 2013, and references therein). Thresholds leading to critical transitions are often crossed when local human impacts are amplified by the synergistic interactions of different ecological processes or through feedback loops (Barnosky et al. 2012). Thus, local extinction of species may produce drastic co-extinctions of their mutualistic partners through feedback processes that cascade across other ecological networks (Valiente-Banuet and Verdú 2013).

14.2 Problem Statement

This chapter is focused on the overexploitation of natural resources related to mezcal boom. Mezcal is an alcoholic beverage obtained from the distillation of plants known as *agaves or magueyes*, belonging to the genus *Agave*. Their center of origin is Mexico, where 159 of the 210 known species occur, of which 119 are endemic (García-Mendoza 2002, 2007, 2012; Colunga García Marín 2006). Mezcal production takes place in 27 states of the country (Colunga García Marín 2006) and is carried out by traditional producers who use more than 40 agave species and great amounts of firewood from different species obtained from nature. Mezcal's production exponential growth rate has increased the overexploitation of agaves and firewood for cooking agaves and distillation which may affect a plethora of ecological interactions at local, regional, and probably geographic scales impacting biodiversity and eventually leading to collapse of ecosystems.

14.3 Sociological Setting

Mezcal is one of the most emblematic alcoholic beverages of Mexico whose production has been carried out by indigenous and peasant groups for centuries and constitutes the livelihood of thousands of families. Its traditional production, whether artisanal or ancestral, is characterized by a great organoleptic diversity. It is based on the extraction of agaves and firewood from natural vegetation, the former used for cooking *piñas* (i.e., agave stems whose leaves have been removed) and the latter as energy for distillation. Traditional production is the most widely practiced and constitutes the livelihood of at least 9000 peasant and indigenous families (Hernández-López 2018). Electric or fossil fuel-driven technologies are not involved in the traditional manufacturing process of mezcal. After cooking *piñas* with firewood, producers macerate them manually using wooden clubs (*marros*) or by means of rock wheels (*tahona*) which are moved by animals such as donkeys or horses. Fermentation is carried out in a variety of containers such as wood or animal skins, using yeasts associated with agaves. The resulting product is consumed locally and during festivities.

Mezcal's recognized organoleptic diversity and richness is a result of variation in local environmental characteristics such as climate, soil, and microorganisms, as well as diverse techniques that vary among regions and among producers in the same region (Colunga-García Marín and Zizumbo-Villarreal 2007; Gutiérrez 2015). Mezcal holds centuries or even millennia of knowledge (Zizumbo-Villarreal et al. 2009; Serra and Lazcano 2015), which is backed and enriched by Mexico's diverse traditional, cultural, and religious context.

In contrast, industrial production, focused on obtaining profits and the expansion of capital in the shortest possible time, is based on the modernization of production processes and the use of minimal labor (Pérez Hernández et al. 2016). To do this, they resort to planting large areas with agave monocultures, following the rules of the technified agriculture to achieve production. There is no cooking of *piñas* but rather a processing with diffusers. Industrial mills are used to obtain juices and few producers ferment naturally, accelerating the process using commercial yeasts and chemicals, contravening one of the basic laws of oenology: "the organoleptic richness of the final product is directly proportional to the fermentation time". They use stainless-steel stills or even distillation towers, instead of copper stills (Gutiérrez 2015).

From the second half of the last century, the production of mezcal has undergone unusual industrialization, favoring international trade supported by the Mexican government as part of a neoliberal policy promoted since the eighties (Plascencia de la Torre and Peralta Gordon 2018). The creation of the Mezcal Regulatory Council (MRC) has played a central role through the regularization of production and the intellectual protection schemes with denominations of origin (DO). These regulations affect their organoleptic diversity, forcing traditional producers to homogenize their production under "quality standards," which are difficult to reach. In addition, only 10 out of 27 mezcal producing states have DO. Therefore, 17 states are unable to officially name their product mezcal, hampering its commercialization. This is a paradoxical scenario given that international demand should increase the opportunities and contribute to improving the quality of life of all mezcal producers while culturally maintaining their traditions. This situation pushes the traditional production system to a disadvantaged position, with respect to the industrial one, since traditionally they move away from the capitalist mercantile criteria, with limited economic and technological capacity to comply with the regulations imposed by the State (Hernández-López 2018; Plascencia de la Torre and Peralta Gordon 2018).

When produced outside the DO states, mezcal producers manufacture clandestinely in order to comply with regulations, including tax regulations. On the contrary, the demand for their high-quality mezcal by intermediaries encourages extractivism and the accelerated destruction of natural resources as a subsistence strategy. Paradoxically, the objective of the DOs was originally to protect socioeconomic, cultural, and environmental sustainability (Bowen 2015).

The Mezcal Regulatory Council (MRC) indicates that production follows an exponential increase rate that was 2.7 million liters in 2015 to 8 million in 2020. More than half of the mezcal volume was exported to 60 countries (CRM 2020). Nevertheless, these rates are underestimated since the MRC registers only industrial associate members.

Overall, the growing mezcal demand has increased the overexploitation of wild agaves, and their seeds through their overcollection, which negatively affects the natural regeneration of populations. Added to this is the extraction of firewood from nature and large-scale deforestation in different areas of Mexico. This phenomenon faithfully reproduces the industrialized tequila expansion that began in the nineteenth century, which promoted the destruction of thousands of hectares of natural vegetation to convert them into monocultures (Huerta and Luna 2015). The overexploitation of agaves ended up extinguishing wild populations, so the production of agaves was carried out through clones obtained from the suckers and through tissue culture techniques under laboratory conditions. The selected clonal agave lines with the best performance were used to plant monocultures, which greatly reduced genetic diversity, affecting their ability to tolerate environmental changes and attack by pathogens. Over time, the depletion of soil fertility in monocultures and the attack by pests encouraged the use of agrochemicals (fertilizers, insecticides, and herbicides) polluting the soil and water, with a negative impact on pollinators.

14.4 The Agave Ecosystem

Most agave species are distributed in arid and semiarid environments with a marginal distribution in temperate areas of Mexico and a null presence in wet environments of Tabasco, Campeche, and Quintana Roo (García-Mendoza 2007). The highest diversity occurs in South-Central Mexico in the Tehuacán-Cuicatlán Valley (VTC) (García-Mendoza 2007). Two continuous distribution belts derive from South-Central Mexico: one along the Pacific coast and the other along the coast of the Gulf of Mexico. Both belts generally have fewer agave species. This distribution pattern matches with the distribution of other taxonomic groups with high endemicity such as columnar cacti (CC; tribe Pachycereeae) (Valiente-Banuet et al. 2002), Burseraceae (Becerra 2005), and animal groups such as nectar-feeding bats, among others (Valiente-Banuet et al. 1996, 2002; Fig. 14.1).

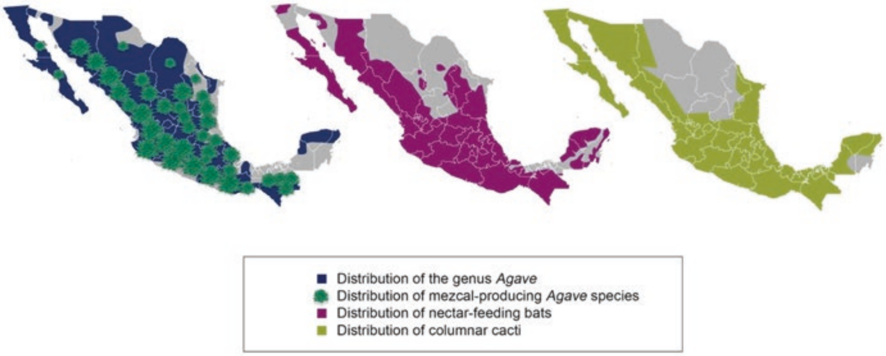

Fig. 14.1 Distribution maps of agave species, columnar cacti, and nectar-feeding bats in México

Fig. 14.2 A typical agave ecosystem in the Tehuacán-Cuicatlán Valley dominated by the columnar cactus *Neobuxbaumia mezcalaensis*. Agave inflorescence belongs to *Agave marmorata* one of the most important species for mezcal production in the region

For example, in the Tehuacán-Cuicatlán Valley (VTC) agave and CC species are dominant elements of vegetation in 13 plant communities, 11 are columnar cactus forests, and the other ones are a rosetophyllous vegetation community (Valiente-Banuet et al. 2000) and the evergreen sclerophyllous vegetation or Mexical (Valiente-Banuet et al. 1998). CC form forests with densities between 1200–1900 ind ha^{-1}, whereas *Agave marmorata* and *A. potatorum*, used for the production of mezcal, reach densities of 2620 and 1830 ind ha^{-1}, the highest among agave species (Valiente-Banuet et al. 2000; Fig. 14.2).

14.5 Interdependence Among Species Through Biotic Interactions

Different studies show that CC exhibit obligate pollination by nectarivorous bats. *Leptonycteris yerbabuena*e, *L. nivalis*, and *Choeronycteris mexicana* are the most important pollinators. This is also the case for agave species that depend on bat pollination, such as *A. marmorata*, *A. peacockii*, *A. salmiana*, *A. potatorum* (Valiente-Banuet and Verdú 2013). Additionally, nectar-feeding bats are also the most important seed dispersers of various CC (Godínez-Alvarez et al. 2002; Castillo and Valiente-Banuet in prep), being able to remove most of the seeds and most of them are deposited under bushes and trees. Of all these bats species, *L. yerbabuenae* is the most effective pollinator and seed disperser and is resident throughout the year in the TCV. This annual residence depends on agave flower resources provided by Agave species and *Ceiba* spp. during almost seven months, and on flower and fruit resources provided by CC for 5 months, respectively (Rojas-Martínez et al. 1999; Valiente-Banuet and Verdú 2013).

Studies analyzing seedling establishment of all plant species at the community level ($N = 5$) indicate that on average 96% of the species recruit through the process of facilitation (Valiente-Banuet and Verdú 2013). Facilitation is a process by which one species generates the conditions for the establishment of another one under its canopy (Valiente-Banuet and Verdu 2007). This process is species-specific, since only phylogenetically distantly related species are able to enhance establishment (Verdú et al. 2010). Notably, legumes stand out for their ability to favor the regeneration of a great number of species, up to 95% in a community (Valiente-Banuet and Verdu 2007). The benefit of this cooperative interaction is maintained until distantly related species reach the adult stage (Verdú et al. 2010). Through the ontogeny of the interaction, the gradual arrival of seeds of other species results in the formation of patches of vegetation made up of several species (range 1–12) under the same one canopy. These patches are the structural components of all the plant communities constituting the arena in which plant regeneration occurs, indicating that regeneration niches of species depend on a complex context of multispecific interactions between plants (Castillo et al. 2010). In fact, microbial communities, mainly bacteria and arbuscular mycorrhizae inhabiting the rhizosphere of the different species, which also may be species-specific (Montesinos-Navarro et al. 2012), supply nutrients such as nitrogen and phosphorous, and the connection of roots through hyphae of different species, enabling a selective nutrient transference between them (Montesinos-Navarro et al. 2016, 2017). This indicates that in the facilitation process, besides the modification of the physical microenvironmental beneath plant canopies, microbiome–plant interaction networks play an outstanding role. This occurs through the acquisition of nutrients by plants, up to 80% of the phosphorus and 90% of the nitrogen used by plants, as well as their transference among plants through hyphae (Van Der Heijden et al. 2008; Montesinos-Navarro et al. 2017).

14.6 Mezcal Production and Extinction Debts

Exponential growth rate of mezcal production due to a growing national and international demand may be already generating extinction debts. Here, I expand the concept of extinction species debt (Tilman et al. 1994; Wearn Oliver et al. 2012) and biotic interactions debt (Valiente-Banuet et al. 2015) to cultural debt. Accordingly, an extinction debt is any loss of species, ecological interactions, and cultural aspects, including the potential disappearance of thousands of traditional producers, which occurs due to the different social and environmental dimensions of mezcal production.

A previous study (Valiente-Banuet and Verdú 2013) was designed to document how an ecosystem may collapse by the disruption of interaction networks. The study was conducted in the TCV in Los Reyes Metzontla, a town whose economic subsistence largely depends to ceramic pottery production. This context was considered by the authors as an ideal scenario because both firewood and agave overexploitation occur in this locality.

To alleviate poverty, since the 1960s pottery production was encouraged leading to an increase of firewood extraction (de la Vega Doria 2006). Annual wood extraction using for firing ceramics sums up 1.66 × 10^6 kg which has been increasing during the last two decades. Besides the overexploitation of species that are crucial in the networks of ecological interactions, the extraction scheme also has created large, degraded areas containing very few species with no evidence of recovery for more than 30 years after abandonment. Intermixed with these degraded areas, it is possible to find well-conserved areas protected by the inhabitants that represent the natural vegetation found in all the area, a columnar cacti forest dominated by *Mitrocereus fulviceps* and *Neobuxbaumia macrocephala*. Besides authors documented the requirements underlying overexploitation among the inhabitants, they obtained information about the extraction of agave species for mezcal production.

Under a realistic scenario, these authors documented quantitatively how human effects on a facilitation network may, through feedback loops, impact concomitant pollination and seed dispersal networks. By including feedback loops in mutualistic networks, it is assumed that extinction in one guild may produce co-extinctions in other guilds, which in turn may cause additional co-extinctions in the first guild and so on. Thus, many of the species exploited for firewood are nurse species that facilitate many species in the network (acting as hubs in the facilitation networks). Similarly, most of the species harvested for mezcal are facilitated species providing nectar and fruits for animals (acting as hubs in pollination and seed dispersal networks (Flores 2005; Estrella Ruiz 2008; Verdú et al. 2010).

By linking facilitation, pollination, and seed dispersal networks into a series, Valiente-Banuet and Verdú (2013), provided evidence for their hypothesis that human-induced extinction of a nurse plant will lead to co-extinction of its facilitated species, especially agaves and columnar cacti, which are primarily pollinated by bats.

The facilitation network was constructed as a matrix, linking the number of individuals of each facilitated species (<30 cm) growing associated with each nurse species and open space. Different experimental studies in the study area confirm that these spatial patterns of association between juvenile and larger plants are due to facilitation and not to mere spatial coincidence (Valiente-Banuet and Ezcurra 1991; Castillo and Valiente-Banuet 2010; Castillo et al. 2010). For the pollination and seed dispersal networks, they focused on the relationships established between bats and columnar cacti and agaves, the most abundant plant species in the area, whose flowers are strongly associated with pollination by animals and whose fleshy fruits (cacti only, since agave seeds are dispersed by wind) are dispersed by animals. Consequently, they worked with only a subset of species within the entire pollination and dispersal networks. The pollination network was based on experimental data and focal observations (Valiente-Banuet et al. 1996, 1997; Flores 2005; Estrella Ruiz 2008) and, for phenological reasons, was split into two stages: (1) early (February to April), the most nectar-limited time of the year, when most Agave species are in bloom and when columnar cacti start blooming, and (2) late (May to January), when most columnar cacti and *A. potatorum* are also blooming. Likewise, the seed dispersal network was constructed based on previous studies for dominant species in the TCV, *Neobuxbaumia tetetzo* and *N. mezcalaensis* (Godínez-Alvarez et al. 2002; Castillo and Valiente-Banuet in prep). For *Cephalocereus columna-trajani*, *N. macrocephala*, and *Mitrocereus fulviceps*, focal observations on fruits during day and night were performed, as well as the seed identification analyzing the frugivore feces captured using five mist nets (20 × 3 m), including that obtained from bat refugia as evidence of transport (Rojas-Martínez et al. 2012). Additionally, for *N. macrocephala*, the contribution of diurnal and nocturnal seed dispersers was sampled by placing 16 seed collectors of 0.25-m^2 plastic net squares nailed to the ground under the canopy of eight different plant species and in open space in an area occupied by the species. All these observations indicate that nectar-feeding bats disperse most of the seeds of these columnar cacti.

Based in the fact that the study system depicts a cyclical dynamics governing facilitation processes in which species *x* acts as a nurse for the recruitment of species *y*, species y acts as a nurse for species *z*, and species *z* acts as a nurse for species *x* (see Fig. 1 in Verdu et al. 2009), they simulated co-extinction cascades across these ecological networks quantitatively in order to incorporate metrics reflecting the dependence of facilitated plant species on nurse species and to relate this dependence not only to species abundance but also to the specificity of each particular interaction (Verdú et al. 2010). In addition, it was considered that the concomitant pollination and seed dispersal networks collapse when all the plant species supplying nectar and pollen resources to the bats went co-extinct with their nurse species. Thus, the consequence of removing a particular species from the network is most important in analyzing mutualists, which are more strongly dependent on it.

To simulate a quantitative scenario in which nurse species extinction produces coextinction of their facilitated species, they calculated the dependence *dij* of facilitated plant species *i* on nurse species *j* (i.e., the proportion of the total number of individuals of species *i* recruiting under nurse species *j*) (Bascompte et al. 2006). Because *dij* measures the importance of nurse species for each facilitated plant species, they considered a facilitated plant species to become co-extinct when the sum of its dependencies across nurse species (*di*) was lower than a particular threshold. They also considered open ground (as possible sites of plant recruitment) as an element in the network. Several extinction thresholds ranging from 0 to 1 were simulated. A threshold equaling 0 indicates that a facilitated species is removed from the network only when the sum of its dependencies is zero (that is, when all of its nurse species have disappeared). When the threshold is 0.5, a facilitated species is removed from the network when the sum of its dependencies is less than 0.5. This threshold can be achieved by removing a very important nurse species for the facilitated species or by removing several less important nurse species.

Valiente-Banuet and Verdú (2013) found that their co-extinction simulations of a facilitation network populated by 50 nurse species and 90 facilitated species triggered by the removal of only 16% of species show that extinctions are dramatically accelerated. In other words, a reduction in the abundance of nurse plants, but not their total extinction, contributes significantly to the co-extinction of species. This means that the extinction of interactions precedes the extinction of species (Valiente-Banuet et al. 2015).

A distinct threshold appears at *dij* = 0.24, indicating that the ecosystem collapses when the nurse species habitat availability is reduced to below 76% of its original extent (Fig. 14.3). The presence of complex interdependent networks of species and their interactions emphasizes the inherent fragility of ecosystems governed by

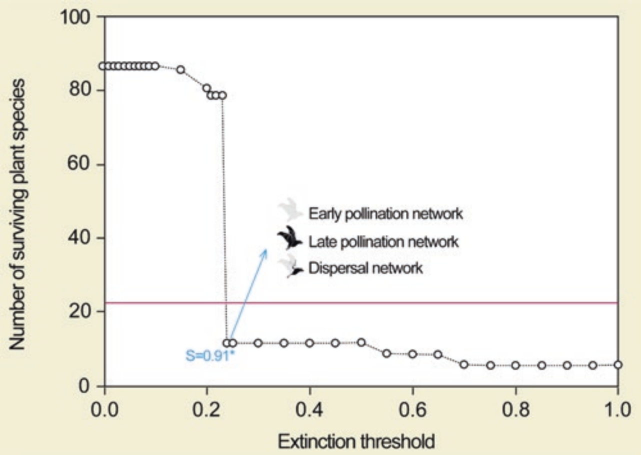

Fig. 14.3 Co-extinction simulation in facilitation networks. Thresholds indicate the dependence dij of facilitated plant species i on nurse species j (proportion of individuals of a species recruiting under a given nurse species). A facilitated plant species becomes co-extinct when the sum of its dependencies across nurse species (di) was lower than a particular threshold. The horizontal line shows the number of species surviving in the degraded community. The maximum similarity between predicted and observed extinctions occurred when the threshold was equal to 0.24 (Sorensen index S = 0.91). The asterisk denotes that all thresholds ≥0.24 in the cyclical scenario revealed a significant association between observed and predicted extinctions ($\chi 2$ test). The arrow indicates collapses in pollination and dispersal networks. (Modified from Valiente-Banuet and Verdú 2013. Copyright license number 5134920539265)

facilitation and their reduced capacity for resilience. In other words, the disruption of the multi-network structure contributes greatly to ecosystem collapse, consequently affecting ecosystem services.

In addition, simulations correctly predicted 75 out 77 extinctions and 8 out of 22 survivals observed in the degraded area (scientific names in blue text in Fig. 14.4). The model also predicted 14 extinctions that were not observed in the degraded area (scientific names in red text in Fig. 14.4) which correspond to species able to resprout (*Acacia constricta*) or peasant managed species (*Lippia graveolens*, *Stenocereus stellatus*). Others are able to recolonize through bird-mediated dispersal (*Cordia curassavica, Opuntia spp*, *Lantana spp*) or abiotic dispersal (*Ipomoea arborescens, Viguiera grammatoglossa, Aeschynomene compacta, Ayenia fruticosa, Cardiospermum halicacabum, Croton ciliato-glanduliferus*).

Authors noticed also that none of the incorrectly predicted extinctions due to strong recolonization ability corresponded with bat-dispersed plants (e.g., columnar

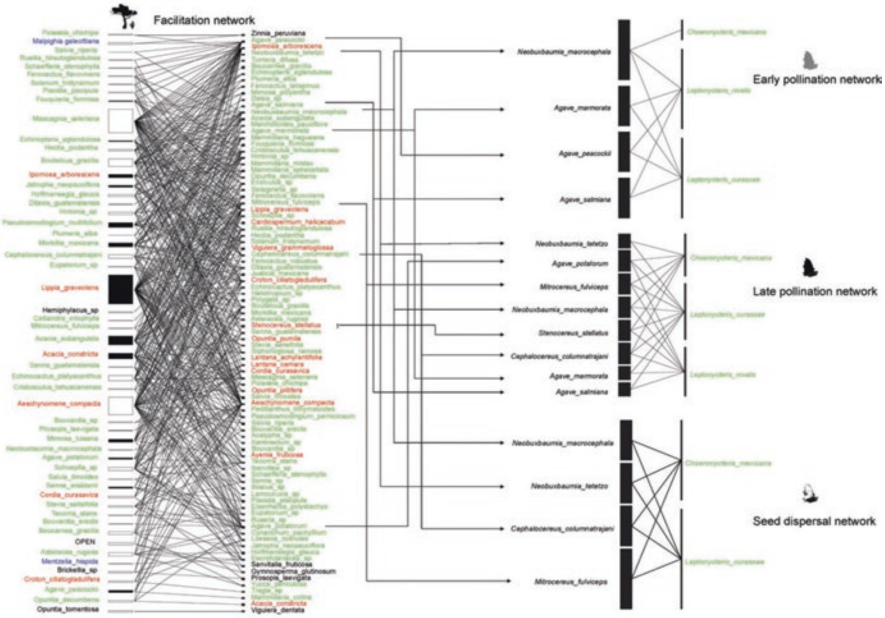

Fig. 14.4 Co-extinction cascades produced by the overexploitation of a few nurse species in the facilitation network propagate toward pollination and seed dispersal networks. The quantitative facilitation network in the conserved vegetation connects nurse species (left) with facilitated species (right). Open ground was also considered as a site for recruitment. The size of each rectangle is proportional to the number of interactions. Black rectangles indicate the overexploited nurse species. Scientific names in green text indicate species in which extinction was predicted and observed; in black text, that extinction was neither predicted nor observed; in blue text, that extinction was observed but not predicted; and in red text, that extinction was predicted but not observed. *Stenocereus stellatus* extinction would have occurred in the degraded community but the species is artificially maintained. (Taken from Valiente-Banuet and Verdú (2013). Copyright license number 5134920539265)

cacti), and the simulations correctly predicted their extinction. Recruitment of bat-dispersed plants in the degraded area is completely absent despite the presence of protected sites provided by nurse species in the community and the opportunity for seeds to potentially establish below them. To test this hypothesis, the authors performed seed sowing experiments with three species of columnar cacti (*Neobuxbaumia macrocephala*, *N. tetetzo*, and *Mitrocereus fulviceps*) (see methods in Valiente-Banuet and Verdú 2013), showing that seedling establishment is not limited by the availability of safe sites, but by dispersal limitation. This result is consistent with the impact that co-extinctions in the facilitation network have in the concomitant pollination and dispersal networks at local scale (Fig. 14.5). Without the nectar and pollen of agaves and columnar cacti, nectar-feeding bats must migrate out of this part of the valley and consequently are no longer available as pollinators and seed dispersers. Pollination and dispersal services performed by bats may abruptly

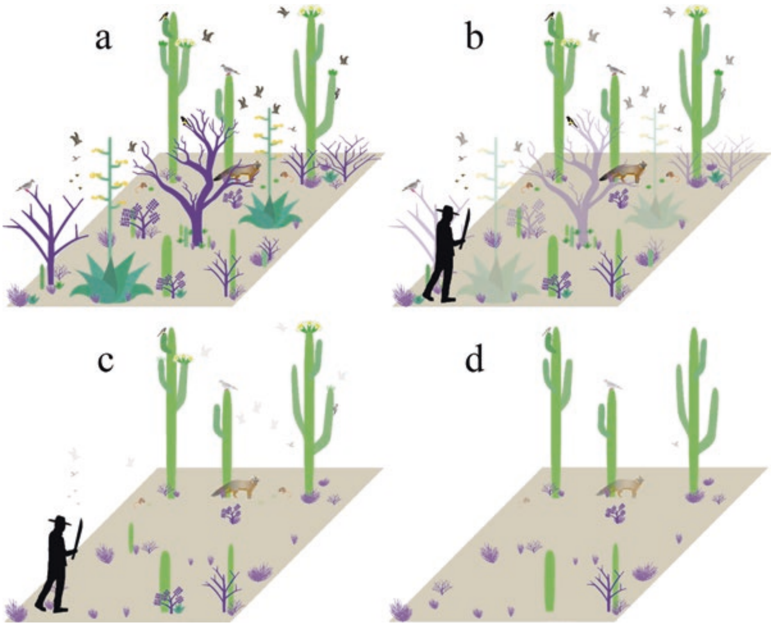

Fig. 14.5 (**a**) Pristine scenario of a community of the TCV depicting the multiple positive ecological relationships that conform the network of interactions that allows the presence and maintenance of a high biological diversity. (**b**,**c**) Nurse species and agaves have gone locally extinct due to intensive extraction. By this point, most interaction networks have undergone co-extinction processes. Without nurse plants, seedlings are not able to establish, impeding regeneration. Bats can be considered functionally extinct, stopping fruit production for columnar cacti and agaves. (**d**) Collapsed ecosystem after man intervention. The remaining vegetation is composed by adult columnar cacti that had established long before the elimination of regeneration sites. Due to the low density of floral and fruit resources, bat populations no longer visit this community. Regeneration becomes virtually impossible due to the lack of safe sites provided by nurse plants

disappear when a critical abundance threshold is crossed (McConkey and Drake 2006). The feeding behavior of the nectar-feeding bat *Leptonycteris yerbabuenae*, the most important pollinator of Agave and CC, is highly affected by floral availability (Estrella Ruiz 2008). This author found that visitation rates and pollination of the nectar-feeding bat to *A. potatorum*, one of the most important species for mezcal production, is the highest in localities with the highest overall floral density, at medium floral densities bat pollination is inefficient, whereas at the lowest floral density pollination is totally absent (Estrella Ruiz 2008).

Clearly, mismatches expected through the network simulations and observed ones may be a consequence of working with a limited number of interaction networks. In addition, this limitation precludes to have a complete real evaluation of the effects of species overextraction. For example, columnar cacti can produce between 815 kg ha^{-1} to 1100 kg ha^{-1} fruits (Rojas-Martínez et al. 2012). According to our preliminary observations, fruits, pulp, or seeds are consumed by at least 119 species, among invertebrates (ants which mostly are granivores) and vertebrates, (mainly birds, rodents, and some carnivores such as *Canis latrans* and *Urocyon cinereoargenteus*), which means that a reduction in the number of fruits, as a consequence of bat-abundance reduction may affect the maintenance of these species. Moreover, and considering that the TCV vegetation is a mosaic of plant communities dominated by columnar cacti and agave species below 2000 m of altitude, it is possible that mezcal boom may collapse different ecosystems at a regional level. In fact, the mezcal boom has the potential to scale up considering that the distribution of columnar cacti and agaves follows a similar pattern in Mexico. As long as the national and international demand for mezcal increase at an exponential rate, different regions of the country's 27 producing states will be strongly affected by overexploitation, as well as by deforestation to establish agave monocultures.

This will have great impacts, especially the co-extinction of species and eventually the collapse of ecosystems mainly in arid environments and possibly with variants, depending on the degree of interdependence between species to those already described.

The arid ecosystems of Mexico, which are those that maintain the highest percentage of the country's endemic flora (Rzedowski 1962) and which are ecosystems governed by facilitation processes (Valiente-Banuet and Verdu 2007), and inhabited by at least 30 ethnic groups (Casas et al. 2010) and unquantified number of peasant communities, are in danger because they depend on their ecosystems' services for survival.

Acknowledgments Special thanks to Tania Sánchez Ortiz for her valuable revision to the manuscript which improved it considerably and for her help with the figures' elaboration. Thanks to Regina Lira who provided important suggestions to the manuscript. Financial support was obtained from PAPIIT-DGAPA-UNAM (IN-214020) and Consejo Nacional de Ciencia y Tecnología (CONACyT-FOP07-2021-04-319061).

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Chapter 15
Deep-Sea Life

Elva Escobar Briones

Contents

15.1 Introduction

Funding science to update the infrastructure needed to carry out exploration, capacity building and mapping of the deep-sea through major national programmes will help to fill in the gaps and advance deep-sea knowledge and its connectivity with the shallow and coastal ecosystems and the neighbouring ocean regions. The ongoing efforts have been of great relevance to the economy. Society will benefit from the continuous efforts to improve ocean literacy to better understand the relevance of the deep-sea life in Mexico and have forecasting capacities to understand the spatio-temporal changes.

E. E. Briones (✉)
Laboratorio de Biodiversidad y Macroecología, Instituto de Ciencias del Mar y Limnología,
Universidad Nacional Autónoma de México, Ciudad Universitaria,
Ciudad de México, Mexico
e-mail: escobri@cmarl.unam.mx

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_15

15.1.1 Analysis of the Current Conservation Status of Deep-Sea Biodiversity in Mexico and Their Habitats

In Mexico, its ocean territory is larger than its continental surface, and extends 3,160,490 km^2, equivalent to 62% of the total territory (INEGI). Below the ocean surface, the pelagic ecosystem is vertically stratified by light, pressure, temperature, and carbon flux into five depth zones, as is the seafloor. The deep ocean, waters below 200 m depth, represents 97% of the water column and 72–92% of the seafloor in the Mexican Exclusive Economic Zone (Tables 15.1 and 15.2). The abyssal zone is the largest ecosystem of the territory, ranging from 2 to 6 km in depth and spanning from 50% to 82% of the seafloor with diverse geomorphological structures mapped. These percentage values vary between the Eastern Pacific Ocean, with an active continental margin, and the Gulf of Mexico and Caribbean, a basin with a passive margin. The water column structure varies too, and is not a homogeneous ecosystem.

The boundaries in the water column are defined by different clines (temperature, salinity, dissolved oxygen, and other ocean chemical essential variables). An extended minimum oxygen zone is present in the Eastern Pacific, expanding from 30 m to over 1500 m depth. It is absent in the Gulf of Mexico and Caribbean. The

Table 15.1 Estimated relative water column volume of the Mexican marine territory. Values in percentage

Depth range (m)	Depth zone	E Pacific	Gulf of Mexico and Caribbean
0–200	Epipelagic	3	4
201–1000	Mesopelagic	24	28
1001–2000	Bathypelagic	29	29
2001–6000	Abyssopelagic	44	38
>6000	Hadopelagic	0.0004	0
Percentage below 200 m		97	96

Source UNINMAR (www.icmyl.unam.mx)
E Eastern

Table 15.2 Estimated relative seafloor surface area of the Mexican marine territory. Values in percentage

Depth range (m)	Depth zone	E Pacific	Gulf of Mexico and Caribbean
0–200	Continental shelf	8	28
201–1000	Upper continental slope	5	10
1001–2000	Lower continental slope	6	12
2001–6000	Abyssal plain	82	50
>6000	Hadal zone	0.09	0
Percentage below 200 m		92	72

Source UNINMAR (www.icmyl.unam.mx)
E eastern

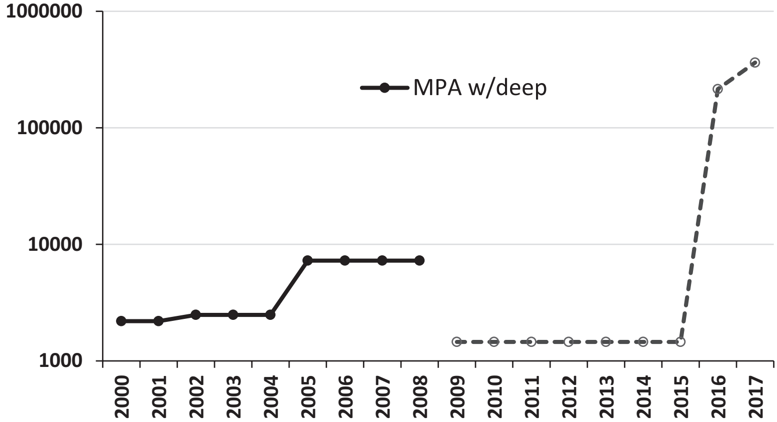

Fig. 15.1 National marine protected areas (MPA) designated after the year 2000; year vs extension in km^2. Island and coastal protected areas with open water and deep seafloor (solid line) and specifically designed deep protected areas and networks (dotted line). (Source of data: https://www.protectedplanet.net/en/thematic-areas/marine-protected-areas)

Table 15.3 Extension, percentage contribution, number, and timeframe of creation of the national marine protected areas encompassing the deep ecosystems

Type	Surface km^2	%	Num. MPA	Year span
Marine protected area with open ocean and deep seafloor	7254.83	1.96	6	2000–2002
Deep marine protected areas	362,999.78	98.04	5	2009–2018

deep ocean is interconnected across habitats, seascapes, ecosystems, and regions, from the surface to the seafloor through circulation, lateral transport, upwelling, heat transport, biota migration, passive and active egg and larvae movement, and the flux of biogenic carbon. All these connectivity mechanisms are important. They help recognize the sources of recruits and sinks where species successfully aggregate (Allen et al. 2018). This knowledge is used in the design of conservation areas, their management, and their restoration.

A key component of the national conservation agenda is guided by the 2016 International Union for Conservation of Nature that calls for a full protection of 30% of each marine habitat and its biodiversity. The current percentage of marine conservation in Mexico is 21.55%. The number of protected areas and the extension of each one has significantly increased in the past 20 years (Fig. 15.1). The deep protected areas in Mexico, in particular hydrothermal vents, were among the first worldwide. In general, these have been designated within the last decade and contribute with a larger extension (Table 15.3).

In contrast to the terrestrial protected areas that have clearly defined borders, ocean biodiversity conservation challenges the managers with its fluid nature, its 3D spatial arrangement, and its required connectivity (Sayre et al. 2017). The extension of the

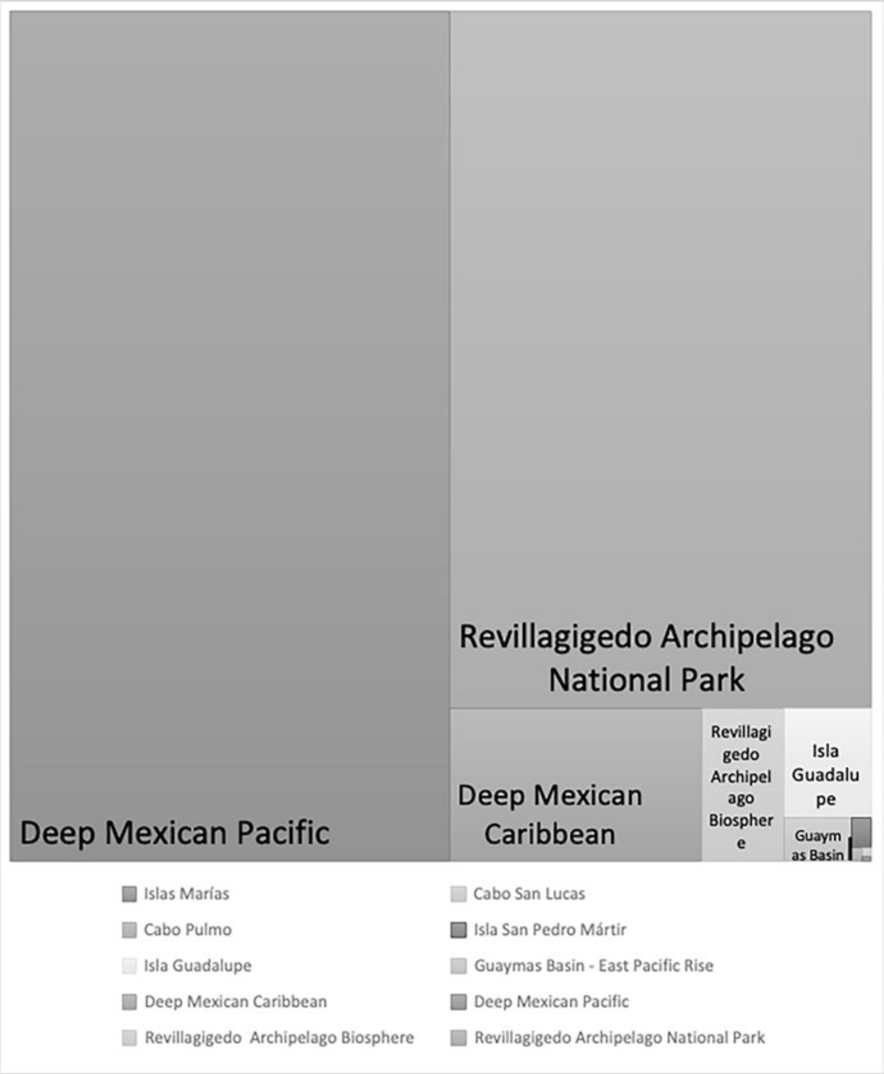

Fig. 15.2 Relative extent of the deep national protected areas created after 2009 in contrast to the areas created between 2000 and 2002 that include open ocean and deep-seafloor elements. (Source of data: https://www.protectedplanet.net/en/thematic-areas/marine-protected-areas)

national deep protected areas is significantly larger (98%) and dwarfs the size of the protected area counterparts that have deep-seafloor elements (Table 15.3, Fig. 15.2).

Globally, the very large marine protected areas (>100,000 km^2) contribute with a significant part of the conservation ocean coverage (Brooks et al. 2016). Such a large extent represents an enormous commitment to conservation. Some of these very large marine protected areas are in areas beyond national jurisdiction for which international collaboration is required. The spatial extent is one of the metrics used to define protection and express the conservation efforts, targets, and progress (Spalding et al. 2016). To ensure that biodiversity and ecosystem services conservation are achieved, ecological effectiveness, connectivity, and representativity are factors that need to be present and monitored.

The ecologically or biologically significant marine areas are biological diversity area-based conservation and sustainable use tools, and are part of strategies to recognize well-represented ecosystems and habitats in the open ocean and deep ocean. The average size of EBSAs is 239,283 km^2 (Secretariat of the Convention on Biological Diversity 2021).

These criteria are defined specifically for each site and network. One or more of the seven criteria (uniqueness, importance for species life history, threatened species and/or habitats, vulnerability, productivity, diversity, and naturalness) are required to sustain in expert workshops the EBSA description based on the best available scientific knowledge and integrate the traditional knowledge of indigenous and local communities (CBD 2009). In contrast, network criteria (representativity, connectivity, replication, and adequacy) are supported only by systematic analyses.

Protecting the deep-seabed ecosystems considers areas of environmental interest (APEI), and sites and areas in need of protection based on criteria such as fine scale or large areas with self-sustaining populations, a broad range of habitat variability, absence of direct and indirect mining effects, and unknown impacts (Donovaro et al. 2020).

The seafloor and its habitats are dynamic in geological timescales, but they are relatively fixed in our timescale. Water, organisms, and flux of particles move and connect within different scales of time and space in an “aqueous materiality” (Acton et al. 2019). It is under these conditions that boundaries for species, seascapes, and biogeographic regions are defined for the conservation of the deep ocean and with it challenge the decision making (Brooks et al. 2016).

15.2 The Energy Sources That Support Deep-Sea Life

The deep ocean is an energy-poor environment. It is with this limited availability of energy, only ~1% of the carbon fixed at the surface deposited on the seafloor below 1000 m depth, that the patterns of diversity are shaped in time and space (Woolley et al. 2014). This important energy source, on which deep-sea life depends on, originates from the sinking of photosynthetic particles through the water column. The organic carbon exported from the surface water below the thermocline exponentially declines with increasing depth. Most of the organic carbon particles are consumed in the water column and transferred along the food web and shed of their labile compounds by microorganisms releasing energy and elements into the deep ocean. The biological pump, as this important process is known, connects the shallow with the deep ocean and the coastal with the offshore ecosystems. It is based on the flux and storage of organic carbon to the deep ocean in timescales of over thousands to millions of years. The amount of carbon exported varies with time and geographically according to the dynamic nature of the ocean, in constant movement and in a 3- or 4-dimensional space (Sayre et al. 2017).

Despite the scant knowledge from deep ocean exploration in Mexico, we understand that the geomorphologies, seascapes, and diversity of habitats are crucial to sustain a biodiversity that provides important ecosystem services of value to the society because of their function. These are classified according to the Millennium Assessment into supporting, provisioning, regulating, and cultural services many of which occur on a very small scale. The vastness of the deep ocean over which these processes occur have a large impact on the planet. Monetary values associated to some of these ecosystem services have been reported including those that support life, sustenance, element recycling, C flux, and storage; services that provision O_2, food, water, energy, mineral, genetic, and bioprospecting resources; services that regulate climate by storing heat, C_{org} and CO_2, lifecycles, and gene pools; and services that enrich culture, traditions, knowledge, and inspire art and music. The services provided become relevant for the functioning of a healthy and resilient ocean and benefit life in the planet (Thurber et al. 2014). The ocean's important role is as a memory keeper of past processes, of the ocean linked to the human history and of the key information for life in the planet.

The unsustainable uses of resources in deep-sea habitats cause disturbances that lead to the loss of biodiversity. This loss of species affects ecosystem services and have higher ecosystem significance. The recovery of ecosystems in the deep sea, like every process in this ecosystem, is extremely slow, in the order of thousands to millions of years. So effectively, the damage done by the loss of diversity will be irreversible. Our tools and understanding to restore the deep-sea biodiversity, processes, and ecosystems are still poor. Recognizing vulnerability of deep ocean and counting with early warning system criteria can help to protect species from extinction. By protecting their populations, habitats, and ecosystems, we prevent the loss of deep-sea biodiversity and ecosystem services from the cumulative human impacts including the synergy with climate change. In the meantime, with the limited knowledge, a precautionary approach and ecosystem-based management measures are a guidance to protect and effectively conserve areas and their key biodiversity components in the long term. In Mexico, this limited knowledge of the deep ocean defies decision making and understanding of why a network of protected areas and full protection of 30% of each habitat is needed to attend the International Union for Conservation of Nature call. In most ocean regions, the trend is that 30% of prioritized areas for conservation are mainly coastal (Zhao et al. 2020).

The effects that the unsustainable use of deep ocean resources could have on deep-sea species occurrence, abundance, and distribution patterns are unknown in different scales of time and space. The global patterns of sea-floor diversity remain poorly known, having so far been described only at local and regional scales (Woolley et al. 2014). In Mexico, the patterns of deep-sea biodiversity are limited to the local scale of the bathyal zone in the North Pacific and the Gulf of Mexico, where a negative correlation exists between the diversity of shelf and slope soft sediment environments and POC flux to the sea floor. These results have poorly supported identifying potential protected areas.

The deep ocean is vast and changes on long residence times (Thurber et al. 2014). Therefore, even the processes that occur on microscopic spatial scale are important and have long-lasting impacts. Biodiversity loss and its effect on resilience and deep ocean restoration respond to these scales in time and space.

15.3 Review of Existing Information of Life Below 200 m in Mexico

Deep ocean research, exploration, and exploitation have been led by a small group of developed nations from the northern hemisphere and have historically resulted in a sampling effort bias with a significant coverage in the northern ocean regions. Deep-sea research is too expensive for Mexico. Collaborative efforts and access to large infrastructure such as research vessels with dynamic positioning, submersibles, and ROV have helped the study of the deep-sea biodiversity in the Mexican Exclusive Economic Zone in specific locations of interest to the international community. This is manifested in the availability of data, samples, and specimens for a few sites only. To engage in deep-sea research nationwide, more capacity building is required with courses in the undergraduate and graduate programmes so that research expertise and training opportunities are available.

Among the most important research efforts carried out with Mexican research vessels and their basic infrastructure is the “Talud” dredge sampling programme in the eastern Pacific carried out by Michel Hendrickx, from Instituto de Ciencias del Mar y Limnología, UNAM, and collaborators. The outcomes of this research are reported in over 200 new species records and species of megafauna described. Other studies focus on local collaborative collections in the California deep-sea basins with and without chemosynthetic processes. These include descriptions of escarpments, minimum oxygen zone, hydrothermal vent, seep and whalefall communities by scientists from CIBNOR, CICESE, and UNAM. Many of these studies focus on the megafauna; larger animals typically traverse greater areas in their larval, juvenile, and adult stages to locate and benefit from the most adequate resources (Allen et al. 2018).

The largest and long-lasting deep-sea sampling effort has been carried out in the Gulf of Mexico. Many of these deep-sea sampling programmes are related to assess oil spills and generate different baselines to forecast the effects on the deep-sea biota. Among these large programmes are CIGoM led by CICESE, C-IMAGE where Mexican and USA institutions partnered to tell the story of two oil spills, studies carried out by UNAM to explore potential deep-sea fishery resources (OGMEX, PROMEBIO, PROGMEX, BIOREPES, COBERPES, SOGOM), and scavengers, using traps and trawls. The infaunal biodiversity has been studied in a

Long-Term Ecological Research programme through the SIGSBEE and DGoMB cruises by UNAM and a partnership with a TAMU-USGS effort. A time series station has been sampled since 1997 through 2019 and halted by the COVID-19 closedown. The mesophotic corals are being studied in an international collaborative effort with the Universidad Veracruzana.

Efforts carried out in the northern Caribbean Sea include the deep-sea corals by local federal institutions. The exploration of the benthic communities along the upper bathyal escarpment from Chinchorro atoll to Arrow Smith Bank is conducted through collaborative research between Harbor Branch Oceanographic Institution and UNAM.

Deep ocean tropical habitats, including both the water column and the deep seafloor and its associated biodiversity, receive much less attention than coastal ones. The pelagic zone below 200 m is perceived as uniform; however, it comprises a multitude of habitats and therefore it harbours one of the largest proportions of the planet's species including amazing large numbers of prokaryotes, 10^{28} (Thurber et al. 2014). The biodiversity peak in tropical latitudes (0–30°) occurs in the shallower depth zones (continental shelf to upper-slope); however, little is known in many ocean regions (Woolley et al. 2014), including Mexico. The water column requires further study. Technology, tools, and capacity development are required to assess the biodiversity of the twilight zone and the deep, dark water column and the important processes provided by its biodiversity. The changes of the Eastern Tropical Pacific minimum oxygen zone with climate change will require intense monitoring.

Our current knowledge recognizes that maximum diversity in the deeper depth zone peaks at higher latitudes (30–50°). This interpretation, explained mainly by the species-energy hypothesis (higher carbon export), is defined as well by a larger knowledge of the deep-sea studies in higher latitudes. Habitats of the deep-sea seafloor have been poorly sampled, too. We know little of canyons, escarpments, seamounts, and the bathyal habitats impacted by the minimum oxygen zone. We need to document the small-scale biodiversity and the spatial changes of the polymetallic covered abyssal seafloor. With a small percentage of the ocean fully protected (<1%) from premeditated and rising anthropogenic impacts, conservation actions in the deep ocean have great opportunity for the next decade. Some of our largest deep-sea national protected areas lack information, among these the trench habitats, the Caribbean borderland, and effects of the possible export of *Sargassum* to the deep seafloor.

The gaps in scientific knowledge and data of the life in the deep ocean in Mexico are related to the limited samples collected both in time and space related to the declining budget for ocean science, the constrained infrastructure, equipment, and skills to study and collect in the small-scale, the small number of taxonomists that can identify the deep-sea taxa, and the derived lack of information of the deep ocean. These limit capacity building and the chances of developing a competitive international deep-sea scientific framework. The absence of reaching the public and to the decision makers stands out in contrast to the size of the deep ocean representation (Thurber et al. 2014), both globally as in the national territory. We have a basic understanding of how the deep sea is relevant to the regulation of climate change. We have a better knowledge of how temporal and spatial processes of the deep ocean diversity are linked to society through the ecosystem services it provides.

However, the current gaps, lack of detailed knowledge and data, make deep ocean decision making and management extremely difficult. This, with regards to the use of biodiversity in areas beyond national jurisdiction and the future exploitation of resources (deep-sea mining). The former can provide great benefits to humankind. The latter, of interest to the economy, can lead to diversity loss, and it is presently impossible to know the cost to pay for exploiting specific resources (Thurber et al. 2014).

15.4 Prognosis of Future Challenges and Expanding Threats Inherent in the Anthropocene

Coastal and surface ocean observations are less complex and expensive to measure. In the same way, biological observations are more difficult to measure than physical, geological, or chemical observations. The Global Ocean Observing System Biology and Ecosystem of the Biology and Ecosystem Panel and the Marine Biodiversity Observation Network of the Group on Earth Observations Biodiversity Observation Network, and the UN Ocean Biogeographic Information System are programmes that measure essential biological and ecological variables from the deep ocean. Biological samples require a significant amount of time and expertise to process, to interpret and to monitor. During the next 10 years, further information will be collected, and historical data analyzed from the Mexican deep ocean regions to help determine threats from human activities. The use of machine learning and artificial intelligence will be of great help to recognize patterns of occurrence of species in real time.

Because the deep ocean is larger, climate change effects on it will be long lasting and have a larger impact. Among these are warming, acidification, deoxygenation, and expansion of the minimum oxygen zones and changes in currents and circulation (IPCC 2019). Of all these, the changes in temperature have influence on individual's metabolism, physiology, growth rate, and size, and may have adverse consequences to diversity in the deep-sea ecosystems at time scales of 10^1–10^4 years (Yasuhara and Danovaro 2016). The water column temperature leads to thermal stratification that is intertwined with the quantity and quality of particulate organic carbon flux, carbon export, food availability and biotic interactions in the deep ocean.

Because climate change is taking place, it affects and will be affecting the deep-sea habitats and their diversity. Some of the critical elements such as deep ocean future climate change associated hazards, the time of climate change emergence and development were identified and modelled for the Clarion-Clipperton ISA contract area (Levin et al. 2020), which lies next to Mexico's Exclusive Economic Zone and shares specific deep-sea habitats and ecosystems. This vastness and how diversity defines the deep ocean processes take relevance under drastic changing climate (Danovaro et al. 2017). More science is required to understand the drivers that will transform the life patterns in the deep-water column and the seafloor while still maintaining key regulating ecosystem services such as carbon fixation under the potential use of deep-sea mineral resources (Levin et al. 2020).

15.5 The Context of the Unique Physical, Ecological, and Cultural Aspects of the Nation

At the largest scale, Mexico's eight unique ecological marine regions are defined by Wilkinson et al. (2009) by the large water masses and currents, the large, enclosed seas, the processes, and response to the surface temperature which extends from surface to the deep ocean. A level II is defined by depth and the seafloor physiography. However, the Global Open Oceans and Deep Seabed's biogeographic classification (UNESCO 2009) delineate Mexico's bathyal and abyssal regions. Mexico's deep-sea uniqueness is described by its geology, processes associated to the active and passive margins, diversity of geomorphological features, connectivity by currents, and by the presence of an extended minimum oxygen zone that impacts the eastern Pacific bathyal zone. A borderland characterizes the Caribbean deep-sea and escarpments, in contrast, a salt dome province and bathyal ridges with oil seepage characterize the Gulf of Mexico.

The deep-sea culture, research, and studies have developed slowly in public research centers, universities, and ocean science institutions. Scientists contribute to deep-sea biodiversity from research intitutes and univeirsities of CICESE, CINVESTAV, UNAM, ECOSUR, UAM, CICIMAR-IPN, UV, CIDESI, UAEM, and UABC. Many of these institutions and scientists are members of the Gulf of Mexico Research Consortium (CIGoM). In some cases, these institutions have laboratories that are in different states in the country. In the case of the universities, many faculties, departments, institutes, and laboratories cover different oceanographic fields. The scientific community in Mexico has built and developed infrastructure, observation platforms and tools to study and monitor the deep ocean biodiversity. Among them are three regional size research vessels (35–55 m) that have joined the CONACyT National Research Vessels Laboratory until 2022. Deep-sea fishery resource exploration counts with one international size research vessel (55–65 m) administered by INAPESCA. Other federal research vessels ran by the Mexican Navy describe the upper ocean hydrography and map the seafloor. On average, these vessels were built more than 35 years ago. Other types of tools to study the deep ocean include human-operated vessels (submersibles), and ROVs, which are unoccupied and operated by someone at the water surface.

Some of the major national research programmes that have contributed to the knowledge of deep-sea life are in the Caribbean Sea: the HBOI collaborative cruise with UNAM. In the Gulf of Mexico porgrammes include: the CIGoM consortium, the OGMEX, and PROGMEX cruises, the 23 year-long SIGSBEE LTER programme, and the international collaborative project Centre for Integrated Modelling and Analysis of Gulf Ecosystems (C-IMAGE) in the Gulf of Mexico. Collaborative cruises with German institutions have led to the discovery of asphalt volcanoes with characteristic chemosynthetic biota spanning from 3000 to 3900 m depth. In the Pacific the "Talud" cruises have had a major contribution regarding the megafauna. In addition, international collaborative cruises include the Gulf of California deep basins with MBARI, other cruises with the Smith Institute, Ocean Exploration Trust, and IFREMER that have led to discover new chemosynthetic sites. New opportunities will enhance our knowledge through the UN Ocean Decade endorsed deep-sea programmes such as Challenger 150, and iDOOS among others.

Capacity building and new knowledge through scientific research are commitments that the Mexican education and research institutions seek to achieve both at the sea and in the laboratory. The next 10 years will see a major change in innovation, technology, and tools to explore and study the ocean. Mexican participation in the IOCARIBE and the UN Decade of Ocean Science for Sustainable Development 2021–2030 offers once in a lifetime opportunity to partner in building capacities in deep-sea taxonomy, in understanding marine genetic resources, in acquiring data that help build a Digital Twin of the Deep-Ocean Ecosystems and deliver better forecasting scenarios. Building these capacities are a requirement to predict the effects of use of resources in the deep sea, impact of pollution, climate change, and species loss.

The benefit of deep-ocean literacy and capacity development efforts to society lie in acquiring a deep-sea culture and knowledge needed to grab new economic prospects that are in hand with society and its health. Outreach, ocean literacy and awareness, citizen science and undergraduate and graduate teaching are some of the mechanisms that will provide tools to make ocean knowledge available, usable, and empower stakeholders. The establishment of higher-education programmes on deep-sea issues at the national and regional levels, and the theses and studies resulting from research will contribute to future leadership in science; implementing these actions in the long term is still challenging.

The study of deep-ocean life and ecology needs to be supported by the development of national ocean and blue economy strategies from a research policy core framework. The framework requires to replace the existing infrastructure with new research vessels, with state-of-the-art sampling equipment and instrumentation onboard, access to laboratory equipment, and in the case of deep ocean: qualified technicians and deep-sea scientists. Understanding deep-sea biodiversity requires to develop capacities in taxonomy, e-DNA technology, data processing and analysis, environmental management, and monitoring. Ensuring that young scientists in Mexican coastal laboratories have access to on-board research vessels for training and undertake deep-sea research in the two ocean regions of Mexico, and to land-based laboratory training in national and regional training and research centers, promoting gender equality and increased participation of women in scientific research activities.

The data repositories and data bases that contain deep-sea life data and metadata from scientific research are UNAM's UNIBIO and UNINMAR, CONABIO's REMIB and SNIB which are open access databases, CICESE and CINVESTAV CIGoM's Sistema Integral de Manejo de Datos (SMID). UNAM's UNINMAR repository have internal regulations and includes not only the biodiversity records, but also essential environmental variables, images, and video transects from the deep-sea collaborative cruises that are currently being updated to have better annotation capacities. The data are shared with the international databases such as OBIS, WoRMS, the World Data Center PANGAEA, Ifremer's BIOCEAN database (Deep Sea Benthic Fauna), MBARI's Spatial Temporal Oceanographic Query System with data, image gallery and video library and the Ocean Exploration Trust data and ROV video footage repository. Other data repositories exist because of cruises from national and international consortia (CIGoM; C-IMAGE) in the bathyal Gulf of Mexico that are not open access but available on demand and collaboration.

The major deep-sea specimen collections in Mexico are in public research institutions and centres at UNAM, CINVESTAV, CICESE, and Universidad Autónoma del Carmen, among others. Some of these collections have a national status, others are reference collections. Some are open access for scientific research, others have limited or no access at all, defined by the curator (CRIM, Colección Regional de Invertebrados Marinos), and on the origin of the financial resources (i.e. CIGoM). Some of these have loan and user regulations (i.e. ICML UNAM). The largest biodiversity knowledge effort has focused in describing megafaunal deep-sea vertebrates and invertebrates from the Gulf of California and the NE Pacific Mexican EEZ followed by those from the bathyal zone in the SW Gulf of Mexico. There are reference collections for infauna with the limitation in their identification. It is for the same reason that monitoring of deep water and benthic habitats should prioritize megafauna and consider starting a capacity development in infaunal taxonomy.

The Mexican ongoing efforts in ocean literacy are the Laboratorio Oceanográfico Virtual CICESE and the Cultura Oceánica project from ICML UNAM, both include the deep-sea biodiversity topics, the former will integrate local and traditional knowledge, while the latter is based in the essential principles, fundamental concepts, and basic understanding of the ocean. The Cultura Oceánica project follows the models of UN Ocean Sciences Decade Ocean Literacy programme and the Ocean Teacher Global Academy seeking to communicate deep sea and general ocean concepts in a meaningful way (Thurber et al. 2014). Ocean literacy is important in deep-sea conservation efforts. By having better knowledge of how biodiversity in the ocean is structured and functions, how it contributes to human well-being and raising its economic value to society, will help understand its priority in the design and implementation of effective conservation management strategies, their observation and reducing its vulnerability (Donovaro et al. 2020).

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Chapter 16
Mexican Fauna in Agroecosystems: Challenges, Opportunities and Future Directions

Juan Fernando Escobar-Ibáñez, Johnattan Hernández-Cumplido, William D. Rodríguez, Romeo A. Saldaña-Vázquez, and Veronica Zamora-Gutierrez

Contents

J. F. Escobar-Ibáñez (✉)
Gnósis – Naturaleza con Ciencia A.C., Zapopan, Jalisco, México

Doctorado en Ciencias de la Sustentabilidad, Instituto de Estudios Superiores de la Ciudad de México “Rosario Castellanos”. Centro Gustavo A. Madero, Ciudad de México, México

Maestría en Ciencias en Biosistemática y Manejo de Recursos Naturales y Agrícolas, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, Jalisco, México

J. Hernández-Cumplido
Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, UNAM, Ciudad de México, México

W. D. Rodríguez
Departamento de Salud Pública, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Zapopan, Jalisco, México

R. A. Saldaña-Vázquez
Instituto de Investigaciones en Medio Ambiente Xabier Gorostiaga, S.J. Universidad Iberoamericana Puebla, Puebla, México

V. Zamora-Gutierrez
CONACYT- Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional Unidad Durango (CIIDIR), Instituto Politécnico Nacional, Durango, México

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_16

16.1 Environmental Crisis Due to the Impact of Human Activities

Human activities are modifying global ecosystems at unprecedented rates and magnitudes. This has caused an environmental crisis that puts the proper functioning of the planetary ecosystem at risk and directly impacts the planet itself (Vitousek et al. 1997; Díaz et al. 2019). Major modifications include climate change, land-use change, fragmentation and overexploitation of ecosystems, alteration of biogeochemical cycles, and environmental pollution (Turner et al. 1990; Steffen et al. 2015). The magnitude of these modifications is such that in stratigraphic analysis it is already possible to detect the so-called "technofossils" (e.g., aluminum, plastics, concrete), as well as black carbon and inorganic ash (Waters et al. 2016), pristine ecosystems no longer exist in the world (Vitousek et al. 1997) and many believe that this has provoked the sixth mass extinction (Dirzo and Raven 2003; Ceballos et al. 2020). Our planet has changed so dramatically due to human actions that a new geological era is recognized, known as the "*Anthropocene*" (Crutzen and Stoermer 1999; Waters et al. 2016). The term "*Capitalocene*" has also been proposed, in recognition of the socioeconomic system that prevails in the world as one of the main causes of the excessive use of the natural resources (Moore 2017). In the face of these modifications and the impacts they entail, it is essential to question the concepts of progress, development and unlimited growth, as well as the paradigms that have contributed to humanity reaching this point of environmental degradation that have put at risk our civilization (Leff 2011).

For thousands of years, domestication of animal and plant species constituted fundamental advances for human societies, paving the way for the development of urban centers and representing a turning point in the history of humanity and the planet (Smith 2001). In recent decades, agriculture has drawn special attention as one of the human activities with the most detrimental impacts on ecosystems, and the largest use of land in the world, occupying around 45% of global land surface (Foley et al. 2005; Hooke et al. 2012). Agricultural activities can be divided into two main areas: (1) livestock activities, related to the production of animal products, and (2) arable farming, focused on the production of fibers or food of plant origin, also called croplands or agroecosystems. The main focus of this chapter will be towards agricultural activities of the second group.

16.2 The Impact of Agroecosystems

Arable farming, or agroecosystems, emerged in different regions of the world at different times in human history (Pongratz et al. 2008), but it is believed that the first agricultural practices occurred independently about 10,000 years ago in: (1) Middle East, where domesticated varieties of emmer wheat (*Triticum dicoccum*), einkorn wheat (*T. monococcum*), and barley (*Hordeum vulgare*) were found; and (2) Mexico, where an ancient predecessor of zucchini has been identified (*Cucurbita pepo*; Smith 2006). Following millennial processes of domestication and expansion, agroecosystems currently occupy around 14% of the earth's surface and are the second largest land use in the world, only after livestock production (Hu et al. 2020). In addition to the huge amount of land surface area that they cover, there is also great concern about their impact on ecosystem functioning, mainly because: (1) the expansion of agroecosystems has occurred mostly at the expense of the world's forests and is the main cause of deforestation and loss of biodiversity and ecosystem services in high-biodiversity sites such as the tropics (Pongratz et al. 2008; Defries et al. 2010; Hansen et al. 2013); (2) together with livestock, agroecosystems are the land use that contribute most to greenhouse gas emissions (Tubiello et al. 2015) and freshwater consumption (Mekonnen and Hoekstra 2011; FAO 2020); (3) it is among the activities with the highest inputs of chemicals into the environment (Zhang et al. 2011).

Although agroecosystems have shaped the distribution of organisms since their inception (Kathleen et al. 2016), in recent decades they have led to population declines in different animal and plant species around the world (Newbold et al. 2015; Stanton et al. 2018; Sánchez-Bayo and Wyckhuys 2019), mainly due to the search for greater production at lower costs by intensifying agricultural practices (Pellegrini and Fernández 2018; Benton et al. 2021). This is alarming, given that biodiversity plays a central role in many processes that are essential for the proper functioning of ecosystems and agroecosystems per se. Therefore, its loss represents a decrease in environmental quality, ecosystem services from which humans' benefit, and the resilience of ecosystems to environmental change (Dirzo et al. 2014; Ceballos et al. 2020). One of the clearest examples of this is the dependence of agroecosystems production on ecosystems services provided by animals such as pollination, nutrient cycling, biological pest control and even improved water quality (Foley et al. 2005; Duru et al. 2015).

Agroecosystems threaten the very fauna on which they depend and consequently requiring the need to replace these services with external inputs at a high economic and environmental cost (Altieri 1999; Phelps et al. 2013). Therefore, the search for sustainability in landscapes dominated by human activities currently represents one of the highest global priorities (Melo et al. 2013). This is even more relevant in megadiverse countries like Mexico, where the main conservation strategies (i.e., Protected Areas) have not been enough to stop environmental degradation by anthropogenic activities (Figueroa and Sánchez-Cordero 2008; García-Bañuelos et al. 2019), and where the loss of biodiversity threatens the country's own cultural identity (Arriaga-Jiménez et al. 2018).

16.3 Mexican Agroecosystems

Agroecosystems in Mexico date back to pre-Hispanic times and have been closely related to the country's enormous biocultural diversity (Toledo et al. 2019). These unique agricultural systems have been recognized globally, from the milpas of the Mayans to the chinampas of the Mexicas (Gómez-Pompa 1987; Moreno-Calles et al. 2013). In fact, there are still regions in the country where traditional techniques are conserved, which, in addition to reflecting indigenous peoples' worldview and relationship with their environment, are also areas where significant biodiversity is conserved (Barrera-Bassols and Toledo 2005; Moreno-Calles et al. 2013). Mexico is also a center for the diversification and domestication of numerous species that are a fundamental part of the world's food supply (e.g., corn, chili, pumpkin; Perales and Aguirre 2008). However, because of global trends towards the intensification of agricultural practices (Pellegrini and Fernández 2018), market interests, and even government initiatives (Moguel and Toledo 1999), traditional practices have been severely altered and reduced, which has not only affected biodiversity and the functioning of ecosystems, but also promoted unwanted social and cultural effects such as social inequality and loss of traditional knowledge (Klepeis and Vance 2003; Bohn et al. 2014).

With more than 142 million tons of crops produced in 2019, Mexico is the 11th largest agricultural producer in the world (FAO 2021). In order of the geographical area that they occupy, the main crops grown in the country are: corn (6,690,449 ha), sorghum (1,324,783 ha), beans (1,207,395 ha), sugar cane (795,984 ha), and coffee (629,300 ha), while those that grew the most between 2009 and 2019 were: corn (+467,402 ha), seed cotton (+135,197 ha), barley (+118,938 ha), avocados (+94,451 ha), and sugar cane (+85,399 ha; FAO 2021). As in most of the tropics, the expansion of agroecosystems is the leading cause of deforestation in Mexico (Mendoza-Ponce et al. 2018; Fig. 16.1), which is the main threat to Mexican vertebrates' populations (Sánchez-Cordero et al. 2005; Challenger and Dirzo 2009; De Jong et al. 2010; Zamora-Gutierrez et al. 2018).

The ecosystems that have been most affected by agricultural expansion are tropical dry forests, grasslands, and scrublands of arid regions of Sonora and Chihuahua (Mendoza-Ponce et al. 2018). Tropical dry forests are one of the ecosystems with the highest degree of endemism in Mexico, while the northern scrublands shelter a high diversity of large mammals of conservation concern (Koleff et al. 2008). The expansion of agroecosystems is expected to continue in the coming years at the expense of natural ecosystems and affecting areas of special interest for the conservation of Mexican biodiversity (Mendoza-Ponce et al. 2020). Therefore, understanding its impact on fauna is essential to move towards the conservation of biodiversity in human-modified landscapes.

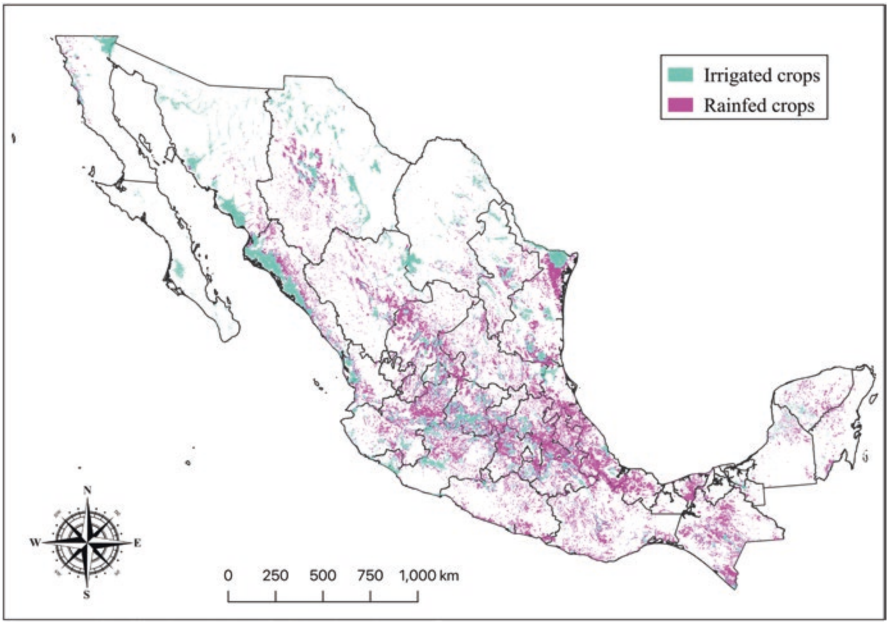

Fig. 16.1 Distribution of agroecosystems across Mexican territory. (Data obtained from INEGI (2017))

16.4 Which Elements of Biodiversity May Benefit/Lose from Agroecosystems?

In addition to their expansion and the loss of habitat that this entails, the impact of agroecosystems on biodiversity depends on the environmental characteristics of the impacted area (e.g., availability of resources and its distribution). These include the inherent characteristics of the affected species (e.g., feeding habit), the age of the plantation, the number of planted crop species (monoculture or polyculture), its structure (plant diversity, stratification and phenology) and temporality (i.e., annual, perennial), and the management given to the crop (e.g., organic, conventional or intermediates). In Mexico, some of these aspects have been mainly evaluated in coffee agroecosystems (Moguel and Toledo 1999; Perfecto et al. 2003; Williams-Guillén and Perfecto 2010, 2011), leaving important information gaps on the general understanding of the impacts of most agroecosystems in the Mexican fauna.

Here, we provide a summary of the responses of some of the main fauna groups in Mexico and for which there is more information available.

16.4.1 Bats

Mexico ranks third in mammal diversity worldwide with about 564 species, of which 157 are endemic (Sánchez-Cordero et al. 2014). This group is distributed throughout the country, but human activities have caused population declines of many species (Sánchez-Cordero et al. 2014). Within mammals, bats are the group with the broadest diet representation, they also have morphological adaptations specialized to use specific habitats (e.g., open areas, clutter vegetation), and additionally their echolocation system also is highly specialized within their guilds (Denzinger and Schnitzler 2013). In terms of bat diversity, Mexico holds fifth place, hosting around 140 species from 8 families (Wilson and Mittermeier 2019). Its high-species richness and wide ecological niche occupancy makes them an ideal taxonomic group to study assemblage responses to anthropogenic disturbances (Jones et al. 2009; see also Chaps. 11 and 14, in this volume).

There is a growing interest in understanding what makes agroecosystems attractive for bat species, especially because of the ecosystem services that they provide to cultivars (i.e., pollination, suppression of insect populations; Kunz et al. 2011). However, most of the studies about the effects of agricultural areas on bat diversity in Mexico have focused on coffee plantations (Fig. 16.2) and *Agave* cultivars (Chap. 14, this volume).

Although bats can move between different habitats due to their flying capacity, studies have shown that not all species benefit from agricultural areas, being the habitat and diet generalists, as well as the most mobile species the usual "winners" (Estrada et al. 1993a, 2006; Madrid-López et al. 2020). For bats, the degree of isolation of forests more than the size of the patches plays an important role in determining species richness (Estrada et al. 1993a; Numa et al. 2005). It is likely that bats use a combination of different habitat patches (i.e., forest, agroecosystems) as stepping-stones to move across the landscape, but the use of a particular habitat does not equate to being able to survive exclusively in that habitat (Estrada et al. 1993a). Moreover, bats use specific landscape features to move across the habitat matrix (e.g., hedgerows, linear features; Estrada and Coates-Estrada 2001, 2002), but not all bat species use landscape cues equally. Therefore, agriculture affects their mobility differently depending on the resulting agricultural–natural habitat mosaic (Russ and Montgomery 2002; Williams-Guillén and Perfecto 2010; Cortés-Delgado and Sosa 2014; Madrid-López et al. 2020).

A general trend emerges from studies on bat assemblages in coffee plantations and in mango orchards, which shows that frugivores and nectarivores are more adaptable to disturbance than other guilds and are less affected within these agroecosystems, mainly due to food availability (Pineda et al. 2005; Williams-Guillén and Perfecto 2010; Castro-Luna and Galindo-González 2012; Madrid-López et al. 2020; but see Saldaña-Vázquez et al. 2010). Studies focusing on the responses of insectivorous bats have found that activity of aerial insectivores decreases with agricultural intensification (Williams-Guillén and Perfecto 2010). Insectivorous bats that forage in clutter environments tend to have reduced activity but not species richness when management intensifies, while species that usually forage in open and semi-open habitats seem to be less affected (Williams-Guillén and Perfecto 2011).

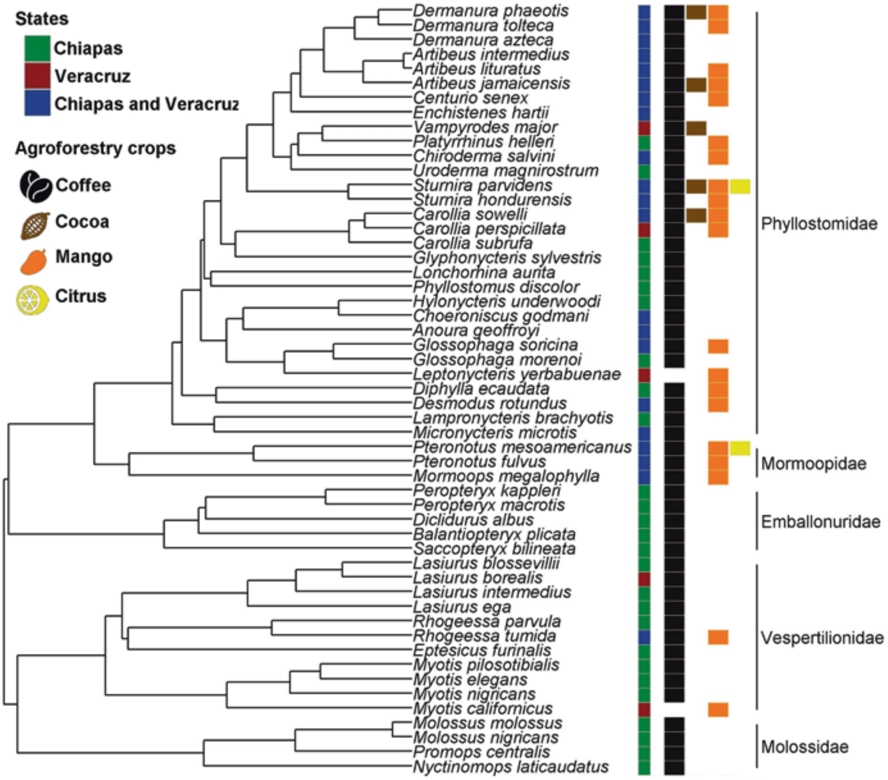

Fig. 16.2 Representation of bat species in agroecosystems studies of Mexico. (Information was obtained through a literature search. Phylogeny based on Shi and Rabosky (2015))

Most studies assessing the response of bat assemblages to agroecosystems in Mexico have focused on only one element of biodiversity, species richness. However, it is crucial to determine community responses at different levels. For example, (Saldaña-Vázquez et al. 2013) compared population structure of the highland yellow-shouldered bat (*Sturnira hondurensis*) in coffee agroecosystems in Veracruz finding that bat populations within forest fragments had a higher female ratio than coffee patches, while the percentage of reproductive females was similar between habitats. These trends may be due to greater food resources within forest habitats, which also promote more stable populations within the natural patches (Le Galliard et al. 2005).

16.4.2 Birds

Birds are one of the best-known groups of fauna and have been widely used to assess the response of biodiversity to agroecosystems. It is estimated that around a third of the world's bird species occasionally use agroecosystems (Sekercioglu et al.

2007), contributing to multiple ecosystem services, as well as with some disservices (Whelan et al. 2015). Mexico is home to around 1130 species of birds (~10% of the world total richness), occupying tenth place of bird species diversity in the world (see also Chap. 9, this volume). In addition, along with mammals, birds have been one of the most studied group of vertebrates in agroecosystems in Mexico (Escobar-Ibáñez unpublished), registering up to 180 species in the agroecosystems in the southern region of the country (Estrada et al. 1997).

As mentioned earlier, the presence of biodiversity in agroecosystems can be highly variable and is determined by factors related to the characteristics of the crop, the intensity of management, and the surrounding conditions (Tscharntke et al. 2008). In the case of birds, the structural complexity of the vegetation within the plots plays a fundamental role in their diversity (Gordon et al. 2007). In general, a decrease in species richness is observed when comparing tree crops with shrub or herbaceous crops (Estrada et al. 1997; MacGregor-Fors and Schondube 2011), or between the same crop type but with less plant cover (Tejeda-Cruz and Sutherland 2004; Tejeda-Cruz and Gordon 2008; Philpott and Bichier 2012). This decrease in bird diversity may result in lower predation of insects, thus reducing pest control services and causing a greater impact on their productivity (Perfecto et al. 2004). In this sense, some studies have found a decrease of functional diversity (i.e., ecological functions) under the presence of agriculture (Tinajero et al. 2017) and with the reduction of forest cover within the crops (Philpott and Bichier 2012), although others report up to 91% of functional similarity between some crops and natural systems (MacGregor-Fors and Schondube 2011).

Landscape characteristics, such as distance to vegetation fragments, are decisive for the diversity of birds within agroecosystems (Estrada et al. 1997). Furthermore, some landscape elements such as live fences or vegetation on the margins of crops can facilitate the movement of species between land use covers (Ramírez-Albores 2010). However, this depends on several factors of these elements, such as the width and number of tree species as well as, vertical complexity (Zuria and Gates 2012). On the other hand, it has been observed that the presence of trees within crops may be of greater relevance for species richness than the size of the plot itself, reaching an increase of the number of species by up to 49% (Mellink et al. 2017), although this may depend on the region and the agroecosystem analyzed (see Ramírez-Albores 2013).

It should be noted that agroecosystems represent important sites for groups of bird species such as Neotropical migrants (Estrada et al. 1993b; Van Der Wal et al. 2012). However, despite this and the fact that agroecosystems can host around 40% of the species in a region (González-Medina et al. 2015; Mellink et al. 2016), it is important to consider that they generally do not have the same conservation value as natural systems. This is because many specialist forest species are not present in crops, indicating that conservation of original forest fragments should be a priority (Gordon et al. 2007; Tejeda-Cruz and Gordon 2008; Alvarez-Alvarez et al. 2018).

16.4.3 Arthropods

During the last decade, a vast array of reports highlighting a strong decline of arthropods have been published (Dirzo et al. 2014; Sánchez-Bayo and Wyckhuys 2019; Janzen and Hallwachs 2019; Wagner et al. 2021). The main drivers of this decline and the synergies that they can display are related to the effects of global change and may vary between regions (Wagner et al. 2021). Contrary to other groups, arthropods show deeper gaps in terms of the evaluation of their response to agroecosystems. For example, it is estimated that only about ~20% of the total estimated arthropod species in the world have been described (Stork 2018), while for Mexico the number of species recorded is estimated to be 5.23% (47,853 spp.; CONABIO 2009). Moreover, there is a notable bias to the study of few orders of arthropods (i.e., Coleoptera, Lepidoptera, Diptera, Hymenoptera, Odonata; Wagner et al. 2021), and several orders remain markedly understudied in Mexico (see Chap. 3, this volume).

Studies that have evaluated the influence of agricultural practices on arthropod diversity have found contrasting results, since the responses of species depend on the group of arthropods and the crop under study (i.e., surrounding weeds and foliar tissue in mangos) (Cabrera-Mireles et al. 2011). For example, some studies have found that with greater intensification there has been both a decrease in the richness and abundance of Lepidoptera larvae (Sosa-Aranda et al. 2018), but an increase in spider diversity (Marín and Perfecto 2013). Regarding insect pollinators, Briggs et al. (2013) found differences in abundance, estimated richness, and composition of Euglosine bees (Hymenoptera: Apidae: Euglossini) between monospecific and diverse shade coffee agroecosystems. Furthermore, they found that polyculture coffee plantations had a similar composition of these bees when compared to natural forests, although the abundance of bees decreased by half in monocultures when compared with polycultures.

Multiple species of arthropods have been recorded in Mexico whose characteristics and habitat requirements make them potential crop pests. A clear example is the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae), which is native from the Americas and is able to feed on 353 different host plant species (Montezano et al. 2018). However, this species is especially destructive in monocultures such as maize, whereby the pest can cause up to 45% losses in crops of some regions of Mexico (Blanco et al. 2014). Similarly, *Helicoverpa zea* (Lepidoptera: Noctuidae) is a polyphagous species which can feed on 100 plant species like soy, corn, and cotton (Karpinski et al. 2014), causing a loss of up to 23% of the production of maize in Mexico (Blanco et al. 2014). However, when this species is exposed to the push and pull system (polycultures) combined with pigeon pea, its damage was attenuated reducing the amount of eggs laid, the number of larvae per plant, and the damage in fruiting bodies in cotton (Jadhav et al. 2008).

16.5 Effects of Agriculture on Ecosystem Services Provided by Wildlife in Mexico

Another way to understand and measure the impact of agricultural activity in Mexico over the natural ecosystems is through the comparison of changes in biodiversity and their impact on ecosystem functioning and services. Currently, it is recognized that the ecological functioning of ecosystems and their capacities to provide ecosystem services depends on biodiversity (Hooper et al. 2012; Dirzo et al. 2014). In Mexico, there is a considerable lack of information regarding the effects of agricultural activities on the ecosystem services provided by fauna, which contrasts with taxonomic groups such as plants (Arias-González et al. 2016). Among the few studies that compare the role of fauna diversity in the functioning of ecosystems and agroecosystems shows that here are negative results in terms of ecosystem services. On the one hand, the seed dispersal service provided by phyllostomid bats decreased in shade coffee plantations compared to that recorder in montane cloud forests (Hernández-Montero et al. 2015). This reduction is associated with the low abundance of the most common bat species of the bat communities. While in the case of invertebrates such as termites (Hexapoda, Isoptera), Mendez and Equihua (2001) found that monocultures of sorghum were highly infested by termites compared to sorghum with the legume *Dolichus* sp. used as intercrop. These few examples show that ecological functions in agroecosystems are strongly related with the abundance of animal species. Therefore, it is urgent to know other ecosystem processes that are regulated by fauna diversity in Mexican agroecosystems.

16.5.1 Native Fauna and Ecosystem Services in Agroecosystems

Despite the lack of studies comparing the faunal diversity and the provision of ecosystem services, there is a wide variety of studies that have evaluated the role of the native fauna of Mexico as providers of ecosystem services in agroecosystems. The Mexican native fauna is an essential provider of pollination services, where 85% of the crop's species depend on animal pollination (Ashworth et al. 2009; see also Chap. 24, this volume). For example, when coffee flowers are pollinated by native bees, they produce more seeds and fruits than when they are pollinated by domesticated exotic bees (Badano and Vergara 2011). Likewise, native flies and wasps are important pollinators of crops such as avocado (*Persea americana*) and squash (*Cucurbita moschata*; Delgado-Carrillo et al. 2018; Dymond et al. 2021). Vertebrates are also important pollinators of plant species of economic and cultural importance. For example, nectarivorous bats are the most efficient pollinators in plantations of pitaya (*Stenocereus queretaroensis*) and *Agave* spp. (Trejo-Salazar et al. 2016; Tremlett et al. 2020).

In addition to pollination services, the native fauna also provides insect population suppression services in agroecosystems. It has been shown that both birds and bats, individually or together, reduce the biomass of small (<2 mm) and large (>3 mm) arthropods in coffee plantations in Chiapas, Mexico (Williams-Guillén et al. 2008). Another example of the suppression of insect populations in agroecosystems comes from the ant *Azteca sericeasur* and lizards of the genus *Anolis*. Both are controllers of the larva of the coffee berry borer, *Hypothenemus hampei* (Ferrari; Coleoptera: Curculionidae), which damages coffee fruits (Morris et al. 2015; Monagan et al. 2017). The reintegration of organic matter by soil microfauna is another important ecosystem service, and soil fauna has been documented to be more diverse in forests when compared to agroecosystems (Marquez et al. 2018). However, we found no studies assessing the impact of the decrease in the diversity of soil microorganisms on the reintegration of organic matter into the soil of agroecosystems.

Other ecosystem services reported to be provided by the fauna in the agroecosystems of Mexico are food, ornamental, and recreational, which are not material ecosystem services. It has been documented that 148 animal species provide these services, 20% being use as food and 34% as ornamental and recreational (Moreno-Calles et al. 2016). Finally, animals can provide fertilizer for agroecosystems. For example, bat guano is used as fertilizer for some Mexican crops (Torres-Jiménez et al. 2020). The role of native fauna in the provision of ecosystem services in agroecosystems in Mexico is broad. However, we still do not know the factors that can increase the provision of these services, nor the threats for their disruption.

16.6 Agroecosystems as Complementary Tools for Biodiversity Conservation: From Protected Areas to an Integral Management of Anthropized Habitat Matrices

Protected areas (PAs) are the main strategy for the conservation of biodiversity worldwide, but they face many challenges that hinder their proper functioning and therefore efficient conservation (Rodrigues et al. 2004; Naughton-Treves et al. 2005; Joppa and Pfaff 2011; Watson et al. 2014; Visconti et al. 2019). Some authors point out that it is essential that 30% of the Earth's surface be conserved and that 20% be used as sites to stabilize climate change (Dinerstein et al. 2019), which would undoubtedly allow progress towards the goal of reducing species extinction. However, others suggest that it is also essential to reduce the impacts of activities outside protected areas because they directly influence processes within them (Laurance et al. 2012). Thus, the focus of a new conservation paradigm should be to create high-quality agricultural matrices to allow the movement and maintenance of species among fragments to maintain or promote meta-population dynamics (Vandermeer and Perfecto 2007).

Agricultural landscapes have been traditionally viewed as an impermeable habitat isolated from islands of natural covers and incompatible with biodiversity conservation (Tscharntke et al. 2005; Mendenhall et al. 2014). However, it is important to consider the dynamics of animal assemblages across the different land use covers across the matrix to develop better management strategies at the landscape level (Mendenhall et al. 2014). With the examples of studies analyzed within the chapter, it has been shown that adequately managed agroecosystems can harbor a good proportion of biodiversity and ecosystem services of several taxa. Agroecosystems are becoming important refuges as natural areas decrease and may serve as important sources of population exchange among areas with different levels of disturbance. They can serve also as steppingstones to improve landscape connectivity and help with dispersal and migration of several species (Tscharntke et al. 2005; Vandermeer and Perfecto 2007; Perfecto and Vandermeer 2008; Cortés-Delgado and Sosa 2014).

Agroecosystems are usually viewed as simplified systems assuming that species have single one-way interactions, but the reality is that species interactions are complex even in "simple" agricultural habitats (Perfecto and Vandermeer 2015). It is important to understand the different levels of species interactions and the modularity of those interactions to incorporate them in management practices and pest control plans (Perfecto and Vandermeer 2015). For example, biological control plans should consider the importance of the species niches and how they are integrated into the agroecosystem (Tscharntke et al. 2005). To develop agricultural management plans, it is also important to determine what we are interested in managing and conserving, species richness (as a surrogate of biodiversity), abundances, system functionality, or ecosystem services.

There are key ecosystem services for agroecosystems that need important consideration in the development of management plans. For example, maintenance of crops genetic diversity, pollination, pest suppression, nutrient cycling, water regulation, and soil retention, among others (Swift et al. 2004). However, most management is done to substitute those natural services by human labor, external sources of energy, or human-made products, which translate into unnecessary expenses of money, human energy, time, and environmental pollution. For example, 75% of agroecosystems depend on pollination by wildlife, and it is estimated that this service would cost approximately $165 billion dollars per year worldwide in the absence of natural pollination (Gallai et al. 2009). Human management of systems is usually more simplified than the natural functioning of agroecosystems, and often substitutes for some functions such as natural pest control for agrochemicals which can damage other important functions like animal-mediated pollination or nutrient turnover (Swift et al. 2004).

It is important to recognize that not all agroecosystems are "biodiversity friendly," indeed, they must maintain certain conditions that promote and maintain that biodiversity. The conservation value of agroecosystems depends on their management intensities, as different management schemes create different microhabitats, where high-management intensity usually relates to low biodiversity and more homogeneous habitat structures (Perfecto et al. 2003; Somarriba et al. 2004;

Williams-Guillén and Perfecto 2010; Castro-Luna and Galindo-González 2012). Sometimes, an increase in the intensity of management within agroecosystems is not necessarily related to a reduction in species richness but can also reduce species abundances (Williams-Guillén and Perfecto 2010; Castro-Luna and Galindo-González 2012) or change the composition of the community. Mixed plantations with complex understory and a variety of plant richness and structure can provide a good habitat for many species since they provide diverse food resources and shelter (Estrada et al. 1993b, 2006; Pineda et al. 2005; Numa et al. 2005).

There are several efforts to reduce the impact of pesticides and fertilizers over the environment and the native biodiversity in Mexico (Table 16.1). These efforts have been mostly related with a consumer demand to have healthier and environmentally friendly products and to comply with export regulations for pesticide residues. Organic farms maintain more similarity to semi-natural habitats because their lower input of agrochemicals can translate to more food sources (like insects) for some species and better water quality for species associated with water bodies (like some *Myotis* bat species) (Racey et al. 1998; Wickramasinghe et al. 2003, 2004; Pineda et al. 2005). For example, a higher species richness (up to 61%) and foraging activity (up to 84%) of bats have been documented in organic versus conventional farms in Britain (Wickramasinghe et al. 2003). Other studies about poly-specific and organic coffee plantations, especially those growing under shade, have shown similar bat assemblages when compared to natural surrounding habitats (Pineda et al. 2005; García-Estrada et al. 2006).

There is a popular discussion around two strategies to mediate the production of food with the conservation of biodiversity: land sharing versus land sparing (Phalan et al. 2011; Hulme et al. 2013; Gilroy et al. 2014; Williams et al. 2017). Land sharing refers to lowering agricultural yield to favor biodiversity in agricultural areas, while land sparing favors high-agricultural yields in exchange for restoring/conserving non-farmed habitats. Studies have encountered different results that relate to the metrics used to assess biodiversity, where most studies only considered species richness without considering individual populations (Williams et al. 2017). A study done on Mexico, specifically with livestock practices in the Yucatan Peninsula, found that the strategy of land sparing favored richer and more abundant animal communities of birds, beetles, and tree species (Williams et al. 2017). Landscapes with land-sharing strategies benefit species that are tolerant to disturbance since "forest" species can only survive in the few remnants of conserved habitats (Williams et al. 2017). However, the effectiveness of land sparing also depends on the strict conservation, management, and restoration of the remaining natural areas (Williams et al. 2017). This trade-off lies in a compensation of biodiversity loss caused by intensive management, by a gain in biodiversity by keeping landscape complexity and natural habitats (Tscharntke et al. 2005).

Table 16.1 Agriculture certifications with environmental criteria most used in Mexico in the productive sector. The name of the institutions and certificates are in the original language (Spanish)

Institution	Certification	Description	Website information
Pronatura	Sello de biodiversidad	Distinctive granted by Pronatura-Veracruz, to products from areas voluntarily destined for conservation in Veracruz, (Mexico) to stimulate the conservation of ecosystems and their biodiversity	https://pronaturaveracruz.org/sellodebiodiversidad/
Control union certifications	México orgánico	It is the national distinctive of organic products as a result of the official certification and accreditation processes	https://certifications.controlunion.com/es/certification-programs/certification-programs/organic-sagarpa-mexico
Colectivos y mercados agroecológicos locales	Certificación Orgánica Participativa: SPG o SCOP	Participatory certification is a collective process between producers, consumers, and other actors, which guarantees the organic and healthy quality of local products, generated on a small scale, based on relationships of trust and that promote commitments to health, ecology, equity, and environmental certainty (Mexican Network of Local Organic Markets and "Tianguis"). It does not currently have a distinctive seal or general logo	https://www.gob.mx/senasica/documentos/certificacion-organica-participativa?state=published
Smithosonian Migratory Bird Center (SMBC)	Bird friendly	Certification of 100% organic coffee grown under shade and produced under agroforestry processes, which also promotes the conservation of habitats for migratory birds	https://es.global.si.edu/success-stories/smithsonian-migratory-bird-center%E2%80%99s-bird-friendly%C2%AE-coffee-program-protects-migratory
Tequila interchange project	Bat friendly	Promote and incorporate bat friendly practices in the agave management and spirit production derived from these plants by allowing a 5% of the agave population to flower to ensure there is food for the nectar feeding bats of the *Leptonycteris* genre, and in consequence we have pollination	https://www.batfriendly.org/index.php/

Rain forest alliance	Rain forest alliance	The certificate shows traceability towards sustainable processes, highlighting the relationships between forest communities that invest in sustainability processes, committed companies and responsible consumers. It is the result of a program that promotes sustainable agriculture to protect nature and improve the quality of life of farmers, spreading shared responsibility throughout the supply chain. Products: coffee, cocoa, bananas, teas, ferns and flowers	https://www.rainforest-alliance.org/business/es/tag/2020-programa-de-certificacion/
Network of Small Bio Producers	Small producer system	Families of small producers that produce without chemicals and that promote the economy of their communities. This seal is present in different countries	https://spp.coop
Flo-Cert	Fair trade	Trade certification that allows visibility and recognition of products with fair social and environmental practices. They promote sustainable processes throughout the chain. It is in close connection with Fair Trade	https://www.flocert.net/es/

(continued)

Table 16.1 (continued)

Institution	Certification	Description	Website information
Private institutions in Mexico	Agricert México	Certification bodies approved for the certification of organic products in Mexico, endorsed by SENASICA and SAGARPA	https://www.agricert.mx/
	OCIA		http://www.ocia.org
	TILTH		https://esp.tilth.org/certificacion/mexico/
	Ceres-cert		http://www.ceres-cert.com
	Mayacert		http://www.mayacert.bio
	México Cert		https://mexicocert.com
	CCOF Organic		https://www.ccof.org
	Kira México		https://www.kiwa.com/lat/es/acerca-de-kiwa
	Pamfa A.C.		https://www.pamfa.com.mx
	Control Union certificacions		https://certifications.controlunion.com/en
	Ecocert		https://www.ecocert.com/es
	Auditig Ops		https://primusauditingops.com/index.php/es/
	Agricert México		http://www.agricert.mx
	Metrocert		http://www.metrocert.com
	imocert		https://imocert.bio
	Certimex		https://certimexsc.com/cmx/

This table was made by Rocío García-Bustamante

16.7 Concluding Remarks and Future Directions

In many regions of the world, information about the impacts of agroecosystems on biodiversity combined with an evaluation of the efficiency of agricultural production have served as a starting point for the development of public policies for planning the expansion and regulation of agricultural practices. Although the positive impact of these strategies for the efficient conservation of biodiversity appears to be currently limited and costly, decades of information are available that could allow governments to map out the best routes to reduce impacts in the coming years (Lambert et al. 2007; Batáry et al. 2015).

Information about the native fauna in agroecosystems in Mexico is biased towards perennial crops such as shade coffee and cacao, as well as the study of birds and mammals (i.e., bats; Escobar-Ibáñez unpublished). It is essential to generate information from other biological groups, as well as from the most widespread crops in the country and from those that are expanding in different regions (e.g., agaves, avocado, and walnut). This will allow us to make informed decisions concerning agricultural management to reduce its impacts on the country's biodiversity.

To have a broader picture of the impacts of agroecosystems on fauna, it is also essential to implement long-term studies to evaluate and monitor population trends, since short-term studies can mask relevant phenomena such as local extinctions (Kleijn et al. 2011; Şekercioglu et al. 2019). In addition, it is important to incorporate other measures of diversity, besides species richness and abundance, such as phylogenetic or functional diversities (Gill et al. 2001). Furthermore, integrative analysis such as multitrophic approach, multi taxa comparisons, community functionality, and ecosystem services analyses are also necessary to improve our understanding of the dynamics of the species involved in the high-input agroecosystems but also in the traditional systems such as "milpas" (corn, bean and other polycultures) and "traspatios" (backyards).

In Mexico, special attention should be paid to the threats posed by agroecosystems to endemic or threatened species, since it is known that ~20% of the distribution of endemic and threatened vertebrates overlaps with the presence of agroecosystems (Mendoza-Ponce et al. 2020). In this sense, specific information on the habitat requirements of the species is necessary, as this could serve to establish guidelines on the type of agroecosystems that can be implemented in sites of relevance for threatened species. In fact, in some regions of the country, crop expansion is occurring in sites that were previously occupied by pastures for livestock (Bonilla-Moheno and Aide 2020), which should be prioritized in regions where patches of large native vegetation remain due to the higher habitat quality that crops represents for wildlife (Escobar-Ibáñez unpublished).

Finally, most of the agricultural production systems in Mexico are organized in *ejidos* and backyards plots, which are especially dominant in the southern region of the country. These small-scale agroecosystems have not been evaluated enough by researchers in terms of quantitative ecology, but some studies suggest that these systems shelter a high biodiversity and have the potential to act as steppingstones that are needed by species to connect and allow dispersal among monocultures, polycultures, and natural remnants (Guarneros-Zarandona et al. 2014). For these reasons, it is critical to develop more comparative studies on biodiversity in these transitional agroecosystems, to improve our understanding of the tradeoffs between land sharing and land sparing, and to better integrate ecological solutions such as integrated pest management (IPM) into agricultural practices.

Acknowledgments The authors would like to thank Natalia Mesa-Sierra for making Fig. 16.1, and Jorge D. Carballo-Morales for made Fig. 16.2.

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Chapter 17
The Amphibians of the Mexican Montane Cloud Forest

Angel F. Soto-Pozos, M. Delia Basanta, Mirna G. García-Castillo, and Gabriela Parra-Olea

Contents

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/978-3-031-17277-9_17.

A. F. Soto-Pozos · G. Parra-Olea (✉)
Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria,
Coyoacán, Ciudad de México, México
e-mail: gparra@ib.unam.mx

M. D. Basanta
Centro de Ciencias Genómicas, Universidad Nacional Autónoma de México,
Cuernavaca, Morelos, México

Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria,
Coyoacán, Ciudad de México, México

M. G. García-Castillo
Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria,
Coyoacán, Ciudad de México, México

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_17

17.1 The Mexican Montane Cloud Forest

Mexico's Montane Cloud Forest (MCF) is one of the scarcest terrestrial ecosystems in the country, whose cloudy landscapes evoke mystery and mysticism. This forest has received a great number of denominations, which reflects the ecological and physiognomic heterogeneity of its plant communities in different regions of the country (Gual-Díaz and González-Medrano 2014). Although the name "Montane Cloud Forest"'is typically used for the Atlantic Slope region, in this chapter we use this term to also encompass areas in the Pacific region called *Bosque Mesófilo de Montaña* by Rzedowski (1978), under the understanding that dense fog is a constant feature and encompasses all forests of this type (Rzedowski 2006; Fig. 17.1).

Fig. 17.1 Photographs of Montane Cloud Forest in Mexico. Pristine forest (**a**–**e**) from El Triunfo, Chiapas and anthropized forest (**f**, **g**) from Zongolica, Veracruz. (Photo credit: Ángel F. Soto-Pozos (**a**, **c**, **f**), Omar Becerra Soria (**b**, **d**, **e**), and Mirna G. García-Castillo (**g**))

17.1.1 Environments of the MCF

In Mexico, the areas with the atmospheric humidity that this forest requires to developing are restricted, generally to the windward of mountain massifs. Here, they receive the humid and warm air from the sea, in glens protected from the desiccating effect of the wind and the sun, exclusively in certain elevational ranges (Gual-Díaz and González-Medrano 2014; Gual-Díaz and Rendón-Correa 2017). Typically, the MCF in Mexico occurs between 1500 and 2500 m altitude (Rzedowski 2006), however, it has also been recorded as low as 400 m and as high as 3200 m altitude (Rzedowski 2006; González-Espinosa et al. 2012). These extreme distributions are explained by the fact that these plant communities develop where they find favorable conditions of temperature and humidity, which can vary depending on topographical effects, due to the physical conformation of the mountain systems (Grubb 1971).

This forest is characterized by a high-environmental humidity, ranging from 48% in the state of Mexico to 98% in the state of Oaxaca. Rainfall usually ranges between 1000 and 3000 mm per year, but in some regions of Oaxaca it reaches up to 6000 mm per year (Gual-Díaz and Rendón-Correa 2017). This precipitation is significantly augmented by the interception through condensation of cloud cover by the forest canopy, often called "horizontal precipitation" (Hamilton 1995). Furthermore, cool temperatures characterize this forest, from about 12 °C to a maximum of 23 °C (Rzedowski 2006).

17.1.2 MCF Distribution

The MCF in Mexico is found on approximately 1% of the surface of the national territory (CONABIO 2010); however, occupying small areas, these forests are found in 18 states of the country (INEGI 2016). The main areas of MCF are distributed from south of San Luis Potosí through the windward side of the Sierra Madre Oriental, to the center of Veracruz, and southwest into the mountains of northeastern Oaxaca. Important MCFs are also found in the Chimalapas region of Oaxaca, the northern highlands of Chiapas, and the Sierra Madre of Chiapas. Smaller and more dispersed MCFs are found in the states of Guerrero, Tamaulipas, Nuevo León, and along the Sierra Madre Occidental (Gual-Díaz and González-Medrano 2014). Therefore, this forest has a naturally discontinuous and fragmented distribution, like a system of archipelagos in which each "island" inhabits a high proportion of endemic species, which lies in a high-species turnover (Peterson et al. 1993). This has implications in terms of the high biodiversity that the MCF is capable to host in the relatively small areas that it occupies.

The current distribution and extent of the MCF are considered natural and anthropologically residual. It is estimated that this forest originated before the Pleistocene, more than 2.6 million years ago, therefore, it was probably subject to glacial and interglacial periods that caused expansions and recurrent retractions of its extension, processes that in turn affected the fauna associated with this forest (Toledo 1982). Later, during the Holocene, approximately 10,000–11,000 years ago, the conditions of its recent distribution settled (Toledo 1982). Currently, the extension of MCF has been strongly affected by the influence of anthropological activities, so in recent decades its distribution has been further retracted, and the fragmentation and isolation of its remnants have increased (Figueroa-Rangel et al. 2012).

17.1.3 MCF Plant Composition

The MCF in Mexico is composed of elements of both the Holarctic and Neotropical realms. Due to its biogeographic history, it was consolidated as a transitional habitat between the temperate and tropical forests of America (Rzedowski 1978). It shares elements with forests of North America, Europe, and East Asia, apparently since the Tertiary period, more than 2.6 million years ago (Rzedowski and Palacios-Chávez 1977). Then, there was an influx of Neotropical elements by both the land bridge with South America and by previous migrations through islands with the appropriate ecological conditions (Gentry 1982). As a result of these events, the very particular composition of the MCF is explained by the mixture of species with Holarctic affinities that occupy mainly the canopy of the forest, and the neotropical contribution that occupies the sub-canopy and the understory (Rzedowski 1978). In these forests, the exuberant epiphytic component of mosses, ferns, orchids, and bromeliads has a higher diversity and endemicity than other ecosystems (Fig. 17.1a–e; Rzedowski 1978; Challenger 1998; Gual-Díaz and González-Medrano 2014). The complex plant structure and physiognomy of the MCF have also allowed it to host a high diversity of animal species and, in some cases, provide exclusive habitats for some of them.

17.2 Diversity

The MCF highlights among the rest of the terrestrial ecosystems from Mexico by its high diversity of different biological groups. It is the most diverse habitat in Mexico in terms of mammals, with more than 50% of the country's total richness (González-Ruiz et al. 2014). For birds, it is home to 18% of the country's species (Navarro-Sigüenza et al. 2014), and it hosts 39 and 33% of the total richness of reptiles and amphibians, respectively (Flores-Villela and Navarro 1993). According to our updated data (Supplementary Material 17.1), 216 amphibian species occur in the Mexican's MCF which accounts for more than 50% of the total species number in the country. It is also notable that of these 216 species, more than 70% (152 spp.) are endemic to the country (Supplementary Material 17.1), and more than 100 of these species are exclusively found in the MCF (Flores-Villela and Navarro 1993;

Wake 1987). The MCF in Mexico may host up to 22 amphibian species in one square km (Fig. 17.2). The sites of highest amphibian richness (from 15 to 22 species) are located in forest patches in Veracruz, Oaxaca, and Chiapas (Fig. 17.2), while the lowest richness (one to three species) is observed mainly in northern states, such as Nayarit and Tamaulipas. Cruz-Elizalde et al. (2022) identified similar trends in amphibian species richness from the Mexican MCF; furthermore, they incorporated phylogenetic information by a taxonomic distinctiveness index, and found that the MCF from southern Mexico not only hosts the highest number of species, but also genera and families.

The MCF has been the stage for the radiation and speciation processes of tropical amphibians. In this habitat, several groups have found favorable environmental conditions, food resources, and a variety of high-humidity microhabitats provided by epiphytic plants (bromeliads), moss, trunks, rocks, ferns, orchids, and the leaf litter (Campbell and Frost 1993; Wake 1987). According to the richness distribution and phylogenetic species variability, amphibian diversification has been more conspicuous in MCFs from southern Mexico than in mountains from the north pacific, Sierra Madre Oriental, and Trans-Mexican Volcanic Belt, although it may be due to the subsampling in these last areas (Flores-Villela et al. 2005; Cruz-Elizalde et al. 2022). Among the amphibians that have been particularly successful at colonizing and diversifying in the MCF are the salamanders of the family Plethodontidae (the only salamanders family distributed in this forest), and frogs of the families Hylidae, Craugastoridae, and Eleutherodactylidae.

17.2.1 Plethodontid Salamanders

In terms of urodele amphibians (salamanders), only one group, the tribe Bolitoglossini of the family Plethodontidae, has adapted to tropical regions. However, their diversification has been of such magnitude that they represent more than 40% of the total number of salamanders in the world (AmphibiaWeb 2022; Frost 2021). The successful diversification and adaptive radiation of tropical salamanders occurred in the middle region of the Americas (Wake 1987; Wiens et al. 2007). Within this region, Mexico's forests have been important for the evolutionary processes of tropical salamanders, highlighting the role of MCFs, where the Plethodontidae family is the most diverse amphibian family with 35% of species representation (Supplementary Material 17.1, Fig. 17.3).

The life history of the plethodontid salamanders makes them common species of the MCF. High-ambient humidity and cool temperatures found in the MCF are physiologically optimal conditions for these salamanders because they have direct development and their reproduction depends entirely on environmental humidity (Wake and Lynch 1976). Some species have specialized in the use of specific microhabitats in the MCF, such as the use of bromeliads, which are a common habitat of the genera *Chiropterotriton* (Fig. 17.3c, d), *Nototriton*, and *Dendrotriton* (Fig. 17.3e; Rovito et al. 2012). These species, although distinct genera, have converged on

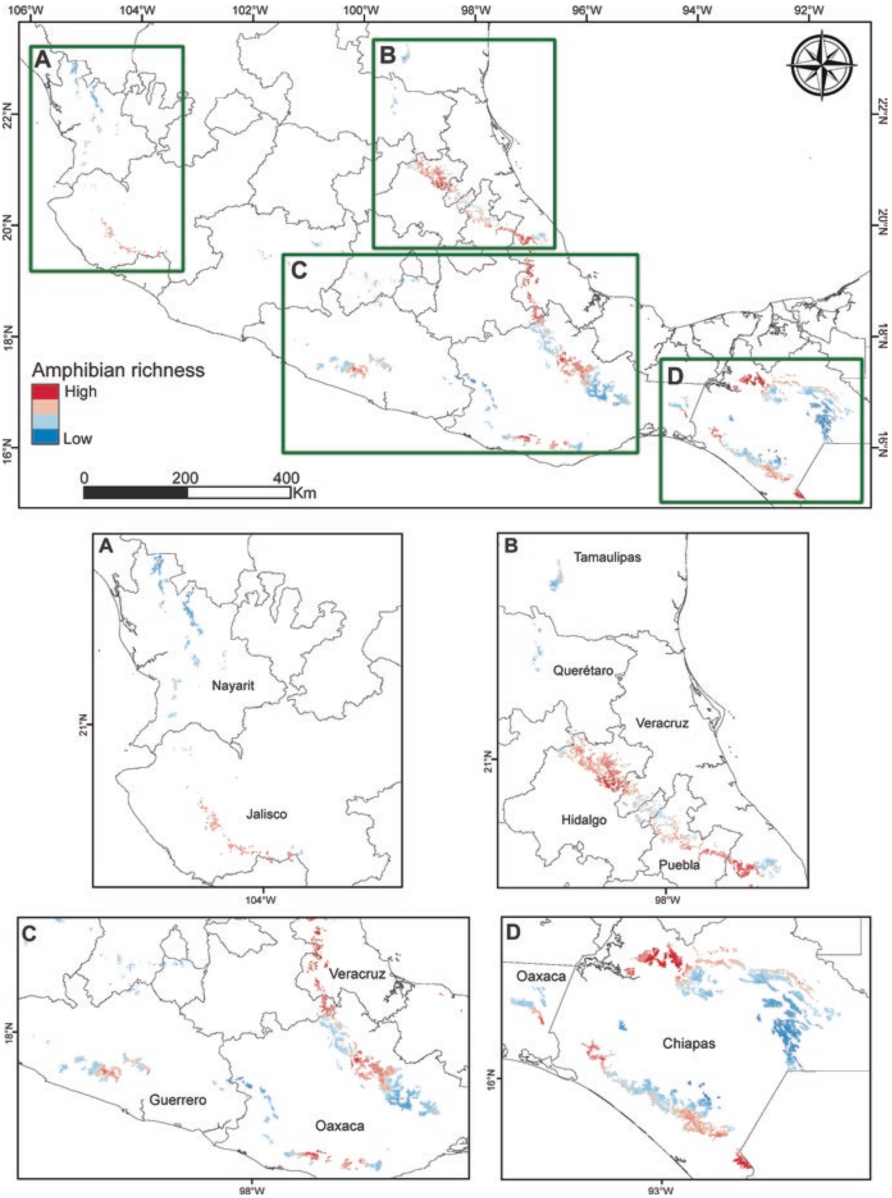

Fig. 17.2 Map of amphibian richness in Montane Cloud Forest of Mexico. Warm colors represent high-species richness and cold colors correspond to low-species richness. Rectangles show main richness areas; (**a**) Sierra Madre Occidental, (**b**) Sierra Madre Oriental, (**c**) Sierra Madre del Sur and Sierra Madre Oriental, and (**d**) Chiapas. (Amphibian distribution maps were obtained from IUCN (2020a) and literature)

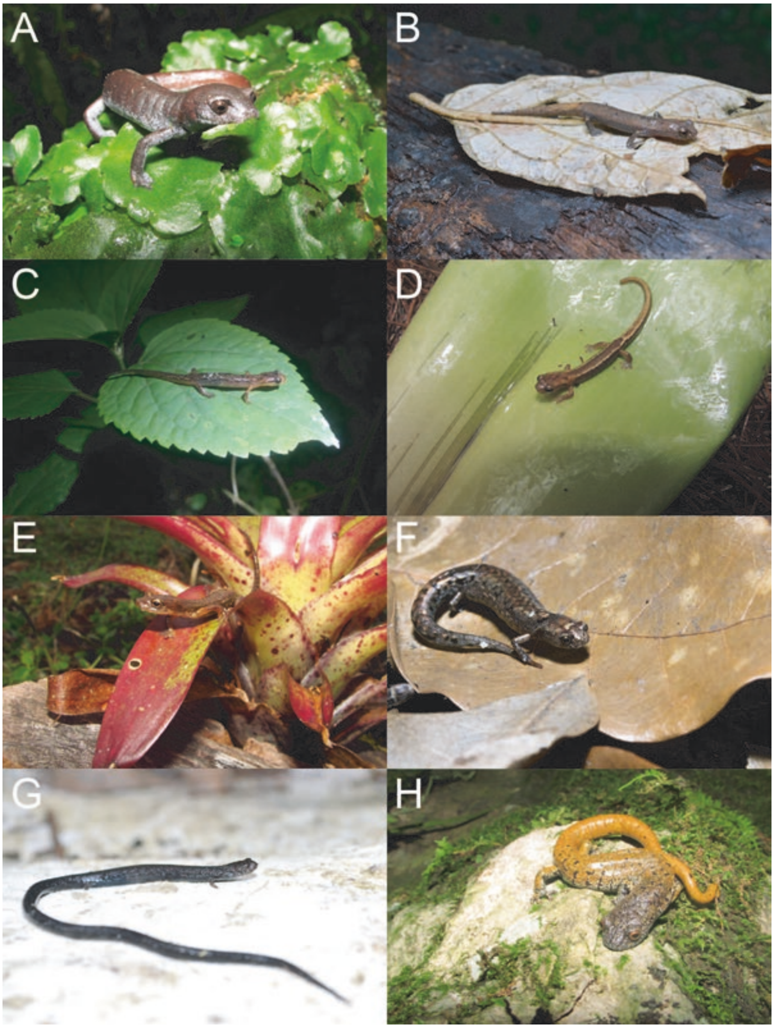

Fig. 17.3 Plethodontid salamanders from Montane Cloud Forest in Mexico. (**a**) *Aquiloeurycea cafetalera*, (**b**) *Bolitoglossa rufescens*, (**c**) *Chiropterotriton lavae*, (**d**) *Chiropterotriton nubilus*, (**e**) *Dendrotriton xolocalcae*, (**f**) *Parvimolge townsendi*, (**g**) *Pseudoeurycea lineola*, (**h**) *Pseudoeurycea granitum.* (Photo credit: Ángel F. Soto Pozos (**a**, **d**, **e**, **h**), Mirna G. García-Castillo (**c**), and M. Delia Basanta (**b**, **f**, **g**))

many shared adaptations to the bromeliad niche (Wake 1987). These specialized salamanders are characterized by a long, thin and prehensile tail, prominent eyes directed towards the front, long fingers developed for climbing, and slender and agile shapes (Wake and Lynch 1976; Wake 1987). On the other hand, species considered generalists are also found in bromeliads. For example, species of the genus *Bolitoglossa* (Fig. 17.3b) are found in a high proportion in this microhabitat (Wake and Lynch 1976; Wake 1987); a few species of the genus *Pseudoeurycea* (Taylor 1941; Shannon and Werler 1955; Fig. 17.3g, h) and *Thorius* (Wake 1987; Hanken and Wake 1998) are specialists of this microhabitat. In general, several species occasionally use these microhabitats, especially during the dry season (Hanken 1983; Wake 1987), even fossorial species, such as *Pseudoeurycea lineola* (Sandoval-Comte et al. 2022).

In addition to bromeliads, the MCF offers a variety of refuges for tropical salamanders, occupied by species of terrestrial and generalist habits. Moss, trunks, rocks, ferns, orchids, and leaf litter are occupied, sometimes by high densities of these species (Wake 1987). Therefore, the elevational range where the MCF is distributed is also where the greatest diversity of tropical salamanders is distributed, mainly between 1500 and 2500 m (Wake 1987; Kozak 2017).

17.2.2 Hylid Frogs

The family Hylidae is the most diverse frog family in the Mexican MCF with 49% of species present there (Supplementary Material 17.1, Fig. 17.4). There are two genera of hylid frogs endemic to Mexico (*Charadrahyla* and *Megastomatohyla*) whose species occur exclusively in the cloud forest (Fig. 17.4a, b, d). All the 10 described species of *Charadrahyla* are distributed in Hidalgo, Puebla, Veracruz, Guerrero, Oaxaca, and Chiapas in elevations between 1100 and 2200 m (Campbell et al. 2009), likewise, all four species of *Megastomatohyla* are distributed in the cloud forests of Veracruz and Oaxaca at elevations between 900 and 1800 m (Frost 2021). Another genus endemic to Mexico is the genus *Sarcohyla* (Fig. 17.4g) which consists of 26 species occurring from the northern states of Durango and Nayarit and San Luis Potosí, and in the southeast to Guerrero. All these species occur primarily in pristine habitats along streams in pine-oak woodlands, with 19 of the 26 species occurring exclusively in the cloud forest from 1500 to 3100 m elevation (IUCN 2020a). Finally, although the taxonomic limits of the genus *Ptychohyla* are in debate, the four species of *Ptychohyla* (Fig. 17.4e) that occur in Mexico are found in the cloud forests of Oaxaca, Puebla, Veracruz, Guerrero, and Chiapas between elevations of 600 and 2000 m (Frost 2021).

17.2.3 Robber Frogs

Species of the families Craugastoridae and Eleutherodatylidae (known as robber frogs) share the characteristic of having a direct development and are frequently found in the cloud forest. The family Craugastoridae (Fig. 17.5a–d) is the second most diverse frog family in the Mexican MCF with 21% of species representation (42 species of which 30 are endemic to Mexico, Amphibiaweb 2022; Supplementary

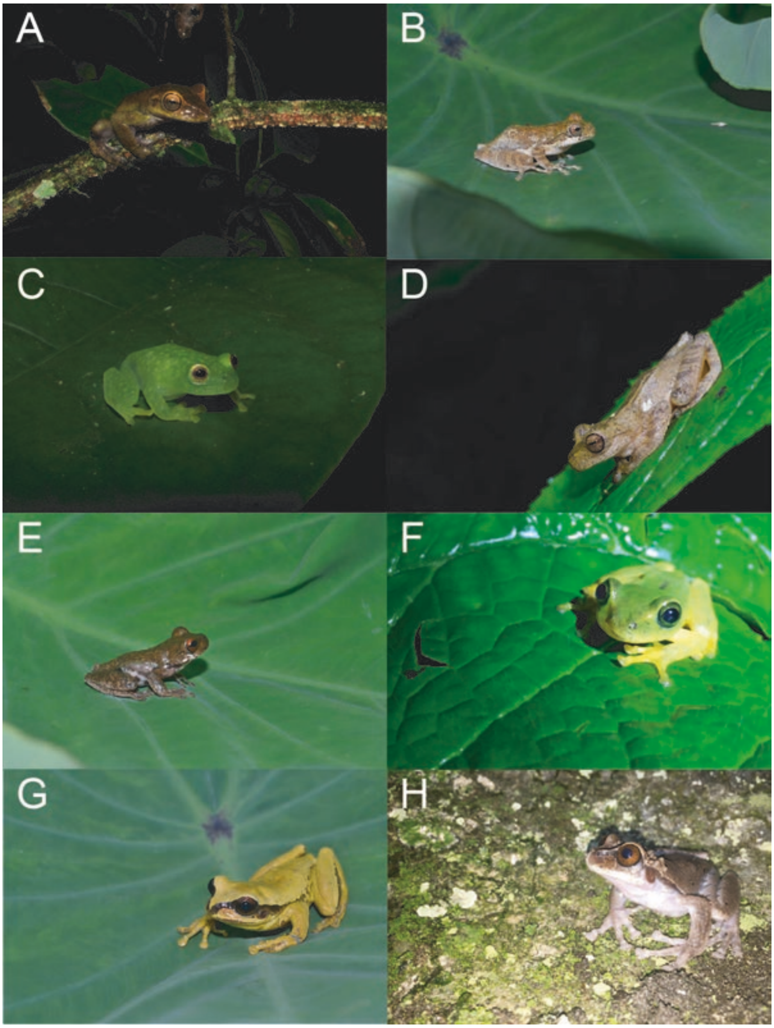

Fig. 17.4 Hylid frogs from Montane Cloud Forest in Mexico. (**a**) *Charadrahyla taeniopus*, (**b**) *Charadrahyla pinorum*, (**c**) *Hyalinobatrachium viridissimum*, (**d**) *Megastomatohyla mixomaculata*, (**e**) *Ptychohyla leonhardschultzei*, (**f**) *Rheohyla miotympanum*, (**g**) *Sarcohyla pentheter*, (**h**) *Triprion spinosus*. (Photo credit: Ángel F. Soto-Pozos (**a**, **c**, **f**, **h**), M. Delia Basanta (**b**, **e**, **g**), and Rene Ávalos Vela (**d**))

Material 17.1). The genus *Craugastor* is distributed throughout Mexico and 73% of its species are present over the entire elevational range of the MCFs of the country.

The third most diverse frog family in the Mexican MCF is Eleutherodatylidae (Fig. 17.5e–h) with 12% of species representation in this forest (16 species belonging to the genus *Eleutherodactylus*, of which 13 are endemic to Mexico; Supplementary Material 17.1). The genus *Eleutherodactylus* is represented by 43%

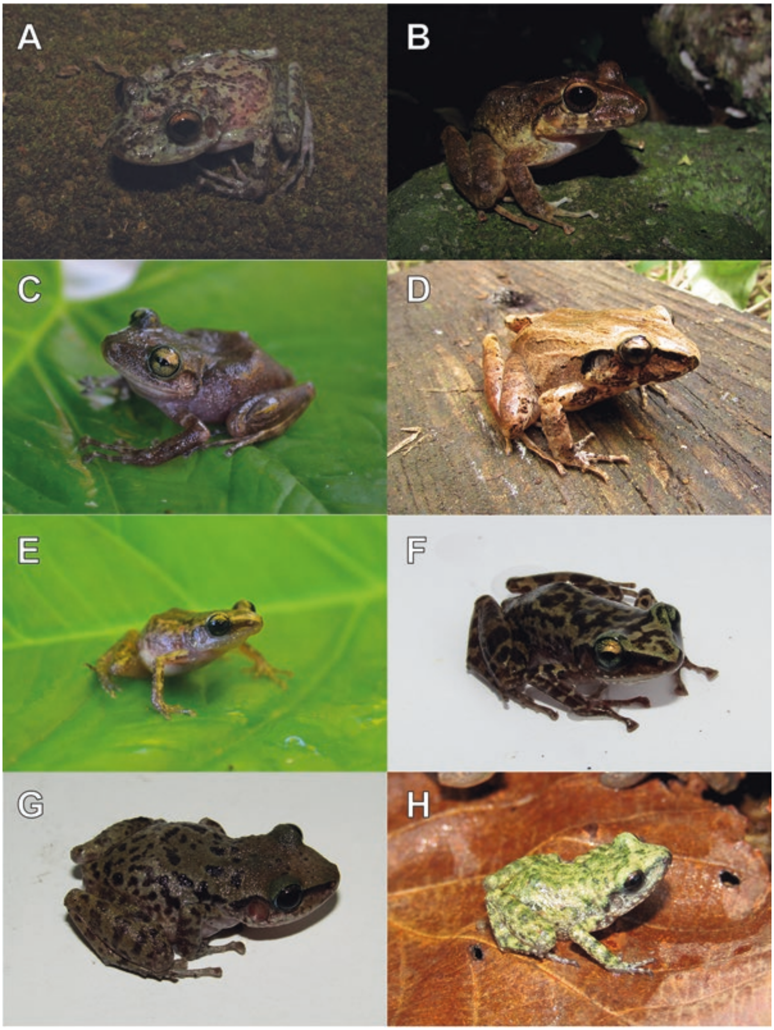

Fig. 17.5 Direct-developing frogs from Montane Cloud Forest. Family Craugastoridae; (**a**) *Craugastor alfredi*, (**b**) *C. berkenbuschii*, (**c**) *C. decoratus*, and (**d**) *C. rhodopis*. Family Eleutherodactylidae; (**e**) *Eleutherodactylus cystignatoides*, (**f**) *E. dennisi*, (**g**) *E. longipes*, and (**h**) *E. verrucipes*. (Photo credit: Ángel F. Soto-Pozos (**a**, **b**, **d**), M. Delia Basanta (**c**, **e**), and Raquel Hernández-Austria (**f**, **g**, **h**))

of its species in the MCF and one of the endemic species inhabits exclusively in this forest (*Eleutherodactylus verruculatus*, IUCN 2020b; Fig. 17.5h). Our knowledge about the diversity of these genera has recently increased; previous reviews considered Eleutherodactylidae as the fifth richest family in species of frogs in the cloud forest (Gual-Díaz and Mayer-Goyenechea 2014). In this sense, the increase in species descriptions (Hernández-Austria et al. 2022; Grünwald et al. 2018; Grünwald et al. 2021) have changed the status of this family and showed the underestimation of their diversity.

17.3 Conservation Status of the MCF

Estimating the current extent of the MCF is a complex task due to the rapid rate at which it is transformed and destined for anthropological uses. A current study from satellite images, cartographic and bibliographic compilation, and field verification (INEGI 2016) estimated an extent of 19,855 square km for cloud forest including secondary vegetation. The comparison of current areas with previous land use and vegetation maps from aerial photographs taken in 1968–1986 (INEGI 1997) indicates a cloud forest loss of 478 square km (including secondary vegetation; Fig. 17.6). The accelerated loss of this habitat during subsequent years has been continued, thus updated information on the extent and quality of the remnants of this forest are needed (Calderón-Aguilera et al. 2012).

At the global level, MCFs are considered of critical value for sustainable development, given their role in maintaining the hydrological cycle and as a reservoir for a large number of endemic species (Toledo-Aceves et al. 2011). These forests are widely valued for their water-regulating function, as well as for providing protection against landslides and soil erosion, carbon storage, climate regulation, and the vast diversity of floristic and faunal resources (Jardel-Peláez and Santiago-Pérez 2014). Mexico’s MCFs provide different types of resources that surrounding communities utilize although not always in a sustainable way. The cultural and socioeconomic conditions of these communities influence the anthropogenic pressure on forests and on the species that inhabit them (Toledo-Aceves et al. 2011).

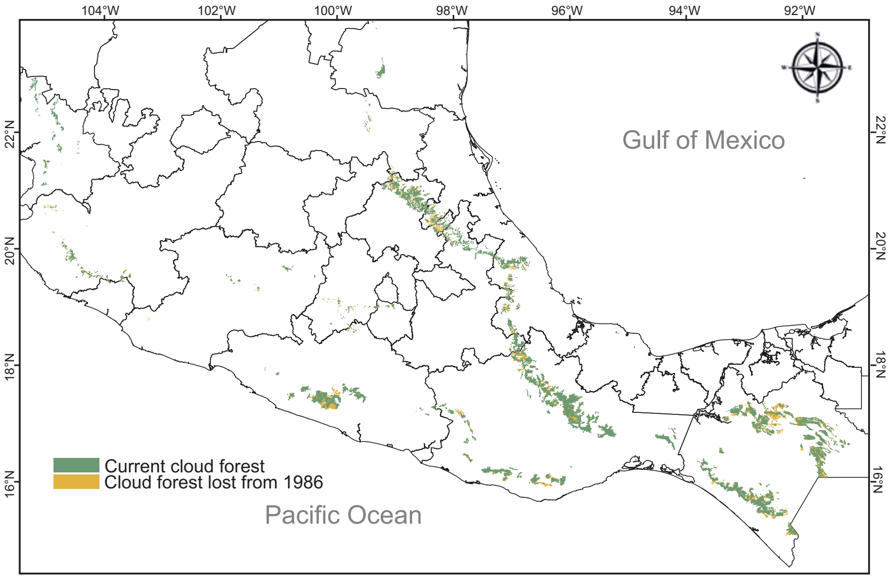

Fig. 17.6 Current and lost area distribution of Montane Cloud Forest in Mexico. Green polygons correspond to the current distribution and yellow to the distribution from 1986. (Maps extensions were obtained from INEGI (1997, 2016))

One of the main issues with MCF of Mexico is that its fragments are immersed in matrices with different anthropogenic impacts, with forests in different successional states, distinct anthropogenic land uses, and even urban areas, which complicate the evaluation of the threats it faces in each region. Moreover, the habitat conditions within each fragment of this forest are highly variable. Toledo-Aceves et al. (2011) recognized 42 priority subregions for conservation distributed in different points of the country, each weighted by different criteria that constitute threats or opportunities for its conservation. For example, the mountain region of northern Oaxaca has the largest continuous extension of MCFs in the country, however, it has subregions at high risk due to the high demand for agricultural soils by local communities (Toledo-Aceves et al. 2011). Also, the low level of social organization in this region is a factor that limits the opportunities for the implementation of conservation actions.

In other regions, such as the mountainous region of North-Central Chiapas, the MCF is severely fragmented and deteriorated, with a low-alpha diversity of species per fragment. However, at the regional level, it has remarkable beta diversity (Toledo-Aceves et al. 2011). Furthermore, its subregions stand out for the presence of endemic and threatened species. These are priority areas due to the threats posed by the high density of roads that intersect them, combined with a strong human presence. Conflicts in land tenure also complicate the scenario for implementing conservation measures. On the other hand, these subregions have points in their favor due to the amount of scientific research that has been produced in them (Toledo-Aceves et al. 2011).

The main threat to the MCF in Mexico lies in its eradication by the expansion of agricultural and livestock borders, deforestation (Fig. 17.1f, g), and the deterioration and affectation of its functionality by improper management. Despite slopes and terrains between 30° and 45°, human settlements have sought to locate themselves near these forests due to the resources they provide of water, food, forestry, and cultural use (Bubb et al. 2004; Gual-Díaz and González-Medrano 2014). This has led to the overexploitation of its resources with the loss of fertile soils that are quickly transformed into a variety of crops, among which the coffee stands out that has disproportionately displaced much of the MCF (Vandermeer and Perfecto 2007).

On the other hand, the modification of the habitats surrounding the MCF may also have an influence on its conservation. When lowland humid forests are converted to livestock pastures or intensive crops, this results in lower humidity of winds that form the clouds in the highlands (Gual-Díaz and Rendón-Correa 2017). This deforestation of lowlands has been correlated with more cloud-free days in adjacent MCFs (Lawton et al. 2001).

In general, anthropological activities have resulted in the reduction of the distribution of MCFs (Figueroa-Rangel et al. 2012), and conservative estimates consider that 60% of its tree component is in some degree of threat (González-Espinosa et al. 2012). These reductions and alterations of the forest community lead to a deterioration in the habitat that also causes the loss of species sensitive to these changes. In amphibian communities of the MCF, salamander species have been observed to be highly sensitive to land-use changes by both coffee plantations and pastures

(Soto-Pozos 2015). Due to all of the above, it is of vital importance that the constant monitoring of this type of communities warns us about the irreversible alterations to which we are subjecting this habitat.

17.4 Conservation Status of Amphibians from the Mexican MCF

According to a recent evaluation performed by the International Union for Conservation of Nature (IUCN 2020a), of the global number of amphibian species occurring in the MCF (216 spp.), 65% (139 spp.) are in some category of concern: 15% (33 spp.) are Vulnerable, 7% (14 spp.) are Near Threatened, 26% (57 spp.) are Endangered, and 17% (37 spp.) are Critically Endangered (CR). Of the 37 CR species, all but two (*Pseudoeurycea brunnata* and *P. goebeli*) are endemic to Mexico and all but four (*Craugastor taylori, Ecnomiohyla valancifer, Megastomatohyla pellita*, and *M. mixe*) are micro endemic to the MCF. A large component of the CR species are plethodontid salamanders (23 spp.) and frogs of the genus *Sarcohyla* (8 spp.). Among the main threats to the amphibian species are the habitat alteration due to anthropogenic activities of land use change, been the change to coffee plantations, the most common to the case of the MCFs (Toledo-Aceves et al. 2011).

Because of the close relationship between MCF and coffee plantations, Murrieta-Galindo et al. (2013) described the effect of different types of coffee plantations on amphibian communities in MCFs of central Veracruz. They found that the traditional coffee planting systems that maintain original tree species of the forest, and where coffee plants take the place of the understory and maintain a thick layer of leaf litter, can harbor an important level of diversity of amphibians like the original forest (Murrieta-Galindo et al. 2013). In general, coffee plantations, and especially traditional systems, are considered to be refuges for amphibian species, although a low richness of salamander species has been recorded in these habitats (Macip-Ríos and Casas-Andreu 2008; Murrieta-Galindo et al. 2013; Soto-Pozos 2015).

Plethodontid salamanders are an important component of the MCF given their evolutionary history and life-history traits which allow them to occupy a variety of habitats away from bodies of water. As a result of their adaptive radiation, these salamanders were able to partition a wide variety of available microhabitats within any given locality. In remnants of considerable size and good quality of the habitat, high-alpha diversity and density of these species have still been recorded (Meza-Parral and Pineda 2015), and even new species discoveries continue to be added (Sandoval-Comte et al. 2017; García-Castillo et al. 2018; García-Bañuelos et al. 2020). For example, in a specific area of Cloud Forest in the center of Veracruz state, one might find terrestrial species (*Aquiloeurycea cafetalera*, *Parvimolge townsendi*, *Thorius pennatulus*), fossorial species (*Pseudoeurycea lineola*), and arboreal species (*Chiropterotriton lavae, C. nubilus*; Wake et al. 1992; Sandoval-Comte et al. 2012; García-Castillo et al. 2018). Furthermore, there are even examples of sympatric speciation where the each of the two sister species occupy either arboreal or terrestrial microhabitats: for example, *Thorius dubitus* (arboreal) and *Thorius troglodytes* (terrestrial) in Veracruz and *Ixalotriton niger* (terrestrial) and *I. parvus* (arboreal) in MCFs from Oaxaca. Fragments with a more deteriorated habitat seem to remain capable of hosting these species, as long as they contain micro habitats necessary for the salamanders, such as bromeliads and moss mats (Parra-Olea et al. 1999; Aguilar-López et al. 2017). Unfortunately, it has been shown that some populations of salamanders have severely declined, especially during the 1980 decade, when also many declines and extirpations in frogs' species occurred (Parra-Olea et al. 1999, Lips et al. 2004, Rovito et al. 2009). On the other hand, some species considered possibly extinct have been recently rediscovered in the MCF, both the salamanders (Fernández-Badillo et al. 2020; Sandoval-Comte et al. 2022) and frog species (Caviedes-Solis et al. 2015; García-Bañuelos et al. 2017). Nonetheless, these have been found in low abundances and after long periods without records; thus, evaluations about their conservation status are required. Several factors have been associated with the population fluctuations, and extinctions in perturbated habitats, such as pollution, deforestation, or habitat transformation; and others such as emerging infectious diseases and climate change explain species declines in pristine habitats.

Chytridiomycosis is an emerging infectious disease caused by chytrid fungi *Batrachochytrium dendrobatidis* (*Bd*) that has been linked to the declines of many species of amphibians (Scheele et al. 2019). The environmental conditions found in the MCF in terms of temperature and humidity are coincident with optimal conditions for the growth of the pathogen *Bd* (Familiar-López 2010), which has affected a large proportion of amphibian species in the mountainous regions, especially those found in the MCFs. In Mexico, more than 100 species have tested positive for the presence of *Bd* (Bolom-Huet et al. 2019; Basanta et al. 2021), and this disease has been linked to the decline of several populations of amphibians from the MCF (Parra-Olea et al. 1999; Lips et al. 2004, Rovito et al. 2009; Cheng et al. 2011). Nonetheless, not all species are being affected equally, and habitat and species traits, as well as biotic interactions, could be playing a relevant role in the amphibians' response to these threats. The most recent update (Supplementary Material 17.1) indicates that 94 species inhabiting the MCF have been tested for the presence of *Bd*, of these, 63 were *Bd*-positive.

17.5 Conservation Actions

In Mexico, the main government policy focused on solving the loss of forests has been the Payment Program for Hydrological Environmental Services (DOF 2013). However, this does not reverse the damage in those areas with a higher rate of deforestation, since it has been seen that they are mostly assigned in areas of low risk of deforestation (Muñoz-Piña et al. 2008). This type of support is insufficient in those areas most affected, associated with marginal populations, with a high need for economic resources. Therefore, the protectionist vision of this scheme is limited and should be balanced by sustainable land use, and not just a restrictive policy. This would allow landowners to obtain additional resources from their lands to offer their families a dignified life (Fonseca et al. 2012).

There are regions of the country where the establishment of archipelago-type reserves has been promoted, a scheme according to the natural conformation of the MCF. In the state of Veracruz, there is an archipelago of reserves in the central region that includes MCF remnants, which, despite being relatively recent efforts (published in the Official Gazette on January 5, 2015), could have a positive effect on forest species, especially if managed in conjunction with initiatives that improve the connectivity between fragments. Some environmental protection zones in the upper altitudinal limit of MCFs have demonstrated positive results for the conservation of amphibian species that have suffered population declines in recent decades, as in the case of some tropical salamanders (Juárez-Ramírez et al. 2016).

17.6 Projections and Challenges for the Future

MCFs of Mexico are one of the most diverse terrestrial habitats, in terms of its taxonomic diversity, eco-physiological conditions, and social characteristics. However, the conservation measures implemented so far have proved insufficient given the magnitude of the processes of deterioration of these forests. Although the ongoing loss and deterioration of this habitat, scientific research are still making important contributions to the diversity of this forest (Sandoval-Comte et al. 2017; Garcia-Castillo et al. 2018; Grünwald et al. 2018; García-Bañuelos et al. 2020; Hernández-Austria et al. 2022; Jameson et al. 2022), and the role of MCF remnants in the survival of amphibian species (Meza-Parral and Pineda 2015; Sandoval-Comte et al. 2012, 2022). Furthermore, amphibian diversity is still considered underestimated (Jameson et al. 2022), meanwhile, it has been found that these species could hold the key to face global health problems (de Amaral and lenes-Lima 2022).

Biological and cultural heterogeneity of the MCF has been a difficulty in the evaluation and implementation of actions for its conservation. Toledo-Aceves et al. (2011) state that it is important to consider that the criteria for conservation evaluated for this forest in different regions (alpha and beta diversity, roads density, human presence, etc.) are not isolated factors, and the analysis of their interaction allows us to contemplate a complete and realistic picture of the situation of these forests in the country. It is, therefore, necessary to implement management and conservation measures at the landscape level, which contemplate the range of mosaics that make up the current MCF landscapes in the country: fragments of primary forest, fragments of secondary forest in different successional states, and their spatial distribution pattern, the socio-economic situation of the surrounding urban and semi-urban areas, and the presence of other types of vegetation cover that could maintain the connectivity and functionality of the forests (Challenger 1998; Williams-Linera 2007; Murrieta-Galindo et al. 2013).

Human populations residing in these forests or surrounding areas will inherently seek to meet their basic needs, so conservation policies must be directed towards the sustainable use of their resources. These types of forests provide highly relevant ecosystem services and directly represent natural capital for their inhabitants. They, in turn, possess a wealth of knowledge of the flora and fauna, that needs to be taken advantage of, reconciling the interests of the people and sustainable use of the resources they provide (food, fodder, wood, firewood, water, leaf litter, medicine, ornamental and ceremonial or religious plants) (Challenger 1998; Eleutério and Pérez-Salicrub 2006; Endress et al. 2006; Wolf and Konings 2001).

The reconciliation between the interests of the communities and the conservation of this forest will lead to the possibility of implementing plans for the management, restoration, and even reintroduction of highly threatened species, such as tropical salamanders. These species face several threats, as the progressive disturbance of their habitats makes them more susceptible to the threat of emergent diseases, so offering them a habitat with a good state of conservation will promote their survival and ensure the preservation of these lineages for the future.

Acknowledgments We would like to thank Raquel Hernández Austria, Omar Becerra Soria, and Rene Avalos Vela for their photographs. This research was supported by grants from the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT-UNAM) IN205521. Angel Soto thanks the Programa de Posgrado en Ciencias Biológicas, UNAM and CONACyT (CVU/Becario: 742781) for granting scholarships to complete his PhD program.

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Chapter 18
Human Impacts on Mexican Caves

William R. Elliott, José G. Palacios-Vargas, Rodrigo A. Medellín, and Omar Calva

Contents

18.1 Distribution of Caves and Karst

Mexican caves were naturally formed in many different rocks: limestone, gypsum, sandstone, lava, and others. Our discussions of caves are arranged in broad regions: Northwest, Northeast, South, and the Yucatán Peninsula. Figure 18.1 shows an

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W. R. Elliott (✉)
Association for Mexican Cave Studies, and Missouri Department of Conservation, retired, Georgetown, TX, USA
e-mail: speodesmus@gmail.com

J. G. Palacios-Vargas
Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México and Unión Mexicana de Agrupaciones Espeleológicas (UMAE), Mexico City, México

R. A. Medellín
Instituto de Ecología, UNAM, Ciudad de México, México

O. Calva
Posgrado en Biociencias, Universidad de Sonora, and UMAE, Hermosillo, Sonora, México

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_18

Fig. 18.1 The 2019 expedition to Nacimiento del Río Uluapan, Oaxaca, which involved technical cave diving and vertical caving by an international team. Photo by Adam Haydock

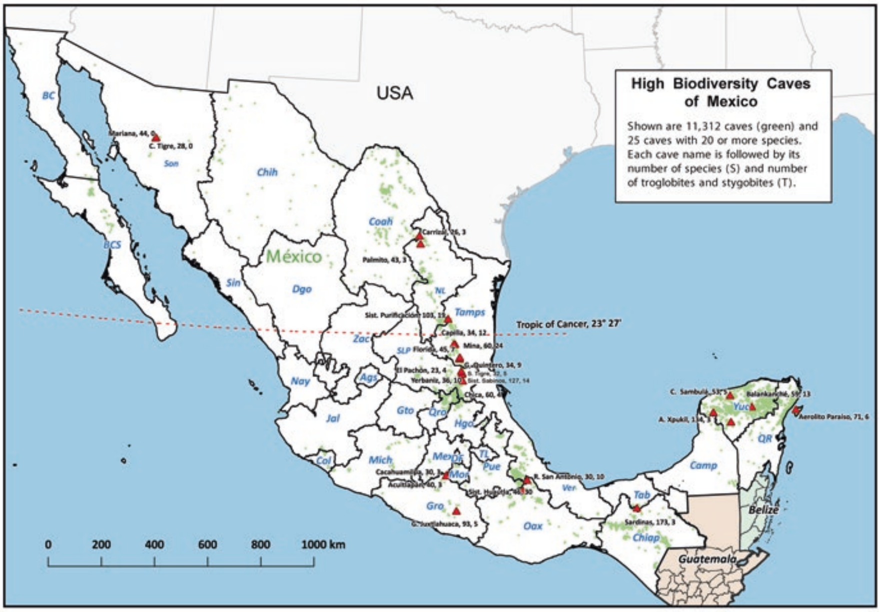

Fig. 18.2 Distributions of 11,312 known caves in Mexico (data courtesy of AMCS, Peter Sprouse). Twenty-five caves are shown having 20 to 40 species of troglobites and stygobites, but there are hundreds with rich and diverse animal communities. Besides invertebrates, bats are an important component of Mexican caves. By William R. Elliott

important resurgence cave, or nacimiento, currently being explored in Oaxaca.

Karst occurs across Mexico, and it is composed of landscapes formed by groundwater dissolution of limestone or gypsum rocks (Fig. 18.2). The Trans-Mexican

Volcanic Belt (Eje Volcánico Transversal) runs from Nayarit on the west coast to Veracruz on the Gulf coast. Lava caves are formed by drainage channels inside hot, flowing lava. Baja California contains rock shelters and littoral (shoreline) caves. All cave types may contain bats and interesting cave-adapted fauna. The AMCS (Association for Mexican Cave Studies) database contains nearly 12,000 cave locations, and the AMCS Index to Cave Maps of Mexico currently includes nearly 4000 maps (Elliott https://cavelife.info/maps/ and AMCS http://www.mexicancaves.org/maps/). Exploration and study of the caves attracts speleological groups from across México and the world. See UMAE https://umae.org/, the Unión Mexicana de Agrupaciones Espeleológicas. Numerous groups of speleologists can be found at those websites.

18.2 Biodiversity

Biodiversity is high in Mexican caves, with about 800 obligate cave species and many more associated with subterranean environments (Fig. 18.2). In this chapter, we refer to all cave-adapted forms as "troglobites," including terrestrial troglobites (troglobionts), and aquatic or marine stygobites (stygobionts) (Palacios-Vargas and Reddell 2013). Fourteen stygobitic fish species live in about 84 sites (Elliott 2018; Graham Proudlove pers. comm.). The other troglobites are invertebrates. Troglophiles are somewhat cave adapted but may occur in other habitats. Trogloxenes, like bats (Fig. 18.3) and cave crickets, come and go from the cave (Table 18.1).

Fig. 18.3 Distribution map which includes 351 bat caves and mines, some with large colonies, usually Tbra or "Mexican free-tailed bats," (common name in English, with a tail mostly free of the caudal membrane), or guano bat. Twenty-four caves have 9–15 bat species, 89 have 3–8, 132 have 1 or 2, and 105 are probable bat caves based on names like "murciélagos," "guano," "diablo," and "salitre" (saltpeter). Cueva San Francisco = Grutas de Zapaluta is included here as it may have 8–16 bat species. By William R. Elliott

Many of the species depend directly or indirectly on bat guano and other organic detritus or waterborne nutrients and detritus. These cave dwellers are scientifically interesting, and they provide evolutionarily significant insights into past climates, plate tectonics, and natural communities.

Terrestrial and some aquatic cave food chains often are based on bat guano from species roosting in different areas of the cave (Reddell 1981; Palacios-Vargas et al. 2011b, 2015; Hoffman et al. 1980, 1986, 2004; Elliott 2018). Cave bats include species that feed on insects, fruit, pollen, nectar, or blood (vampire bats). *Astyanax* cavefishes feed on floating bat guano (Elliott 2018). Collembola (springtails; Fig. 18.4) provide much of the base of the terrestrial food chains (Castaño-Meneses and Palacios-Vargas 2012), along with guano-dwelling mites, which include micropredators and those that feed on guano. More than 17 families and 180 species of Collembola have been recorded from Mexican caves, representing about 20% of the Collembola known from the country; this includes 12 families and 22 genera of troglobites (Palacios-Vargas et al. 2015). The food chain continues with millipedes, flies, moths, beetles, and many small arachnid predators.

Table 18.1 The top 25 general biodiversity caves in Mexico

Name	State	Municipio	Bat species	T	S	T/S	Risk
Sistema Huautla	Oaxaca	Huautla de Jiménez	2	30	48	0.63	2
Cueva de la Mina	Tamaulipas	Gómez Farías	2	24	60	0.40	1
Sistema Purificación	Tamaulipas	Hidalgo	2	19	103	0.18	1
Sistema de los Sabinos	San Luis Potosí	Ciudad Valles	4	14	127	0.11	2
Grutas de Balankanché	Yucatán	Tinum	7	13	59	0.22	2
Cueva de la Capilla	Tamaulipas	Gómez Farías	1	12	34	0.35	1
Cueva del Nacimiento del Río San Antonio	Oaxaca	Acatlán de Pérez Figueroa	1	10	30	0.33	1
Sótano de Yerbaniz	San Luis Potosí	Ciudad Valles	2	10	37	0.26	1
Grutas de Quintero	Tamaulipas	El Mante	13 (11)	9	34	0.26	5
Cueva de la Florida	Tamaulipas	Antiguo Morelos	8	7	45	0.16	1
Cueva Aerolito de Paraíso	Quintana Roo	Cozumel	?	6	71	0.08	1
Cenote Sambulá	Yucatán	Motul	?	5	53	0.09	4
Grutas de Juxtlahuaca	Guerrero	Quechultenango	8	5	93	0.05	2
Sótano del Tigre	San Luis Potosí	Ciudad Valles	1	5	32	0.16	1
Cueva Chica	San Luis Potosí	Ciudad Valles	6	4	60	0.07	3
Cueva de El Pachón	Tamaulipas	Antiguo Morelos	6	4	23	0.17	4
Actún Xpukil	Yucatán	Opichén	10	3	134	0.02	2
Cueva de las Sardinas	Tabasco	Tacotalpa	7	3	173	0.02	2
Gruta de Acuitlapán	Guerrero	Taxco de Alarcón	?	3	40	0.08	1
Gruta de Carrizal	Nuevo León	Lampazos de Naranjo	1	3	26	0.12	1
Gruta del Palmito	Nuevo León	Bustamante	0	3	43	0.07	2
Grutas de Cacahuamilpa	Guerrero	Pilcaya	7	3	30	0.10	3
Gruta Xtoloc	Yucatán	Tekax de Álvaro Obregón		2	86	0.02	1
Cueva de la Mariana	Sonora	San Miguel de Horcasitas	7	0	44		2
Cueva del Tigre	Sonora	San Miguel de Horcasitas	9	0	28		1

They are ranked in descending order for T = number of troglobites and stygobites. Another measure of general biodiversity is S = number of species. Some of these caves have many bat species or large bat colonies, but generally not. Risk means the likelihood of losing one or more species in the cave because of human activity; 1 is a natural cave, 2 had minor degradation, 3 and 4 are increasing levels of damage, 5 is severely impacted, gutted means a cave where life is absent. Risk was based on several factors: known loss of species, reduced bat populations, loss of habitat, level of human visitation, degree of human alteration, vandalism, etc.

Fig. 18.4 Collembola (springtails) provide much of the base of terrestrial food chains in caves. This *Pseudosinella* springtail is 1–2 mm long. Photo by Andy Murray

Few population estimates of cave invertebrates have been done in México, but these can be very large in bat caves. Osorio-Tafall (1943) studied the aquatic species in Cueva Chica, San Luis Potosí. Mitchell estimated a population of 11,000 ricinuleids (Arachnida) on guano in Cueva de la Florida, Tamaulipas (1970a). Mitchell (1970b) reported very large populations and densities of guanophiles in Fern Cave, Texas, associated with a large Mexican free-tailed, or guano bat, colony, similar to caves in Mexico. Palacios-Vargas (1983, 1988, 1993) conducted invertebrate surveys in many caves. Palacios-Vargas et al. (2011a, b) studied the ecologically rich Cueva de las Sardinas, Tabasco. Four different biotopes were studied over the course of a year: bat guano, litter, soil under chemoautotrophic bacteria colonies, and the control, plain soil without litter or guano. A total of 27,913 specimens of 169 species were collected. Guano had the highest densities recorded. Many reports by Palacios-Vargas et al. (1995, 2013, 2015) on cave invertebrate populations and by Calva (2017) in arid land caves are found in issues of *Mundos Subterráneos* (https://umae.org/mundos-subterraneos).

Endemism is relatively high among troglobites, with some taxa known only from one cave, or even a small part of one cave. In this study, we measured the endemism in a cave as the troglobite component, T/S, or fraction of troglobites (T) among all species (S) in the cave (Table 18.1). We also tabulated the number of bat species. Sistema Huautla, in mountainous Oaxaca, is the deepest cave in the Americas at 1560 m vertical relief, and it contains 48 species with at least 30 troglobites, a 63% troglobite component, the highest in México. Cueva de la Mina, in the tropical montane cloud forest of Tamaulipas, contains 60 species, 24 of which are obligate cave forms, nearly all terrestrial. An extremely different cave, Cenote Aerolito de Paraíso, Isla Cozumel, Quintana Roo, is submerged, most of it continuous with the Caribbean Sea. It hosts 71 species, 6 or which are stygobitic marine forms. All of these communities are vulnerable to disturbance. To date, some of the caves with high biodiversity have been impacted. Bat caves are disturbed by some visitors, but most severely by mining and human intervention, including harassment.

Table 18.2 The top 26 caves for bat diversity and abundance

Name	State	Municipio	Bat species	Tbra pop	Nmex pop	S	T	T/S	Total bats	Risk
Cueva Cerro Huatulco	Oaxaca	Santa María Huatulco	15						No census	1
Cueva Las Vegas	Puebla	Tenampulco	13		300				300	1
Grutas de Quintero	Tamaulipas	El Mante	13 (11)	100,00 1999		34	9	0.26	10,000	5
Cueva Cuaxilotla	Guerrero	Cuetzala del Progreso	12						>80,000	1
Aktún Loltún	Yucatan	Oxkutzcab	12						No census	2
Cueva El Salitre, Colima	Colima	Colima	11		>350				>350	1
Cueva El Salitre, Morelos	Morelos	Tlaltizapán	11							1
Cueva Los Laguitos	Chiapas	Tuxtla Gutiérrez	10		>10,000 [>1000]				100,000	1
Grutas Karmidas	Puebla	Zapotitlán de Méndez	10						No census	1
Mina Armadillo	Sonora	Alamos	10	Tbra	1000				1000	2
Mina La Aduana	Sonora	Alamos	10	Tbra	present before, absent 2010				No census	2
Actún Xpukil	Yucatán	Opichen	10		Present before, absent 2010	134	3	0.02	No census	2
Volcán de los Murciélagos	Campeche	Calakmul	9						3,000,000	2
Cueva La Fábrica	Colima	Coquimatlán	9						No census	1
Cueva Mina América	Morelos	Tlaquiltenango	9						No census	1
Cueva del Cerro	Morelos	Puente de Ixtla	9						No census	1
Cueva del Tigre	Sonora	San Miguel de Horcasitas	9	1,000,000	100	28	0	0	1,000,000	1
Mina Santo Domingo	Sonora	Alamos	9	Tbra	>500				>500	2
Cueva de Don Luis	Tabasco	Teapa	9						Big	1

(continued)

Table 18.2 (continued)

Name	State	Municipio	Bat species	Tbra pop	Nmex pop	S	T	T/S	Total bats	Risk
Cueva El Ojo de Agua	Tamaulipas	Gómez Farías	9		100				100	1
Cueva de El Abra	Tamaulipas	Antiguo Morelos	9	Large flights 1950s, now uncertain					Thousands	4
Cueva El Socavón	Veracruz	San Andrés Tuxtla	9		Present before, absent 2010				No census	1
Gruta Tzamnah	Yucatán	Tecoh	9						No census	1
Cueva San Francisco = Grutas de Zapaluta	Chiapas	La Trinitaria	8 (16?)	"Big"					"Big"	3
Grutas de Juxtlahuaca	Guerrero	Quechultenango	8		>1000	93	5	0.05	70,000	2
Cueva del Ídolo	Morelos	Jojutla	8							Gutted

See Table 18.3 for free-tailed bat caves) in Mexico. Another 18 caves contain 8 or 9 bat species, but most have not been censused. We assigned a risk value of 1 unless we had specific information. Tbra refers to *Tadarida brasiliensis*, Nmex refers to *Natalus mexicanus*; these are common cave bats, censused often. T = number of troglobites and stygobites. Another measure of general biodiversity is S = number of species

Table 18.3 (below) Details of 23 "free-tailed bat caves," containing *T. brasiliensis mexicana*, which is important for control of agricultural pest insects

Name	State	Municipio	Bat species	Notes	Total bats	Risk
Cueva de Allende	Coahuila	Allende	1	Villa-R (1966)		1
Cueva de El Abra	Tamaulipas	Antiguo Morelos	9	Large exit flights 1950s, uncertain in 2020. Málaga Alba, Villa-R 1957: 560 Tbramex. Reddell (1965), thousands of dead bats. Torres-Flores and López-Wilchis (2010)		4
Cueva de la Boca	Nuevo León	Santiago	3	5–10 million before guano mining. Arita (1992): 5 million. Roemer (2003), winter 2002: 100,000. 2001: 2.5 million; 2021: 2 million. Villa-R (1966), Torres-Flores and López-Wilchis (2010): Nmex, Tbra	2,500,000	4
Cueva de la Chinacatera	Sinaloa	Angostura	4	Roemer (2003): Likely summer roost. Locals mined three hundred sacks of guano in 1999		2
Cueva de la Isla de Janitzio	Michoacán	Patzcuaro	1	Villa-R (1966). Small colony 1999, Roemer (2003). Now gutted of life.	<10	Gutted
Cueva de la Mariana	Sonora	San Miguel de Horcasitas	7	Calva (2017): 500,000.	500,000	2
Cueva de la Mula	Tamaulipas	Jaumave	3	Mollhagen (1971)		1
Cueva de las Torrecillas	Jalisco	Toliman	8	Ayala Téllez et al. (2018)	400	1

(continued)

Table 18.3 (continued)

Name	State	Municipio	Bat species	Notes	Total bats	Risk
Cueva del Guano	Durango	Lerdo	2	Map 1972, Roemer (2003): 53 Tbra 1999-12-12.	53	2
Cueva del Real	Jalisco	Tecaliltlán	5	Ayala Téllez et al. (2018). Except for *D. rotundus*, species were identified using echolocation calls. Low human disturbance	40	1
Cueva del Rincón de la Virgen	Nuevo León	García	1	Villa-R (1966), Roemer (2003): 10 + large guano deposit, 1999-12-10, summer roost for Tbra	10	1
Cueva del Tigre	Sonora	San Miguel de Horcasitas	9	Arita (1992): 9 bat species, very high abundance, 1 fragile species, a major free-tail colony. Torres-Flores and López-Wilchis (2010): Nmex, Chmex, Lniv, Mcal, Mmeg, Mvel, Pdav, Ppar, Tbra. 1000,000 Tbra, bats declined from 9 to 4 species from 1991 to 2017. Calva (2017)	1000,000	1
Cueva Higuerilla	Jalisco	Tecalitlán	2	Ayala Téllez et al. (2018). Human disturbance is low.	20 (echolation calls)	1
Cueva La España	Durango	Lerdo	1	11 specimens examined, Villa-R (1966)		1
Cueva San Francisco = Grutas de Zapaluta	Chiapas	La Trinitaria	8 (16?)	"big" colony of *Tadarida brasiliensis intermedia*, Villa-R (1966). Map at AMCS website	"big"	3

(continued)

Table 18.3 (continued)

Name	State	Municipio	Bat species	Notes	Total bats	Risk
Cuevas de Las Garrochas	Jalisco	Mixtlán	3	Roemer (2003): Banded Tbra from Carlsbad Caverns 1952-11-26. Tbra bones and odor 1999-12-21. No Tbra but Drot with young. Torres-Flores and López-Wilchis (2010): Nmex, Drot		1
Grutas de Quintero	Tamaulipas	El Mante	13 (11)	13 bat species max. Mollhagen (1971), 9 species. Reddell (1981). Arita (1992): 9 species, very high abundance, 1 fragile species. Roemer (2003): 10,000 Tbra 1999-12. Hernández-Vázquez (2005): 11 bat species. Torres-Flores and López-Wilchis (2010)	10,000	5
Las Cuevas	Baja Cal. Sur	Los Cabos	3	Torres-Flores and López-Wilchis (2010)		1
Mina Armadillo	Sonora	Alamos	10	Torres-Flores and López-Wilchis (2010)	1000	2
Mina La Aduana	Sonora	Alamos	10	Torres-Flores and López-Wilchis (2010)		2
Mina Santo Domingo	Sonora	Alamos	9	Torres-Flores and López-Wilchis (2010)	>500	2
Resumidero del Cerro Toxin	Jalisco	Toliman	4	Ayala Téllez et al. (2018)	300	1
Ventana Jabalí	San Luis Potosí	Ciudad Valles	1	Bonet (1953): guano mining. Mollhagen (1971)		2

See range maps in Villa-R. and Cockrum and Bradshaw. T = number of troglobites and stygobites. Another measure of general biodiversity is S = number of species. Only three caves have biodiversity scores to date: Mariana 3 S, 0 T; Tigre 28 S, 0 T; Quintero 34 S, 9 T, 0.26 T/S

Arita (1992, 1993, 1996, 1997) Arita and Vargas (1995), and Arita and Ortega (1998) studied the ecology and conservation of Mexican bats, especially in Yucatán. Arita developed a table, "Critical Caves for the Conservation of Mexican Cave Bats," in his 1992 dissertation, which listed 12 important caves with 9–12 bat species each. Since 1992, our knowledge has increased to 25 caves with 8–15 bat species each, detailed in Table 18.2. Nine of Arita's 12 bat caves are in our tables in this chapter, and the other 3 are in our GIS (geographic information system) and maps. It is important to document diversity and protect additional caves with multiple bat species and diverse invertebrate communities.

18.3 Human Impacts on Caves

Human impacts on caves are many, the main ones being disruption and killing of bats, mining, vandalism, trash dumping, overuse and degradation of cave environments, and contamination of groundwater. Palacios-Vargas (1995) proposed the inclusion of subterranean environments in ecological laws for the Mexican Government to protect caves and karst areas. Several authors have recommended conservation actions for individual caves.

Below is a descending list of impacts that have occurred at American and Mexican caves (Elliott 2000). These impacts are ranked on general frequency and severity, so they may vary in importance in the list depending on the region and cave type.

1. Destruction of caves by quarrying or inundation.
2. Unregulated, uncontrolled, and unsustainable mining of phosphates, guano, and other materials resulting in bat disturbance or extirpation.
3. Killing of multiple species of bats by locals or rabies control workers against vampire bats.
4. Disturbance of bats by cave visitors, mostly by tourists, but sometimes by cavers and scientists.
5. Alteration of entrances that affects access by wildlife or the cave environment itself.
6. Alteration or contamination of water inputs.
7. Pipeline breaks, dumping of toxic materials or medical waste.
8. General cave abuse, graffiti, trash, trampling, and breakage.
9. Some kinds of ecotourism cave development, environmental alteration, cave lint, algae growth (from artificial lights), loss of bats and troglobites.
10. Over-collecting by biologists (infrequent).
11. Infrequent visitation and unintended bat disturbance (harmful during critical times, such as birthing and nursery periods).

These impacts are ranked on frequency and severity, so some impacts may move up or down the list depending on the information available at any given time.

18.4 Review of Caves by Geographic Region

The international importance of Mexican cave biology is reflected in its large scientific literature, with more than 4200 papers, 123 cited here. There are more than 1000 papers on a single model species (i.e., *Astyanax mexicanus jordani* cavefishes) alone, and many papers and books on exploration, cave fauna, taxonomy, evolution, ultramorphology, genomics, cultural use of caves, geology, hydrology, and environmental problems.

Mexico has at least 139 species of bats, 60 of which occur in caves, with 36 reported in this chapter (Arita 1992; Ayala-Téllez et al. 2018). The largest impact reported on bats has been the mining of phosphates, nitrates, and guano (Elliott 2000). Some were mineralized deposits from bat guano and bones, but many affected caves had living bat colonies and fresh guano. In the past, federal rabies control workers killed vampire bats and sometimes other species living in the same caves (Elliott 2000). Guano mining in Ventana Jabalí, San Luis Potosí, and the need for protection of bat caves for agriculture were noted in 1953 by Federico Bonet, a prominent cave scientist. Population estimates of bats were difficult and imprecise until about 1980. Recurrent counts by experts of hibernating bats are now reliable. Large maternity colony emergences are more difficult to estimate, but there have been advances since 2000 in infrared videography for counting (Elliott 2008; Elliott et al. 2011). For the migratory Mexican free-tailed bat (*Tadarida brasiliensis mexicana*), it is important to identify and protect migratory routes and critical cave roosts in both the United States and Mexico (Wiederholt et al. 2013).

The following caves are detailed because of their high biodiversity or notable impacts. Other caves are listed in Tables 18.1 and 18.2. Many had documented human impacts, but some are important caves that have received little or no impact, but deserve additional protection.

18.4.1 Northwest Region

18.4.1.1 Cueva El Tigre and Cueva de La Mariana, Sonora

Both of these karstic caves are located between the towns of San Miguel de Horcasitas and Carbó in the central region of Sonora. They are located approximately 60 km NE of the capital, Hermosillo. Cueva El Tigre is 156 m long and 46 m vertical development. Cueva de la Mariana is 700 m long and 44 m deep (Calva 2017). The two caves were used for guano extraction. Landowners collected guano in winter, when bat populations decrease. Cueva El Tigre is still visited by the land owner to collect guano; however, guano extraction ceased in Cueva de la Mariana years ago.

Cueva El Tigre was explored in the 1960s. Despite the proximity between the caves, Cueva de la Mariana was not recorded by Sonora cavers until 2014. Cockrum

Fig. 18.5 *Myotis velifer*, the cave myotis, one of 60 bat species commonly found in Mexican caves. Photo by Rodrigo A. Medellín

and Bradshaw (1963) made several trips to Sonora as part of a bat-banding program. At Cueva El Tigre, they recorded 9 species, with 2 specimens of *Pteronotus mexicanus*, 32 *Pteronotus fulvus*, 19 *Mormoops megalophylla*, 18 *Macrotus californicus*, 1 *Choeronycteris mexicana*, 4 *Leptonycteris nivalis* (probably *L. yerbabuenae*), 4 *Natalus mexicanus*, 1 *Myotis velifer* (Fig. 18.5), and 10 *Tadarida brasiliensis*. *L. nivalis* is absent from the region, and there probably was a misidentification with its close relative *L. yerbabuenae*, which has been recorded in Cueva de la Mariana, and it is present in the region.

Arita (1993) compared Mexican bat caves, and he rated Cueva El Tigre as having high diversity and great bat abundance. Calva (2017) reported only four bat species corresponding to *T. brasiliensis*, *P. fulvus*, *N. mexicanu*s, and *M. californicus* in Cueva El Tigre. Calva recorded these four species in Cueva de la Mariana, plus three more: *Leptonycteris yerbabuenae*, *Myotis velifer*, and *Mormoops megalophylla.* The most abundant species was *T. brasiliensis* with an estimated population of more than one million individuals in Cueva El Tigre, and half a million in Cueva de la Mariana. Both caves are important because 50% of the species use them as maternity roosts. We have assigned a risk factor of 2 for Mariana and 1 for Tigre.

In his thesis, Calva (2017) collected and recorded invertebrates and other vertebrates in both caves. No troglobites were found. Despite the hot conditions inside both caves, 52 taxa were determined at least to generic level. In Cueva de la Mariana 43 species of invertebrates and vertebrates were recorded, whereas in Cueva El Tigre only 28 species were found. The two caves shared 19 species. For invertebrates, the unique groups were arthropods represented by centipedes, arachnids, and insects, and for vertebrates he recorded amphibians, reptiles, birds, and mammals.

18.4.2 Northeast Region

18.4.2.1 Cueva del Cañón El Buey, Coahuila

The cave is 20 m long and 8 m deep, and it is strongly affected by medical waste, including biologically infectious material such as syringes, photographed in 1996 at the bottom of a pit cave, Cueva (Pozo) del Cañón El Buey (Elliott 2000). We have assigned a risk factor of 5 for El Buey.

18.4.2.2 Toxic Sink, Coahuila

In July 1996, used drums of the insecticides, the organochlorine chlordane, and the organophosphate methamidophos were found and photographed in Toxic Sink, Coahuila, a pit cave (Elliott 2000). Both chemicals are highly toxic. We could not enter the cave and the fauna is unknown, but we have assigned a risk factor of 5 to Toxic Sink.

18.4.2.3 Cueva de la Boca, Nuevo León

The huge, 27 by 27 m entrance to Cueva de la Boca (Fig. 18.6) opens on the south side of Cañon Garrapatas, 1.5 km E of Santiago and Presa de La Boca. Cueva la Boca is a single chamber, 295 m long and 14–30 m wide. Near the entrance the ceiling is almost flat, but at the rear two large domes extend 152 m above the floor. A

Fig. 18.6 Cueva de la Boca, Nuevo León. The 27-m entrance is high on a ridge above Cañon Garrapatas. The cave now contains about 2 million *Tadarida brasiliensis.* Photo by Alejandro Gómez

30-m tower was formerly used for accessing and extracting phosphates from the walls. A jeep road was used to carry the rock and guano to the cave entrance, where an aerial tramway carried the ore in buckets across the canyon to the road below (Russell and Raines 1967).

Cueva La Boca is the focus of a major conservation effort to restore the colony of *Tadarida brasiliensis mexicana*, Mexican free-tailed bat or guano bat. It was estimated that 20 million bats formerly inhabited the cave, but 5 or 10 million is more likely. The colony is mostly *Tadarida brasiliensis mexicana*, but there is a small colony of *Mormoops megalophylla* and a seasonal colony of *Leptonycteris nivalis.* Unfortunately, because of human impacts, such as guano and phosphate extraction, uncontrolled tourism, pollution, and vandalism (bonfires, fireworks, etc.), the bat population was reduced to less than 100,000 in 1991, but it started increasing in 1994. The Program for Conservation of Bats in Mexico (PCMM) began working there in 1995 with a very active program on research, conservation, and environmental education (Medellín 2003; Medellín et al. 2004). They drafted a management plan for conservation of this cave, and provided it to a local organization in 1999. They obtained a mining permit to prevent future guano extraction and its disturbances. Medellín and his team continued research in the cave, and the colony recovered to about 2.5 million bats in 2001. The colony continued to grow in the next 5 years. Unfortunately, only a second fence was built in 2004, which was vandalized within months. Both fences are inadequate, and a video posted on YouTube on 22 March 2019 shows intruders entering the cave through holes in the fences. We assume that the bats are disturbed at times. The local organization continues to work sporadically in the area, but the Covid-19 pandemic has hindered efforts. The colony currently is about 2 million, an improvement, but we have rated the risk factor for La Boca at 4 because of frequent intruders.

18.4.2.4 Sistema Purificación, Tamaulipas

This large cave system includes 33 caves in a remote mountain region, the source for Río Purificación. Many years were required to explore and map the system. Purificación is the fourth longest cave in México at 94,889 m, the longest "dry" Mexican cave (mostly above water) and 11th deepest at 957 m. The cave, at 1916 m elevation, has 103 total species, 19 troglomorphic species (4 aquatic, 15 terrestrial), 2 aquatic and 46 terrestrial troglophiles (Reddell 1981, p. 20; Table 18.3). There are at least two bat species: unidentified insectivorous bats and *Desmodus rotundus*, the common vampire (Peter Sprouse and James Reddell, pers. comm.). The system receives massive floods during heavy rains, which flow out of the lower entrance to the Río Purificación. Access to the cave is available only to experienced speleologists, and we have rated the risk factor at 1.

18.4.2.5 Cueva de la Mina, Tamaulipas

Cueva de la Mina, at 1527 m elevation in the Sierra de Guatemala, has a small entrance, and is only 160 m long and 25 m deep. There is much flowstone over soil creep and roots reach down from the cloud forest. The cave has 60 species with 24 confirmed troglobites, for a troglobite component value of 40%. The cave was mapped in 1971 by Elliott and others from Texas Tech University. The cave is within the Reserva de la Biósfera El Cielo, hidden in the forest at about 1500 m asl (above sea level), near an abandoned logging road that is rarely traveled. It probably receives very few visitors (Reddell 1965, Reddell and Mitchell 1971b; Elliott 1973; Reddell and Elliott 1973b; Palacios-Vargas et al. 2015). Two species of bats were reported: *Anoura geoffroyi* and *Leptonycteris nivalis* (Mollhagen 1971). The most notable troglobite there is the endemic *Typhlochactas rhodesi*, the first blind scorpion discovered in México. For many years, Cueva de la Mina was the most biodiverse Mexican cave, but it is now number 2. Ecotourism in the area could affect this cave in the future, but we have rated the risk factor at 1 for now.

18.4.2.6 Cueva de la Capilla, Tamaulipas

This is a very biodiverse cave at high elevation (about 2100 m asl) with 34 species, including 12 troglobites, within the Reserva de la Biósfera El Cielo. Mapped in 1971 by Elliott et al., the cave is 250 m long and 22 m deep, with an entrance at each end. A bat collected here was lost, but it probably was *Corynorhinus mexicanus*. The cave is in an isolated area with very few visitors (Reddell and Mitchell 1971a, b; Elliott 1973; Reddell and Elliott 1973a, b; Palacios-Vargas et al. 2015). We have rated the risk factor at 1 for now.

18.4.2.7 Grutas de Quintero, Tamaulipas

Also called Cueva de Quintero, it is 1030 m long and 15 m in vertical relief. The cave is an old spring that was extensively mined and torn up for minerals since 1965; however, bat domes still exist and spring-fed rimstone pools remain at the far end. Russell and Raines (1967) described the cave in its better days as having a succession of travertine dams up to 3-m high filled with water, flowstone slopes, and large speleothems. They noted that foot traffic and some vandalism had marred the cave before the 12-m pit at 500 m from the entrance. Most of the scenic value of the cave has been destroyed since then.

Grutas de Quintero was listed as an “Important Cave for Conservation” (Arita 1992 and section below). Quintero is a cave of national importance, but it has suffered abuse for a long time. Figure 18.7 shows the damage to the cave from 1965 to 2007; formerly there were many pristine, travertine, or rimstone pools, but later most of the calcite crusts and speleothems were removed, and the pools were ruined and drained. Hernández-Vázquez (2005), noted 11 bat species and large amounts of

Fig. 18.7 Grutas de Quintero, the cave's condition in 1965 (left) compared to 2007 (right). The cave was extensively mined, destroying much habitat, and bats have been reduced. Photos by Francis Abernethy (left) and Peter Sprouse. Pictured are Jean Louis Lacaille Múzquiz (left) and Vince Massey

trash and vandalism; he recommended specific actions for the cave's restoration, management, and sustained use.

Quintero's general biodiversity is, or was, high (34 species, 9 troglobites). On 20 July 1983, Wilson et al. (1985) recorded three bat species: *Glossophaga soricina, Eptesicus fuscus miradorensis*, and a flight of about 100,000 *Tadarida brasiliensis mexicana*. In 1999, the cave contained only 10,000 *T. b. mexicana* (Roemer 2003). It is one of 24 sites for this species in Mexico. In 2005, Hernández-Vázquez netted 698 *T. b. mexicana* but made no population estimate.

The cave still is important as a diverse bat roost, with 13 species identified since 1971. Two of the species have not been reported since Mollhagen's 1971 survey of 9 bat species: *T. brasiliensis mexicana* (Fig. 18.8), *Artibeus jamaicensis*, *A. lituratus*, *Desmodus rotundus*, *Diphylla ecaudata*, *Eptesicus fuscus* (captured in small holes in the entrance vault*), Glossophaga soricina*, *Leptonycteris yerbabuenae*, *Micronycteris microtis*, *Mormoops megalophylla, Natalus mexicanus*, *Pteronotus mesoamericanus*, *P. psilotis*. The missing species are *Artibeus lituratus* and *Micronycteris microtis*.

Aquatic cave species include the cirolanid isopods *Speocirolana bolivari* and *S. pelaezi*, ostracod *Sphaeromicola cirolanae*, and mysid *Spelaeomysis quinterensis*. Terrestrial troglobites include the isopod *Brackenridgia bridgesi*, thysanuran *Anelpistina quinterensis*, schizomid *Sotanostenochrus mitchelli*, ricinuleid *Pseudocellus osorioi*, and pseudoscorpion *Paravachonium bolivari*.

Quintero has been the site of many studies, but there has been no long-term project to scientifically monitor the cave and conserve its resources (Jean Louis Lacaille

Fig. 18.8 A nursery colony of *Tadarida brasiliensis mexicana*. The babies are pink. A human disturbance may cause the mothers to drop their babies, but they cannot retrieve them from the floor. These bats control moths and other agricultural pests. Photo by Rodrigo A. Medellín

Múzquiz, pers. comm.). As a result, the cave has suffered, two bat species were lost, and habitat has been lost. We have assigned a risk factor of 5 to Quintero because of these documented losses and the continuing risk to the cave. This risk applies in three ways: biodiversity, bat biodiversity, and *T. b. mexicana* in particular. Quintero has the best documented losses of any Mexican cave, including a Master of Science thesis by Hernández-Vázquez (2005), and papers by Russell and Raines (1967), Mollhagen (1971), Elliott and Mitchell (1973), Reddell (1981), Wilson et al. (1985), Arita (1992), Roemer (2003), and Torres-Flores and López-Wilchis (2010).

18.4.2.8 Cueva de El Abra, Tamaulipas

This famous cave has a prominent, large entrance high above the Mexico 85 highway in the El Abra pass, south of Ciudad Mante. “Cave near Ojo de Agua” is a synonym for the cave, named for the village of El Abra (Ojo de Agua) 2 km SE. At 500 m long and 119 m deep, the cave has attracted countless visitors over many years. It was first explored to the bottom of its pit by Texas cavers in 1956. Málaga Alba and Bernardo Villa-R. collected bats in 1957. A skylight at the top of the hill also is a portal for up to 9 species of bats. In recent years, Jean Louis Lacaille Múzquiz (pers. comm.) and the Grupo Espeleológico Mante (GEM) from Ciudad Mante have removed graffiti and many bags of trash from the cave. There are warning signs placed by the local government, but there is no adequate safeguard against the continued abuse by visitors.

It is interesting that bats still use this cave, despite all the disturbance, but probably at a reduced number. The current bats are *Tadarida brasiliensis mexicana*, *Nyctinomops laticaudatus*, and *N. aurispinosus* from the cave (Málaga-Alba and Villa-R 1957; Torres-Flores and López-Wilchis 2010). Other species reported:

Artibeus jamaicensis, *Desmodus rotundus*, *Myotis nigricans*, *Glossophaga soricina*, *Pteronotus mesoamericanus*, *Natalus mexicanus*. Reddell (1965) reported, "Throughout the first section of the cave thousands of dead bats were seen on the floor during the most recent visit (27 January 1965) that were evidently the victims of some epidemic." We have assigned a risk value of 4 to this cave and its fauna, as the large flights of the 1950s no longer occur. A new bat census is needed.

18.4.2.9 Cueva de la Florida, Tamaulipas

Locally, Florida is called "Cueva Misantla," and a survey monument nearby called it "Mina la Florida." The elevation is 230 m asl. It is 1830 m long and 57 m deep. The cave apparently is an ancient resurgence similar to nearby Cueva de El Pachón, but now it is a dry cave with eight bat species and a rich invertebrate fauna, including a prolific population of two guano-dwelling ricinuleids, *Pseudocellus osorioi* and *P. pelaezi*. The map, lost since 1968, will be published by Elliott and Lacaille Múzquiz in 2021 or 2022. There are 45 total species with 7 troglobites. The ricinuleids were statistically estimated by Mitchell (1970a) in the left-hand tunnel, where there are copious guano deposits supporting a population of 11,000 *Pseudocellus osorioi* ricinuleids, and millipedes, schizomids, amblypygids, and other fauna. *P. pelaezi* is found more in the right-hand tunnel, Elliott Lacaille Múzquiz (2022).

Bat diversity, eight species: *Artibeus jamaicensis*, *Desmodus rotundus*, *Diphylla ecaudata*, *Glossophaga soricina*, *Mormoops megalophylla*, *Natalus mexicanus*, *Pteronotus mesoamericanus*, *P. psilotis* (Mollhagen 1971; Torres-Flores and López-Wilchis 2010; Elliott 2015a, 2018). The risk factor for Florida is 1 for now.

18.4.2.10 Cueva de El Pachón, Tamaulipas

Pachón is an important site for the study of *Astyanax* cavefishes (Fig. 18.9; Mitchell et al. 1977; Wilkens and Strecker 2017; Elliott 2018). The cave is 583 m long and 8 m deep. The cave has moderately high biodiversity and six bat species: *Artibeus jamaicensis*, *Desmodus rotundus*, *Diphylla ecaudata* (De la Torre 1954), *Glossophaga soricina*, *Natalus mexicanus*, *Pteronotus mesoamericanus* (Martin and Martin 1954).

In 1971, using a two-census, mark-recapture method involving a caudal fin clip (Lincoln Index), Mitchell et al. (1977) statistically estimated the Pachón population of cave *Astyanax* conservatively as $\hat{N} = 9781 \pm 8502$). In 2009, Reynoso et al. (2009) reported a new population estimate using a similar fin clip method in Pachón of $\hat{N} = 2750 \pm 1927$. The 2009 Pachón $\hat{N}$ is only 28% of the 1971 $\hat{N}$, but the confidence limits are wide in both cases. There has been a decline of cavefishes in Pachón, but it is difficult to say how large the decline was. Reynoso said, "We conclude that the scientific community should be concerned about the vulnerability of blind cave fish populations, since fishes are constantly extracted, or populations are manipulated for scientific purposes…." This conclusion was mainly for Pachón, which is often

Fig. 18.9 *Astyanax mexicanus jordani*, the cave *Astyanax* or Mexican cavefish, model system in evolutionary and genomics research. About 70–100 mm long. Photo by Jean Louis Lacaille Múzquiz

visited by scientists. The cavefishes of this cave ought to be censused again. We have set the risk factor for Pachón at 4 (Table 18.1).

18.4.2.11 Sistema de los Sabinos, San Luis Potosí

Sistema de los Sabinos contains three hydrologically connected caves: Cueva de Los Sabinos, Sótano del Arroyo, and Sótano de la Tinaja. The highest elevation is 320 m asl at Tinaja. The system is inhabited by the fish *Astyanax jordani*, (Hubbs & Innes 1936) and is 13,206 m long and 155 m deep. The cave receives large floods during the rainy season and drains to the Nacimiento del Río Choy.

Because of studies by scientists from México, USA, and Canada from 1942 to 1974, the three caves are known to contain 127 species, including 14 troglobites, 42% of the known cave species of the Sierra de El Abra region. More concentrated study of other large cave systems is needed, but it seems likely that the Sistema de Los Sabinos will remain the richest in cave biodiversity in the region because of the concentration of bats (in Sabinos and Tinaja) and flood detritus. Only nine species occur across all three caves; five are troglobites and four are troglophiles. Sabinos and Arroyo share 23 species, Arroyo and Tinaja share 8 species, and Sabinos and Tinaja share a different set of 9 species. The 14 troglobites range more widely in the system. Four bat species are known: *Balantiopteryx plicata*, *Desmodus rotundus*, *Diphylla ecaudata*, and *Glossophaga soricina* (Mollhagen 1971). The caves are still wild, but there is occasional disturbance of bats by ecotourists (Elliott 2018). We have set the risk factor for this system at 2.

18.4.2.12 Sótano de Yerbaniz, San Luis Potosí

Sótano de Yerbaniz is 2238 m long, 97 m deep, and has three levels below the entrance at 242 m asl. It has a large catchment area of 16 km^2 and it floods violently. Eyed *Astyanax* fish are sometimes found on levels 1 and 2, cavefishes on level 3.

The cave has a rich fauna of 37 species with 10 troglobites and at least 2 bat species. Surface fish and hybrids are sometimes found in shallow pools in the cave. A two-census, mark-recapture study estimated the total number of cavefishes at 8671 with 95% confidence limits 1810–15,534 (Mitchell et al. 1977; Elliott 2018). Food input is from flood debris, guano, and dying surface fish (Elliott 2014, 2015a, b, 2018).

Yerbaniz hosts the blind scorpion, *Sotanochactas elliotti*, in one damp gallery of the cave. Three trips found only three specimens total in that one passage. It is still considered the world's most troglomorphic (cave-adapted) scorpion. The cave schizomid, *Agastoschizomus lucifer*, also was discovered in the cave. Bats: *Desmodus rotundus*, and unidentified bats in the main roost over Level 3 lake. We consider the risk factor as 1 for Yerbaniz.

18.4.2.13 Sótano del Médico, San Luis Potosí

The cave is 10 m long and 37 m deep and is also known as Sótano Caracoles Médicos. The name of this cave near Tlamaya reflects the large amount of medical waste, including used syringes that had been dumped into it (Minton 1992). Although the fauna is poorly known, a risk factor of 5 is assigned.

18.4.3 South Region

18.4.3.1 Cave near Mezcala, Jalisco

In the mid-1990s, a colony of *Leptonycteris sp.* bats was killed or driven off by local people from an unnamed cave near Mezcala. The people probably went after the common vampire bat, *Desmodus rotundus*, which inhabits another cave nearby (Mario Sgro, pers. comm. in Elliott 2000). Although the fauna is poorly known, a risk factor of 4 is assigned.

18.4.3.2 Cueva de la Isla de Janitzio, Michoacán

The cave had a small colony of free-tailed bats. Villa-R (1966) examined two specimens of *T. b. mexicana* from Cueva de Janitzio. In December 2000, Roemer (2003) went there because bats banded from Carlsbad Cavern in the United States were found there before. We have reports that the cave has been gutted.

18.4.3.3 Three Bat Caves in Guerrero: Grutas de Cacahuamilpa, Cueva Cuaxilotla, and Grutas de Juxtlahuaca

Three large bat caves lie within 140 km of each other in northern and east central Guerrero: Grutas de Cacahuamilpa (7 bat species), Cueva Cuaxilotla (12), and Grutas de Juxtlahuaca (8). Cacahuamilpa is 1380 m long and 120 m deep. The subterranean stream of Río Chontalcoatlán runs below Cacahuamilpa and extends 6 km to exit at the famous Dos Bocas. Cuaxilotla is 1620 m long, but the depth was not mapped as the cave is relatively level. Grutas de Juxtlahuaca is a show cave, 5,099 m long, depth unmapped, but at least 60 m deep at the greatest ceiling height.

Cacahuamilpa has moderate biodiversity and high-human disturbance (7 bat species, 20,000 total bats, 3 troglobites, and 30 total species). In contrast, Juxtlahuaca has moderately high biodiversity and less human disturbance (8 bat species, 70,000 total bats, 5 troglobites, and 93 species). Of the three caves compared here, Cuaxilotla has the highest bat diversity and population and the lowest disturbance (12 bats, >80,000). This is the best existing dataset comparing human impacts on cave biodiversity in México. Details for each cave are given below.

Grutas de Cacahuamilpa, Guerrero

Cacahuamilpa is an historical show cave, used like Juxtlahuaca by the Olmec people, and later by the Chontal tribe for ceremonial purposes. The first biological investigation of this cave was conducted in 1866 by the Austrian Reverend, Dominik Bilimek, who accompanied Maximiliano of Habsburg on a cave visit. Bilimek (1867) reported 11 species with one troglobite, *Anelpistina* (ex *Lepisma*) *anophthalma*. The next important contribution to the fauna of this cave was that of the Mexican biologist, Alfonso L. Herrera (1891, 1911). Federico Bonet and Cándido Bolívar y Pieltain made an intensive study of cave fauna for 20 years. They began with a visit to Grutas de Cacahuamilpa in 1939, then in 1941 to Grutas de Juxtlahuaca. Bonet in 1962 studied Grutas de Acuitlapán (Guerrero), and from 1951 to 1963, he published several articles on his excursions to caves, and finally in 1971 on the paleontology of the Cacahuamilpa region. In 1969, the Accademia Nazionale dei Lincei of Italy sponsored the first Italian speleological expedition to Mexico, conducted by Valerio Sbordoni, Roberto Argano, and Vittorio Parisi. They visited 17 caves in several states, including the Cacahuamilpa region. Descriptions were published of a large number of new troglobitic and stygobitic species.

A Master of Science thesis by Galicia-Castillo (2004) of Cacahuamilpa, Cuaxilotla, and Juxtlahuaca found the following (translation):

1. The recorded number of bat species using the caves as day shelters was 4 species (7 species total) for Cacahuamilpa, 8 species for Juxtlahuaca, and 12 species for Cuaxilotla. In Juxtlahuaca and Cuaxilotla, one of these species is *Leptonycteris yerbabuenae*, which is a migratory species and very sensitive to disturbance. In Cacahuamilpa, three other species, *Artibeus jamaicensis*, *Sturnira parvidens*, and *Glossophaga soricina*, were observed using the cave as a night shelter only.
2. Bats avoid using roost sites that are frequented by humans.
3. Even if the roost sites are off the tour, this activity contributes to reducing the diversity of bats. The diversity and abundance of guanobious organisms appear to be correlated with the diversity and abundance of bats.

4. Intensity in tourist use negatively affects the diversity and abundance of bats. The type of management given to each of the caves has a decisive influence on the degree of effect on the species present.

Galicia-Castillo's final conclusion is translated as follows: "We found a clear tendency of bats to avoid using human-frequented sites as a roost site. A negative relationship was observed between the number of visitors each cave received and the diversity and abundance of bats that were recorded. There was also a direct relationship between the diversity and abundance of bats and the diversity and abundance of microarthropods. These results suggest that human presence in caves is a factor that negatively influences bat populations, causing an imbalance in the cave ecosystem, the food chain of which is initiated from bat guano."

The cave has been open to the public with trails and lights for many years. Cacahuamilpa has some 20,000 bats of 7 species (4 day-roosting and 3 night-roosting species) and is subjected to an extremely high level of tourist disturbance, with dynamiting decades ago, electric lights, concrete throughout much of the cave, and much vandalism due to poor surveillance.

Seven bats still occur in Cacahuamilpa (Galicia-Castillo 2004): *Balantiopteryx plicata*, *Pteronotus psilotis*, *Glossophaga soricina**, *Artibeus jamaicensis**, *Sturnira parvidens**, *Mormoops megalophylla*, *Pteronotus fulvus* (* = night roost).

The ricinuleid *Pseudocellus boneti* has been cited from Acuitlapán and Cacahuamilpa, and it has been used for important contributions of ultramorphology and oogenesis. Cacahuamilpa is moderately low in biodiversity with 3 troglobites and 30 total species. We have assigned Cacahuamilpa a risk factor of 3.

Cueva Cuaxilotla, Guerrero

Cuaxilotla by far has the lowest disturbance levels of the three Guerrero bat caves discussed here. It houses over 80,000 bats of 12 species (Galicia-Castillo 2004): *Macrotus waterhousii*, *Leptonycteris yerbabuenae*, *Anoura geoffroyi*, *Glossophaga soricina*, *Natalus mexicanus*, *Pteronotus fulvus*, *P. mesoamericanus*, *P. psilotis*, *Mormoops megalophylla*, *Artibeus jamaicensis*, *Desmodus rotundus*, *Balantiopteryx plicata.* The invertebrate fauna is not well known. We have assigned a risk factor of 1.

Grutas de Juxtlahuaca, Guerrero

An important cave with ancient Olmec features, this show cave also is well known. Juxtlahuaca and Aguachil have rhagidiid mites. The amblypygid (whip spider) *Paraphrynus mexicanus* has been cited in 5 caves from Guerrero; the biggest population occurs in Juxtlahuaca. Juxtlahuaca has moderately high biodiversity with 8 bat species, 5 troglobites, and a fauna of 93 species (Table 18.1).

Eight bats are recorded from Juxtlahuaca (Galicia-Castillo 2004): *Mormoops megalophylla*, *Pteronotus mesoamericanus*, *Natalus mexicanus*, *Glossophaga soricina*, *Leptonycteris yerbabuenae*, *P. fulvus*, *Macrotus waterhousii*, *Desmodus rotundus*, with a total population of about 70,000, varying seasonally.

The large population is likely due to a good level of management and surveillance conducted by the private owners, who have protected the cave for over 50 years. It has very restricted and controlled tourism under constant surveillance, and the number of visitors is a few hundred per month versus tens of thousands per month in Cacahuamilpa (Galicia-Castillo 2004). However, the constant use of the cave has resulted in the decrease of the invertebrate fauna (Palacios-Vargas et al. 1985; Galicia-Castillo 2004). We have assigned a risk factor of 2.

18.4.3.4 Cueva Las Vegas, Puebla, Municipio Tenampulco

Also known as Cueva de las Vega, Cueva de la Vega, and Cueva El Sapo. Not in AMCS databases, no map, but listed by Arita (1992): 13 species, highly abundant; (Avila-Flores and Medellín 2004; Torres-Flores and López-Wilchis 2010). A total of 13 bat species have been reported for this cave: *Natalus mexicanus*, *Artibeus lituratus*, *A. jamaicensis*, *Carollia perspicillata*, *Desmodus rotundus*, *Diphylla ecaudata*, *Glossophaga soricina*, *Leptonycteris nivalis* (IUCN endangered), *Mormoops megalophylla* (IUCN decreasing), *Myotis keaysi*, *M. nigricans*, *M. velifer*, *Pteronotus mesoamericanus* (IUCN 2021). We have assigned a risk factor of 1, because there are no accounts of bat losses to date.

18.4.3.5 Sistema Huautla, Oaxaca

Sistema Huautla is the deepest cave in the Americas at 1560 m, and the fifth longest in Mexico at 89,000 m. The system at Huautla de Jiménez has been explored and mapped by skilled speleologists since 1966. There are six major caves: Sótano de San Agustín, Sótano del Río Iglesia, La Grieta, Sótano de Agua de Carrizo, Li Nita, and Nita Nanta (top of the system at 1760 m asl). With at least 28 entrances, the system continues to be pushed to new depths and lengths by PESH (Proyecto Espeleológico Sistema Huautla), an international organization. There are long, deep sumps at the bottom, Sump 9.

The system contains 48 species with at least 30 troglobites, a 63% troglobite component, the highest in México (Oscar Francke, pers. comm.; Table 18.1). The troglobites include amblypygids, schizomids, scorpions, opilionids, spiders, millipedes, Collembola (springtails), and silverfish. In Li Nita, a new troglobitic scorpion of the genus *Typhlochactas* was collected in 2014. At least two species of bats occur, *Desmodus rotundus*, common vampire, is not far inside one of the three Sótano del Río Iglesia entrances; and a small group of other bats is not far inside the Sótano de San Agustín entrance. Three caves were impacted by local garbage and medical waste dumping, but that has ceased and the PESH cavers have begun a clean-up campaign (Cruz-López and Francke 2019; Krejca 2016; Mendoza and Franke 2018; Steele 2019). We have assigned a risk factor of 2.

18.4.3.6 Cueva del Nacimiento del Río San Antonio, Oaxaca

This large cave is a drainage network under a ridge at 90 m asl, the source of the Río San Antonio. There are 30 species with 10 troglobites, including the blind catfish, *Rhamdia reddelli*, and the small-eyed crayfish, *Procambarus oaxacae reddelli*. At least one unidentified bat species inhabits the cave, noted from guano.

The fauna of the cave is as follows: "A rich invertebrate cave fauna is associated with the catfish. Four species of troglobitic crustaceans inhabit the cave: *Potamalpheops stygicola* Hobbs (Decapoda: Alpheidae), *Macrobrachium villalobosi* Hobbs (Decapoda: Palaemonidae), *Procambarus (Austrocambarus) oaxacae reddelli* Hobbs (Decapoda: Cambaridae), and *Speleomysis olivae* Bowman (Mysidacea: Lepidomysidae). A specimen of the alpheid shrimp *Potamalpheops stygicola* was disgorged by a catfish upon preservation. The rarity of shrimps and mysids in pools containing catfish is doubtless related to predation by the fish on the crustaceans. The cave is also inhabited by a possibly troglobitic clam, which is abundant in various parts of the cave but awaits study. The terrestrial fauna is extremely abundant and includes troglobitic trichoniscid isopods, nicoletiid *Zygentoma*, millipedes, spiders, and opilionids." Northern Oaxaca's Municipio Acatlán de Pérez Figueroa has at least three blind catfish caves (Reddell 1981; Miller 1984; Mejía-Ortiz et al. (1997); Palacios-Vargas et al. 2015; Elliott 2020). We have assigned a risk factor of 1.

18.4.3.7 Cueva Cerro Huatulco, Oaxaca

Huatulco contains 15 species of bats, the highest confirmed count among Mexican caves. It lies at 450 m asl, surrounded by patches of tropical forest with medium-sized semideciduous trees, shade coffee plantations, and grasslands. Most bats were captured for a study of bat flies (Streblidae) using mist nets placed 20 m from the cave entrance. Despite the relevance of this cave, there is no map of it. A total of 732 individuals of all bats were captured, corresponding to the families Phyllostomidae (10 spp.), Mormoopidae (4 spp.), and Natalidae (1 sp.). About 53% of the bats carried 1 or more streblid species, totaling 1317 streblid specimens belonging to 24 species and 8 genera. 15 bat species: *Artibeus jamaicensis*, *Artibeus lituratus*, *Dermanura phaeotis*, *Dermanura tolteca*, *Dermanura watsoni*, *Carollia subrufa*, *Sturnira hondurensis*, *Desmodus rotundus*, *Glossophaga soricina*, *Leptonycteris yerbabuenae*, *Natalus mexicanus*, *Mormoops megalophylla*, *Pteronotus fulvus*, *Pteronotus mesoamericanus*, and *Pteronotus psilotis* (Tlapaya-Romero et al. 2019). We have assigned a risk factor of 1.

18.4.3.8 Cueva San Francisco, Chiapas

Cueva San Francisco near La Trinitaria is 1750 m long and 288 m deep; elevation is about 1500 m asl. The cave may have the highest number of bat species among Mexican caves, but not all are documented. Also called Cueva or Grutas de Zapaluta or La Trinitaria, it was reported by Villa-R (1966) as a *Tadarida brasiliensis intermedia* roost. It was recognized by Arita (1992) as a critical cave for the conservation of Mexican cave bats at 8 species (but without a list), with very high abundance, and 2 "fragile" species. Chávez and Horváth (2009) reported 7 resident species and claimed another 9 species (but did not list them), a possible total of 16 bat species. Known bats: *Pteronotus mesoamericanus*, *Artibeus jamaicensis*, *Artibeus lituratus*, *Glossophaga comissarissi*, *Desmodus rotundus*, *Tadarida brasiliensis intermedia.* The cave also hosts many interesting guanophiles and troglobites. In 2014, the cave was badly polluted, receiving a direct discharge of raw sewage from the nearby village (Oscar F. Francke, pers. comm.) We have assigned a risk factor of 3.

18.4.3.9 Cueva de las Sardinas, Tabasco

Called Cueva de Villa Luz by many, its original name in the literature is Cueva del Azufre and/or Cueva de las Sardinas locally. At an elevation of 72 m asl, the cave is 1987 m long and 23 m deep. With a total of 173 species, Sardinas has the highest richness among Mexican caves; 3 troglomorphic species, with 8 bat species: *Balantiopteryx plicata*, *Mormoops megalophylla*, *Pteronotus fulvus*, *Pteronotus gymnonotus*, *Pteronotus mesoamericanus*, *Pteronotus psilotis*, *Desmodus rotundus*, *Myotis nigricans*. It is now famous for its large population of partially cave-adapted *Poecilia mexicana* fishes, H_2S, sulfur-fixing bacteria, and "snotites" (microbially created, soft stalactites).

Troglobites: *Robustocheles* sp. (Rhagidiidae mite), *Dugesia* sp. (planarian), and *Poecilia mexicana* (cavefish; Torres-Flores and López-Wilchis 2010; Sánchez-Hernández and Romero-Almaraz 2011; Palacios-Vargas et al. 2011a, b; Northup and Jones 2011).

"La Pesca de la Sardina" is the annual, sacred ceremony in the cave by local Zoque Indians on Palm Sunday weekend. The fish are stunned with rotenone, contained in the ground-up bark of the Barbasco vine. The toxin inhibits the use of oxygen by tissues, causing the fish to become sluggish, and to cluster along the shallow edges of the stream, where they are scooped up. In 2001, about 20 kg of cave-adapted fish were caught and consumed in local dishes. The event seems to have only minor, short-term impacts on the cave and its rich biological community. The abundant energy of the cave's ecosystem and the dynamic nature of the ecology of the cave appear to make this exploitative event sustainable (Hose 2001). We have assigned a risk factor of 2.

18.4.4 Yucatán Peninsula

18.4.4.1 Volcán de los Murciélagos, Campeche

Nine bat species inhabit this extensive cave located in the public reserve of Balamkú, in the area of influence of the Reserva de la Biósfera de Calakmul, part of the ecosystem called La Selva Maya. Also called the Calakmul Bat Volcano, the cave is 670 m long and 117 m deep. The entrance is a deep funnel or sinkhole, followed by a steep slope down to about 120 m below the surface, where there is collapse area and breakdown pile. Another slope down comes to a high chamber, then another slope down to the nearly level bottom of the cave, about 450 m long, ending in a slope up to the ceiling (Rojo and Gheysens 2006; Arroyo-Cabrales et al. 2011; Vargas-Contreras et al. 2011, 2012).

El Volcán had perhaps 800,000–1000,000 bats in the early 2000s (Escalona-Segura et al. 2002, 2019). Bat emergences recorded with a camcorder in 2010–2011 lasted 30–45 min, and with a thermal camera 90 min, which suggests an estimated population over 3 million bats. In an unpublished chapter, Vargas-Contreras et al. (2011) reported that, "We observed cave visitors littering the surroundings. This cave can be used for tourism following some recommendations, establishing visitors' carrying capacity, and visiting after the reproductive season."

With a total bat diversity of 9 species, including the following trophic groups: insectivorous bats: *Mormoops megalophylla*, *Pteronotus mesoamericanus*, *P. fulvus*, *P. psilotis*, *P. gymnonotus*, *Natalus mexicanus*, *Myotis keaysi* and *Nyctinomops laticaudatus.* Nectivorous bats: *Glossophaga soricina* (Vargas-Contreras pers. comm.).

The cave contains some invertebrates: *Stenophysa* aquatic snails, *Mayaweckelia cenoticola* amphipods, and *Antricola mexicanus* soft ticks. Carbon-dioxide concentrations are dangerously high at 3–5%. The cave also harbors *Histoplasma capsulatum*, the fungal agent of histoplasmosis, a lung disease (Rojo and Gheysens 2006). Only qualified and safely equipped visitors should visit the cave's interior.

A large management plan was published in 2019, analyzing multiple aspects of the ecology and agroeconomy of the cave bats and the surrounding reserve (Escalona-Segura et al. 2019). We have assigned a risk factor of 2.

18.4.4.2 Cenote Sambulá, Yucatán

Also known as Cueva Sambulá and Cueva del Rancho Sambulá, this cenote is used for recreational purposes. The entrance is circular, about 5 m in diameter and 6 m deep. A slope with concrete steps supported by pillars leads to a large chamber with a concrete floor 10 m wide. Under the steps, the passage extends for about 20 m before ending in a series of low passages. In the opposite direction, the passage extends 15 m before meeting the flooded floor, which gradually becomes deeper, from 0.8 to 2 m. There is an excavated well with an extraction pump; 12 m beyond the pool ends and there are two low passages with a height of 1 m over a stretch of

10 m. The water temperature is between 26.7 and 27 °C and pH 6.5. (Barba-Macías, Palacios-Vargas 1998).

This is a cave with moderately high biodiversity, 53 species with 5 troglobites, but no bats, although they should be present. We set the risk factor at 4 based on the disturbed condition of the cave and loss of biodiversity.

18.4.4.3 Cueva de El Pochote, Yucatán

A pig farm (Agropecuaria Yucatán) was constructed above Cueva de El Pochote, which contained a unique cave fauna, including the cavefishes *Ogilbia pearsei* and *Ophisternon infernale*. The consequences of this action have not been reported in the literature. Only five caves contain both of these fishes. The cave also contains the isopod *Creaseriella anops* and the shrimps *Creaseria morleyi* and *Typhlatya pearsei*. Cenotes provide important habitat for stygobites and other species, such as the Morelet's crocodile, and provide drinking water for endangered mammals, such as the jaguar (Hall 1936). No studies of pollution effects on cave species of the Yucatán Peninsula have been published to date (Elliott 2000). Details about the cave's fauna are lacking, but we have set the risk factor at 2.

18.4.4.4 Cenote Dzitya, Yucatán

In Mérida, some wastewater is disposed of by deep-well injection, but its fate has not been traced. Pig farms and cattle ranches are another potential source of pollution, and use of fertilizers and pesticides threatens the karst groundwater in some areas. Solid waste is often dumped at the edges of towns or into dry caves. Cenote Dzitya, near Mérida, was contaminated by a nearby pig farm, according to water chemistry and algal data (Elliott 2000). Some cenotes in the Yucatán Peninsula are being cleaned by cavers and citizens, who are removing tires and trash (Sergio Grosjean and Roberto Rojo groups). Details about the cave's fauna are lacking, but we have set the risk factor at 2.

18.4.4.5 Grutas de Balankanché, Yucatán

Balankanché is an important cultural site as well as a high-biodiversity cave, with 59 species, 13 troglobites, and a diverse bat fauna with 7 species. The cave entrance is at 28 m asl, and the cave is 1400 m long and 15 m deep, with a trail about 500 m long through the main, dry passages. It is operated as an educational show cave in an archaeological zone. It is one of the few Mexican caves with two stygobitic fishes: *Ophisternon infernale* and *Typhliasina pearsei.* The aquatic fauna includes four troglobitic crustaceans: *Caecidotea* sp., *Antromysis cenotensis*, *Typhlatya pearsei*, and *Creaseria morleyi.* The terrestrial troglobite fauna includes a squamiferid isopod (*Trichorhina pearsei*), a trichoniscid isopod (*Cylindroniscus maya*), a pseudoscorpion (*Vachonium maya*), an amblypygid (*Paraphrynus chacmool*), an oonopid spider (*Oonops coecus*), a collembolan (*Troglopodetes maya*), and a gryllid cricket (*Tohila atelomma*). The cave is noted for a large population of the ricinuleid, *Pseudocellus pearsei*.

Even though the bat colonies are not large (Reddell 1977), three bat species were initially identified by Jones, Smith, and Genoways in 1973. Later Torres-Flores and López-Wilchis (2010) reported 7 bat species: *Natalus mexicanus*, *Artibeus jamaicensis*, *Desmodus rotundus*, *Glossophaga soricina*, *Mormoops megalophylla, Myotis keaysi*, and *Pteronotus mesoamericanus*. We have assigned a risk factor of 2 for Balankanché.

18.4.4.6 Cueva (Cenote) Aerolito de Paraíso, Isla Cozumel, and Other Systems, Quintana Roo

Many extensive, submerged, freshwater, and anchialine cave systems exist on the Caribbean coast of Quintana Roo. These world-class systems are actively explored by large numbers of serious cave divers and ecotourists. The longest is Sistema Sac Actún (+ the Dos Ojos system) at 371,958 m, the longest submerged cave in the world. Sistema Ox Bel Há is second at 271,026 m, and Sistema K'oox Baal (+Tux Kupaxa system) is third at 100,431 m (Minton 2020). Few of these cave systems have been well-studied biologically, and some of them are vulnerable to groundwater pollution from nearby tourist areas. A groundwater study by Kane and Lenczewski (2016) showed that the primary contaminants were bacteria, with high amounts of total coliform and *E. coli* fecal bacteria. Nutrient levels and metals were in low concentrations, and antibiotic tests produced negative results. Cavers and local citizens have embarked on trash removal and restoration projects at cenotes, sinkhole entrances to the systems (Fig. 18.10).

Sistema Aerolito or Cueva (Cenote) Aerolito de Paraíso (18,288 m long) is an anchialine cave on the west coast of Isla Cozumel, which connects to the Caribbean Sea and contains many unusual marine species. There are at least six stygobites of marine origin: *Copidaster cavernícola*, brittlestar; *Ophionereis* n. sp., brittlestar; Order Canalipalpata, an undescribed genus and species of polychaete worm is a possible stygobite; *Macrochaeta* is a possibly stygobitic polychaete worm; *Bahadzia bozanici*, hadziid amphipod; *Yagerocaris cozumel*, alpheid "snapping" shrimp (Pisanty et al. 2010; Frontana-Uribe and Solís-Weiss 2011; Ortiz and Cházaro-Olvera 2015; Ortiz and Winfield 2015, 2016). No remipedes or isopods are documented yet, but they would be expected based on similar caves. Threats to the cenote include groundwater pollution by land development and tourist facilities. We have assigned a risk factor of 1 for Aerolito.

Fig. 18.10 Trash removal by cavers and local citizens from Cenote Chancom, Yucatán. Photo by Sergio Grosjean-Avimerhi

Table 18.4 Summary of the risk values for 62 caves documented in this chapter

Risk	Caves
1	*36*
2	*16*
3	*3*
4	*4*
5	*3*
Gutted	*2*
Total	*64*

18.5 Conclusions and Recommendations

Mexico is superlative not only in the number of caves, but in their biodiversity and the scale of ecosystem services they provide. Knowledge of the fauna in Mexico's nearly 12,000 caves has increased greatly over 200 years. The fauna is still incompletely explored, but we have enough information to recommend strong conservation policies.

In 1995, Palacios-Vargas proposed adding the cave environment to the GEEPA Act, passed by the Mexican Congress in 1988 and amended in 2021 (El Congreso de los Estados Unidos Mexicanos, 2021), Article 55 establishes sanctuaries (reserves) for "grutas, cavernas, cenotes" and other natural features, but there are no specific penalties for causing harm, and cave fauna and bats are not mentioned.

In this chapter, we have specifically documented 64 caves (including 3 mines) in tables and text, but many thousands remain to be evaluated. Table 18.4

summarizes the risk values for the 64 sites, 28 (44%) of which present clear signals of human impact. Thirty-six caves have a risk value of 1 (a normal wild cave) and 16 have a mild risk of 2. Three caves have a moderate risk value of 3: Cueva Chica, Grutas de Cacahuamilpa, and Cueva San Francisco. A risk value of 4 was assigned to Cueva de la Boca, Cenote Sambulá, Cueva de El Abra, and Cueva de El Pachón because of species losses or threats. Grutas de Quintero lost two bat species, much aquatic habitat, and is at risk 5 of further damage to the cave and its rich fauna. In Coahuila, Cueva del Cañón El Buey and Toxic Sink were severely degraded with toxic trash and were rated at risk factor 5. Cueva del Ídolo, Morelos, and Cueva de la Isla de Janitzio, Michoacán, were gutted of life and may never recover their lost fauna.

Probably hundreds of Mexican caves have been impacted by humans. A similar trend has occurred in the USA (Elliott 2000). Disruption and destruction of bat roosts is the most damaging activity, but recent activities, including unregulated tourist use of caves, have strongly affected them.

About 800 obligate cave species are endemic to Mexican caves. The largest concentrations of wild mammals in Mexico are in caves, and the largest bat cave in the Neotropical biogeographic realm, the Volcán de los Murciélagos (Calakmul Bat Volcano), contains over 3 million bats. No other cave in the Neotropics has more bats.

In the Nearctic biogeographic realm, roughly including the northern half of Mexico, many caves are essential providers of ecosystem services. McCracken (1986) estimated that in the southwestern USA there might be 120–150 million Mexican free-tailed bats from spring to autumn. Although this may be an overestimate, it is likely that the Mexican states that border the USA have between 20 and 30 million *Tadarida brasiliensis*. This is an important resource for both nations (Russell et al. 2005, López-Hoffman et al. 2017).

Our data in Table 18.3 have 23 *T. brasiliensis* caves, with 12 having an aggregate of about 5 million bats. Many others host smaller colonies. Cave exploration is still preliminary across Mexico, but with our estimate of 20–30 million just in northern Mexico, bats consuming insects at the rate of 10 tons every night per million bats, would yield an ecosystem service that is in the order of magnitude reported by Lopez-Hoffman et al. (2017), Medellín (2009), Wiederholt et al. (2013, 2015, 2017), Federico et al. (2008), and Gándara et al. (2006). The order of magnitude goes from US $578,000 per year in the vicinity of Monterrey, Nuevo León, provided by Cueva de la Boca alone (Gándara et al. 2006), which is still at risk, to US $3.7 billion for the conterminous USA (Boyles et al. 2011). Furthermore, we know that *T. brasiliensis* moves far away from its roost caves each night, but even underestimating the area covered with a radius of only 50 km, the area of influence of 7850 km^2 around each cave (Medellín et al. 2017) yields an area of about 100,000 km^2 around the known *T. brasiliensis* caves.

18.6 Conservation Guidelines

Considering the losses that already occurred in at least 28 Mexican caves and mines, we recommend the following conservation guidelines that could be implemented at different levels of government:

1. Enact and enforce national legislation for caves (cavernas, cenotes, cuevas, grutas, sótanos) on private, state, and federal lands that prohibit vandalism, trash dumping and sewage discharges into caves, destruction and degradation of caves, and disturbance and killing of cave life, except the minimum sampling necessary for scientific study.
2. Prohibit mining of resources in all natural caves except under federal permits that ensure no disruption or harm to bats and other fauna, and only sustainable extraction of bat guano.
3. Prohibit disturbance, harassment, and killing of bats in caves and abandoned mines, which often contain bats beneficial to agriculture, except for precise, selective control of the Common Vampire Bat, *Desmodus rotundus.*
4. Establish a university institute to map and document Mexico's caves, abandoned mines, cave life, and cave-related geology, hydrology, and cultural resources, and to educate the public about the value of cave resources. The institute should work cooperatively with existing Mexican and international speleological groups, INEGI (Instituto Nacional de Estadística y Geografía), and other resource agencies. A repository of data and literature is needed, with a central, secure database. A geographic information system should be maintained in cooperation with existing speleological groups and INEGI.
5. Precise cave locations must be protected from general public view to avoid overuse or exploitation of caves by vandals. Protection of cave location data applies to the central cave database, INEGI, and other mapping agencies. Registered contributors and individuals with a valid need to know would be able to borrow limited cave location data for exploration, science, and conservation. Limited data may be available to those proposing possibly sustainable use of caves, which must be detailed in a written proposal. Data users would be encouraged to share new and corrected cave locations and data with the central database.
6. It is important to allow reasonable cave access to qualified explorers, scientists, conservationists, and cultural experts provided that they conform to conservation rules and laws for the caves and abandoned mines, and that they provide reports and data to the central database.
7. A new Federal initiative should create natural reserves (reservas naturales) to protect caves of all types, karst, volcanic caves, associated groundwater, and abandoned mines. Federal, state, and private funding should be sought for cave and bat conservation projects at all levels. Restoration of natural caves should be promoted. Traineeships should be offered at resource agencies to foster a new generation of cave and bat conservationists.

8. Steel cave gates should be built according to the best practices of the American Cave Conservation Association and their partners; see Elliott (2006, 2011) and Hildreth-Werker and Werker (2006). Cave gates are needed for a few caves and abandoned mines to prevent intruders from entering, but construction must be followed by a program of surveillance, inspection, and repair, as most gates are eventually broken or defeated by vandals.
9. Resource and mapping agencies should be included in these efforts and are encouraged to create new positions for cave specialists, biologists, and conservationists. Research and support projects dealing with cave life must be promoted and financially supported.
10. The operators of tourist (show) caves should write environmental plans to prevent, mitigate, or restore damage to their caves and fauna. The operators should set the maximum number of visitors and the proper season for use, especially when bats are present.

Acknowledgments We would like to thank Patricia Ornelas-García (review, editing), Robert W. Jones (editing), Jean Louis Lacaille Múzquiz (data), Peter Sprouse (data), José Alfredo Hernández-Vázquez (literature), Oscar F. Francke (review, data), Graham Proudlove (data), Jorge A. Vargas-Contreras (data, literature), Adam Haydock (photo), Alejandro Gómez (photo), Sergio Grosjean-Avimerhi (photo), Andy Murray (photo), James R. Reddell (literature), Francis E. Abernethy (photo, deceased), and Robert W. Mitchell (photo, deceased).

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Chapter 19
Fauna of Inland Waters

Javier Alcocer and Verónica Aguilar-Sierra

Contents

19.1 Introduction

The geographic location around the Tropic of Cancer involved a dominant tropical-subtropical seasonality in Mexico. The latter, combined with an irregular topography with seven mountainous ranges, extended high-altitude plateau, and coastal plains, originated a great variety of epicontinental water bodies inhabited by a diverse aquatic biota, rich in endemic species (Alcocer and Aguilar-Sierra 2019).

J. Alcocer (✉)
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

V. Aguilar-Sierra
Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Tlalpan, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_19

Epicontinental aquatic resources include lentic and lotic ecosystems. Lentic ecosystems comprise lakes, ponds, and reservoirs, while lotic ecosystems include rivers and streams.

The integrity of the epicontinental water bodies and their biological diversity is increasingly threatened by human activities worldwide (UNEP-WCMC 2016). The great variety of cross-sectoral activities are at odds with each other and with the species' needs. The reduction in the volume of surface and groundwater available and the deterioration of its quality demonstrate that inland waters are not inexhaustible resources. The social and economic well-being of a country depends, to a large extent, on the capacity of these aquatic ecosystems to provide their environmental goods and services, hence the importance of its use being rational and sustainable (Aylward et al. 2005). The epicontinental water bodies play a fundamental role from the ecological point of view (Balvanera et al. 2016) and as such, it is necessary to address the many problems related to their integrity, the sustainability of the ecosystems, and the survival of their species.

The biodiversity of inland waters is an essential part of the national heritage and is currently highly degraded by inefficient management and lack of planning. The "Comisión Nacional para el Conocimiento y Uso de la Biodiversidad" (CONABIO), a Mexican governmental commission, organized a workshop to diagnose the relationship between epicontinental aquatic resources and biological diversity. The idea was to provide a reference framework for the different sectors involved in developing research, conservation, use, and management plans of epicontinental aquatic resources. This exercise identified 110 priority hydrological regions (PHRs) according to their biodiversity (Arriaga-Cabrera et al. 2000). Among these, 82 (74.5%) corresponded to areas of high use, 75 (68.2%) had high biodiversity with potential for conservation, 75 (68.2%) were threatened, and 29 areas (26.4%) were biologically important but poorly known.

The PHRs are a mosaic of aquatic environments that maintain a good state of ecological conservation that represents aquatic resources in need of preservation due to their current and potential economic importance, ecological functions, and natural value. Concerning the problems identified in the PHR, the overexploitation of surface and groundwater stands out, causing a notable decrease in the amount of available water. Other problems are saline water intrusion, desertification, and contamination of shallow and deep aquifers, mainly by urban, industrial, agricultural, and mining discharges that cause a decrease in water quality and eutrophication. Additionally, accelerated erosion processes caused by changes in land use for agriculture, livestock, forestry, and urban and industrial growth through activities that modify the environment, such as deforestation, alteration of watersheds, construction of dams and canals, desiccation, or filling of flooded areas, modification of natural vegetation, loss of soil, and fires, are occurring. Finally, the introduction of exotic species to epicontinental water bodies with the consequent displacement of native species and a decrease in biological diversity is another important threat.

19.2 Hydrological Background

According to the "Comisión Nacional del Agua" (CONAGUA 2018), the surface area of Mexico is around 1.96 × 10^6 km^2; 67% of the country is arid and semiarid (precipitation <500 mm per year or as low as <100 mm per year), while 33% is humid (precipitation >2000 mm per year or as high as >4000 mm per year). Mexico has a limited volume/area of inland waters representing around 0.1% of the world's fresh water reserve. Although lentic aquatic resources are comparatively unimportant regarding the lotic aquatic resources, they are considered critical regional resources.

There are administrative bodies for 13 basins ("organismos de cuenca") for the administration and preservation of Mexican inland waters, geographically delimited regions for governmental hydrological and administrative management. There are approximately 12,000 lakes, 611 reservoirs (82% of total storage is in 180 large dams), and 633,000 km of rivers (though 51 rivers drain 87% of the total runoff of the country) distributed in the 757 main drainage basins (Alcocer and Escobar 1996; Alcocer and Bernal-Brooks 2010).

The largest lakes are Chapala in Jalisco, Cuitzeo and Pátzcuaro in Michoacán, Catazajá in Chiapas, Del Corte in Campeche and Bavícora, and Bustillos and Encinillas in Chihuahua, while the largest dams are El Caracol in Guerrero, El Humaya (Presidente Adolfo López Mateos) in Sinaloa, La Amistad in Coahuila, Las Adjuntas (General Vicente Guerrero) in Tamaulipas, Aguamilpa in Nayarit, Temascal (Presa Presidente Miguel Alemán) in Oaxaca, Infiernillo in Michoacán, and Netzahualcoyotl (Malpaso), La Angostura (Doctor Belisario Domínguez), and Chicoasén (Presa Manuel Moreno Torres) in Chiapas.

The more extensive drainage basins are the Bravo River (Chihuahua, Coahuila, Nuevo León, and Tamaulipas) and Balsas River (Guerrero and Michoacán), while the longest rivers are the Bravo and the Grijalva and Usumacinta (Chiapas and Tabasco). The Lerma and the Nazas and Aguanaval (Durango and Coahuila) are the most important interior watersheds. Regarding lakes, the largest are more numerous in the Gulf of Mexico and southeast regions, while the largest reservoirs are along the Pacific coast and in the north-central area of Mexico (Alcocer et al. 2000a).

19.3 The Anthropocene

The Anthropocene is the name used to identify a geological epoch, the most recent period in Earth's history, when anthropogenic activities have impacted significantly the planet leading to global planetary-scale environmental changes. Anthropocene is still nonofficial and needs to fit formal requirements for its recognition as a new epoch. The beginning of this epoch is also still in debate, but two dates are the most appointed: 1610 and 1964 (Lewis and Maslin 2015).

Earth's climate has changed between warmer (e.g., Medieval Warm Period) and colder (e.g., Little Ice Age) periods. General colder conditions took place AD 1580 and 1880 while warmer in recent times (AD 1971–2000). This recent warming reached higher temperatures than in any other time in nearly 1400 years (Pages 2k Consortium 2013). Preindustrial (1300–1800 CE) climate variability relates to volcanic aerosols. However, the second half of the twentieth century displayed the largest – and unusual – warming trend in recent decades (Pages 2k Consortium 2019).

During the last 1500 years, the climate has experienced short- and long-term variability with several megadroughts. Solar insolation minima coincide with megadroughts suggesting these hemispheric phenomena are solar forcing (Asmerom et al. 2013). Nonetheless, the climatic variability is also due to the differential impact of other forcing agents (e.g., Pacific Decadal Oscillation, Atlantic Multidecadal Oscillation) on precipitation seasonality (Metcalfe et al. 2015). There was a reduction in the summer precipitations in the north, in the center, and even in the country's southern regions, with extreme drought events in the twentieth century (Lozano-García et al. 2015).

Other anthropic activities (e.g., sewage, agriculture, deforestation, erosion, eutrophication) add up to climate change (e.g., droughts) adversely affecting inland water bodies. Diverse studies exhibit the intense anthropic disturbances in Mexican lakes from the 1950s or 1960s onward like Lago Verde, Veracruz (Caballero et al. 2006); Lake Balamtetik, Chiapas (Caballero et al. 2020); Lake Santa María del Oro, Nayarit (Lozano-García et al. 2021; Rodríguez-Ramírez et al. 2015); and Lakes El Sol and La Luna, Estado de México (Alcocer et al. 2020).

19.4 Fauna of Inland Waters

Mexico is considered a megadiverse country. It is one of the few countries that possess, when taken all together, 70% of the vertebrate and vascular plant diversity worldwide (Llorente-Bousquets and Ocegueda 2008). However, little is known about the biodiversity of Mexican epicontinental water bodies, and it is unknown whether these ecosystems present the same trend of high biodiversity that terrestrial communities show. Probably one of the better known groups is freshwater fish. Miller et al. (2005) mentioned that Mexican freshwater fish biodiversity is two-thirds of the USA and Canada.

However, Mexican freshwater fish fauna is highly diverse, with 536 species and high levels of endemism (Lyons et al. 2020). Also, research on Mexican freshwater decapods, starting in 1815, recognizes 172 species with many endemisms, most of them with highly restricted distributions (Alvarez and Villalobos 2016). Unfortunately, the biodiversity of freshwater ecosystems is inadequately known and described, particularly for small invertebrate groups (Cortés-Guzmán et al. 2019).

Moreover, unsustainable water use in Mexico is leading to inland aquatic habitat loss and degradation. Overextraction and diversion of surface and groundwater mainly for agriculture and human use for industrial and urban development have largely depleted or even exhausted valuable hydric resources. Pollution, eutrophication, exotic species introductions, and construction of large dams have altered the natural flow and regime of many major rivers and imposed additional pressure on aquatic biota (Lyons et al. 2020).

Many Mexican inland water species are endangered. For example, 40% of the freshwater fish species in Mexico are threatened with extinction. Of the 536 freshwater fish species, 291 are endemic to Mexico. According to the IUCN Red List Categories, 12 species are already extinct, and 8 are extinct in the wild; these 20 species are endemic. Forty-four species, all of them endemic, are critically endangered. Seventy-one species, 64 of them endemic, are endangered. Fifty species, 38 endemic, are vulnerable. Other 351 species, 125 of them endemic, are considered as near threatened (5.1%), least concerned (66.7%), and data deficient (28.1%). The families with more species included in the IUCN Red List are Poeciliidae with 86, Cyprinidae with 77, Cichlidae with 50, Goodeidae with 40, Atherinopsidae with 38, and Cyprinodontidae with 33 (Lyons et al. 2020).

Fifteen species of "axolotl" (*Ambystoma*), a well-known Mexican iconic species, are already listed in the Official Mexican Standard NOM-059-SEMARNAT-2010; all of them are endemic and some, for example, *A. taylori*, with a very restricted distribution area (Escobar et al. 2021; Parra-Olea et al. 2021). Eleven species of *Ambystoma* are classified as *Pr* or subject to special protection (i.e., those species that could be threatened by factors that negatively affect their viability, thus determining the need to promote their recovery and conservation or the recovery and conservation of populations of associated species). Three species are categorized as *A* or threatened (i.e., those species that could be in danger of disappearing in the short or medium term, if the factors that negatively affect their viability continue to operate, by causing the deterioration or modification of their habitat or directly reducing the size of their populations). Finally, one is listed as *P* or in danger of extinction (i.e., those species whose areas of distribution or size of their populations in the National Territory have drastically decreased, putting their biological viability at risk throughout their natural habitat, due to factors such as the destruction or drastic modification of the habitat, unsustainable exploitation, and diseases or predation, among others). The better known cases are the Mexican axolotl (*A. mexicanum*) and Taylor's salamander or the Alchichica's axolotl (*A. taylori*). All the same 15 species are also included in the IUCN Red List of threatened species. Six species (40%) are critically endangered (CR), six (40%) endangered (EN), two (13.3%) least concern (LC), and one (6.7%) data deficient (DD). The six critically endangered species are *A. amblycephalum*, *A. andersoni*, *A. mexicanum*, *A. dumerilii*, *A. leorae*, and *A. taylori.*

Mexican freshwater decapods (Crustacea) belong to eight families: Atyidae, Palaemonidae, Alpheidae, Cambaridae, Parastacidae, Pseudothelphusidae, Trichodactylidae, and Glyptograpsidae. As well as most biological groups, Mexican freshwater biota is composed of Nearctic and Neotropical lineages. Biodiversity hotspots are distributed along the Trans-Mexican Volcanic Belt, where orography generates numerous endorheic basins promoting an "endemism belt." Only 12 out of the 172 freshwater decapod species are listed in the Official Mexican Standard

NOM-059-SEMARNAT-2010. Differently, the IUCN Red List includes 172 species of Mexican freshwater decapods, of which 70 (40.7%) are data deficient (DD), 52 (30.2%) least concern (LC), 7 (4%) near threatened (NT), 22 (12.8%) vulnerable (VU), 9 (5.2%) endangered (EN), 9 (5.2%) critically endangered (CR), 2 (1.2%) extinct (EX), and 2 have not been assessed (Alvarez and Villalobos 2016).

An essential reference compiling the fauna inhabiting Mexican epicontinental water bodies is "Aquatic Biota of Mexico, Central America and the West Indies" (Hurlbert and Villalobos 1982). Many species listed there may be extinct nowadays. Although no update of this valuable information is available yet, Alcocer and Aguilar-Sierra (2019) present an essay on the biodiversity of inland waters.

19.5 Inland Water Ecosystems

Diverse human impacts threaten Mexican inland aquatic resources. Among them are catchment/drainage basin activities (e.g., deforestation, erosion), diversion of inflows (e.g., agriculture), pollution (e.g., urban and industrial development), physical impacts on drainage basins (e.g., overextraction of surface and groundwater), and direct impacts on the biota (e.g., overfishing, exotic species introduction).

Twenty basins show a very high eco-hydrological alteration qualifying as "basins of extreme priority" and cover 35.74% of the national territory. This category contains numerous large river basins (Bravo, Pánuco, Grijalva-Usumacinta, Balsas, Lerma-Chapala, Santiago, and Papaloapan, among others), the basins of important lakes (Cuitzeo, Zirahuén, and Pátzcuaro), and several small but relevant basins with high aquatic biodiversity, which are located mainly in the coastal plain of the Pacific Ocean and the western slope of the Baja California Peninsula. These basins display an ample variety of ecosystems and habitats, high species diversity, high endemism and microendemism, and important wetlands (Aguilar et al. 2010).

Seven river systems in Mexico show a very high eco-hydrological alteration: the rivers of the Mexico basin, the Balsas River, the rivers of Lake Cuitzeo basin, the Bravo River, the Santiago River, the Pánuco River, and the San Luis Potosí River. These seven rivers correspond to 31% of the total length of the hydrographic network of the country. Their basins' surfaces occupy 26% of the national territory, where 52% of the Mexicans inhabit. Regarding their volume, the most important Mexican rivers, the Grijalva and Usumacinta Rivers, display high eco-hydrological alteration (Garrido et al. 2010).

Multiple drivers impact the Mexican territory and groundwaters. The governmental (CNA) surface water network consists of 3493 monitoring sites covering the Mexican territory and measures eight water quality-related parameters (i.e., BOD_5, COD, total suspended solids, fecal coliforms, *E. coli*, enterobacteria, dissolved oxygen saturation, toxicity). Only 31.2% of the monitoring sites met the acceptable water quality limits, while the remaining 68.8% failed in fitting one or more of the eight water quality limits. Similarly, the groundwater network consists of 1068 monitoring sites measuring 14 water quality-related parameters (fluorides, fecal coliforms, nitrate-nitrogen, total arsenic, total cadmium, total chromium, total mercury, total lead, alkalinity, conductivity, hardness, total dissolved solids, total manganese, and total iron). In this case, 40.6% of the monitoring sites met the acceptable water quality limits, while the remaining 59.4% failed in fitting one or more of the 14 water quality limits (Comisión Nacional del Agua 2018).

Changes in the water quality, pollution, eutrophication, and exotic species introduction, among other variables, have led to inland aquatic biodiversity loss. Primarily but not exclusively, species extinction occurs in the water bodies close to large urban and industrial developments of Central Mexico (e.g., 39% of Mexico's freshwater fishes are threatened with extinction, Lyons et al. 2020). Climate change adds to these anthropic impacts to accelerate inland aquatic ecosystems' deterioration and desiccation. Examples illustrating the significant impacts on Mexican inland water ecosystems leading to ecosystem alterations or even disappearance (Fig. 19.1) are presented next.

Fig. 19.1 Location of the inland water ecosystems mentioned below: (1) Lake Chapala, Jalisco; Lakes Cuitzeo and Pátzcuaro, Michoacán, and Valle de Santiago, Guanajuato; (2) Lakes Totolcingo, Puebla-Tlaxcala, Tepeyahualco, and Alchichica, Puebla; (3) Lakes El Sol and La Luna, Estado de México; (4) Cuatro Ciénegas, Coahuila; and (5) Montebello, Chiapas

19.5.1 Lakes Chapala, Cuitzeo, and Pátzcuaro

Chapala in Jalisco and Cuitzeo and Pátzcuaro in Michoacán are three of the most emblematic lakes in Mexico. Located in the central-western part of the country, the federal and state governments have long-term information on level fluctuations. The water level in these lakes presents two components. The first component, seasonal, depends on the recurring dynamics of the rainy and dry seasons, which increases or decreases the lakes' water level as a function of the morphometric characteristics different for each lake basin.

The second component constitutes the long-term trend superimposed on the seasonal fluctuations, which encompasses decades, coincident approximately in the three lakes. Worldwide, the cyclical variation in solar activity induces lake level oscillations with periods between 20 and 50 years. Decadal phenomena (e.g., ENSO) also influence the hydrometeorological regime on lakes, as found for Lake Chapala (Filonov et al. 2016; Tereshchenko et al. 2002).

In general, from 1935 to 1955, the long-term component involves a decrease in the water level of the lakes to resume with a recovery at the end of the decade of the 1960s as a closing of a cycle. This trend remains stable until approximately 1978. From then on, the lake levels again progressively lose depth until 2001 when they acquire a lower position compared to 1955 (−519 mm in the case of Lake Pátzcuaro; Bernal-Brooks et al. 2002; Gómez-Tagle et al. 2002). However, the expected recovery of the water volume to conclude the cycle and start a new one between 1998 and 2008 did not occur, just a slight increase trend that lasted until 2005. As a synchronous phenomenon in the three largest lakes in central-western Mexico, the influence of the long-term climate component raises concern as to why there are currently no signs of recovery in these lakes to higher levels. In the long-term component, the lakes of the western central part of Mexico reach an exceptional filling condition at the end of the 1930s decade relative to the current condition. Such evidence clarifies the net loss of water in the lakes and a progressive advance of desertification.

19.5.2 Lakes Totolcingo and Tepeyahualco

In the south-easternmost portion of the Mexican Altiplano lies the Oriental basin occupying part of Puebla, Tlaxcala, and Veracruz. It is a large (~5000 km^2) endorheic basin holding at the central and lowest portion of two shallow lakes extended for ~290 km^2: Laguna de Totolcingo or El Carmen and Laguna de Tepeyahualco or El Salado (Fig. 19.2). Although climate change can not be discarded, agriculture, groundwater overextraction, and growing urban and industrial developments largely depleted these lakes. Laguna de Tepeyahualco was the first one that became dry. At the same time, Laguna de Totolcingo changed its hydrological regime from permanent to temporal drying in the dry season while flooding in the rainy season. Later,

Fig. 19.2 Lake El Carmen after the rainy season. (Photograph by Javier Alcocer)

Laguna de Totolcingo turned to episodic flooding only under extraordinary rainfall seasons (Alcocer et al. 1998).

19.5.3 Lakes of the Valle de Santiago

The Río Lerma-Salamanca basin, in the central and western region of Mexico, holds numerous volcanic cones. The Valle de Santiago region, in the southern portion of the state of Guanajuato, has four crater (maar) lakes: Rincón de Parangueo, San Nicolás de Parangueo, La Alberca, and Cíntora. Increasing groundwater overextraction for agriculture and urban development, perhaps together with climate change, resulted in the progressive desiccation of the lakes (Alcocer et al. 2000b; Escolero and Alcocer-Durand 2004). Old photographs (1970) show the four lakes flooded. Nonetheless, San Nicolás de Parangueo dried up in ~1979 while Cíntora in ~1984. Rincón de Parangueo and La Alberca still had a water column ~35 m (from an original ~50 m deep) in 1985, but in 2002, both lakes were highly reduced down to 1–2 m deep (Alcocer 2012; Alcocer et al. 2002). La Alberca is today already and Rincón de Parangueo nearly dried (Fig. 19.3).

19.5.4 Cuatro Ciénegas

Another critical site threatened by anthropic activities is Cuatro Ciénegas in the Chihuahuan Desert, Coahuila, Northern Mexico. This arid region holds ponds, wetlands, and streams. It is well known for its high terrestrial and aquatic biodiversity

Fig. 19.3 Desiccation process (top 1995, bottom 2002) of lakes La Alberca (left) and Rincón de Parangueo (right); the white arrows indicate the original water level. (Photographs by Javier Alcocer)

and the high degree of endemism that justified its designation as a Biosphere Reserve in 1994 (e.g., Álvarez and Ojeda 2019; García-Oliva et al. 2018; Souza et al. 2018). Cuatro Ciénegas is well known for its spring-fed ponds that are inhabited by diverse microbialites, including stromatolites and microbial mats, with a unique microbial community structure (Fig. 19.4). The enormous microbial biodiversity of the microbialites seems to be associated with low nutrient concentrations, particularly phosphorous (Souza et al. 2018).

Agricultural diversion and extractions starting in the 1880s are the most important but not the only activities impacting the aquatic resources of Cuatro Ciénegas; unregulated tourism, species introduction, and climate change added to the desiccation trend already evident in some of the water bodies (e.g., pozas – ponds – of the Churince System; Ortiz-Acosta and Romo-Aguilar 2016; Pisanty et al. 2013).

Cuatro Ciénegas display a high degree of endemism, particularly microendemisms, with numerous species being endemic to a single pond (Alcocer and Aguilar-Sierra 2019). The wetland ecosystem fragmentation and the reduction or even drying up of many ponds and streams threaten the persistence of this aquatic biodiversity severely. Among the aquatic biota of Cuatro Ciénegas with endemics are fish (Espinoza-Pérez and Lambarri-Martínez 2019) and crustaceans (Álvarez and Villalobos 2019).

The fish group comprises 18 species from 6 orders (Cypriniformes, Siluriformes, Characiformes, Cyprinodontiformes, Cichliformes, and Perciformes). Nine fish

Fig. 19.4 Poza Azul, Cuatro Ciénegas, Coahuila. (Photograph by Elva Escobar)

species are endemic (the Cyprinidae *Cyprinella xanthicara* and *Dionda* cf. *episcopa*, the Fundulidae,

Lucania interioris, the Cyprinodontidae *Cyprinodon atrorus* and *C. bifasciatus*, the Poeciliidae *Gambusia longispinis* and *Xiphophorus gordoni*, the Cichlidae *Herichthys minckleyi*, and the Percidae *Etheostoma lugoi*).

There are 45 species of crustaceans representing four classes, 18 families, and 32 genera. Copepods with 26 species are the most diverse group. Seven crustacean species are endemic (the Cladocera *Ceriodaphnia laticaudata*, the copepods *Eucyclops cuatrocienegas* and *Leptocoris stromatolicolus*, the amphipods *Mexiweckelia colei* and *Paramexiweckelia particeps*, the isopod *Speocirolana thermydronis*, and the decapod *Palaemonetes suttkusi*).

19.5.5 El Sol and La Luna

Even high mountain lakes, mainly because their high altitude is usually considered remote zones and therefore sheltered from pollution, are not safe from the long-range reach of anthropic airborne pollutants. Unique in Mexico are the high mountain Lakes El Sol and La Luna at an altitude of 4139 m above sea level inside the crater of the Nevado de Toluca volcano, Mexico State (Fig. 19.5). Bulk (i.e., wet and dry) deposition pH reaching the area remained acidic all year-round but acquired extreme low values from July to September. Consequently, anthropogenic impacts threaten to acidify Lakes El Sol and La Luna through acid precipitation (Ibarra-Morales et al. 2020).

Fig. 19.5 High-mountain Lake La Luna, Nevado de Toluca, Estado de Mexico. (Photograph by Mariana Vargas)

The deposition of human-induced windblown particles derived from activities at the volcano slopes, that is, soil erosion at lower elevation (3000 m) in areas surrounding the Nevado de Toluca and long-distance transport from nearby highly urbanized areas (Toluca and Mexico cities), augmented the atmospheric dust deposition increasing the sediment accretion and the organic carbon concentration (Alcocer et al. 2020). In addition, the pH of both lakes unexpectedly augmented and became more variable. Also, the air and lake water temperature increased 0.5 °C, and the lakes' water level declined 1.5 m, suggesting effects related to climate change. These changes also impacted the benthic macroinvertebrate communities with a drastic reduction (up to 90%) in density and biomass (Alcocer et al. 2021).

19.5.6 The Montebello Lakes

The natural protected area and RAMSAR site "Parque Nacional Lagunas de Montebello" (PNLM) is a karstic lake district with more than 130 lakes in the SSE region of Chiapas. Modification on some lakes was observed beginning in 2003, with changes from crystal clear waters to the occurrence of a yellowish-green supernatant, fetid odors, and fish mortality. As an important national and international tourist attraction, this alteration caused alarm among residents and local authorities due to the associated adverse social, tourist, and economic effects. Moreover, the modifications initially observed in a single lake have now extended to other nearby lakes. Almost 50 years of land-use changes, deforestation, and accelerated urban, agricultural, and tourist growth led to environmental deterioration (Fig. 19.6).

Fig. 19.6 Oligotrophic Lake Cinco Lagos (left) and eutrophic Lake La Encantada (right), Montebello, Chiapas. (Photographs by Mariana Vargas)

Agriculture, deforestation, urban development, and wastewater disposal imposed severe ecological and socio-economic pressure on the lake district resulting in the eutrophication of lakes mostly in the NW plateau portion of the PNLM. In the SE mountainous and still forested region, the lakes remain pristine with crystal clear waters (Alcocer et al. 2018). The turbidity and green color of the eutrophic lakes of Montebello originate in the large amount of suspended particulate matter mainly composed by sediments eroded from deforested areas and by the increase of phytoplankton biomass promoted by the entrance of nutrients associated with agricultural fertilizers and wastewaters (Vargas-Sánchez et al. 2022).

Mora-Palomino et al. (2017) found that agriculture and sewage negatively impacted the water quality of the lakes on the NW portion of the PNLM. Nonetheless, it seems the deterioration of the Montebello lakes started as early as in the 1950s when changes in land use occurred, due to the Agrarian Reform that had started during the 1940s. Fifty years of impacts accumulation went unoticed by the locals, until 2003 when the lakes shifted from blue (oligotrophic) to green (eutrophic), and the problem became evident (Caballero et al. 2020).

The anthropic eutrophication of Montebello lakes is also detrimental to aquatic biodiversity. These lakes show an elevated regional taxonomic richness but large singularity; each lake has different species composition from the other lakes. As a group of lakes, the species richness is high, but species richness is low per lake. Eutrophication reduces deep benthic community (Cortés-Guzmán et al. 2019) and zooplankton (Fernández et al. 2020a, b) species diversity, threatening these fragile ecosystems characterized by high taxonomic richness and singularity. Moreover, the phytoplankton of the eutrophic lakes of Montebello harbor cyanotoxin-producing cyanobacteria that can cause harm to human and animal health, aquatic ecosystems, and local economies (Fernández et al. 2021).

19.5.7 Lake Alchichica

Lake Alchichica exemplifies a paradigm of low species richness but a strikingly high degree of endemism for such a small (surface area 2.3 km^2) water body (Alcocer 2019). It is located mostly in Puebla; however, a small portion of the crater that holds this maar lake is in Veracruz. Numerous species inhabiting Lake Alchichica show restricted occurrence, most of them occur only in this lake and therefore fall within the category of microendemic (i.e., distribution range <5% of the national territory, Table 19.1).

Lake Alchichica became worldwide famous for its stromatolites (Fig. 19.7). Their ring-like shape parallel to the coast is unique in the world (Valdespino-Castillo et al. 2019). Microbialites are recognized as hotspots of microbial diversity. Stromatolites are among the oldest examples of life on the planet. They are commonly found in the fossil record from the Precambrian, so they can be considered living relics, as they are currently scarce. These "living fossils" of the same lineage as those that appeared approximately 3.5 billion years ago are truly a scientific

Table 19.1 Microendemic species of Lake Alchichica (Ortega-Mayagoitia et al. 2022)

Bacteria	
Xenococcaceae	*Xenococcus candelariae*
Eurycoccales	*Gloeomargarita lithophora*
Chroococcales	*Entophysalis atrata*
Chroococcales	*Entophysalis lithophyla*
Chamaesiphonaceae	*Chamaesiphon halophilus*
Merismopediaceae	*Mantellum rubrum*
Synechococcales	*Heteroleibleinia profunda*
TSAR	
Bacillariophytina	*Cyclotella alchichicana*
Amorphea	
Isopoda	*Caecidotea williamsi*
Diaptomidae	*Leptodiaptomus garciai*
Canthocamptidae	*Cletocamptus gomezi*
Candonidae	*Candona alchichica*
Limnocytheridae	*Limnocytherina axalapasco*
Corixidae	*Krizousacorixa tolteca*
Chironomidae	*Chironomus alchichica*
Brachionidae	*Brachionus* sp. Mexico
Atherinidae	*Poblana alchichica*
Ambystomatidae	*Ambystoma taylori*

Species organization follows the classification system of SILVA rRNA database project (https://www.arb-silva.de/) (v138, release 11-2020), Algaebase (https://www.algaebase.org/), while Eukarya by Adl et al. (2019). *L. axalapazco* also inhabits Lakes La Preciosa and Quechulac, and *Brachionus* sp. Mexico also inhabits Lakes Atexcac and La Preciosa

Fig. 19.7 Lake Alchichica, Puebla. (Photograph: Mariana Vargas

treasure that allows us to go back to the origin of life on the planet (Valdespino-Castillo et al. 2022).

The water level decline of the lake is related to climate variability and groundwater (its primary water source) exploitation (Alcocer et al. 2004). In this way, a direct impact is driven by agriculture and urban development, leading to groundwater overextraction and an indirect effect of anthropic climate change. Additional potential impacts are pollution from agriculture (e.g., herbicides) and industrial expansion (e.g., pig and poultry farms, automobile industry) in the watershed.

The lake's desiccation has the most critical impact on the aquatic biota. Alcocer and Escobar-Briones (2007) showed historical aerial photographs evidencing the water level reduction. Originally formed underwater, living stromatolites died when exposed to air by water level descend, leaving behind only the carbonaceous deposit easily seen in the aerial photographs as white rocks. Unfortunately, not only the lake's desiccation process threatens stromatolites but also the rise in temperature (climate change) and water pollution (eutrophication).

19.6 Conclusion

The integrity of inland water bodies and their biological diversity is increasingly threatened by human activities, particularly during the Anthropocene. The extensive changes taking place in short periods characteristic of the Anthropocene are rapidly deteriorating the quantity and quality of inland water bodies and their biodiversity. Climate change and increasing water quality deterioration and pollution associated with human development have severely impacted lakes and rivers throughout the Mexican territory. The social and economic well-being of a country depends, to a large extent, on the capacity of these aquatic ecosystems to provide their environmental goods and services, hence the importance of their sustainable use.

Acknowledgments This work had financial support from the Consejo Nacional de Ciencia y Tecnología (CONACYT) and Dirección General de Asuntos del Personal Académico (PAPIIT, UNAM) through several projects. The author acknowledges Mariana Vargas for providing several photographs that illustrate the chapter.

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Part IV
Processes

Chapter 20
Contemporary Climate Change Impacts on Mexican Fauna

Enrique Martínez-Meyer and Julián A. Velasco

Contents

20.1 Introduction

The newest information is conclusive: Contemporary global warming is unequivocally a consequence of carbon dioxide (CO_2) and other greenhouse gas (GHG) emissions produced by human activities, with ongoing and irreversible outcomes in the climate system, affecting both the biotic and human dimensions (IPCC 2021). Global temperature has increased around 1.1 °C relative to 1850–1900 mean temperature, with a more significant increase over land (1.59 °C) than over the ocean (0.88 °C), and in the northern hemisphere than in the southern (IPCC 2021).

E. Martínez-Meyer (✉)
Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico
e-mail: emm@ib.unam.mx

J. A. Velasco
Instituto de Ciencias de la Atmósfera y Cambio Climático, Universidad Nacional Autónoma de México, Mexico City, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_20

Moreover, CO_2 and GHG emissions have affected the whole climate system, mainly since the second half of the twentieth century. For instance, heat waves and droughts (and concomitant wildfires) have become more frequent and intense; global precipitation has increased, boosting the frequency and intensity of heavy rains and high-category tropical hurricanes. In addition, global heating has produced a thermal expansion of the oceans. It has melted sea and land ice, rising sea level by 0.20 cm in the last century. Also, growing atmospheric CO_2 has increased ocean acidification and decreased oxygen levels. Worrisome, many of these climatic disruptions already have inertia that will last for decades, centuries, and beyond, even under early net-zero emission scenarios (IPCC 2021).

The future climate is uncertain because it depends on actions taken today regarding GHG emissions (Tollefson 2021). Therefore, scientists have developed possible future climate scenarios based on different socioeconomic pathways (Riahi et al. 2017), with global warming levels ranging, on average, from 1.5 up to 4.5 °C compared to the preindustrial mean temperature by the end of the present century. Furthermore, projections estimate that by 2040 we may reach 1.5 °C warming, regardless of the scenario (IPCC 2021). Therefore, the multiple disruptions observed until now, like the increase in frequency and intensity of extreme climatic and weather events, are expected to exacerbate in the coming decades. In other words, we are looking at the tip of the iceberg. This picture poses critical challenges for adaptation to biotas and human populations (Pecl et al. 2017).

Consequently, biotas of all realms (terrestrial, marine, and freshwater) are already reacting to changes in the climate system all over the world, and evidence is palpable in different patterns and processes at all levels of organizations (from genes to biomes) in most taxonomic groups (Scheffers et al. 2016). For the faunal component, at the organismal level, genetic, physiological, and morphological changes attributed to climate change have been documented from invertebrates (e.g., van Asch et al. 2012) to long-living mammals (Forcada and Hoffman 2014). Populations of several taxonomic groups are responding in different ways, including changes in abundance, recruitment, and sex ratios (e.g., mammals; Myers et al. 2009), as well as phenological adjustments, such as spawning times in aquatic vertebrates (Phillimore et al. 2010; Asch 2015), reproductive activity in amphibians (Todd et al. 2011), and migration in birds (Travers et al. 2015). Alterations at the population level reverberate at the species and community levels in different ways. In the former, probably the most extensively documented aftermath, both over land and the oceans, are distributional shifts as a means of tracking suitable environments (Sunday et al. 2012; Lenoir and Svenning 2015), where terrestrial species are, in general, lagging behind thermal niches more than marine species (Lenoir et al. 2020). Population changes at the local scale, such as phenology, abundance, local extinctions, and colonizations, have implications in the community structure and function – and ultimately the biomes – by affecting interspecific interactions (Ockendon et al. 2014) and community composition (Tingley and Beissinger 2013; Vergés et al. 2014). Despite the quickly mounting evidence of the impacts of climate change on biodiversity, we can make few generalizations, in part because climatic changes and their concomitant biotic responses are dependent on the local geographic and ecological contexts (Gaüzère et al. 2018; Antão et al. 2020; Vandvik et al. 2020) but also due to a lack of long-term studies in most regions of the world, particularly in the tropical regions, where most biodiversity has accumulated (Mantyka-Pringle et al. 2012; Ockendon et al. 2014).

Unsurprisingly, most evidence-oriented studies in the context of climate change have been carried out in the northern hemisphere, particularly in Western Europe and North America (Ockendon et al. 2014; Lenoir and Svenning 2015), regions with a long tradition of systematic data gathering and scientific research. However, to better realize the magnitude of the phenomenon and the challenge to face it, it is necessary to broaden our knowledge to the tropical and subtropical regions, the biodiversity-richest regions of the planet. This chapter summarizes our knowledge of current and future climate change impacts on Mexican fauna, identifying major taxonomic, geographic, and research topics gaps, aiming to outline a research agenda that hastens our understanding of this critical topic for biodiversity and human well-being.

20.2 Contemporary Climate Change in Mexico

20.2.1 Observed Climatic Changes

Mexico is highly vulnerable to climate change given its geographic position in the tropical-subtropical transition zone and the influence of climate change-sensitive phenomena, like the El Niño-Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO), and the Pacific Decadal Oscillation (PDO). Also, Mexico is in the impact and influence zone of both the North Atlantic and Pacific hurricane systems (Quintanar Isaías et al. 2015). Therefore, climatic variables, particularly precipitation, are naturally highly variable (Murray-Tortarolo 2021). This condition, coupled with a limitation in the amount and length of high-quality observational climatic data across the country, has made the detection and attribution of change somewhat challenging (Estrada Porrúa et al. 2015). Nonetheless, recent works have identified the degree of anthropogenic signal on warming at regional scales. In particular, Estrada et al. (2021) found evidence that at least 0.8 °C is attributable to radiative forcing for Mexico.

Furthermore, countrywide analyses have shown that the climate in Mexico is changing in various ways. For instance, Pavia et al. (2009) analyzed surface temperature trends of ~1400 weather stations in two time periods from 1940 to 2004. They found that, in general, there was a cooling trend in the first half of the studied period (1940–1969) and warming in the second one (1970–2004) that were consistent with the PDO behavior. This cooling-warming trend was also observed in the gridded datasets analyzed by Cuervo-Robayo et al. (2020) from 1910–1949 to 1950–1979 and from 1950–1979 to 1980–2009, respectively, and by Murray-Tortarolo (2021) between 1951 and 1980. The mean temperature increase for the country between 1970 and 2000 was 0.22 °C (Cuervo-Robayo et al. 2020) and 0.71 °C from 1951 to 2017 (Murray-Tortarolo 2021). However, the country has not warmed up uniformly since the mid-twentieth century. Different studies agree that Northern Mexico has heated more than the central and southern portions of the country (Pavia et al. 2009; see studies cited in Estrada Porrúa et al. 2015; Cuervo-Robayo et al. 2020; Murray-Tortarolo 2021).

Changes in precipitation trends have been more challenging to detect. In general, precipitation has increased countrywide in the last century (Méndez González et al. 2008). However, no clear trend can be observed because the wettest and driest years between 1951 and 2017 were interspersed, probably driven by ENSO (Murray-Tortarolo 2021). Authors agree that precipitation has generally increased in the last decades in the arid and semiarid regions of Northern Mexico (Méndez-González et al. 2008; Cuervo-Robayo et al. 2020; Murray-Tortarolo 2021). In contrast, the tropical region (except the Yucatán Peninsula) has suffered a decrease of around 5% in the annual precipitation from 1970 to 2000 (Cuervo-Robayo et al. 2020). However, geographic patterns show high spatial heterogeneity with zones of increment and decrement across the country.

Probably, the most conspicuous pattern is regarding seasonal precipitation and water balance (precipitation minus potential evapotranspiration). In the last 70 years, the wet season has become wetter and the dry season drier across the country. Areas with a strong negative year-round balance are located in Baja California and Sonora and with a positive balance are found in the Yucatán Peninsula (Murray-Tortarolo 2021). In our reanalysis of Cuervo-Robayo et al.'s (2020) data, we found several areas in the Chihuahuan Desert, some in Sonora, Baja California, and Southern Veracruz that have experienced the most significant temperature increase and precipitation decrease combined in the last decades (Fig. 20.1).

The information for the Mexican oceans is even more scarce than for land; thus, uncertainty is still high. Nonetheless, some observations in the last three decades show some trends. In terms of temperature, the oceans in the Pacific side show different patterns than the Atlantic region. The open Pacific at the central part of the country and the Gulf of California have cooled in the last three decades, being more intense in the former. In turn, the Pacific region of Baja California and the Gulf of Tehuantepec have not shown a clear trend. On the contrary, most of the Gulf of Mexico (except for the southern coast of the United States) and the western Caribbean show a clear warming trend in the order of 0.2–0.6 °C/decade (Lluch-Cota et al. 2013), with rapid warming detected in the Caribbean since 1987 (Bove et al. 2021).

In addition to temperature increases, scientists have documented other significant impacts of current climate change in the marine realm. For instance, the oceans are mostly CO_2 sinks; hence, the increase of global atmospheric CO_2 produces higher oceanic absorption, which changes the inorganic carbon cycle and lowers the pH. This phenomenon is called ocean acidification and has important consequences for marine chemistry and ecosystems, most notably affecting the calcifying organisms, such as shellfish, several phytoplankton species, and reef-building and deep-sea corals, among others (Gledhill et al. 2008). Current estimates indicate that

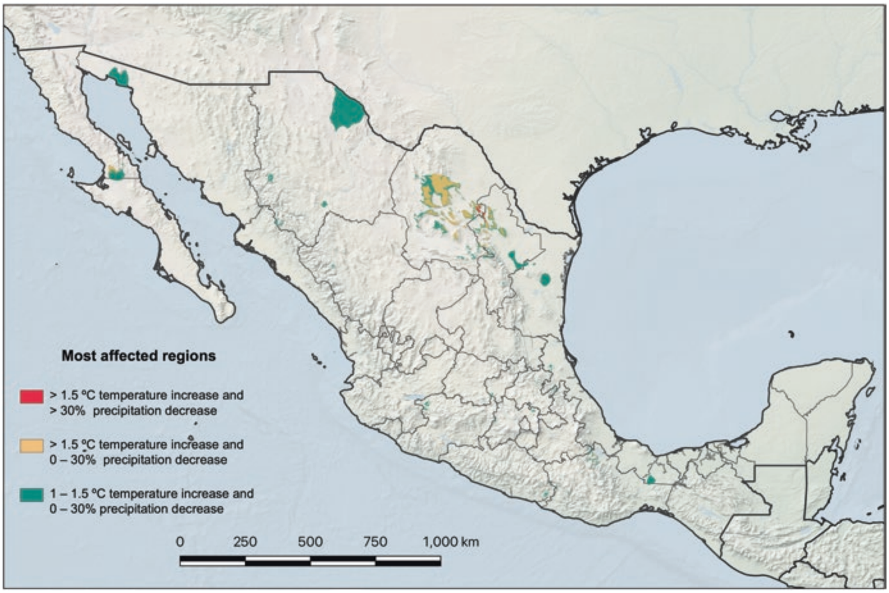

Fig. 20.1 Most affected regions in Mexico due to temperature rise and precipitation decrease between the average values of 1950–1979 and 1980–2009. Climatologies were obtained from Cuervo-Robayo et al. (2020)

global surface waters have decreased 0.1 pH units since the beginning of the industrial era (mid-1700) equivalent to a 13% reduction in the concentration of carbonate ions (Ochoa de la Torre et al. 2015).

Moreover, sea level rose an average of 2.0 mm/year between 1971 and 2010 worldwide (Ochoa de la Torre et al. 2015). However, this rate increased to 3.2 ± 0.4 mm/year from 1993 to 2010 (Zavala-Hidalgo et al. 2015). Sea level rise observed in the Mexican oceans has regional differences. The northern Gulf of Mexico (Tampico-Madero) presents the largest increments, in the order of 9.2 mm/year, but with high uncertainty. The Caribbean also presents a positive trend between 2.4 and 3.4 mm/year. Conversely, the Pacific shows positive (2.0–4.8 mm/year) and negative (−2.7–0.1 mm/year) trends in different locations, although the general trend is positive (Zavala-Hidalgo et al. 2015). Finally, the Gulf of California shows a positive trend ranging from 0.1 to 4.8 mm/year, depending on the location and the period analyzed (Páez-Osuna et al. 2016).

In sum, it is encouraging that an increasingly robust research community in Mexico is interested in understanding the climate change phenomenon and its impacts in its different facets, as evidenced by the expanding number of scientific publications in the last decade. Despite the limitations imposed by the lack of high-quality data, there is evidence that current climate change has clear manifestations in Mexico, both in the terrestrial and marine realms. Therefore, it is reasonable to expect these manifestations to already have an impact on the biotic component in different ways.

20.2.2 Future Climate Change Exposure in Mexico

In this section, we briefly analyze the climate change exposure in Mexico from different emission scenarios and general circulation models (GCMs) and, particularly, on the network of natural protected areas (NPAs). The first attempt to analyze the potential vulnerability of Mexican NPAs in the face of climate change was conducted by Esperon-Rodríguez et al. (2019). They developed a potential vulnerability index calculating current climate space loss (estimated as a hypervolume of 19 bioclimatic variables), geographic area, and the number of species in each NPA. These authors found that most NPAs will have novel climates by 2050.

Here, we present a complementary analysis based on additional spatial climate change metrics to evaluate the exposure of 170 Mexican NPAs to novel conditions in the future and how fast the current climate may vanish (Williams and Jackson 2007; García et al. 2014b; Brito-Morales et al. 2018; Trisos et al. 2020). First, we calculated the climate velocity and the residence time (Loarie et al. 2009; García-Molinos et al. 2019) using a time series of 95 years (2006–2100) for annual mean temperature obtained from the CCSM4 model for an RCP8.5 scenario. We obtained this scenario from the CMIP5 (Climate Model Intercomparison Project phase 5) repository and processed it using the statistical delta downscaling method at 2.5 minutes of spatial resolution (Ramírez-Villegas and Jarvis 2010). Climate velocity (Fig. 20.2) describes the speed and direction that a given NPA should move to remain in the baseline climate space (1960–1990). In contrast, residence time represents the number of years for the current baseline climate to cross a protected area. To do so, we used the *gVoCC* and *resTime* functions from the *VoCC* R package (García-Molinos et al., 2019). We found that only 31% NPAs (i.e., 54) are projected to exceed the residence time after 100 years (Fig. 20.3). Thus, we ranked NPAs according to the residence time and identified which NPAs will be more exposed to novel and disruptive temperatures before 2050 (Fig. 20.3). Many NPAs with residence times below 50 years from now are relatively small and might experience substantial impacts from increases in temperatures (Fig. 20.3). It is important to note that we do not assume anything about the thermal tolerances of species occurring in the NPAs. However, it is reasonable to consider that endemic- or restricted-range species, particularly in small NPAs, likely face higher extinction risk than species with more extensive ranges.

We also calculated the emergence of novel climates (no-analog climates; Williams and Jackson 2007) based on the Euclidean distance of a combination of 19 bioclimatic variables for an ensemble of 11 General Circulation Models and 2 Representative Concentration Pathways (RCP; RCP2.6 and RCP8.5) from the CMIP5 database for 2050 and 2070. Most no-analog climates emerged for 2050 and 2070 in the northern portion of the Sierra Madre Occidental in Sonora, the Trans-Mexican Volcanic Belt, the southern part of the Sierra Madre Oriental, the central portion of the Chihuahuan Desert, and the mountains in Coahuila (Fig. 20.4). Combining these metrics with faunistic changes observed recently (e.g., Peterson et al. (2015a) might help evaluate the vulnerability of already affected faunistic assemblages to future climates.

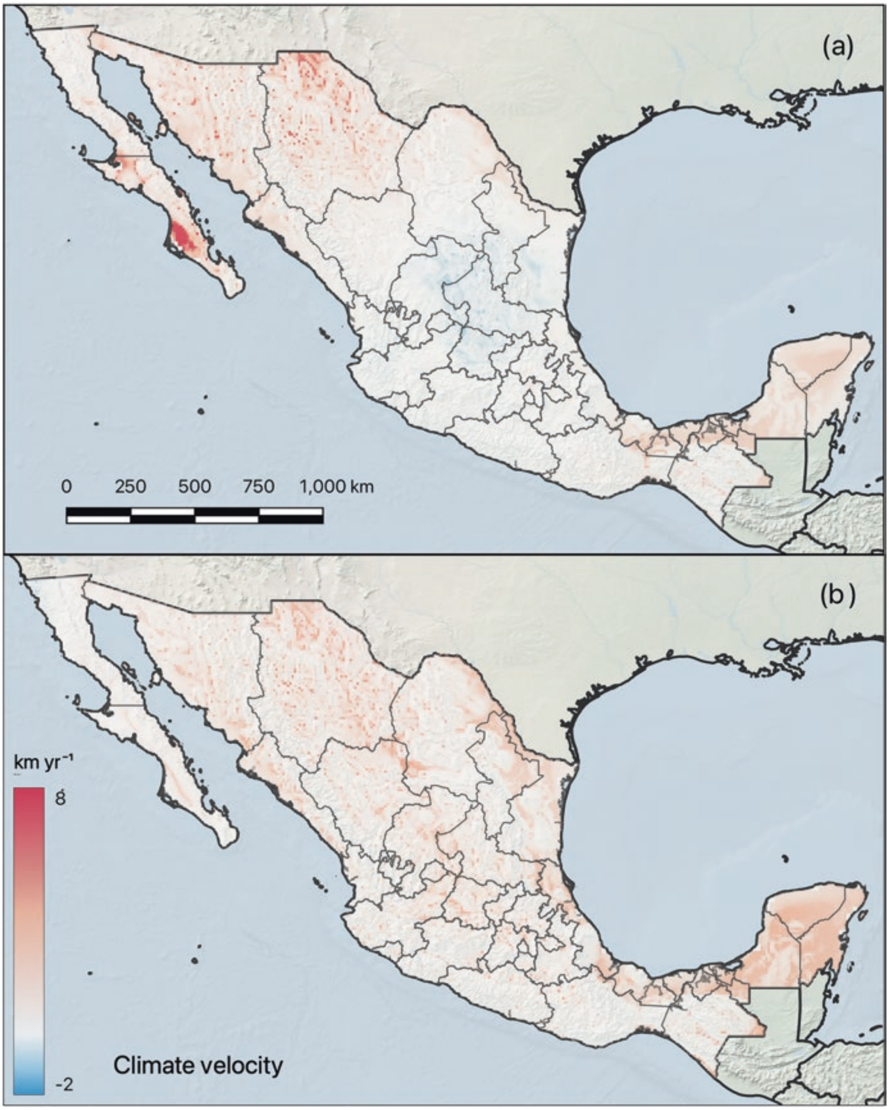

Fig. 20.2 Climate velocity (km yr.$^{-1}$) of (**a**) minimum and (**b**) maximum temperatures across the country with respect to the baseline climatology of 1960–1990

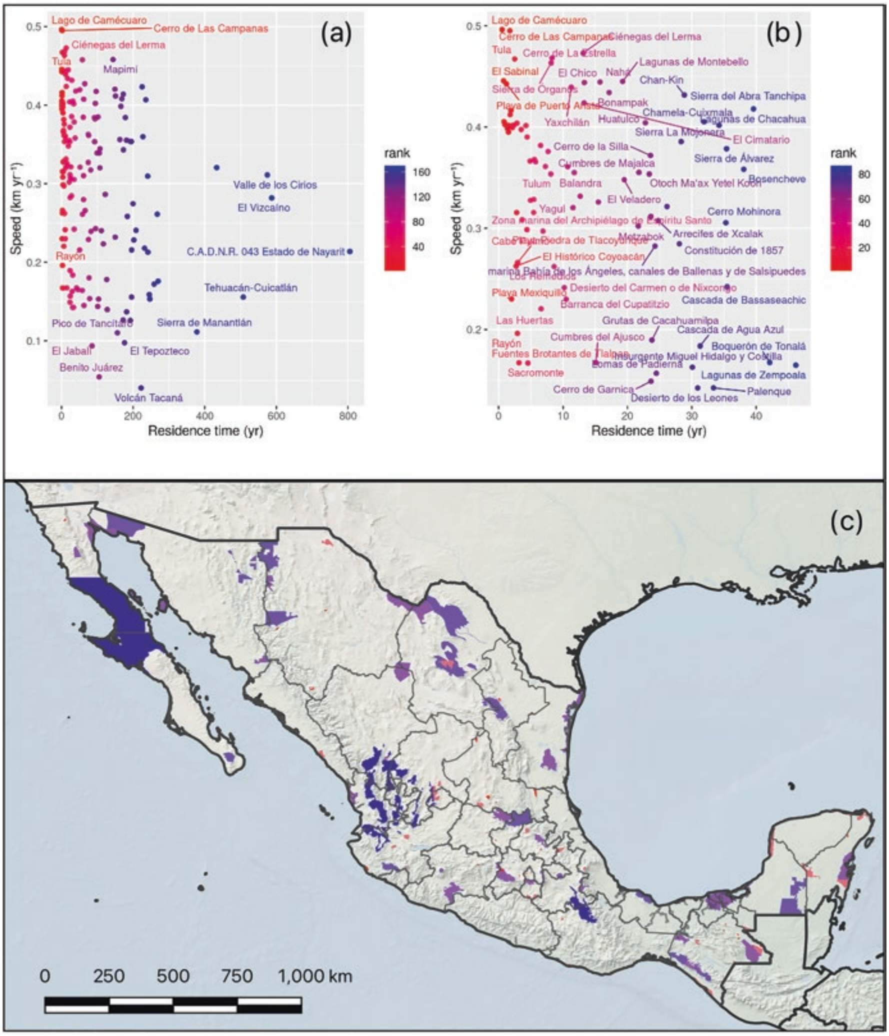

Fig. 20.3 Climate velocity (km yr.$^{-1}$) and residence time (years) for (**a**) all Mexican Protected Areas (PAs) and (**b**) for a subset of PAs with residence times below 50 years. PAs were ranked from lower to higher residence time. Residence time reflects the time for current climate conditions to cross a PA (Loarie et al. 2009). (**c**) Map showing the Mexican Protected Areas following the same color scheme of panel (**a**)

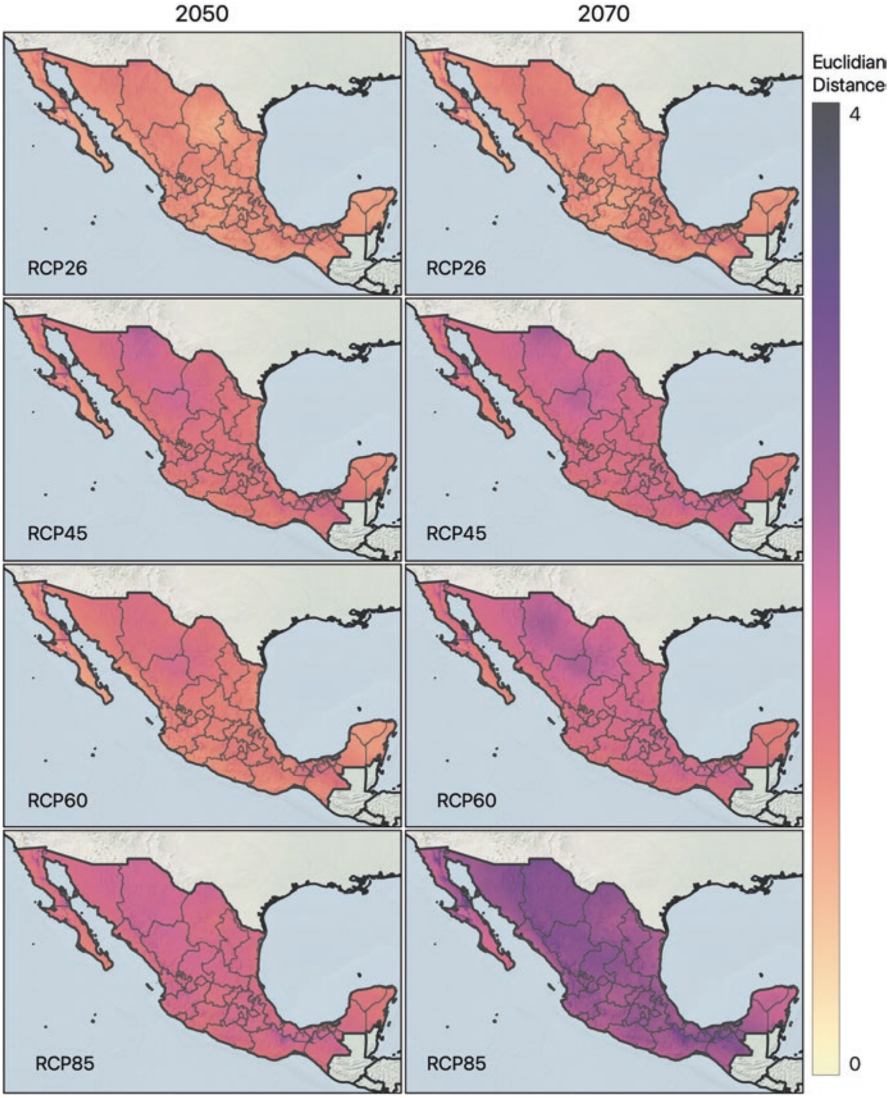

Fig. 20.4 Spatial emergence of novel climate combinations captured as Euclidean distances (ED) between the baseline (1960–1990) and future (2050 and 2070) climatic conditions

20.3 Climate Change Impacts on the Mexican Biota

The information generated worldwide about climate change impacts on the biota can be broadly classified into two main research streams: evidence-oriented and projective/predictive analyses. In the former, researchers have utilized two complementary approaches to detect changes in one or more biological traits (e.g., physiology, phenology, demographics, distribution) at different levels of organization (i.e., genetic, organismal, population, species, community, and ecosystem) attributable to climate change: long-term field observations and analysis of historical biological and climatic data (Scheffers et al. 2016). In the latter, experimental approaches and correlative-, mechanistic-, and process-based models have been applied to species, communities, and ecosystems under future climate scenarios to infer the potential impacts to biodiversity (Peterson et al. 2015b).

The biology of climate change is an expanding yet immature research field in Mexico. For many years, very few people worked in the biological aspects of recent climate change, and it was exclusively under a projective approach at the ecosystem (Villers-Ruíz and Trejo-Vázquez 1998) and species (Peterson et al. 2001, 2002) levels. Fortunately, both established and early-career scientists have turned their eyes to this research topic in recent years, including significant contributions from paleoecologists and paleobiologists (e.g., Pérez et al. (2021)). Thus, today, we have a growing scientific community producing novel information and forming a new generation of climate change scholars. However, this research community is still young and small to achieve, at least, a general view of the magnitude of the impacts that current climate change is exerting and may exert on the Mexican biota in the future. Consequently, we find biases and gaps in the research developed in Mexico, resulting in an incomplete view of the phenomenon.

The three major biases that we detected are in (a) the research stream, (b) realm, and (3) taxonomic. The first one refers to the asymmetry between evidence-oriented and projective studies since most publications involve projections of species and ecosystems under future climatic scenarios (e.g., Peterson et al. 2002). In turn, there are very few studies addressing the actual impact of climate change on biodiversity (Cuervo-Robayo et al. 2020). Second, freshwater ecosystems have been largely neglected, whereas most studies have been developed in the terrestrial realm and the oceans. Finally, most studies are for vertebrates and plants on land and corals in the ocean, whereas information for the remaining taxonomic groups is almost nil. We think these three biases obey the same reason: most scientists conduct their investigations in the research field, biodiversity groups, and realms for which data (biological and climatic) and methodological approaches are more readily available. For instance, it is much easier to analyze the future potential impacts of climate change on birds than to analyze the actual impacts on freshwater invertebrates. In the first case, occurrence data are abundant, future climate scenarios are already processed, and methodologies are well established. In contrast, in the latter, occurrence or any other biological data are scarce, and historical climatic data are fragmentary or lacking.

Despite these shortcomings, the research community in Mexico has generated valuable information that begins to unveil some patterns and draw preliminary conclusions. In the next section, we summarize what we know about current climate change impacts on the Mexican fauna in the present and the future.

20.3.1 Observed Impacts on Mexican Fauna

Evidence of climate change impacts upon Mexican biota is generally scarce and, in some cases, indirect. The first publication documenting climate change impacts on any faunal component in the terrestrial domain in the country was only in 2010 (Sinervo et al. 2010). These authors demonstrated that 12% of local populations of 48 *Sceloporus* lizard species had gone extinct since 1975 due to regional warming (Sinervo et al. 2010). In addition to the historical analysis, the authors also implemented a mechanistic modeling approach that has been widely used in Mexican species to estimate the extinction risk of reptiles under future climatic conditions (e.g., Arenas-Moreno et al. 2021; Lara-Reséndiz et al. 2021). Further studies with reptiles include analyses of the thermoregulatory behavior and nesting strategies of oviparous and viviparous *Sceloporus* lizards to avoid overheating potentially harmful to their offspring (López-Alcaide et al. 2017a, b). Finally, another group of reptiles for which there is some information is the crocodilians. In a long-term study in the Mexican Caribbean islands Banco Chinchorro and Cozumel, the authors found that the body condition of the American crocodile (*Crocodylus acutus*) is sensitive but resilient to hurricanes (Labarre et al. 2020). However, the increase in the frequency of high-category hurricanes in the northern Atlantic (Elssner 2006) may negatively affect populations of this species in the Caribbean and Gulf of Mexico in the longer term.

Amphibians are of great concern among Mexican herpetologists, with studies addressing some of the causal factors affecting their conservation status. However, only a few studies have evaluated climate change directly or indirectly as a causal factor of species or population declines. For instance, Lips et al. (2004) resurveyed historical localities in the mountains of Southern Mexico (Guerrero, Oaxaca, and Chiapas), finding a worrying 52–81% of species that exhibited local population extinctions in the last 16–40 years. However, the study was not focused directly on the impact of climate change but instead on the prevalence of the chytrid fungus *Batrachochytrium dendrobatidis*. Climate change may have played a direct role by affecting water availability and an indirect one by facilitating chytrid fungus dissemination and establishment (Lips et al. 2004), but reanalysis integrating climatic data would be necessary to determine a connection between climate and these declines.

Other studies have looked for genetic clues of climatic change impacts in amphibians. For instance, Velo-Antón et al. (2013) analyzed the genetic diversity of *Pseudoeurycea leprosa*, an endemic salamander of the Transvolcanic Belt, in the context of historical climatic changes. They found that the distribution and thus the gene flow among the salamander populations were broader during cooler periods. Therefore, warming since the Last Glacial Maximum has isolated its populations, thus causing genetic divergence. This effect can exacerbate as a consequence of current warming with potentially detrimental effects for the species.

Birds are the taxonomic group for which more biological information exists, so conducting large-scale analyses and drawing more general conclusions are feasible. One such study compared the community composition across Mexico from historical (1920–1950) and recent (post-2000) surveys relating land use and climatic changes between periods (Peterson et al. 2015a). Their results demonstrated that temperature change had a significant effect on species turnover. Also, they found that the northern deserts (Chihuahuan, Sonoran, and Northern Baja California) and the Usumacinta River basin were the regions with the most significant local extinction and turnover rates. Interestingly, the northern deserts have the highest warming rate in the country (Cuervo-Robayo et al. 2020). At the local scale, in the north of Sierra Madre Occidental, recent species turnovers due to poleward and up-elevation shifts as a response to increasing temperatures and summer-fall precipitation are causing a homogenization of bird communities (Flesch 2019). Similarly, in the upper Balsas River basin, typical tropical dry forest species have expanded upward to oak forests (but not the opposite), probably due to increasing temperatures (Vázquez-Reyes et al. 2017). Finally, the white-fronted parrot (*Amazona albifrons*) have also exhibited an extratropical expansion since 1990, probably due to climate change, but this hypothesis requires further testing (Mota-Vargas et al. 2020).

The information generated for taxonomic groups other than vertebrates in the terrestrial realm is extremely scarce. We only found one study with the Monarch butterfly (*Danaus plexippus*). In an analysis across its full geographic range (Zylstra et al. 2021) and its overwinter distribution in Central Mexico (Barve et al. 2012), the authors concluded that the changing climate has played a role in the declining trend observed in the last three decades. Although other factors, such as pesticides, have also impacted some regions (Zylstra et al. 2021), particularly for the overwintering sites in Mexico, results show a local climate trend toward lethal conditions for monarchs in recent years (Barve et al. 2012).

Freshwater ecosystems are probably the most threatened biomes in the world (Dudgeon et al. 2006), yet in Mexico, they have been largely overlooked for documenting climate change impacts on biodiversity. In fact, we also found only one study in which warming temperatures may be responsible for the successful establishment of the invasive tropical poeciliid fish *Pseudoxiphophorus bimaculatus* in a temperate lake system in Central Mexico, causing the gradual displacement of the native goodeid *Girardinichthys multiradiatus* via competition. If this trend continues, there is a serious extinction risk of that population of the native *G. multiradiatus* (Ramírez Carrillo and Macías García 2015).

In the marine realm, the number of studies is increasing. However, most studies have focused on corals and coral reef ecosystems, probably because one of the most harmful consequences of ocean warming is mass coral mortality. Warmer waters cause coral bleaching since corals expel their zooxanthella symbionts as heat stress increases. If warming events become chronic, corals cannot recover their zooxanthella, producing massive coral bleaching and mortality, thus causing significant degradation in the coral reef ecosystem (Muñiz-Castillo and Arias-González 2021).

The Gulf of Mexico/Caribbean coral reef system is one of the six largest such systems in the world and the one with the lowest temperature increase in 1950–2009 (Hoegh-Guldberg et al. 2017). Nonetheless, the heat stress in the Caribbean has increased over time, particularly since 2003, when overheating events have been more frequent with intermediate intensity values in the Mexican reefs (Muñiz-Castillo et al. 2019). For instance, in 2005, an extreme heat wave and several hurricanes severely affected coral cover (Elías-Ilosavy et al. 2020). Interestingly, coral reefs in the Mexican Caribbean have recovered since then, increasing their cover by 6% (Contreras-Silva et al. 2020; Elías-Ilosavy et al. 2020). However, higher temperatures affect coral growth, so the increasing temperatures and heat wave frequency observed in the region may have decreased the recovery capacity of hard corals (Elías-Ilosavy et al. 2020; Bove et al. 2021; Muñiz-Castillo and Arias-González 2021).

There are a few other studies about climate change and biodiversity in the Mexican oceans. For example, a comprehensive review of the Gulf of California reported an increasing trend in the frequency and number of days with algal blooms in the last three decades, possibly associated with severe La Niña events (Páez-Osuna et al. 2016). Algal blooms of toxic species cause severe damages to the whole food web, from fish and crustaceans to birds and mammals. Furthermore, some benthic species have shown distributional shifts probably associated with sea temperature changes. Such is the case of the endemic hard coral *Porites sverdrupi*, which recorded a southward expansion probably associated with cold events, and the invasive sponge *Chalinula nematifera*, which seems to benefit from warming events that cause coral bleaching (Páez-Osuna et al. 2016).

Finally, climate change has impacted some fisheries in one direction or another. For example, the pink shrimp (*Farfantepenaeus duorarum*) fishery in the Campeche Sound started a pervasive decline since 1980, followed by other species, including sharks, the red grouper (*Epinephelus morio*), and the Spanish mackerel (*Scomberomorus maculatus*) (Arregín-Sánchez et al. 2015). Conversely, other species, like the red octopus (*Octopus maya*) and jacks (family Carangidae), observed an inverse trend (Arreguín-Sánchez 2019). These changes are not due to overfishing but structural changes in the ecosystem productivity likely driven by rising sea temperature (Arreguín-Sánchez et al. 2015).

In sum, documented alterations in different aspects of the Mexican fauna attributable to climate change are widespread geographically and taxonomically (Fig. 20.5). Although the evidence gathered so far is still incipient, it is evident that this is only the tip of the iceberg of what is occurring in Mexico and the beginning of what we will profusely see shortly. This sense of urgency and the need to anticipate how climate change can affect biodiversity is the primary motivation that many research groups in Mexico have developed projective studies relying on the construction of future scenarios. In the next section, we summarize the main findings.

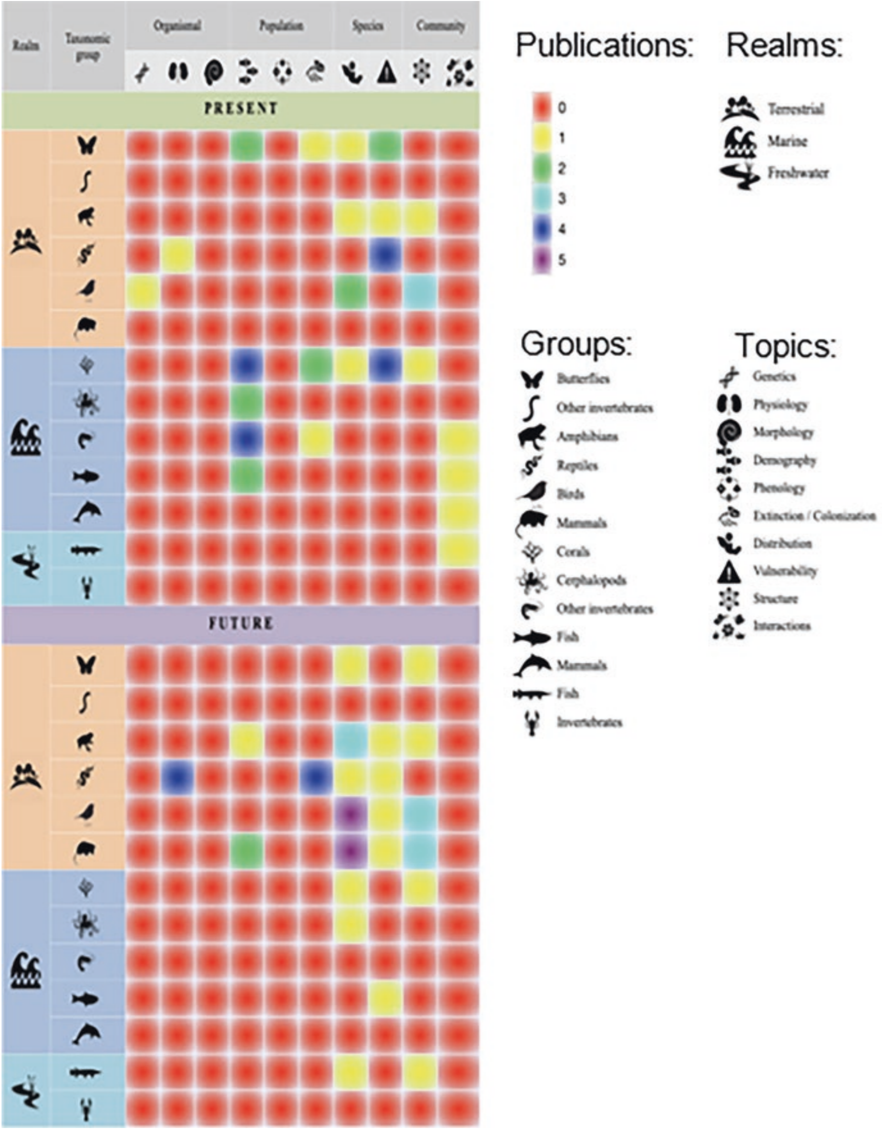

Fig. 20.5 Number of publications regarding climate change impacts on Mexican fauna in which the research topic and taxonomic group from the three realms (terrestrial, marine, freshwater) are analyzed both for the present and the future. Note that one or more topics or taxonomic groups could be included in the same publication

20.3.2 Projected Impacts on Mexican Biota

The information from species' occurrences is rapidly growing and readily available in digital repositories, such as the Global Biodiversity Information Facility (GBIF) for the world or the Sistema Nacional de Información de la Biodiversidad (SNIB) for Mexico (CONABIO 2020). These facilities allow scientists to estimate quickly how future climate change may impact Mexican biota. Using occurrence data and climatic variables under space-for-time substitution approaches (also known as ecological niche modeling (ENM)) makes it possible to estimate a given species' current, past, and future potential distribution. This approach has been widely used in ecology and provides a quick and cheap method to infer future trajectories of geographic ranges under shifting climates (Blois et al. 2013; Urban et al. 2016). Since species (or any other entity) are expected at equilibrium with the current climate (Araújo and Pearson 2005), it is assumed that species' responses to fluctuating environments will be stable across spatial and temporal scales. Accordingly, it is possible to anticipate how species will behave under shifting climates in the future (Blois et al. 2013; Urban et al. 2016). However, the species-climate equilibrium assumption has been challenged by multiple lines of evidence which show that species-climate relationships are not stationary across geographical and temporal scales (Svenning and Sandel 2013; Gaüzère et al. 2018; Loehle 2018; Sandel 2019; Rapacciuolo et al. 2019; Pili et al. 2020; Damgaard 2019). Consequently, current static ENM approaches are insufficient to model these transient (i.e., nonequilibrium) dynamics, producing biased projections under future climate change scenarios (Yates et al. 2018; Rapacciuolo et al. 2019).

The evaluation of impacts of future climate change on Mexican biota has been performed almost exclusively using static ENM (e.g., Peterson et al. 2002; Thomas et al. 2004; Feria-Arroyo et al. 2013; Martínez-Meyer et al. 2011; Trejo et al. 2011; Ochoa-Ochoa et al. 2012; Prieto-Torres et al. 2020) or hybrid approaches incorporating demographic viability analyses (e.g., Anderson et al. 2009; Ponce-Reyes et al. 2013) or physiological information (e.g., Lara-Resendiz et al. 2019, 2021). Here, we briefly review some of the most important studies conducted in Mexico. A summary of the number of publications identified until May 2021 by research subject, taxa and realm, for the present and the future is presented in Fig. 20.5.

Most studies focus on how distributional areas may change in the future under different climate change scenarios using different phases of the Coupled Model Intercomparison Project (CMIP) (e.g., Peterson et al. 2001; Ballesteros-Barrera et al. 2007; Rojas-Soto et al. 2012; Mendoza-González et al. 2013). Most of these studies focused on terrestrial environments and only a few were conducted in the marine realm either on individual species or fisheries stocks (e.g., Stranges et al. 2019; Cisneros-Mata et al. 2019; Ángeles-González et al. 2020). Furthermore, few studies have evaluated how climatic changes may affect entire species assemblages in the biotic composition (e.g., Peterson et al. 2002; Martínez-Meyer et al. 2011; Ochoa-Ochoa et al. 2012; Stranges et al. 2019; Prieto-Torres et al. 2020). In some cases, spatial prioritizations of protected areas (PAs) under climate change were conducted to evaluate whether the network system of PAs would be effective to preserve biodiversity in the future (e.g., Prieto-Torres et al. 2016; Mendoza-Ponce et al. 2020; Chacón-Prieto et al. 2021).

One of the first analyses using an ENM approach evaluated projected distributional shifts of the bird family Cracidae under future climatic scenarios (Peterson et al. 2001). Similarly, Peterson et al. (2002) examined how the potential distribution for 1179 birds, 416 mammals, and 175 butterflies in Mexico may be affected by climate change by 2055. They generated a series of future projections and estimated several widespread local extinctions and dramatic range collapses for many species with a high faunistic turnover among regions, mainly concentrated in the desert regions of the north. Similarly, Thomas et al. (2004) projected that at least 8% of Mexican mammals would be facing high levels of extinction risk driven by climate change on local populations. However, Hannah et al. (2007) found that the Mexican protected area network seems to work adequately for mammal species in the face of future climate change. In the same line, Trejo et al. (2011) modeled potential distributions for 61 mammal species and generated future range projections using six different general circulation models (GCMs) and two emission scenarios. They found individualistic responses in which range contractions might be at least 50% of the current size for half of the species examined. As a particular study case, the charismatic Mexican endemic volcano rabbit (*Romerolagus diazi*) was projected to go extinct by 2050 in all scenarios examined. In another study, Martínez-Meyer et al. (2011) also analyzed a group of priority terrestrial species threatened by illegal traffic or that are endemic. They found that sites with high species richness, particularly the Chiapas highlands, might impoverish under the more pessimistic scenarios. They also estimated that most Mexican conservation priority sites in Coahuila, Sonora, Nuevo León, and Tamaulipas would be susceptible to species losses driven by climate change toward 2030 and 2050.

Few studies were conducted on amphibians across Mexico regardless of their charismatic and endangered status at global and regional scales (Parra-Olea et al. 2005; Ochoa-Ochoa et al. 2012; García et al. 2014a). For instance, Ochoa-Ochoa et al. (2012) evaluated how future climate change (2020 and 2050) may affect microendemic amphibian species and turnover patterns of amphibian assemblages. They found that the regions with high projected species losses were in the northern Pacific coast, southern coast of the Gulf of Mexico, and the Yucatan Peninsula. In turn, the regions with potential species gains were the Sierra Madre Oriental and south of the Istmo de Tehuantepec. In addition, their results projected high turnover toward the south of the Pacific coast (Ochoa-Ochoa et al. 2012). Similarly, García et al. (2014a) built ecological niche models for 29 amphibian species endemic to the Pacific coast. They found substantial changes in individual species distributions and significant reductions in species' potential richness in this region, which is currently neglected in the national terrestrial priority regions for conservation. Finally, Parra-Olea et al. (2005) also analyzed future distributions for two species of plethodontid salamanders in the highlands of Central Mexico and found substantial reductions in range size toward 2050.

Recently, Mexican researchers have coupled ENM approaches with physiological information to estimate future extinction risk in lizards (e.g., Lara-Résendiz et al. 2015, 2019, 2021; Arenas-Moreno et al. 2021). This hybrid approach combines thermal tolerance data from experimental trials with spatial projections generated by ENM techniques to establish sites where future temperatures will be outside the known thermal thresholds. For instance, Lara-Résendiz et al. (2015) estimated future extinction risk in two lizard species in the Chihuahuan Desert (*Phrynosoma cornutum* and *Phrynosoma modestum*) based on restriction hours of the species' activity (i.e., daily hours where the local temperature exceeds the operative temperature of an organism) in each sampled locality under a set of climate change scenarios.

However, not all studies follow a species-specific approach. Several studies have evaluated climate change impacts at the biome or ecosystem level. The first study in Mexico about climate change and biodiversity was this type (Villers-Ruiz and Trejo-Vázquez 1997). They found that, in general, temperate forests would reduce their extent under future climate scenarios, whereas dry and very dry tropical forests were the opposite. More recently, one focus of attention is the cloud forest, given its particular fragility to climate change due to its natural narrow distribution and sensitivity to climatic conditions (Ponce-Reyes et al. 2012, 2013; Rojas-Soto et al. 2012; Mendoza-Ponce et al. 2018, 2020). All analyses coincide that more than 50% of the current extent of this ecosystem could disappear in the second half of this century as a consequence of climate change exacerbated by land cover degradation. This drastic reduction would compromise the persistence of the biotic component endemic to cloud forests (Ponce-Reyes et al. 2012, 2013; Rojas-Soto et al. 2012). Moreover, in a recent countrywide analysis, Mendoza-Ponce et al. (2020) evaluated the exposure of terrestrial vertebrates to future changes in climate and land use simultaneously to propose a spatial conservation prioritization under different scenarios. They found that amphibians are the most vulnerable group and 0.39% of the country holds 30% of the most vulnerable areas, mainly in Guerrero.

The assessments of potential climate change impacts on Mexican biota (Fig. 20.5) have used coupled atmosphere-ocean GCMs from the Climate Model Intercomparison Project phase 3 (CMIP3) and phase 5 (CMIP5) as the climatic basis for model projections. However, the recent development of a new series of climate models (CMIP6) demands further studies to reanalyze how Mexican biota could be affected by future climate change. These new climate models were developed by combining different Shared Socioeconomic Pathways (SSPs; O'Neill et al. 2016) and Representative Concentration Pathways (RCPs; Moss et al. 2010), resulting in five narratives of socioeconomic development at the global scale that facilitates the analysis of impacts at regional and local scales. Moreover, in CMIP6 scenarios, the uncertainty in the equilibrium climate sensitivity (i.e., global surface temperature response to doubling of atmospheric CO_2 concentration) is lower than previous scenarios, and therefore, they are more realistic in simulating the global climate system (Meehl et al. 2020; Zelinka et al. 2020). Therefore, adopting new ecological modeling approaches coupled with CMIP6 is necessary to provide more realistic climate change impact scenarios on the Mexican biota. Luckily, new developments in ecological modeling incorporate eco-evolutionary processes explicitly in the estimates of range shifts or demographic parameters (Norberg et al. 2012; Cotto et al. 2017; Diniz-Filho et al. 2019; Nadeau and Urban 2019; Lyons and Kozak 2020; Miller et al. 2020). Finally, the increasing availability of massive datasets of fossil records and paleoclimates also helps to calibrate ecological models incorporating nonstationarity climate dynamics through time and space (Fordham et al. 2016, 2018).

20.4 Major Knowledge Gaps and Research Opportunities

As observed above, the biology of climate change in Mexico is an emerging field gaining strength, although there is still a long way to go. However, time is growing short; thus, the main challenge is to speed up the generation of relevant information to understand the phenomenon better and make more suitable decisions for conserving biodiversity in a rapidly changing world. Next, we highlight major gaps in our knowledge regarding climate change biology in Mexico and propose some directions to contribute to a national research agenda.

20.4.1 Gaps in Baseline Climatologies

One of the main problems in Mexico is the lack of robust historical baseline climatic data. This problem obeys, in part, to its large extension and rugged topography that has made it very complicated to maintain a representative network of meteorological stations across the country but also because many stations have stopped operating for long periods, producing fragmentary time series that limit long-term analysis. Therefore, it is a priority to devote significant efforts to overcome this limitation and produce high-quality data for at least the last 100 years. This information is the cornerstone for retrospective analyses and the baseline for calibrating models more appropriately to project future trajectories under several climate change and socioeconomic scenarios. In this context, some recent approaches based on machine learning might be helpful to process precipitation and temperature daily data and somewhat fill temporal data gaps (Richman et al. 2009; Kiani and Saleem 2017; Gorshenin et al. 2019).

20.4.2 Long-Term Population Monitoring and Retrospective Analyses

In Mexico, we know very little about how the diverse manifestations of biodiversity respond to the observed changes in climate (Fig. 20.5). However, we can readily advance our knowledge by undertaking two main approaches: (a) analyzing long-term monitoring biological data concomitantly with climatic data and (b) relating historical and current observational data with climatic trends. For the first approach, long-term monitoring efforts are not copious across the country, but some information is available. Initiatives such as the Long-Term Ecological Research (Mex-LTER; Maass et al. 2010) or data gathered from marine fisheries may be a good starting point to find continuous data over significant periods to observe temporal changes and relate these with local climatic trends. Moreover, the new spatially explicit information about recent climate change trends (e.g., Cuervo-Robayo et al. 2020; Murray-Tortarolo 2021) can be advantageous to pinpoint specific sites to establish monitoring programs designed to detect structural and functional biotic responses to climate change.

Under the second approach, Mexico has an enormous advantage. For three decades, CONABIO has led a national effort to gather, systematize, georeference, clean, and make available primary biodiversity data from several sources, primarily natural history collections, and, more recently, from citizen science (CONABIO 2020). This information is highly valuable because it covers most taxa for a long period of collecting and recording efforts that allow before-and-after analyses matching biological and environmental data (e.g., Peterson et al. 2015a). Also, primary biodiversity data are helpful to direct resurveys to specific well-inventoried sites, similar to the Grinnell Project (https://mvz.berkeley.edu/Grinnell/).

Lastly, particularly worrisome is the lack of information from the freshwater realm. Freshwater ecosystems are under enormous pressure from different flanks, and we have no clue to what extent climate change affects their ecological integrity. Our literature search returned only one study with indirect information about the possible impact of climate change in a freshwater system (i.e., Ramírez Carrillo and Macías García 2015). Consequently, this is probably the most urgent pending task for the climate change biology research agenda in Mexico.

20.4.3 New Modeling Approaches

Few efforts currently exist to generate future projections of the Mexican fauna range dynamics using the so-called hybrid models, which incorporate eco-evolutionary mechanisms directly during the calibration processes (e.g., Cotto et al. 2017; Diniz-Filho et al. 2019). Accordingly, we have little information about future climate change impacts beyond static ENM approaches. Although such approaches are handy tools because they provide an initial glimpse of the potential effects of climate change, the associated (usually unknown) uncertainties coming from many sources make them unreliable for some applications, like conservation decision-making (Guisan et al. 2019; Santini et al. 2020). For instance, recent studies have found more uncertainty in future projections from algorithm model selection than GCMs (Guisan et al. 2019). This issue is vital when many algorithms exist, and there is no a priori reason to choose a specific one for climate change studies. Furthermore, the uncertainties and error propagation through different steps during the ENM process can bias the signature of climate change impacts across taxa and regions.

We call for more robust statistical approaches by including additional biological parameters during the calibration model process. For instance, when modelers included demographic parameters, physiological thermal tolerances, or life history traits, the projected range shifts under future climate change were less pessimistic than static ENMs (Benito-Garzón et al. 2019; Lyons and Kozak 2020). These more comprehensive modeling approaches will likely help reduce uncertainty and generate more realistic projections under several narratives of socioeconomic trajectories and emission scenarios. Indeed, some of these data are available from public repositories (e.g., the Open Traits Network – OTN) or can be approximated using imputation methods (e.g., Penone et al. 2014; James et al. 2020). Finally, an effort to adopt an ecological synthesis framework is necessary to reduce our knowledge gap of the Mexican biota in the face of climate change (Halpern et al. 2020).

20.5 Recommendations for Conservation

Mexican fauna, particularly sensitive to alterations to its original habitat, is under great threat because pristine or low-impacted environments are rapidly disappearing (FAO 2015). Furthermore, the ubiquitous nature of climate change and its synergistic effect with other stress drivers paint a worrying picture that calls for decisive actions. In our changing world, species are shifting, communities are rearranging, and biotic interactions are disrupting while new ones are emerging. Consequently, the static conservation model of (disconnected) protected areas and species-oriented efforts is useful but insufficient. Moreover, current data and methodological approaches are not robust enough to accurately project, with reasonable certainty, where in the country or what species we should focus our conservation efforts on in the face of climate change to establish new protected areas. Therefore, we need to come up with novel and creative strategies that consider not only the conservation of biodiversity patterns but also the ecological and evolutionary processes that produce new patterns. In this context, a paramount strategy is to expand spatiotemporal connectivity among natural areas to facilitate the movement of populations as a response to shifting climates, but equally important is to strengthen the collaborative work among disciplines and coordination among stakeholders (Hannah et al. 2008, 2020).

One such endeavor in this direction in Mexico is a consulting tool developed by CONABIO et al. (2021) called *Explorador de cambio climático y biodiversidad* (ECCBio). ECCBio integrates historical and future climatic trends and some possible effects on biodiversity elements in the natural protected areas of the country. Also, it presents a proposal of bioclimatic corridors that favor landscape connectivity, which refers to areas with low human impact and mild climatic gradients that connect natural vegetation fragments. Theoretically, these corridors would facilitate the movement of shifting populations tracking their climatic niches.

This type of collaborative work between the public, private, and academic sectors is vital to guide the urgent actions necessary to be implemented. In the same line, more lively collaboration and coordination among climate change scholars of different disciplines are necessary to hasten the generation of critical information for nourishing conservation decisions in the context of climate change. As the IPCC (2021) and IPBES (2019) have said, this may be our last chance to make the necessary transformative changes to avoid irreversible and unpredictable modifications to life on Earth.

Acknowledgments We thank Oscar Calderón Bustamante for his help during the preparation of climate datasets from CMIP5. We also thank the Programa Universitario de Investigación en Cambio Climático (PINCC-UNAM) for the financial support (EMM project number IB-739, JAV no project number). JAV thanks the Direction General de los Asuntos del Personal Académico (DGAPA) for the support through grant UNAM-PAPIIT IA201320.

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Chapter 21
Invasive Alien Species of Invertebrates and Fishes Introduced Into Mexican Freshwater Habitats

José Luis Bortolini-Rosales and Hugo Enrique Reyes-Aldana

Contents

21.1 Introduction

It is estimated that over a million species worldwide rely on freshwater ecosystems for their survival but the rapid deterioration of freshwater bodies, driven by human population growth and habitat degradation, is having a negative impact on inland aquatic biodiversity (Cumberlidge et al. 2009). Freshwater ecosystems sustain a

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J. L. Bortolini-Rosales (✉)
Departamento de Biología Comparada, Facultad de Ciencias, Universidad Nacional Autonoma de México, Ciudad de México, Mexico
e-mail: jlbr@ciencias.unam.mx

H. E. Reyes-Aldana
Department of River Ecology, Helmholtz Centre for Environmental Research – UFZ, Magdeburg, Germany

Department of Aquatic Ecosystem Analysis, Helmholtz Centre for Environmental Research – UFZ, Magdeburg, Germany
e-mail: hugo.aldana@ufz.de

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_21

high diversity of invertebrates with about 90,000 species in 17 phyla and ~570 families (Strayer 2006). Diversity not only considered as the number of species but also the number of interactions among the biotic and abiotic components, when altered, may present changes at different levels in the dynamics of the ecosystem. Normally such processes have a natural origin and happen over geological time; however, in recent times, anthropogenic sources are influencing the development of these processes with negative consequences on endemic biodiversity. The effects of such anthropogenic processes are called "anthropization," which is the conversion of natural spaces by human action that results in the environmental erosion and degradation of ecosystem components to different extents (Lai et al. 2017).

Alterations such as dam or water reservoir construction, land-use change, and introduction of plant and animal species are usually associated with aquaculture and other commercial activities. The list of impacts continues with the excessive discharge of heavy loads of pollutants, use of water bodies as transport routes, electrical energy production, recreation, and, possibly one of the most notorious disturbances, the loss of native habitats and species and the alteration of the biogeochemical cycles of ecosystems.

In Latin America, Mexico is one of the countries with the largest diversity of both ecosystems and living species ranging from 10 to 17% of the world's biota (Ramírez-Albores et al. 2019). However, a common limitation of environmental studies in Mexico is due to the lack of information available of local communities, biodiversity loss rates, and habitat tolerance to human impact.

For Arriaga-Cabrera et al. (2000), biodiversity finds its critical levels of conservation in underdeveloped countries where environmental conservation does not represent an axis of government agenda, as is the case in Mexico. The disparity between social and private costs in the distribution of water has caused the deterioration of freshwater biodiversity. An important tool to improve the adequate maintenance of aquatic systems at different levels of government and state is the knowledge of broad and local biodiversity, the state of conservation, and the possible actions for its restoration, as well as including multiple levels of social involvement.

21.2 Invasive Alien Species (IAS)

Species outside of their native range can be deemed as alien, non-native, nonindigenous, foreign, exotic, or introduced. These species are defined by the Convention on Biological Diversity (CBD 2000) as "species, subspecies or lower taxa introduced outside its natural past or present distribution, which includes any part, gametes, seeds, eggs, or propagules of such species that might survive and subsequently reproduce." If an alien species represents a threat to the local ecosystems or native biota, it becomes an invasive alien species (IAS; Roy et al. 2011). IAS are considered to be the second most severe cause of biodiversity loss, after habitat destruction. Their introduction and proliferation cause displacement and extinction of native populations due to niche exclusion, competition, predation, or transmission of pathogens (CBD 2000; MEA 2005).

In recent years, IAS have received more attention, in part, because of their dramatic increase in the number around the world. Even though most of the introduced species do not succeed on becoming invasive, the few ones achieving invasion success could become considerably harmful (Mooney et al. 2005; Pluess et al. 2012). There are several factors for an IAS to be successful in its establishment: physical characteristics of the landscape, bottom-up processes, biological characteristics of IAS such as dispersal and reproductive adaptations; top-down processes and the presence of anthropogenic factors since different aspects depend on these, such as the density and/or number of propagules, seeds, or larvae that are introduced to the system; and the life cycle phase of the invading organisms, among others. In addition, IAS cause economic losses and contribute to social instability facilitating the appearance of difficulties in the development and economic growth of associated human populations (Early et al. 2016).

The multiple, physical, chemical, and mainly biological alterations that are observed and that are caused by IAS have the capacity to modulate the availability of resources to other species (Ilarri et al. 2014). In the case of freshwater biodiversity and ecosystems, the threats come from habitat competition, predation, habitat alteration, hybridization in phylogenetically related species, and a great variety of introduced diseases (Mooney et al. 2005; Early et al. 2016). Once established, IAS are often difficult or impossible to control, making their presence and dispersal a widespread pressure on the ecological status of water bodies. When competing for a habitat, IAS put pressure on native species and outcompete them in niche occupation and food resources, altering through this colonization the forms and functioning of the freshwater ecosystems (Mooney et al. 2005; Haubrock et al. 2019; Fagúndez and Lema 2019). Regarding predation, IAS can prey on native species, but becoming prey themselves is a less common consequence as local predators may not have the traits necessary to prey on them. This leads to an excessive growth of the introduced populations as well as overconsumption of food sources.

When there is a certain phylogenetic proximity, IAS may breed with native species, potentially leading to alterations in adaptations, resilience, and genetic diversity in local populations. One of the examples is the so-called hybrid vigor or heterosis, where the product of interbreeding of closely related species leads to the increase in certain functional traits such as biomass, reproductive output, and lifespan, among others, outcompeting one or both parental populations (Bousset et al. 2014).

Introduction of diseases to local populations is another common problem linked to IAS. When introduced to a new habitat, IAS may carry pathogens that at the same time could be considered IAS themselves, as there may not be an existing pool of their populations in the environment. Another possibility could be that IAS alters the equilibrium of species interaction, therefore increasing the incidence of a disease; and this effect can be observed in terms of geographic range, virulence, or adaptation to a new host. For example, if a hypothetical exotic organism manages to fit in a local population, the parasite load it had could spread to the local communities and generate a considerable impact on local populations. However, pathogens are not phylogenetically limited, and if newly arrived individuals are infected, there is a probability to contaminate close lineages or organisms that could share physio-ecological characteristics, with potentially devastating consequences. Diseases carried by IAS can impact native aquatic organisms and their populations by (1) altering predator-prey interactions, (2) affecting host abundance, (3) reducing the native hosts' genetic variation, or (4) producing local extinctions of sensitive species.

21.2.1 Platyhelminthes

Commonly known as flatworms, platyhelminthes are bilateral unsegmented protostomes. With more than 6500 species and diverse life-forms, many of them are parasitic and cause zoonosis with multiple stages through their life cycles. Some 1300 species are unique of freshwater ecosystems. Platyhelminthes occupy a myriad of ecological niches and play important roles in the food webs, such as predation, parasitism, invasions, and feedback controls with other organisms (Brusa et al. 2020; Collins 2017; Noreña et al. 2015).

In addition to that, their multiple functional traits and simple morphology have allowed them to colonize and invade a great diversity of environments and hosts. According to molecular data, freshwater platyhelminthes are a monophyletic taxon which started its dispersal since the Pangean period (Artois 2008; Noreña et al. 2015).

Out of their natural environments and ecological constrains, platyhelminthes can become a nuisance as pests and pathogens to humans and animals. Flatworms are especially successful parasites; this trait has evolved multiple times in this phylum and makes them able to parasitize invertebrates and vertebrates (Hugot et al. 2001; Parker et al. 2003; Zarowiecki and Berriman 2015). Parasitic species are able to get into their hosts by multiple means, and then they establish and develop inside their digestive tract, brain, blood, or other internal organs (Collins 2017). Even free-living species represent a risk to the ecosystem if they are introduced to a non-native area, as they may feed on much larger prey, and sometimes these preys can be fulfilling and play an important ecological role such as earthworms, snails, and insects, therefore altering the processing of organic matter through the food web (Sluys 2016; Stocchino et al. 2019).

It is worth mentioning that the direct voluntary introduction of flatworms is rare, as it is unusual for them to have a primary role in human activities. However, due to their ecological functions, they may be used for biological control of other pests such as snails and insects (Barker 2004; Justine et al. 2014; Tranchida et al. 2009). Accidental transportation is the most common form of introduction of flatworms and their transition to an IAS. Either with plants or animals, flatworms can be transported through eggs in the soil or on surfaces, and depending on the size of the individual, adult organisms can also be transported. Considering that many of them are hermaphrodites and/or are capable of asexual reproduction, the risk of dispersal is high (Boag and Yeates 2001). Additionally, they can be carried by their animal hosts. Such is the example of various species of the genus *Cherax*, Australian

Table 21.1 List of invasive helminths (platyhelminthes and nematodes) reported in Mexican freshwater systems (CONABIO 2020; Fig. 21.1)

Invasive helminths of Mexican freshwater systems		
Bothriocephalus acheilognathi	*Gyrodactylus cichlidarum*	*Ligictaluridus mirabilis*
Centrocestus formosanus	*Gyrodactylus colemanensis*	*Octomacrum mexicanum*
Cichlidogyrus	*Gyrodactylus elegans*	*Onchocleidus principalis*
Cichlidogyrus dossoui	*Gyrodactylus neotropicalis*	*Onchocleidus spiralis*
Cichlidogyrus sclerosus	*Gyrodactylus pseudobullatarudis*	*Posthodiplostomum minimum*
Cichlidogyrus tilapiae	*Gyrodactylus shariffi*	*Proteocephalus ambloplitis*
Cleidodiscus bedardi	*Gyrodactylus ulinganisus*	*Sciadicleithrum bravohollisae*
Crepidostomum cornutum	*Gyrodactylus yacatli*	*Sciadicleithrum mexicanum*
Dactylogyrus vastator	*Haplocleidus dispar*	*Sciadicleithrum splendidae*
Enterogyrus sp.	*Haplorchis pumilio*	*Scutogyrus longicornis*
Enterogyrus cichlidarum	*Ligictaluridus floridanus*	*Urocleidoides reticulatus*
Camallanus cotti	*Pseudocapillaria tomentosa*	

invasive crayfish that were introduced to South African freshwaters through inappropriate handling in aquaculture and aquarism. These crayfishes are hosts of numerous species of temnocephalans, such as *Temnocephala minor*, *T. chaeropsis*, and *Diceratocephala boschmai*, all of them representing a high risk of becoming parasites on the local populations of decapods, which could put an intense ecological pressure on their populations considering that the crayfishes are already exerting a constant stress over them (du Preez and Smit 2013).

In Mexico, there are 33 species of exotic platyhelminthes in freshwater ecosystems (CONABIO 2020; Table 21.1). For example, *Bothriocephalus acheilognathi*, a parasitic flatworm from Russia and China, was introduced with *Ctenopharyngodon idella*, and other species of cyprinids, improper practices, and the alteration of freshwater habitats made it possible for the parasite to spread all along the Mexican territory, infecting native and introduced fishes. This platyhelminth can cause great damage in fish populations, particularly on young individuals as the digestive system results severely damaged through the infection, also causing anemia and chronic infections of bacteria and protozoa. On the long range, it also produces a decrease in the reproductive and swimming capacities, causing massive fish kills as has been observed in cultivated ponds (Salgado-Maldonado and Pineda-López 2003).

Among the 33 IAS of plathelminths in Mexican freshwaters, 8 correspond to the genus *Gyrodactylus*, making it the most abundant of invasive flatworms. This group is known to be mainly parasitic of brackish and freshwater fishes, they resemble leeches in their external morphology and form of parasitism, and they possess a couple of hooks in the mouth which help them attach to the fishes and feed on the epithelium and sometimes on blood. They can cause considerable infections in gills and skin. Once parasitized, fishes show fading of color, loss of scales, excessive mucous on the tail and fins, detachment of skin, ulcers, and necrosis (Grano-Maldonado et al. 2018).

Fig. 21.1 Invertebrate invasive species of Mexico: (1) *Daphnia lumholtzi*; (2) *Pseudodiaptomus inopinus*; (3) *Daphnia magna*; (4) *Argulus japonicus*; (5) *Centrocestus formosanus*; (6) *Haplorchis pumilio*; (7) *Planorbella duryi*; (8) *Pomacea flagellata*; (9) *Amerianna carinata*; (10) *Radix auricularia*; (continued)

Alternatively, if the infection develops on the gills, the fish can die due to the profuse secretion of mucous (Kar 2016; Stoskopf 2015). In Mexico, the introduction of exotic fishes for aquaculture has promoted the invasion of such parasites. For example, *G. cichlidarum*, initially reported in cultured African tilapias in Northern Mexico, is now present in the Gulf of Mexico slope infecting at least three native poeciliids. The invasion seems to continue expanding and represents a threat to fish farms and watersheds where more native biota may result affected (García-Vásquez et al. 2017; Grano-Maldonado et al. 2018).

Most of the platyhelminthes IAS have arrived indirectly with species used for aquaculture; negligent practices such as overcrowding, inadequate storage and transportation, and escapes and releases have created this problem. If it is true that fish farming may be a necessary activity for the development of riverine and lacustrine communities, there should be programs to aid the producers to identify and eliminate the risk of parasitic infections. Although antiparasitics could be used, one has to keep in mind that in the same way as with bacterial infection, the overuse can cause resistance and create a greater health and ecological imbalance.

21.2.2 Nematodes

Commonly known as roundworms, nematodes are one of the most diverse groups of organisms as they occupy niches in almost all the ecosystems of the planet, from the Antarctic and deep oceans to rainforest and high mountains (Ingham 1994). The diversity of this group makes it difficult to estimate accurately how many species of nematodes exist in the Mexican territory, but some of species have been identified to cause gastrointestinal diseases in humans, cattle, crops, and fishes (Moravec et al. 1995; Torres-Acosta et al. 2003; Molina-Ochoa et al. 2003; Canul-Ku et al. 2012; Bruno et al. 2020). These pathogenic characteristics are important when considering the probability of introduced species to become IAS as they could harm natural populations and crops.

According to official records (CONABIO 2020), there are only two species of nematodes considered invasive in Mexico, *Camallanus cotti* and *Pseudocapillaria tomentosa*. In the case of *C. cotti*, it corresponds to a fish parasite which has been introduced worldwide, most probably with ornamental fishes (Levsen 2001). However, its flexible life cycle has allowed it to disperse through other means such as running water (Hugot et al. 2001).

◄

Fig. 21.1 (continued) (11) *Tarebia granifera*; (12) *Biomphalaria glabrata*; (13) *Cipangopaludina chinensis*; (14) *Pomacea canaliculata*; (15) *Marisa cornuarietis*; (16) *Corbicula fluminea*; (17) *Procambarus clarkii*; (18) *Melanoides tuberculata*; (19) *Dreissena polymorpha*; (20) *Cherax destructor*; (21) *Macrobrachium macrobrachion*; (22) *Cherax quadricarinatus*; (23) *Orconectes virilis*; and (24) *Macrobrachium rosenbergii*. (Images 1, 2, and 21 were obtained from the Smithsonian Institution Digital Collection and are under Creative Commons license; the rest of the images were obtained from the Wikimedia Commons and are free to use for noncommercial purposes)

Originally described from Japan, *C. cotti* infects all types of fishes but has been observed mainly in small ornamental species. It is an intestinal parasite known for causing anal inflammation due to the protrusion of the gravid females as a red cord; the color is due to the blood-feeding form of the parasite which can eventually cause anemia, emaciation, and death (Stumpp 1975; Levsen 2001). Despite the information contained in the list of invasive species of CONABIO (CONABIO 2020), no scientific peer-reviewed literature mentions the existence of this species in the Mexican territory; it may be that those records come from other types of publications such as technical reports, thesis, or inventories.

Pseudocapillaria tomentosa is a common parasite of cyprinids and other fishes; the infection can create a range of reactions from subtle inflammation to aggressive neoplasms in the intestine (Kent et al. 2002; Salgado-Maldonado and Quiroz-Martínez 2013). The records of *P. tomentosa* suggest that it was introduced to the country with non-native carps (Pineda-López et al. 2005).

It is evident that the information regarding IAS of nematodes is rather scarce for aquatic ecosystems. It is essential to develop this field of knowledge as nematodes can affect local ecosystems as well as economic activities such as cattle breeding, fish farming, silviculture, and the health of domestic animals.

21.2.3 Crustaceans

Crustacea is the most successful taxonomic group of aquatic alien invaders around the world as they present quite dominant behaviors (examples in Table 21.2). For instance, in European freshwater ecosystems, 53% of invasive alien species are crustaceans (Hänfling et al. 2011) and show higher densities than their native competitors.

The arrival of invasive alien crustaceans (IAC) has three important vectors for their introduction: transport in ballast water, dispersal through canal systems, and aquaculture and stocking practices. The second, artificial canal systems, have contributed to intracontinental invasions of IAC. These artificial waterways provide shortcuts between water bodies, thus leading to a rapid expansion in the geographical range of alien Crustacea. After their first introduction to North America via ballast water, some Ponto-Caspian IAC, including freshwater and brackish water amphipods, cladocerans, copepods, decapods, and mysids, have spread quickly and irrepressibly, via drift and local boating through the systems of canals in the Hudson River catchment and the Laurentian Great Lakes (Mills et al. 1993). The third and main driver of the introductions of IAC in the world is the stock translocation and aquaculture. In North America, the massive introduction of many amphipods and mysids to water bodies was purposed to boost secondary production and increase yields for the fishing industry and recreational angling (Hänfling et al. 2011).

Some crustacean species were introduced into new areas for research or teaching, such as *Orconectes rusticus* and *Carcinus maenas* in North America: living specimens can be readily ordered and air-shipped in large quantities from several

Table 21.2 List of invasive crustaceans reported in Mexican freshwater systems (CONABIO 2020) (Fig. 21.1)

Invasive crustaceans of Mexican freshwater systems		
Argulus japonicus	*Macrobrachium macrobrachion*	*Moina macrocopa*
Cherax sp.	*Macrobrachium rosenbergii*	*Moina macrocopa macrocopa*
Cherax destructor	*Mastigodiaptomus albuquerquensis*	*Orconectes virilis*
Cherax quadricarinatus	*Mesocyclops aspericornis*	*Procambarus clarkii*
Daphnia lumholtzi	*Mesocyclops ogunnus*	*Pseudodiaptomus inopinus*
Daphnia magna	*Mesocyclops pehpeiensis*	*Thermocyclops crassus*
Exopalaemon styliferus	*Mesocyclops thermocyclopoides*	

biological supply houses and are often accidentally or intentionally released to the wild from school or research aquaria. Another example is *Procambarus clarkii* which is widely used for physiological studies (Hänfling et al. 2011). The introduction of invasive species is not always due to the action of man in ecosystems; other organisms can act as vectors, carrying certain life stages, that finally introduce the alien species to the bodies of water.

In the case of Copepoda, there are studies of the native fauna in different places in Mexico, and it is possible to find the existence of introduced species which have been reported in areas such as reservoirs in the State of Sinaloa. For instance, *Skistodiaptomus pallidus*, grazes on algae, but not finding these food resources, can develop cannibalistic behavior. This species has a distribution in Ontario, Canada, Montana, Northern USA, Texas, Mississippi, and Georgia to the south, and in Mexico, it has been found in the abovementioned reservoir which makes this the first record for Northwestern Mexico. A possible vector for introduction is via migrating birds; diapausing eggs have been reported in the American white pelican *Pelecanus erythrorhynchos*, during fall and winter in this reservoir (Suárez-Morales and Arroyo-Bustos 2012).

Another case is the red claw crayfish *Cherax quadricarinatus*, a parastacid crustacean originally from Northern Australia and Papua New Guinea, which was introduced to Mexico in 1995 for aquaculture purposes by the Universidad Autónoma Metropolitana in Mexico City. A small stock was brought to initiate a research program to determine its suitability to be cultured in the country (Bortolini et al. 2007). Wild populations have been recorded in Jamaica, Mexico, Puerto Rico, Ecuador, Singapore, and South Africa. This species is highly invasive due to its high reproductive capacity and to its ability to adapt to multiple environments after escaping from captivity. In Mexico, starting around 1998, this species was transferred to different aquaculture centers throughout most of the countries. To date, it is considered a fully established resource with stable catch rates that represent a fishery already constituted in some sites (Vega-Villasante et al. 2015). Besides the impact that red claws could have on the native fauna, through direct competition, predation, or habitat modification, the spread of new parasites into native populations must be considered. Red claws have been reported to be carriers of a number of pathogens, including viruses, bacteria, fungi, and protozoan and metazoan parasites (Bowater et al. 2002; Edgerton et al. 1996, 2000; Romero and Jiménez 2002). Apparently, more parasites of red claws are discovered as more studies are undertaken, and their spread could be occurring without being noticed. It is now apparent that the reported disease-free nature of *C. quadricarinatus* was an artefact of the lack of surveys for diseases in what was until the mid-1980s a little-known species, which inhabited remote areas of its original distribution (Edgerton and Owens 1999). Another example is *Procambarus clarkii* which has been recorded as an exotic species. *P. clarkii* has its type locality between "San Antonio" and "El Paso" in Texas, USA, on the eastern border of the USA and Mexico. To date, this organism can be collected in Aguascalientes, Baja California, Baja California Sur, Chiapas, Chihuahua, Coahuila, Colima, Durango, Jalisco, Michoacán, Morelos, Nuevo León, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, and Yucatán (Hernández et al. 2008). Invasive crayfishes have reduced or eliminated many species of different taxa, fishes, other crayfish species, amphibians, and plants elsewhere. The effects of crayfish on other species depend on the strength of their mutual interactions. Crayfish can reduce and alter vertebrate and invertebrate distribution and can promote changes in the trophic dynamics (Weber and Traunspurger 2017).

With respect to *Macrobrachium rosenbergii*, its native distribution extends from Pakistan in the west to southern Vietnam to the east, across Southeast Asia, and south to northern Australia, Papua New Guinea, and some Pacific and Indian Ocean Islands. Today it is cultured in at least 43 countries across 5 continents. The larvae require brackish water for survival and early development. The species is characterized by its high fecundity and high resistance to handling and stress conditions; it has a relatively short larval period, and it is omnivorous and has a fast growth rate. In Mexico, between 1930 and 1970, the creation of aquaculture centers was promoted; by 1978, 30,000 individuals of *M. rosenbergii* were introduced to Bejuco in the Municipality of Coyuca de Benitez, Guerrero, from Miami, Florida, USA; in 1979, a second lot of postlarvae from Hawaii was brought to El Lagartero center in El Carrizal, Guerrero. In 1987, there were 48 farms and 13 laboratories producing postlarvae throughout several states in the country (Ponce-Palafox et al. 2003). The most important disease associated with this species is the white tail (WTD) caused by *Macrobrachium rosenbergii* nodavirus (MrNV; Low et al. 2018).

The Mexican crayfish fauna represents 8.7% of the world's crayfish diversity and 13.3% of the total diversity of the family Cambaridae (Crandall and Buhay 2008). Fifty-three of the 56 species of crayfish recorded, except for *Orconectes virilis*, *Procambarus clarkii*, and *Procambarus pilosimanus*, occur only in Mexico, and most of them have small distribution ranges with only four species (*Cambarellus montezumae*, *Procambarus acanthophorus*, *P. clarkii*, *P. llamasi*) presenting large distributions covering several states and basins (Armendáriz et al. 2017).

The pet trade has been responsible for many introductions of non-native species and is likely the major driver of introductions of nonindigenous crayfish in several countries (Chucholl 2013; Soes and Koese 2010). The scale of the trade in pets, particularly aquatic animals, has been difficult to estimate (Rhyne et al. 2012), but online sale and trade websites can provide estimates of the risk of introduction of nonindigenous species (Kikillus et al. 2012). The pet trade in crayfish in North

America has not been studied in depth, even though it is a large potential market for crayfish pets. Three species account for most (83.7%) of the online crayfish trade in North America: the Marmorkrebs (*Procambarus fallax* f. *virginalis*), the Cajun dwarf crayfish (*Cambarellus shufeldtii*), and the Mexican dwarf crayfish (*Cambarellus patzcuarensis*).

21.2.4 Mollusks

After arthropods, mollusks are the second invertebrate group with the highest diversity occupying multiple niches in marine and freshwater ecosystems. They can be found from the deep seas to shallow waters and even terrestrial environments. Some species are not only important ecologically but also economically, as they can be used for human consumption or in undesirable scenarios they could become problematic. In the case of Mexico, the state of understanding of the malacofauna is still developing, and a great deal of it has not been adequately studied and understood (Naranjo-García and Castillo-Rodríguez 2017; Thompson and Hulbert 2011). Aquatic mollusks are susceptible to become invasive species as any other clade, and the same mechanisms of introduction also apply to them.

For Mexico, the state of knowledge of molluscan IAS is not as comprehensive as for other groups. For example, CONABIO (2020) indicates that at least 12 mollusk IAS exist in the Mexican territory; however, 5 of them are only mentioned by their genus which could imply multiple species or overlap with others already mentioned in the document. On the other hand, Naranjo-García and Castillo-Rodríguez (2017) performed a comprehensive analysis of the introduced and invasive mollusk species in which ten freshwater species were found. It is noteworthy that only 4 species coincide between these 2 studies which would mean that there are at least 18 mollusk IAS registered in Mexico (Table 21.3).

One of the coincident species in both lists is *Pomacea canaliculata*, a freshwater snail originally from South America that was found for the first time in Baja

Table 21.3 List of invasive mollusks reported in Mexican freshwater systems (Naranjo-García and Castillo-Rodríguez 2017; CONABIO 2020)

Invasive mollusks of Mexican freshwater systems	
Clea helena	*Melanoides tuberculata*
Amerianna carinata	*Pachychilus* sp.
Biomphalaria glabrata	*Pila* sp.
Biomphalaria sp.	*Planorbella (Semolina) duryi*
Cipangopaludina chinensis	*Pomacea canaliculata*
Corbicula fluminea	*Pomacea diffusa*
Dreissena polymorpha	*Pomacea flagellata*
Helisoma duryi	*Radix auricularia*
Marisa cornuarietis	*Tarebia granifera*

California in 2010 (Campos et al. 2013). It has been hypothesized that the organisms from these records may have come from populations that dispersed from the USA, specifically Arizona. The flow from the Colorado River and the connectivity with other rivers could have been the motor for this dispersion. In other areas of the world, this species which was initially introduced for human consumption or as pet for aquarists and is considered highly harmful. In Japan, *P. canaliculata* is considered a plague which threatens rice fields and other crops; the invasion was facilitated by the wet soils and connectivity between rivers, streams, and ponds; and some strategies such as releasing native predatory fauna have been tested to try to diminish or suppress this invasion (Yusa et al. 2006). Japan has not been the only Asian country in which this species has become problematic, since the 1980s multiple countries from Central Asia have reported the invasion by this commonly known apple snail (Hayes et al. 2008; Martín et al. 2001). Not only the connectivity between water bodies has played an important role in the dispersal of this invasive organism but also the community composition of the areas where it is now found. In Asia, the plant composition seems to be highly nutritious for the apple snail, which in conjunction to the apparently negligible effect of the phytotoxins represents an excellent scenario for its dispersal (Qiu and Kwong 2009).

Bivalves are one of the groups with the highest incidence of invasiveness in aquatic ecosystems, and their attributes can markedly affect biological communities and ecosystem processes and functions (Sousa et al. 2009) due to the characteristics of the organisms/populations where even after death valves continue to cause important modifications in the substrate. The hardness of their shells plays an important role in bivalve ecological success, as it impedes the access of predators. Indeed, it can also contribute to important physical modifications (i.e., provision of substrata for attachment, provision of shelter from predators, and physical and/or physiological stress, also affecting the transport of particles and solutes in the benthic environment that can greatly influence the associated fauna) (Ilarri et al. 2014).

A bivalve and non-coincident species is *Dreissena polymorpha*, a species inhabiting fresh and brackish waters in the region of the Caspian and Black Seas (Nalepa and Schloesser 1992). While CONABIO does not identify this species or even the genus as an IAS, Naranjo-García and Castillo-Rodríguez (2017) found that *D. polymorpha* is already present in the State of Veracruz. Commonly known as Zebra mussel, it is considered as one of the most dangerous invasive species, threatening the ecosystems where it is found (Nalepa and Schloesser 1992; Lowe et al. 2012; Schloesser and Schmuckal 2012). It has been more than 30 years since the first record of this species in North America – the first record can be traced to 1989 – and the damages it has generated to native ecosystems and species are remarkable (Cooper et al. 2019; Strayer 2009). In the USA and Canada, the state of knowledge of this species is solid, and the information regarding their expansion has been kept updated since the first records (Depew et al. 2020; Strayer 2009). However, the current level of understanding is not enough to manage the species yet, as the high level of connectivity among the rivers and lakes has made possible for this species to expand its invasive range, which adds to the human behavior which can aid the dispersal of the mussels (Rodríguez-Rey et al. 2021; Strayer 2009). The proliferation of this species has caused considerable disturbance in North American ecosystems, as filter feeders and mussels consume the phytoplankton, sometimes even the toxic one.

As the populations of introduced mussels become more abundant, the consumption of phytoplankton also increases; this can lead to an increase in the clarity of water and subsequent increase in macrophytes. Those conditions could be considered as positive for the ecosystem; however, the depletion of phytoplankton limits the growth of other species which also depends on this resource such as zooplankton and larval forms of larger organism. This condition leads to the inevitable alteration of the community structure and trophic networks which eventually may lead to loss of diversity and fracture of the ecosystem and its functions and services (Nalepa and Schloesser 1992; Strayer 2009). Around a decade ago, it was forecasted that the presence of the zebra mussel would bring around $4 billion dollars – worth of damage to native ecosystems in North America and the collapse of multiple fisheries and ecosystem services which could have even greater impacts (Strayer 2009). However, an update on this information is needed. Unfortunately, and despite the imminent risk that this species represents, its study in Mexico is limited, a situation that urges the attention of biologists and stakeholders.

In relation to other groups of IAS, the current state of knowledge of mollusks in Mexico is rather insufficient. There is a need to develop more work not only on the inventorying of mollusk IAS but on the understanding of each species ecology.

21.2.5 Fishes

The North American region ranges from the Alaska Peninsula and Canada to Mexico, although the biodiversity distribution varies with the type of weather, it is an area of the world with significant diversity, and in the case of fishes, it harbors approximately 1050 freshwater species.

The Mexican plateau has an estimated diversity of 250 species that are considered endemic and have an affinity with the Neotropics. Around 35 families of strictly freshwater fish are found in North America, 13 of which are endemic (Cyprinidae, Percidae, Poeciliidae, and Catostomidae; Lévêque et al. 2008). According to Lundberg et al. (2000), the ichthyofauna of North America is well documented, and even when new species appear in the registry, the potential to discover new species is toward the south, in the northern region of the Mexican territory.

Exotic fish, like other introduced organisms, can reproduce naturally and replace local species due to the advantages that they present and that have been mentioned previously (Stachowicz and Tilman 2005). They can also cause genetic pollution with uncontrolled hybridization processes, introgression, and genetic swamping.

In the case of fishes, the situation is not easy to generalize, as it is the most diverse group of vertebrates with multiple ecological functions and anthropogenic uses (Espinosa-Pérez and Ramírez 2015). Possibly one of the most common uses of fishes is human consumption; in this case, aquaculture and sport fishing, besides other strategies to increase fish yields, are responsible for leakages of individuals which later on become naturalized and eventually develop invasive traits (Espinosa-Pérez and Ramírez 2015; García-Vásquez et al. 2017; Ochoa-Ochoa et al. 2017).

An example of the abovementioned situations is the introduction of the Nile tilapia (*Oreochromis niloticus*) in multiple regions of Mexico. This fish originally from the African continent has been introduced to Mexico and other regions of the world as part of aquaculture efforts. This fish has aquaculture advantages over many local species as it produces high yields of biomass, reproduce quickly, feed on a high variety of resources, and tolerate low-quality environmental factors such as oxygen and water chemistry. However, these same beneficial traits for aquaculture are the ones favoring their dispersal and proclivity to become an invasive species. In Mexico, the Nile tilapia is found in almost every region of the country where aquaculture is practiced, and unfortunately due to inadequate management, leakages are frequent to the local environments where they have been observed to displace the local fauna by niche competition and predation, in addition to the multiple diseases that they can transmit. Unfortunately, the Nile tilapia is not the only species with aquacultural importance that has been observed to become invasive; the list is extensive and the factors are related to it as well (Espinosa-Pérez and Ramírez 2015; Table 21.4).

Aquaculture for human and animal consumption is not the only source of invasions by freshwater fishes in Mexico. Another important risk factor are ornamental species. More than 40 million ornamental fishes from more than 700 species are annually traded in Mexico (Mendoza et al. 2015). It is an important industry in the country, but the poor conditions of some of the traders and breeders in combination with the lack of regulation enforcement by the authorities have led to multiple events of release and leakages (Espinosa-Pérez and Ramírez 2015; Mendoza et al. 2015; Ochoa-Ochoa et al. 2017). These events have compromised the status of local fauna, as these ornamental species can compete for the ecological niche and prey on the local organisms, disrupting the delicate ecological networks. For instance, guppies (*Poecilia reticulata*) – a relatively popular group of fishes for aquarism – have been found in Central Mexico; these species have been found harassing other fish groups during their mating rituals and trying to copulate with them; of course, this

Table 21.4 List of invasive fishes reported in Mexican freshwaters (CONABIO 2020; Figs. 21.2 and 21.3)

Invasive fishes of Mexican freshwater systems		
Abramis brama	*Chirostoma grandocule*	*Oncorhynchus tshawytscha*
Abramites hypselonotus	*Chirostoma humboldtianum*	*Oreochromis* sp.
Acanthogobius flavimanus	*Chirostoma labarcae*	*Oreochromis esculentus*
Acantopsis dialuzona	*Chirostoma lucius*	*Oreochromis leucostictus*
Algansea lacustris	*Chirostoma patzcuaro*	*Oreochromis macrochir*
Altolamprologus compressiceps	*Chirostoma sphyraena*	*Oreochromis mortimeri*
Amatitlania nigrofasciata	*Chitala chitala*	*Oreochromis mweruensis*
Ambloplites rupestris	*Chromobotia macracanthus*	*Oreochromis niloticus* *Oreochromis spilurus*
Ameiurus catus	*Danio rerio*	*Oreochromis urolepis* subsp. *hornorum*
Ameiurus natalis	*Dimidiochromis compressiceps*	*Oreochromis urolepis*
Ameiurus nebulosus	*Dorosoma cepedianum*	*Oreochromis urolepis* subsp. *urolepis*
Amphilophus citrinellus	*Dorosoma petenense*	*Osmerus mordax*
Andinoacara rivulatus	*Epalzeorhynchos bicolor*	*Osteoglossum bicirrhosum*
Aphyosemion australe	*Epalzeorhynchos frenatum*	*Panaque nigrolineatus*
Apistogramma viejita	*Epalzeorhynchos kalopterus*	*Pangasianodon gigas*
Aplocheilus lineatus	*Fundulus zebrinus*	*Pangasianodon hypophthalmus*
Apteronotus albifrons	*Gila* sp.	*Pangasius bocourti*
Arapaima gigas	*Gila orcuttii*	*Pangio kuhlii*
Astronotus ocellatus	*Gnathonemus petersii*	*Pantodon buchholzi*
Astyanax caballeroi	*Gymnocorymbus ternetzi*	*Paracheirodon axelrodi*
Astyanax fasciatus	*Gyrinocheilus aymonieri*	*Paracheirodon innesi*
Astyanax mexicanus	*Hasemania nana*	*Parachromis managuensis*
Aulonocara nyassae	*Helostoma temminckii*	*Petenia splendida*
Aulonocara stuartgranti	*Hemichromis bimaculatus*	*Puntius conchonius*
Balantiocheilos melanopterus	*Hemichromis letourneuxi*	*Phractocephalus hemioliopterus*
Puntius semifasciolatus	*Hemigrammus erythrozonus*	*Piaractus brachypomus*
Barbodes semifasciolatus	*Hemiodus gracilis*	*Pimelodus pictus*
Barbonymus schwanenfeldii	*Herichthys cyanoguttatus*	*Pimephales promelas*
Beaufortia leveretti	*Heros efasciatus*	*Poecilia petenensis*
Belonesox belizanus	*Heterandria*	*Poeciliopsis gracilis*
Betta splendens	*Heterotilapia buttikoferi*	*Polypterus senegalus*
Botia almorhae	*Hypancistrus zebra*	*Pollimyrus castelnaui*
Botia striata	*Hyphessobrycon eques*	*Pomoxis annularis*
Brachygobius xanthozonus	*Hyphessobrycon herbertaxelrodi*	*Pomoxis nigromaculatus*

(continued)

Table 21.4 (continued)

Invasive fishes of Mexican freshwater systems		
Carassius auratus	*Hyphessobrycon megalopterus*	*Pristella maxillaris*
Carassius gibelio	*Hypophthalmichthys molitrix*	*Hyphessobrycon anisitsi*
Carassius carassius	*Hypophthalmichthys nobilis*	*Pseudorasbora parva*
Carnegiella strigata	*Hypostomus plecostomus*	*Pseudotropheus johanni*
Carpiodes carpio	*Hypostomus punctatus*	*Pseudoxiphophorus bimaculatus*
Cichlasoma geddesi	*Ictalurus punctatus*	*Pterophyllum scalare*
Clarias	*Kryptopterus bicirrhis*	*Pterygoplichthys anisitsi*
Clarias batrachus	*Labidochromis caeruleus*	*Pterygoplichthys disjunctivus*
Clarias fuscus	*Lepisosteus platostomus*	*Pterygoplichthys gibbiceps*
Clarias gariepinus	*Lepomis auritus*	*Pterygoplichthys joselimaianus*
Clarias macrocephalus	*Lepomis cyanellus*	*Pterygoplichthys multiradiatus*
Clarias ngamensis	*Lepomis gulosus*	*Pterygoplichthys pardalis*
Colossoma macropomum	*Lepomis macrochirus*	*Puntigrus tetrazona*
Copadichromis borleyi	*Lepomis marginatus*	*Puntius titteya*
Coptodon zillii	*Lepomis megalotis*	*Pygocentrus nattereri*
Corydoras aeneus	*Lepomis microlophus*	*Pylodictis olivaris*
Corydoras agassizii	*Lepomis punctatus*	*Rineloricaria parva*
Corydoras arcuatus	*Leporacanthicus galaxias*	*Salmo salar*
Corydoras julii	*Leporinus fasciatus*	*Salmo trutta*
Corydoras leucomelas	*Macrognathus aculeatus*	*Scatophagus argus*
Corydoras melanistius	*Macrognathus siamensis*	*Sciaenochromis fryeri*
Corydoras metae	*Marosatherina ladigesi*	*Siphateles bicolor*
Corydoras paleatus	*Mastacembelus armatus*	*Synodontis eupterus*
Corydoras panda	*Mastacembelus erythrotaenia*	*Tampichthys ipni*
Corydoras rabauti	*Maylandia estherae*	*Tanichthys albonubes*
Cribroheros robertsoni	*Maylandia lombardoi*	*Thayeria boehlkei*
Ctenopharyngodon idella	*Maylandia zebra*	*Thorichthys callolepis*
Cyathopharynx furcifer	*Megalobrama amblycephala*	*Thorichthys meeki*
Cyprinella lutrensis	*Melanochromis auratus*	*Tilapia*
Cyprinodon macularius	*Melanotaenia boesemani*	*Tilapia baloni*
Cyprinodon tularosa	*Melanotaenia praecox*	*Tilapia rendalli*
Cyprinus rubrofuscus	*Metynnis*	*Tilapia sparrmanii*
Cyrtocara moorii	*Microglanis iheringi*	*Tilapia zillii*
Chalceus macrolepidotus	*Micropterus dolomieu*	*Tinca tinca*
Channa	*Micropterus salmoides*	*Trichogaster lalius*
Channa argus	*Mikrogeophagus altispinosus*	*Trichogaster trichopterus*
Channa asiatica	*Mikrogeophagus ramirezi*	*Trichopodus leerii*
Channa bleheri	*Misgurnus anguillicaudatus*	*Trichogaster microlepis*

Fig. 21.2 (continued) *Carassius gibelio*; (25) *Chalceus macrolepidotus*; (26) *Channa micropeltes*; (27) *Chindongo socolofi*; (28) *Corydoras rabauti*; (29) *Dimidiochromis compressiceps*; (30) *Corydoras paleatus*; (31) *Cyrtocara moorii*; (32) *Hemigrammus erythrozonus*; (33) *Corydoras julii*; (34) *Epalzeorhynchos frenatum*; (35) *Gnathonemus petersii*; (36) *Gymnocorymbus ternetzi*; (37) *Hasemania nana*; (38) *Helostoma temminckii*; (39) *Hemichromis bimaculatus*; (40) *Heros efasciatus*; (41) *Herichthys cyanoguttatus*; (42) *Copadichromis borleyi*; (43) *Hyphessobrycon megalopterus*; and (44) *Hypancistrus zebra*. (All images have been obtained from the Wikimedia Commons and are free to use for noncommercial purposes)

Fig. 21.2 Invasive fish species of Mexico: (1) *Abramis brama*; (2) *Abramites hypselonotus*; (3) *Acanthogobius flavimanus*; (4) *Altolamprologus compressiceps*; (5) *Amatitlania nigrofasciata*; (6) *Ameiurus catus*; (7) *Amphilophus citrinellus*; (8) *Ameiurus nebulosus*; (9) *Andinoacara rivulatus*; (10) *Aphyosemion australe*; (11) *Apteronotus albifrons*; (12) *Astronotus ocellatus*; (13) *Astyanax fasciatus*; (14) *Astyanax mexicanus*; (15) *Aulonocara nyassae*; (16) *Aulonocara stuartgranti*; (17) *Balantiocheilos melanopterus*; (18) *Barbonymus schwanenfeldii*; (19) *Belonesox belizanus*; (20) *Betta splendens*; (21) *Botia almorhae*; (22) *Botia striata*; (23) *Brachygobius xanthozonus*; (24)

(continued)

Fig. 21.3 Invasive fish species of Mexico: (1) *Kryptopterus bicirrhis*; (2) *Lepomis auritus*; (3) *Labidochromis caeruleus*; (4) *Lepomis macrochirus*; (5) *Lepomis cyanellus*; (6) *Lepomis marginatus*; (7) *Lepomis microlophus*; (8) *Lepomis megalotis*; (9) *Mastacembelus erythrotaenia*; (10)

(continued)

can generate a disbalance in the local populations that requires attention from the researchers and authorities (Valero et al. 2008).

The problem with IA fishes does not become smaller in comparison with other groups of IAS in Mexico. This is by far the most documented and abundant group of IAS that has been registered for Mexico (CONABIO 2020), which is of no surprise considering the ecological, economic, and biological importance and diversity of the group.

21.3 Final Comments

Movement of fauna outside its native distribution causes a series of events that can hardly be controlled. This movement caused by humans for food, transport, and culture or simply as ornaments, has promoted the degradation of natural habitats in almost the entire world. These alterations may arise through a wide variety of processes, including interspecific competition, disturbance, and predation. Many of these causes have been assumed through the correlation of the arrival of an exotic species with the subsequent alteration of its distribution and population density in native species. These introductions are associated with the anthropogenic interest in fostering species for a wide range of interests and have accompanied humans in the colonization of new environments. Trade and transport facilities accelerated the rate of introduction of exotic species since the eighteenth and nineteenth centuries.

Out of the different groups of invertebrates that are known as introduced species, the level of knowledge of the alterations they cause to the ecosystem is variable. There are some groups which are more broadly studied than others; this fact does not allow for a complete or better evaluation of the effects of the introduction of such species. It is also a fact that taxonomic inventories are more reliable for species with commercial relevance or clearly important for ecosystem processes.

Fig. 21.3 (continued) *Maylandia estherae*; (11) *Maylandia lombardoi*; (12) *Maylandia zebra*; (13) *Melanochromis auratus*; (14) *Melanotaenia boesemani*; (15) *Melanotaenia praecox*; (16) *Mikrogeophagus altispinosus*; (17) *Mikrogeophagus ramirezi*; (18) *Misgurnus anguillicaudatus*; (19) *Moenkhausia sanctaefilomenae*; (20) *Morone chrysops*; (21) *Morone saxatilis*; (22) *Myloplus rubripinnis*; (23) *Neolamprologus leleupi*; (24) *Notemigonus crysoleucas*; (25) *Oncorhynchus tshawytscha*; (26) *Oreochromis leucostictus*; (27) *Panaque nigrolineatus*; (28) *Pangasianodon hypophthalmus*; (29) *Paracheirodon axelrodi*; (30) *Parachromis managuensis*; (31) *Petenia splendida*; (32) *Piaractus brachypomus*; (33) *Pimephales promelas*; (34) *Pristella maxillaris*; (35) *Pterophyllum scalare*; (36) *Pterygoplichthys gibbiceps*; (37) *Puntius conchonius*; (38) *Scatophagus argus*; (39) *Sciaenochromis fryeri*; (40) *Pygocentrus nattereri*; (41) *Tanichthys albonubes*; (42) *Thorichthys meeki*; (43) *Trichogaster lalius*; (44) *Xiphophorus hellerii*. (All images have been obtained from the Wikimedia Commons and are free to use for noncommercial purposes)

In addition to landscape alteration by projects that are for the benefit of the human being, there is a conversion of natural spaces due to anthropogenic activities, resulting in the erosion and degradation of ecosystems at different levels, having negative consequences on the biodiversity of the endemic biota. This process is known as anthropization.

In Latin America, a region constituted by underdeveloped countries, where it is difficult to apply policies to conserve the environment or assure its proper management, the lack of information and specific studies lead to mismanagement at different levels and ultimately the loss of biodiversity. In these countries, biodiversity indicators are critical and particularly important when dealing about freshwater environments, where information is even more scarce at the local and national levels. This deterioration has been caused to a large extent by the disparity that exists when accessing these resources by different social groups. Thus, it is necessary to develop comprehensive management tools and, especially, to create awareness about the value of biodiversity at the local, regional, and national levels.

According to Seebens et al. (2017), the number of newly documented invasions has risen continually over the last 200 years, accumulating slowly at first, but accelerating in an exponential fashion, reflecting an average of more than 1.5 new invasion records per day since 1800. In 2018, CONABIO indicated that >300 IAS were present in the country, threatening the economy and biodiversity. Nevertheless, these estimates may be inaccurate; the scientific community is often pessimistic of the possibility of eradicating introduced species, especially invertebrates, plants, and aquatic species. In general, the pessimism is due to a few highly visible, expensive, failed eradication campaigns with notable nontarget damage.

Neighboring countries and local governments within each country need to make larger efforts for the prevention of invasive species introduction. Additionally, authorities are urged to design and apply programs for the eradication of already established species. It is essential to implement techniques that measure the impacts on water bodies and prioritize the knowledge transfer among neighbors and collaborators to develop better management practices. It is clear that IAS are a problem that requires more attention from the researchers, managers, and authorities. They represent a threat to local and already endangered ecosystems, which in addition to phenomena such as climate change and anthropogenic alteration of the landscape can face an enormous risk of disappearance. In addition to that, the replacement of the local diversity by the IAS will mean not only a loss in ecological functions but also on potential information to be researched.

Acknowledgments The doctoral studies at the Helmholtz Centre for Environmental Research – UFZ of Hugo Enrique Reyes Aldana are currently founded by the Helmholtz International Research School TRACER (Trajectories Towards Water Security), grant no. HIRS-0017.

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Chapter 22
Patterns of Distribution in Helminth Parasites of Freshwater Fish of Mexico: Can We Detect Hotspots of Richness and Endemism?

Benjamín Quiroz-Martínez and Guillermo Salgado-Maldonado

Contents

B. Quiroz-Martínez
Laboratorio de Ecología Numérica y Análisis de Datos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de Mexico, Mexico

G. Salgado-Maldonado (✉)
Laboratorio de Helmintología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de Mexico, Mexico
e-mail: salgado@ib.unam.mx

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_22

22.1 Introduction

Mexico is a megadiverse country and concerning parasite diversity for freshwater fishes; Mexico also stands out as a hotspot (Mittermeier et al. 1997; Luque and Poulin 2007), exhibiting high levels of endemicity (Pérez-Ponce de León and Choudhury 2005; Salgado-Maldonado 2006; Salgado-Maldonado and Quiroz-Martínez 2013). While a summary of the geographic distribution of the helminth parasites of freshwater fishes of Mexico has been attempted (Vidal-Martínez and Kennedy 2000; Aguilar-Aguilar et al. 2003; Pérez-Ponce de León and Choudhury 2005; Aguilar-Aguilar and Salgado-Maldonado 2006; Garrido-Olvera et al. 2012; Quiroz-Martínez and Salgado-Maldonado 2013a), a formal quantitative up-to-date analysis of the spatial distribution of endemism of this group is needed.

Understanding the distribution of parasite diversity among geographical areas is central to the study of the ecology and evolution of parasitic systems and their biogeographic characteristics. However, there are still few documented biogeographical patterns concerning the diversity of parasites (Poulin 2007). Endemism is one of the most significant features of geographical distributions because species are rarely cosmopolitan and most species and supraspecific taxa are confined to restricted regions at a variety of spatial scales. Examining the spatial distribution of species restricted to a given region can improve our understanding of its biodiversity and origins. To understand patterns of diversification and geographical distribution, one must also understand patterns of endemism (Cracraft 1985). Endemism patterns are commonly hypothesised to be associated with the geological history, movements and distribution of the biota, that is, with historical processes (Lomolino et al. 2010). Historical processes especially geomorphological changes have determined current patterns of hydrology and freshwater fish distribution that are largely dependent on connections between drainage basins, thus implying a significant interplay between biological and geological evolutions, and may also be responsible for shaping patterns of endemism of their helminth parasites (Miller 1966; Myers 1966; Martin and Bermingham 1998; Doadrio et al. 1999; Concheiro-Pérez et al. 2007; Říčan et al. 2013; Matamoros et al. 2015b; Tagliacollo et al. 2015).

The problem of analysing patterns of endemism within Mexican helminthofauna of freshwater fishes has only been approached by Aguilar-Aguilar et al. (2008), but this previous attempt to make a synthesis of distributional data of endemic helminths is now updated as a substantial amount of new data has become available (Salgado-Maldonado and Quiroz-Martínez 2013). Our understanding of patterns of the spatial distribution of endemic species in Mexico is still in its early stages. For example, while some drainage basins were considered hotspots of richness and endemism for helminth parasites of freshwater fish (Aguilar-Aguilar et al. 2008), recent research suggests a certain degree of endemism in most of the different hydrological basins (Salgado-Maldonado and Quiroz-Martínez 2013).

In this work, we focus on the spatial distribution of endemic helminth species and its variability at a regional scale. We aimed to rate the freshwater drainage basins of Mexico regarding the richness and endemism of helminth parasites of freshwater fish. We address whether drainage basins with high levels of endemism can be objectively detected by the analysis of species presence/absence data, to assess previous statements made using subjective non-analytical methods (Salgado-Maldonado and Quiroz-Martínez 2013). To do this, we consider the relationship between endemism and species richness because a simple count of endemic species in an area is a measure sensitive to artefacts of poor sampling, as well as to the confounding effect of the patterns of distributions of range-restricted versus more widespread species (Crisp et al. 2001; Linder 2001).

However, given the accelerated changes in recent decades and the increase in introduced fish species in the hydrological basins of Mexico, it has become necessary to analyse the patterns at the basin level to have a conservation tool at a regional scale based on this premise. The Anthropocene has been characterised by rapid environmental change promoted in part by the increase in introduced species.

22.2 Material and Methods

We used the distributional records of 184 adult helminth parasite species from freshwater fish in Mexico (trematodes, monogeneans, cestodes, acanthocephalans and nematodes) from the datasets of Salgado-Maldonado (2006) and Salgado-Maldonado and Quiroz-Martínez (2013). A presence-absence matrix, representing every recorded species of adult helminth parasites of freshwater fishes from 26 Mexican hydrological basins, was constructed. Currently, host lineage specificity is a well-documented general pattern for the helminth fauna of freshwater fishes from Mexico. Patterns of host associations have consistently shown a suite of helminth parasites specific to fish families, which are constantly and widely distributed in them (Commito and Rusignuolo 2000; Vidal-Martínez and Kennedy 2000; Pérez-Ponce de León and Choudhury 2005; Salgado-Maldonado et al. 2005; Salgado-Maldonado 2006, 2008; Salgado-Maldonado and Quiroz-Martínez 2013; Choudhury et al. 2016). These associations of helminths with their host taxa make basins appear related not only for their fish fauna but also for their parasite faunas. This concept proves to be a most important factor to explain patterns of distribution of richness and endemism of helminths (Commito and Rusignuolo 2000; Vidal-Martínez and Kennedy 2000; Pérez-Ponce de León and Choudhury 2005). We, therefore, identified the suite of helminths exclusive to each of the 17 fish families included in the matrix.

Endemic species were those with the smallest geographical range, that is, restricted to a single basin, or on a regional scale, restricted to Mexico in such a way that a taxon is here considered endemic to a particular drainage basin or Mexico if it occurs only in that area (Anderson 1994; Crisp et al. 2001). We acknowledge that the concept of endemic species related to a country is artificial and that it could be modified with a better knowledge of the geographic distribution of the helminthofauna of the Americas.

We focus on the regional scale to explore evolutionary diversification as a general biogeographical phenomenon. In this paper, we deal with spatial variation in absolute parasite species richness per se (sensu Poulin and Morand 2004) considering hydrological basins as biogeographical units. We focus on how many parasite species are found in a particular basin. At this scale, host species richness explains most of the variations in parasite species richness across rivers, and correspondingly, the spatial distribution of host species richness is the foremost determinant of the geographic distribution of parasite diversity (Poulin and Morand 2004). Thus, the number of parasite species becomes directly proportional to the number of host species present within a given basin (Poulin and Morand 2004). However, there is a strong phylogenetic component in the helminth fauna of freshwater fishes of Mexico, since certain host species have evolved richer faunas than others (Salgado-Maldonado and Quiroz-Martínez 2013). Some fish lineages harbouring either diverse or less diverse parasite faunas and colonising basins may contribute to explaining the distribution of parasite diversity. Therefore, we also examined richness characteristics per fish groups.

The corrected weighted endemism index (CWEI) was calculated as the sum of the inverse of the ranges of the component species of each drainage and the proportion of the species in each basin that have restricted ranges; CWEI values range from 0 to 1 (Crisp et al. 2001; Linder 2001). This index allows us to separate the pattern of range-restricted species from that of species that are more widespread because it is uncorrelated with the species richness of the drainage (Crisp et al. 2001).

We mapped species distributions and endemism among basins. The extent of congruence between richness and endemism was assessed to identify basins as hotspots for helminth parasites of freshwater fishes using the quartile method proposed by Gaston (1994). We use the term hotspot to characterise basins that rank particularly high in the axes of species richness and level of endemism.

Finally, the latitudinal ranges of each helminth species were also calculated. We assumed that species ranges are continuous between latitudinal sampling points. The latitudinal range of species (V_r) was calculated as the maximum latitude of occurrence (m_x) minus the minimum latitude of occurrence (m_n) (Pineda 1993): $V_r = m_x - m_n$. We plotted the resulting ranges and midpoints.

22.3 Results

22.3.1 General

The compiled dataset includes 184 species of adult helminths from 86 genera and 34 families recorded from 17 families of freshwater species of fishes from 26 drainage basins of Mexico (Fig. 22.1; Tables 22.1 and 22.2). Among the taxa found, trematodes (S = 56, 30%), nematodes (S = 53, 29%) and monogeneans (S = 51,

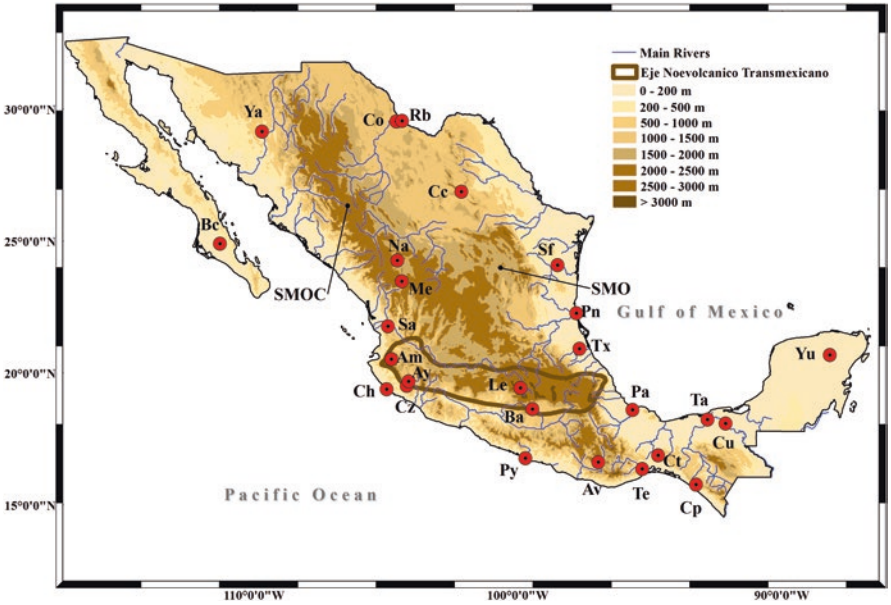

Fig. 22.1 Main river courses of 26 drainage basins in Mexico from which records of helminth parasites of freshwater fish have been obtained. Abbreviations: Am, Río Ameca; Av, Río Atoyac, Verde; Ay, Río Ayuquila, Armería; Ba, Río Balsas; Bc, Oases of Baja California; Cc, bodies of water of Cuatro Ciénegas; Ch, rivers near Chamela Bay; Co, Río Conchos; Cp, short rivers along the Pacific coast of Chiapas state; Ct, upper reaches of Río Coatzacoalcos; Cu, Rio Usumacinta and Rio Grijalva at crossing Chiapas state; Cz, Río Cuzalapa; Le, Río Lerma; Me, Río Mezquital; Na, Río Nazas; Pa, Río Papaloapan; Pn, Río Pánuco; Py, Río Papagayo; Rb, Río Bravo; Sa, Río Santiago; Sf, Río San Fernando and Río Soto La Marina; Ta, bodies of water in the lowlands of Tabasco state; Te, Río Tehuantepec; Tx, Río Tuxpan; Ya, Río Yaqui; and Yu, bodies of water of the Peninsula of Yucatán, mainly cenotes (sinkholes)

28%) contributed 87% of the total species recorded, with cestodes (*S* = 12, 6.5%) and acanthocephalans (*S* = 12, 6.5%) being the taxa with the least species recorded.

22.3.2 Patterns of Richness

Our analyses make evident that basins situated in Southern Mexico are the richest compared to basins situated north of the Transmexican Volcanic Belt (TVB) (Fig. 22.2; Table 22.1). It is noteworthy that the richest basins are situated towards the southwestern Gulf of Mexico versant, including the Río Grijalva and Río Usumacinta (Cu) basins, Río Papaloapan (Pa), bodies of water of the Yucatan Peninsula (Yu), bodies of water of Tabasco (Ta) and Río Coatzacoalcos (Ct). On the opposite Mexican slope, southern basins draining towards the Pacific Ocean, including Río Tehuantepec (Te), Río Balsas (Ba), Río Nazas (Na) and small rivers on the

Table 22.1 Helminth richness and endemism in each basin

Basin (see text for abbreviations)	No. of fish examined	Observed richness	No. of endemic species (single basin)	No. of endemic species (whole Mexican basins)	CWEI
Cu	1917	69	4	25	0.44
Pa	3825	52	10	28	0.57
Yu	4080	49	7	20	0.58
Ta	4340	49	4	18	0.45
Ct	430	27	3	12	0.47
Te	425	21	1	4	0.54
Ba	2245	26	3	12	0.38
Na	1262	21	7	7	0.93
Cp	296	16	1	2	0.67
Rb	318	15	1	4	0.40
Pn	2100	22	1	7	0.27
Sa	619	15	3	7	0.54
Ay	832	15	0	10	0.25
Cc	811	14	0	3	0.27
Ch	171	8	3	7	0.59
Me	1107	12	0	4	0.27
Ay	528	9	0	1	0.17
Tx	59	6	1	2	0.57
Am	103	5	0	3	0.14
Cz	103	5	1	4	0.39
Bc	424	5	0	1	0.33
Sf	39	3	0	1	0.14
Co	352	4	0	1	0.14
Ya	74	2	0	0	0
Py	4151	11	1	4	0.52
Le	8549	23	6	12	0.62

Basins are ranked by residual values, to correct the observed helminth richness considering the uneven sample effort (unequal number of fishes examined from each basin)

Pacific coast of Chiapas (Cp), also display important levels of richness, however, not as high as the southwestern basins. Richness decreases considerably in the basins of Central Mexico's highland plateau and, in general, towards basins situated north of the TVB. Accounting correction for uneven sample effort, considering the number of fish examined, some basins appear as truly depauperate of parasites. For example, comparing the two nearby Río Nazas (Na) and Río Mezquital (Me) basins, where a comparable number of fishes were examined, the Río Mezquital basin appears as notoriously impoverished. Remarkably, because of its size, the Río Lerma basin, (Le) when compared to all other basins, is the less rich in helminth species. The neotropical region emerges as a very rich one, considering both species and genera of helminth parasites of freshwater fish.

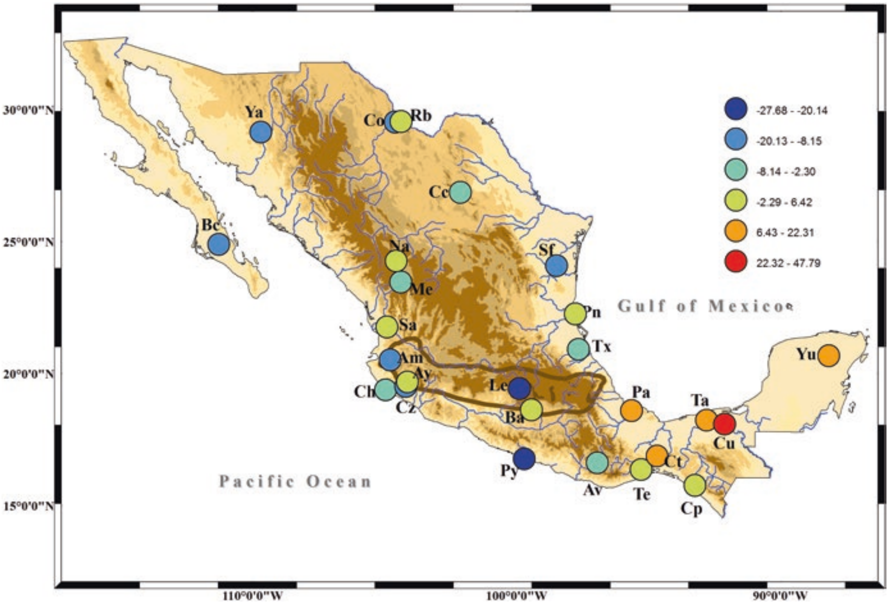

Fig. 22.2 Distribution of corrected helminth species richness (number of fish examined) in 26 drainage basins from Mexico

22.3.3 Helminth Richness in Each Fish Family

Taking into account the number of fish individuals examined in each family, Characidae, Cichlidae, Ictaluridae, Heptapteridae and Eleotridae are the richest families for helminth parasites. Remarkably, given their diversity, the Goodeinae and the Poeciliidae range as rather depauperate fish groups regarding helminth species richness (Table 22.2).

22.3.4 Endemicity

High levels of endemism at the species level characterise the Mexican helminthofauna: 96 of the 184 helminth species (52%) recorded had distributions that are restricted exclusively to Mexican basins. A high number of species had small ranges. We found that 57 of 184 species (30%) can be considered as single basin endemics (which were recorded in a single river basin) based on the present data. The majority of the basins showed high values (>0.3) of CWEI (Table 22.1; Fig. 22.3). Most basins have records of endemic species, excepting the Río Yaqui (Ya), Río San Fernando (Sf) and Río Ameca (Am). A high positive correlation, $r = 0.93$, exists

Table 22.2 Helminth richness and endemism in each fish family

	No. of fish examined	Helminth species richness	Endemism
Characidae	2399	24	12 (50%)
Cichlidae natives	9724	36	24 (66%)
Ictaluridae	1165	16	4 (25%)
Heptapteridae	731	14	7 (50%)
Eleotridae	2167	11	9 (82%)
Synbranchidae	98	5	5 (100%)
Catostomidae	164	4	3 (75%)
Mugilidae Agonostomus	164	4	4 (100%)
Centrarchidae	479	4	4 (100%)
Lepisosteidae	184	3	1 (33%)
Sciaenidae	59	2	1 (50%)
Cyprinidae natives	2325	6	6 (100%)
Gobiidae	184	1	1 (100%)
Poeciliidae	4652	10	3 (30%)
Profundulidae	2262	5	2 (40%)
Atherinopsidae	1597	2	2 (100%)
Goodeinae	9567	12	12 (100%)

Fish families are ranged by residual values, to correct the observed helminth richness considering the uneven sample effort (unequal number of fishes examined from each fish family). Endemism data are the number of endemic species of helminths recorded from the fish family and (between brackets) the percentage that this number of endemic species represents concerning the total number of helminth species recorded for each family

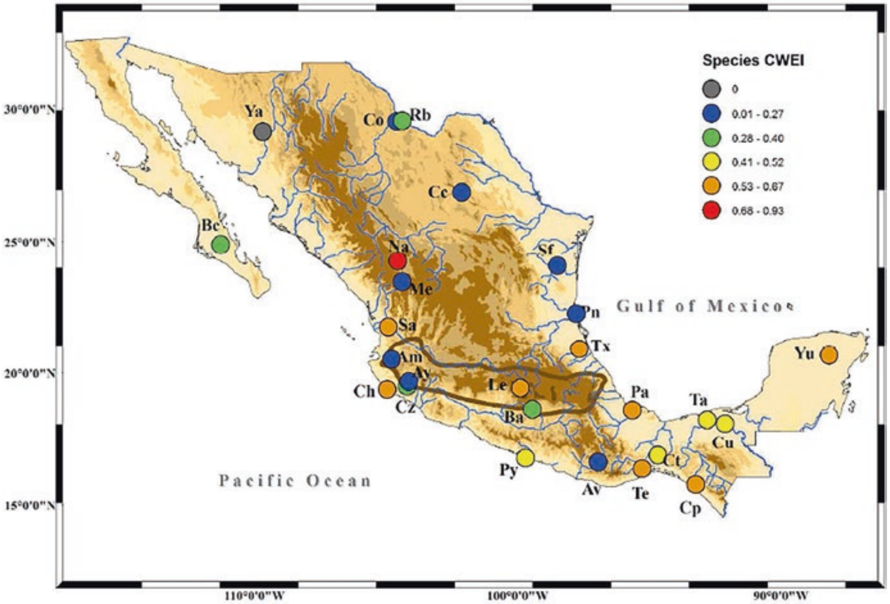

Fig. 22.3 Distribution of the values of the corrected weighted endemism index in 26 drainage basins of Mexico

between the helminth species richness and the number of endemic species recorded from each basin; however, calculated values of CWEI are independent of sample effort (CWEI vs. number of fishes examined from each basin $r = 0.35$).

22.3.5 Endemism by Fish Families

All 17 families of Mexican freshwater fish examined include endemic species of helminths in their records. The number of endemic species of helminths by fish family varies from 1 (Lepisosteidae, Gobiidae, Sciaenidae) to 12 (Goodeinae) and 24 (Cichlidae). However, the proportion of endemic species considering the total number of helminth species recorded from each family remains high, ranging from 25% (Ictaluridae) to 100% (several fish groups) (Table 22.2).

22.3.6 Hotspots of Richness and Endemicity

Ten basins displayed both high species richness and high value of endemism (Fig. 22.4), high enough to be considered here as hotspots of helminth richness and endemism, including Río Nazas (Na), small river of the Pacific coast of Chiapas (Cp), the cenotes of Yucatán Peninsula (Yu), Río Papaloapan (Pa), Río Tehuantepec (Te), Río Santiago (Sa), Río Coatzacoalcos (Ct), Ríos Usumacinta and Grijalva in Chiapas state (Cu), bodies of water of Tabasco (Ta) and Río Bravo (Rb). The Río Balsas basin (Ba) also recorded a high level of richness and endemicity but not enough to rank among the hotspot basins. On the other hand, the basins of Río Lerma (Le), Chamela (Ch), Tuxpan (Tx) and Papagayo (Py) also display high indices of endemism; however, their richness values are not comparable to the above mentioned basins.

22.3.7 Latitudinal Ranges of Species and Genera

In general, latitudinal ranges at species levels were larger for northern Nearctic helminths than for neotropical ones (Fig. 22.5). Helminth parasites recorded south of 21° N (roughly following the course of the TVB) show remarkably smaller ranges than those of the Nearctic that extend their distribution well into the neotropical region of Mexico.

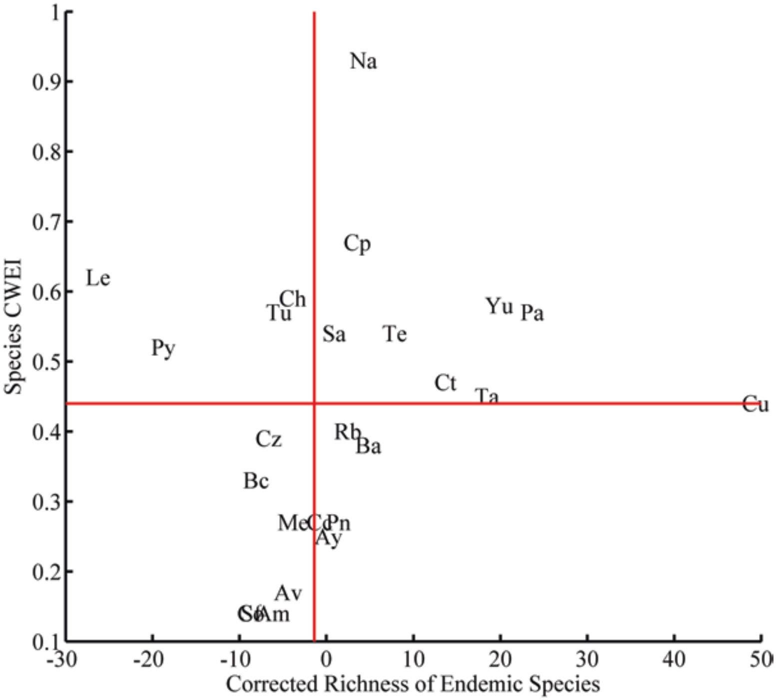

Fig. 22.4 Relationship between corrected species richness (residuals) and endemism (CWEI values) of helminth parasites of freshwater fishes of 26 drainage basins of Mexico. Red lines mark the median of each frequency distribution

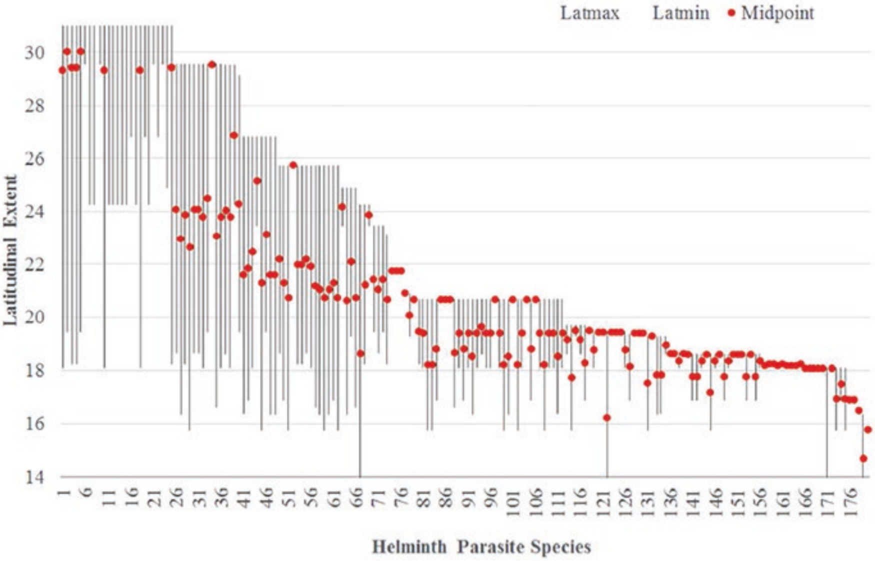

Fig. 22.5 Latitudinal extent of 184 species of helminth parasites of freshwater fish from Mexico

22.4 Discussion

22.4.1 General

High levels of endemism characterise the Mexican helminthofauna: 52% of the species of helminths had distributions that are restricted exclusively to Mexican basins and 30% of these have been recorded only from a single basin. Explanations for the origin of the megadiversity of Mexican biota and the great number of endemisms include the location of Mexico between two great biogeographical realms, the Nearctic and the Neotropical (Morrone 2005), the great latitudinal extent of Mexico's territory, running from 14°N to 32°N latitude including a wide variety of ecosystems. In particular for the freshwater aquatic biota, it is important to consider the complex geological history of Mexico with dynamic orogenic events (Ferrusquía-Villafranca 1993; Ferrari et al. 2002) that shaped the orography of Mexico, which have promoted a complex surface configuration and have determined a very intricate pattern of altitude and relief that conditions the hydrography of the country (Alcocer and Bernal-Brooks 2010). This results in a diverse ecological mosaic of drainage basins in which climate and ecosystem characteristics change abruptly between basins and between sections of the same basin over short distances (Cotler-Ávila et al. 2010). Multiple drainage modifications, such as compartmentalisation of bodies of water, stream captures and the formation of endorheic basins, allow colonisation and dispersal but also lead to isolation and speciation in Mexican freshwater biota, particularly freshwater fishes (Barbour 1973a, b; Contreras-Balderas and Lozano-Vilano 1996; Mayden 1997; Miller et al. 2005) and presumably their parasites (Moravec et al. 1995; Scholz et al. 1996; Vidal-Martínez and Kennedy 2000; Vidal-Martínez et al. 2001). The diversification of host species may contribute to the diversification of their parasites through inheritance as part of the evolutionary baggage, intrahost speciation, cospeciation or colonisation processes (Poulin and Morand 2004).

22.4.2 Richness and Endemism by Fish Families

Our results suggest that the distribution of richness and endemism of helminths among basins can be explained mainly by the ichthyological composition of the basins. Helminths of most fish families currently examined showed important levels of richness and endemism. However, helminths in certain fish families have experienced high diversification, have evolved richer parasite faunas and provide the highest numbers of endemic helminth parasites than others. The helminth fauna of the neotropical Characidae, Cichlidae, Heptapteridae and Eleotridae but also of the Nearctic Ictaluridae have given rise to high levels of richness and endemism. For example, the neotropical basins from Southeastern Mexico that drain towards the

Gulf of Mexico (Pa, Yu, Ta, Cu, Ct) where characids and cichlids are the most abundant hosts correspondingly have abundant and diverse helminth parasites.

Also, it appears that helminths have diversified at a higher rate in the tropics. Helminths of a Nearctic fish family Ictaluridae, one of the few Nearctic fish families that have successfully invaded the neotropical basins of Mexico, have also experienced high levels of diversification. However, these levels are not as notable when compared to the helminth faunas of several neotropical fish families that have given rise to much higher levels of richness and endemism. Taxa in warm waters are expected to experience higher rates of diversification because of the shorter generation times and higher mutation rates that result from higher temperatures (Rohde 1992, 1999; Allen et al. 2002). Nonetheless, these data cannot be used to explain why some fish families exhibit higher numbers of helminth species and endemism as compared to others. However, they provide empirical evidence that the diversification of helminths and the proportion of endemic forms reaches higher values in cichlids, characids, eleotrids, heptapterids and other mostly neotropical fish families than in the centrarchids, cyprinids and poeciliids.

Our present results that the Neotropical basins of Mexico are host to the richest and more diversified helminth fauna, including more families, genera and species, compared to the less diverse helminth fauna in the Nearctic basins, are supported by several previous studies (Vidal-Martínez and Kennedy 2000; Aguilar-Aguilar et al. 2003; Pérez-Ponce de León and Choudhury 2005; Aguilar-Aguilar et al. 2008; Garrido-Olvera et al. 2012; Salgado-Maldonado and Quiroz-Martínez 2013; Quiroz-Martínez and Salgado-Maldonado 2013a). The differences in helminth faunas observed between the Nearctic and the Neotropical Mexican hydrological basins stem from the fact that families from both regions have different origins and have not been exposed to the same set of parasite species. The availability of these two distinct taxonomic sets of parasites in Mexican basins has been already pointed out (Garrido-Olvera et al. 2012; Quiroz-Martínez and Salgado-Maldonado 2013b). The Northern Mexican territories have a different geological and zoogeographical history than those of Central American affinity in Southern Mexico. Paleogeographic scenarios for the present Mexican territory propose that after the breakdown of Pangea, the primitive Laurasia and Gondwana continents became separated during long geological periods (Barrier et al. 1998; Campbell 1999; Iturralde-Vinet 2006). A seaway likely existed at the Isthmus de Tehuantepec during the Pliocene and Pleistocene glacial minima separating Mexico from nuclear Central America (Beard et al. 1982; Mulcahy et al. 2006) in such a way that the Nearctic and neotropical Mexican faunas have evolved separately.

22.4.3 Nearctic Fauna

The Nearctic territory of Mexico extends over the central Highland Plateau between the Sierra Madre Occidental to the west and the Sierra Madre Oriental to the east, bordering to the south by the Transmexican Volcanic Belt (TVB), a range of mountains crossing Mexico east to west at ~21°N (Morrone, et al. 2002). Our data show a clear separation in helminth faunas between basins within these highlands and those situated south of the TVB. Several authors have reported concordant vicariant events underlying the role of the TVB as a biogeographical barrier that separated northward and southward lineages in the Late Miocene and Early Pliocene (Rosen 1978; Contreras-Balderas and Lozano-Vilano 1996; Hulsey et al. 2004; Zaldívar-Riverón et al. 2004; Mateos 2005; Mulcahy et al. 2006; Ornelas-García et al. 2008; Salgado-Maldonado and Quiroz-Martínez 2013; Quiroz-Martínez and Salgado-Maldonado 2013a, b; Quiroz-Martínez et al. 2014).

One outstanding feature that characterises the fauna of helminths in the central highlands of Mexico is the high degree of endemism rather than the number of species. Several endemic helminths found only in Mexican basins have been recorded from cyprinids, ictalurids, catostomids and other Nearctic fish families. On the other hand, 15 generalist species widely distributed in freshwater fish species of North America north of Mexico belong to northern strains that extend their austral distribution along with their freshwater fish hosts (Salgado-Maldonado and Quiroz-Martínez 2013; Quiroz-Martínez and Salgado-Maldonado 2013a).

The endemism of helminths and their fish hosts in the Nearctic basins of Mexico reach a remarkably high level in the Río Lerma basin (Aguilar-Aguilar et al. 2003; Mejía-Madrid et al. 2007), one of the main bodies of water of the Central Highland Plateau of Mexico. The so-called Fauna Lermense is unique because of its high number of endemics. For the Río Lerma basin, in particular, high levels of endemic helminths are associated with the Goodeinae, an endemic subfamily of freshwater Cyprinodontiformes, entirely restricted to the highlands of Central Mexico (Parenti 1981; Doadrio and Domínguez-Domínguez 2004) as are its associated helminth parasites (Pineda-López et al. 2005; Martínez-Aquino et al. 2014). A second unique ichthyological component of the Fauna Lermense is the atherinopsid genus *Chirostoma* which has diversified in this geographical area (Echelle and Echelle 1984; Miller and Smith 1986; Espinosa-Pérez et al. 1993; Miller et al. 2005), giving rise to an impoverished helminth fauna, but is entirely endemic to Mexico. Third, the component of a marine origin of the Fauna Lermense cannot be disregarded, as suggested by the recent records of two helminth species originally described in *Chirostoma estor* of Lago de Pátzcuaro and other bodies of water of the Highland Plateau (Osorio-Sarabia et al. 1987; Choudhury and Pérez-Ponce de León 2001), the trematode *Allocreadium mexicanum* and of the nematode, *Spinitectus osorioi* recently recorded in an atherinopsid from an Atlantic drainage in Southern Mexico (Moravec et al. 2010; Salgado-Maldonado et al. 2014).

22.4.4 Neotropical Fauna

The current state of knowledge of Central American helminths suggests that the region is an evolutionary very recent centre of diversification for the helminth parasites of freshwater fish (Salgado-Maldonado 2008). It has been proposed that from the Late Cretaceous to Early Palaeocene, north and south American landmasses remained separated and were not connected until the final closure of the Isthmus of Panama during the Pliocene about 3–3.5 Mya (Coates and Obando 1996). However, current studies propose that the Central American seaway closure may be as old 8–10 Mya during the Miocene (Coates and Obando 1996; Kirby and MacFadden 2005; Bacon et al. 2015; Montes et al. 2015).

Currently, it is argued that the geographical origin of Central American ichthyofauna and its parasites has multiple sources including components of marine origin (Choudhury et al. 2016), components displaying a close relationship with freshwater lineages from South America (Mendoza-Franco et al. 2003; Salgado-Maldonado 2008; Mendoza-Franco et al. 2009; Choudhury et al. 2016) and as the present data suggest an in situ diversification of helminths in the Central American area, mainly associated with cichlids, characids and heptapterids (Mendoza-Franco and Vidal-Martínez 2005). Helminths of Nearctic origin in Southern Mexico and Central America's neotropical host lineages are very rare, the only case currently known being that of the monogenean genus *Salsuginus* (Mendoza-Franco et al. 2006; Salgado-Maldonado 2006; Salgado-Maldonado 2008). Most models of colonisation and dispersal of Central American and Southern Mexico freshwater fishes of neotropical origin currently propose northwards expansion of the southern taxa (Myers 1966; Martin and Bermingham 1998; Doadrio et al. 1999; Concheiro-Pérez et al. 2007; Hrbek et al. 2007; Říčan et al. 2013; Matamoros et al. 2015b; Tagliacollo et al. 2015). However, some fish lineages like the poeciliid *Pseudoxiphophorus* likely originated in Central Mexico and dispersed from this area southwards (Agorreta et al. 2013). Accordingly, several authors have proposed that the ancestral fish stocks that colonised the area brought their ancestral parasites with them and then both hosts and parasites developed in isolation in Central America and Southwestern Mexico. This could mean independent colonisation events involving a northwards expansion of southern helminth lineages (Vidal-Martínez and Kennedy 2000; Vidal-Martínez et al. 2001; Mendoza-Franco et al. 2007).

The present results suggest that the neotropical bodies of water of Southern Mexico have been highly favourable for helminth diversification mainly associated with cichlids, characids and heptapterids. The few available phylogenies of Central American freshwater helminths also support these findings (Choudhury et al. 2016). The primary factors contributing to the radiation and differentiation of this fauna are highly varied physical geography resulting from a geological history of intense tectonics and periods of marine expansions (Miller 1986; Miller and Smith 1986; Alcocer and Bernal-Brooks 2010). Orography, vulcanism and other geological events provided isolated bodies of water with peculiar biotic and abiotic conditions and favoured speciation processes, including differentiation of endemic forms (Moravec et al. 1995; Scholz et al. 1996).

22.4.5 The Pacific Ocean and Gulf of Mexico Helminth Components

Our present observations clearly distinguishing between helminths from the Pacific Ocean and the Gulf of Mexico slopes are confirmed by numerous studies that divide freshwater taxa into Pacific and Atlantic communities (Morrone and Márquez 2001; Escalante et al. 2004; Escalante et al. 2007; Griffiths 2010; Morrone 2010; Quiroz-Martínez and Salgado-Maldonado 2013b; Quiroz-Martínez et al. 2014; Griffiths 2015). Also, our present findings that richness is higher in basins draining towards the Gulf of Mexico are supported by several other papers (Smith 1981; Mahon 1984; Moyle and Herbold 1987; Latham and Ricklefs 1993; Oberdorff et al. 1997; Stephens and Wiens 2003; Smith et al. 2005; Haag 2010; Smith et al. 2010; Kozak and Wiens 2012; Quiroz-Martínez and Salgado-Maldonado 2013a; Quiroz-Martínez et al. 2014; Griffiths 2015; Matamoros et al. 2015a, b). Some authors have argued that the uplift along the continental plate margin created smaller, steeper catchments and greater barriers to dispersal on the Pacific slope of America which led to higher extinction rates on the Pacific side than in the Atlantic versant (Smith et al. 2010; Griffiths 2015). This, in turn, has led to the neotropical fauna of Mexican helminths having higher species richness and more endemics among communities along the Gulf of Mexico than that in the Pacific communities.

22.4.6 Hotspots of Richness and Endemism

Our results also show that there are hotspot basins in Mexico that feature high levels of endemic species and richness, and our two indices show, in part, congruent patterns of distribution. The ten basins we pointed out as hotspots of helminth diversity and endemism are supported by early results by Aguilar-Aguilar et al. (2003). Basins favouring the development of richness and endemism of parasites are mostly the neotropical ones, but also three Nearctic basins of Mexico were characterised as hotspots. These patterns are thought to be the product of high rates of ecological and allopatric speciation inherent to the hydrological basins themselves and of the distribution of the fish families that favour helminth diversification. Nevertheless, a call of caution is in order because of insufficient taxonomical resolution or poor sampling. For example, the helminths of Río Nazas showed remarkably high CWEI values. However, this can be explained by low taxonomical resolution since seven monogeneans recorded from this basin were determined either as *Gyrodactylus* sp. or *Dactylogyrus* sp. As identification improves, these species could well be identified as Nearctic species from North America, North of Mexico. On the other hand, Río Papagayo (Py) is undersampled as most fish examined from this basin belong to a single species and thus may have greater levels of richness and endemism.

Our results show clearly that the neotropical basins of Southeastern Mexico along the Gulf of Mexico slope including the basins of the Grijalva and Usumacinta rivers (Cu), Yucatán (Yu), Tabasco (Ta), Río Papaloapan (Pa) and Río Coatzacoalcos (Co) have been highly favourable for the development of endemic species, along with a high diversity of helminth species and previous observations. Aguilar-Aguilar et al. (2008) confirm these findings. This region belongs to the Usumacinta ichthyofaunal province (Miller et al. 2005; Matamoros et al. 2015b) and lies in the area of highest availability of water in Mexico (Bunge 2010) and is located in the Central American hotspot (Mittermeier et al. 1997). These river basins are characterised by high levels of endemicity and richness of freshwater fishes (Contreras-MacBeath et al. 2014). They harbour a variety of cichlids, characids, heptapterids and eleotrids that support the greatest number of endemic helminths of all Mexican river basins. Along the Atlantic slope of northern Central America, the continental shelf is very wide allowing river anastomosis and drainage confluence during low sea-level periods (Perdices et al. 2002; Smith and Bermingham 2005). It would seem that these neotropical basins have particular characteristics which, coupled with freshwater fish families, have been favourable for the diversification of the helminths. Most of the other Mexican basins examined in this study reported substantial levels of helminth endemism and diversity, though lesser than these hotspot basins. Explanations for the distribution of richness and endemism concern the basin's magnitude and its geological age and the ichthyofaunal composition (Pérez-Ponce de León and Choudhury 2005; Salgado-Maldonado et al. 2005; Aguilar-Aguilar et al. 2008).

Regardless of the underlying mechanism, our results confirm that the geographical patterns of richness and endemism among helminths are broadly concordant. This means that measures of diversity and endemism at the species level largely locate the same basins, although the rank order among them differs. Congruence between patterns of richness and endemism is far from perfect owing undoubtedly to taxa being of different ages, ecologies or dispersal abilities. Therefore, it would seem that characteristics of several basins have favoured the development of both high diversity and high endemism. This may be because of continued speciation and accumulation of endemics in areas of high richness and endemics (Fjeldsa and Lovett 1997; Brown and Lomolino 1998; Crisp et al. 2001). In addition, latitudinal ranges of distribution at the species level were found to be larger for northern Nearctic helminths than for neotropical species. The tendency for geographic range size to increase with latitude (Rapoport's rule) is a well-known pattern for a wide range of organisms (Stevens 1989, 1992; Gaston 2000, 2003; Hernández et al. 2005). This pattern has been reported also for parasites of marine fishes (Rohde 1996, 1999); now it is reported for the first time for helminth parasites of freshwater fishes from Mexico. The causes of this pattern remain, however, uncertain. It has been proposed that relatively generalised niches and greater capacities of dispersion are needed by temperate species to adapt to their highly variable climatic regions (Rohde 1996, 1999), whereas tropical species inhabit less variable environments, allowing them to occupy narrower niches and geographical ranges under limited pressure to disperse. Consequently, species from temperate regions should be able to cross more barriers resulting in larger geographical ranges (Stevens 1989, 1992; Gaston 2000, 2003).

Finally, this study points out the urgent need for targeted survey work across Mexican basins and fish families, particularly sampling in basins and families highlighted here as hotspots. Also, this study shows that the inventory of helminth parasites of Mexican freshwater fishes is far from being complete since only a limited number of basins and freshwater families of fish have been examined for helminths.

Finally, one of the most serious threats to native fish in Mexico and their native parasite fauna is the introduction of exotic fish species and their parasites. These are virtually ubiquitous in all freshwater basins of Mexico and extremely difficult to eradicate once established (Salgado-Maldonado and Pineda-López 2003). The presence of invasive species of helminths in Mexican freshwater fish is favoured by the anthropogenic introduction of fish for aquaculture, fisheries or aquariums. Invasive species have been introduced primarily through the importation, production and distribution of Asian carp, African tilapia and North American catfish and trout.

Salgado-Maldonado and Rubio-Godoy (2014) recognised at least 40 species of introduced helminths, of which 33 are monogeneans. Based on their extended time in Mexico, these authors recognised five parasites as established invasive species: three monogeneans (*Cichlidogyrus sclerosus*, *Dactylogyrus extensus* and *Gyrodactylus cichilidarum*), the digenean *Centrocestus formosanus* and the cestode *Schyzocotyle acheilognathi*. For example, the Asian fish tapeworm, *Schyzocotyle acheilognathi*, has an extraordinary ability to adapt to different environmental conditions and has been found in more than 110 species of freshwater fish in Mexico and in, at least, 214 localities throughout the country (Chiappa-Carrara et al. 2022). The two species of tapeworms *S. acheilognathi* and *L. intestinalis* are considered highly pathogenic parasites that may produce mortalities among host populations. The Asian fish tapeworm causes severe damage to the intestine of their hosts, whereas the larval form of *L. intestinalis* attains impressive sizes in the body cavity of its intermediate fish host causing extensive systemic pathologies. Another exotic parasite is *Centrocestus formosanus* which was first recorded in 1985 as metacercariae in fry of the first generation of black carp *Mylopharyngodon piceus*, imported from China and subsequently in other fish from a farm in Central Mexico. Since that time, the trematode has spread rapidly over a wide area which includes Central Mexico and both the Atlantic and Pacific coasts. This rapid spread has apparently been enabled by the previous propagation, in Mexico, of another exotic organism, the intermediate snail host, *M. tuberculata* (Scholz and Salgado-Maldonado 2000). Finally, the introduction of fish in Mexico has allowed the introduction of 40 species of parasitic helminths, at least 5 of which have become established and 2 affect native fish populations.

Acknowledgements This study was supported by the Consejo Nacional de Ciencia y Tecnología (CONACyT) through grant no. 155372 SEP-CONACyT and by UNAM DGAPA project PAPIIT IN203016, both to GSM and through grant 628 from the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México to BQM.

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Chapter 23
Comparison of Biomass of Exotic and Native Mammals Between Temperate and Tropical Forests of Mexico

Mariana Munguía-Carrara, Michael F. Schmidt, Raúl Sierra, Juan Carlos López, and David Valenzuela-Galván

Contents

23.1 Introduction

There are many studies linking human activities such as overhunting and habitat loss to the increased risk of extinction of wild fauna, particularly larger animals (Ripple et al. 2019; Smith et al. 2018). This impact may even extend back to the Pleistocene, whereby some evidence suggests that humans played a role in size-selective extinctions of large mammals. In this scenario, a combination of hunting and climate change is contributed to the megafauna extinction between 50,000 and 3000 years ago, which claimed around half of the large (>40 kg) land mammal species (Surovell et al. 2016; Malhi et al. 2016; Broughton and Weitzel 2018). The biomass of wild land mammals before this period of extinction was estimated by

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M. Munguía-Carrara (✉) · M. F. Schmidt · R. Sierra · J. C. López
Comisión Nacional para el Conocimiento y Uso de la Biodiversidad,
Ciudad de México, México
e-mail: mariana.munguia@conabio.gob.mx

D. Valenzuela-Galván
Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Cuernavaca, México

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_23

Barnosky (2008) at 0.02 gigatons of carbon (gT). The same author estimates present-day biomass of wild land mammals to be approximately sevenfold lower, at 0.003 gT.

Loss of large-bodied wild mammal species from ecosystems is a general indicator of human impact, and current trends continue to accelerate with sweeping consequences for the structure and functioning of ecosystems. One of these impacts is a uniquely human activity that started in the beginning of the Holocene. This is the domestication of animals, with the earliest evidence of animal husbandry reaching as far back as 10,500 B.P. Yet, there are stark regional contrasts in the magnitude of this practice, for instance, native societies of Mesoamerica used very few domesticated species. Following the conquest of Mexico, the Spaniards introduced European livestock that were quickly adopted and spread in great quantities (see Chap. 1, this volume). According to the Food and Agriculture Organization (FAO and GDP 2018), there are approximately 1.5 billion bovines in the world as of 2018. Currently in Mexico, cattle breeding for beef production has developed in extensive grazing systems throughout the country, contributing to the livelihood of over one million families with a substantial impact on natural resource use (González-Padilla et al. 2019).

Humans and large domestic mammals are estimated to comprise about 96% of all mammal biomass on Earth (Bar-On et al. 2018), with humans representing 34% and livestock 62% (Barnosky 2008; Smil 2011). The remaining 4% are wild mammals. Exploring this topic for Mexico, we focus an assessment of photographic records from camera traps of medium and large mammals to assess approximate body mass and biomass in two forest ecosystems from a wide range of sites within the country: temperate and tropical forests. Our data provide evidence of a strong widespread invasion of livestock and feral animals into Mexico's remaining wild places. Part of our conclusions shows that estimation of biomass is an indicator that allows a more comprehensive evaluation of the state and condition of natural animal communities, and by doing that, it can be shown that livestock and feral animals can have a much more negative impact on forest ecosystems than what can be estimated by other methodologies like satellite-derived assessments. The consequences of this invasion are discussed in detail and include the amount of energy used by exotic mammals in forest ecosystems in detriment of wild species, the effects that these animals have on biotic interactions among wild animals, an increase in competition for space and food resources, degradation of soil and forests, and disease spreading, among others.

23.2 Monitoring Animal Presence and Abundance Using Camera Traps

Camera traps are a widely used method for the rapid assessment of mammalian biodiversity (Tobler et al. 2008; Sunarto et al. 2015; Burton et al. 2015). The components of camera trapping include a specific deployment of the device relying on knowledge and prediction of target species behavior and activity, the settings of the device, and sometimes the use of different types of attractants. The combination of the three can lead to significant differences in the rate of animals captured and the rate of domestic vs. wild species in the data. In this study, we used data that was previously obtained from a nationwide monitoring effort called the National Biodiversity and Ecosystem Degradation Monitoring System (SNMB for its Spanish acronym). This project employed staff, from each sampling site, previously trained by wildlife experts in an attempt to ensure a homogeneous and successful monitoring effort, mostly within natural protected areas and with a great majority of the sampling sites used as part of the national forest inventory. Cooperation between governmental (Comisión Nacional de Áreas Naturales Protegidas, Comisión Nacional Forestal, and Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) and nongovernmental actors (e.g., Fondo Mexicano para la Conservación de la Naturaleza) was a cornerstone for this effort and conducted between 2014 and 2018 (García-Alaniz et al. 2017).

A great percentage of the camera data from the SNMB does not contain fauna, as the sensors of the devices are commonly triggered by movement of plants by wind or by movement of shadows by sunlight. Of the 370,800 images obtained, only 7604 feature animals, and therefore the data needed to be revised and processed in an automated, machine learning-based approach. Our approach was based on using preprocessing operations for contrast and color enhancement and running a generic animal detector (mega-detector), a computer vision model that is capable of localizing (but not identifying) animals in camera trap images under wide-ranging conditions (Beery et al. 2019). Using only the detections with higher levels of confidence (score equal to or greater than 0.3), we could preselect the images most likely to feature animals. Posteriorly, all preselected images were reviewed by experienced mammalogists to identify species in the photographic records.

Our assessment considered mostly medium-large (>1 kg) domestic and wild mammals. These are the ones most reliably captured with the kind of sensor used. However, we also included several additional records of smaller mammals that could be reliably identified to species level and are important in terms of conservation and ecological understanding (e.g., such as rare or specialist species). For example, we included semiarboreal squirrels such as *Sciurus oculatus*, *Sciurus deppei*, or *Neotamias obscurus*.

We considered data from cameras with a wide spatial coverage in two forest ecosystems, temperate forest (TF) and tropical forest (TRF). In total, we used 285 different sampling sites (187 on TF and 98 on TRF). Each sampling site was assigned to one of the two forest classes (TF or TRF) based on the national vegetation data set of INEGI (National Institute of Statistics and Geography), the National Statistics Institute (INEGI 2001).

23.3 Differences in Abundance and Biomass

The total nationwide sampling effort we considered for these two forest ecosystems was 3164 and 2403 camera trap days, respectively, for TF and TRF. This total amounted to 5679 photographs of 50 (43 wild and 7 domestic) mammal species for TF and 1925 photographs of 45 (41 wild and 4 domestic) mammal species for TRF. Since the sampling period varied between camera traps (García-Alaniz et al. 2017), we calculated a conservative unbiased representation of the relative abundance for all species recorded at each habitat, by only considering the presence of a species at a sampling site (unique record), irrespectively of how many photographs were obtained during the sampling period. Then we multiplied all unique records for each species at each forest ecosystem by its average body mass obtained from the literature (Figueroa 1995; Munguía et al. 2016). We considered that it is a valid approximation of species biomass by habitat (Table 23.1), providing a conservative scenario of differences in abundance and biomass of domestic and wild mammals by forest ecosystem.

Considering all mammals, at TF sites, the following species accounted for over 50% of the unique records considered, *Odocoileus virginianus* (86 records), *Urocyon cinereoargenteus* (60), and *Bos taurus* (70), and at TRF sites, *O. virginianus* (45 records), *Bos taurus* (36), *Didelphis virginiana* (29), *U. cinereoargenteus* (29), *Dasypus novemcinctus* (28), *Cuniculus paca* (27), *Nasua narica* (27), and *Procyon lotor* (12). There were considerably more unique records of wild mammals compared to domestic in both forest ecosystems (Fig. 23.1).

Taking into account only wild mammals in TF sites, five species represented more than 50% of the records considered: *O. virginianus* (18.7%), *U. cinereoargenteus* (13.1%), *Sciurus deppei* (8.49%), *Sylvilagus floridianus* (6.5%), and *Bassariscus astutus* (6.1%). While at the TRF, seven species represented together more than 50% of all records considered: *U. cinereoargenteus* (9.2%), *D. virginiana* (9.2%), *D. novemcinctus* (8.8%), *Cuniculus paca* (8.5%), *N. narica* (8.5%), *P. lotor* (3.8%), and *Dicotyles tajacu* (3.5%). In contrast, more than 50% of all biomass of

Table 23.1 Comparison of biomass (t) and percentage (parenthesis) among each of the seven recorded domestic species and combined totals for all wild species

	Bos taurus	*Equus caballus*	*Felis silvestris catus*	*Equus asinus*	*Ovis armies*	*Canis lupus familiaris*	*Capra hircus*	Wild mammals
Temperate forest	49 (67.1)	11.4 (15.7)	0.03 (0.04)	1.68 (2.3)	0.82 (1.1)	0.23 (0.3)	0.24 (0.3)	9.54 (13.1)
Tropical forest	25.2 (73.3)	2.2 (6.4)	0.13 (0.04)	–	–	0.4 (1.04)	–	6.59 (19.2)

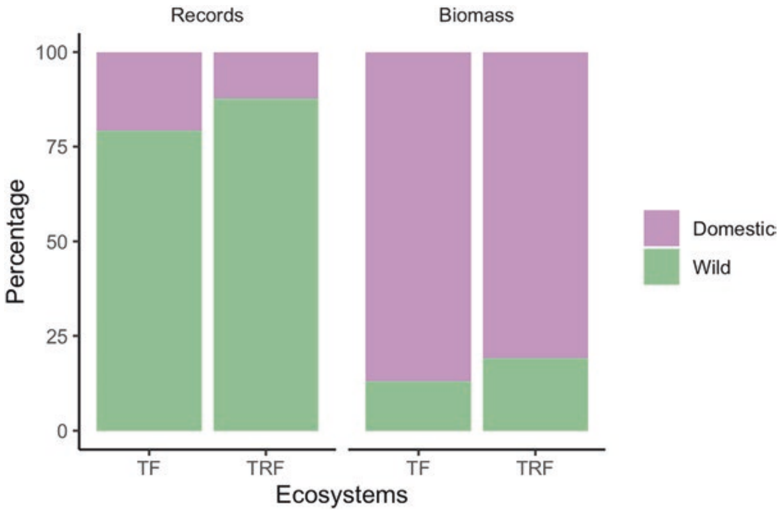

Fig. 23.1 Percentage of the number of unique records and biomass of domestic vs. wild mammals in both forest ecosystems. TF temperate forest, and TRF tropical forest

wild mammals is composed of *O. virginianus* (73% at TF and 55% at TRF), followed by *O. hemionus* (8%) and *Canis latrans* (4%), in TF, and by *Panthera onca* (6%) and *O. hemionus* (4%), in TRF.

We estimated a total of 63.4 tons (t) of domestic mammal species and 9.5 t of wild mammals recorded from our sites of temperate forests and in contrast 27.8 t of domestic species and 6.6 t of wild species in the tropical forest. *Bos taurus* is featured most prominently by biomass in both forest ecosystems (Table 23.1) albeit with higher biomass in TRF than in TF. Wild mammals accounted for less than 20% of the total biomass in both ecosystems, although they have slightly lower values in TF than in TRF sites (Table 23.1).

These results show an even higher percentage of domestic mammal biomass (70.2%) than reported (62%) in the global-scale study by Bar-On et al. (2018). However, our work includes only domestic animals, and we would need to incorporate human biomass to compare both studies.

23.4 Functional Groups

To understand the potential competition between exotic and native species in the same ecosystem, we integrated information of their functional groups. We followed two proposals of functional group classifications (Frisch 1995; González-Salazar et al. 2014). We considered 7 exotic and 59 wild mammal species detected in the camera traps in the sampled forest ecosystems (Fig. 23.2). Fifteen species occurred in both ecosystems. The recorded exotic species can be included on 4

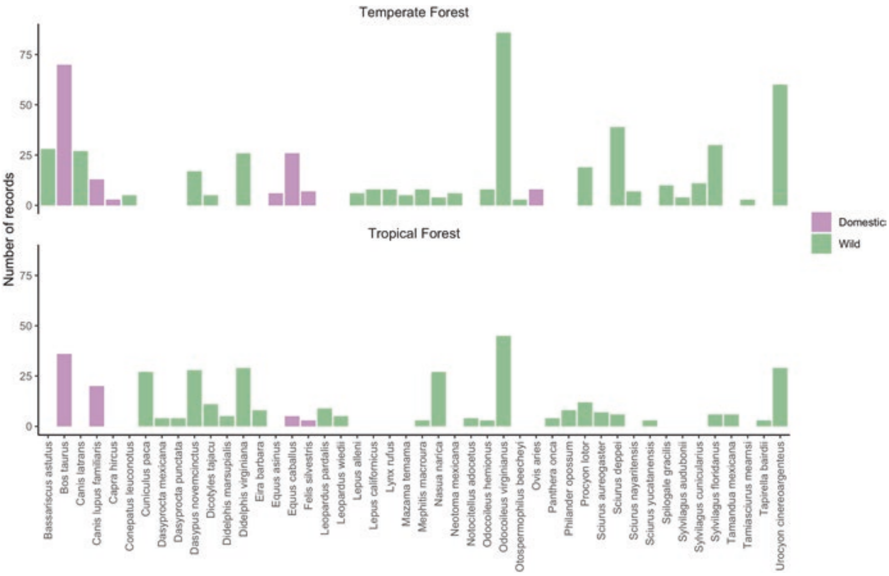

Fig. 23.2 Number of records of the species composition detected by camera traps in each forest ecosystem (species with <2 records were not included in the graph)

different functional groups (2 of them are exclusive), while the detected wild mammals are representative of 32 different functional groups.

There are two functional groups that are exclusive for exotic species: (1) large-sized herbivores-grazers (HPTL), represented here by cattle and sheep, and (2) large-sized carnivores-omnivores (COTL), represented only by dogs. However, depending on the average body mass considered for dogs, they could be placed a different group shared with *Canis latrans.*

Only two functional groups occur in exotic and wild species alike: (i) large-sized herbivores-browsers (HRTL), composed of horses, donkeys, and goats and native deer species, *O. viginianus* and *O. hemionus*, and (ii) semiarboreal carnivores (CSCB), among which domestic cats together with ocelot, margay, and jaguarundi can be counted (Fig. 23.3).

This overlap of functional groups between exotic and wild species represents a potential scenario of resource competition (Amstrong and Harmel 1981), while functional groups exclusive for exotic species may be considered as outside of resource competition. Yet, although cows and deer forage on different plant species, cattle can negatively affect local wild herbivores such as deer because their presence restricts other species from foraging in the same place at the same time (Cohen et al. 1989; Chaikina and Ruckstuhl 2006). This interference can reduce the potential foraging area of deer and can affect their population size (Fig. 23.4). Foraging by cattle of large biomass reduces local plant diversity, compacts soils, and reduces recruitment of many plant species, thus impacting species not directly consumed by cows but that are part of the diet of deer and other native herbivores, altering food

Fig. 23.3 An ocelot, *Leopardus pardalis* (above), a semiarboreal wild cat, and a domestic cat, *Felis silvestris catus* (below), caught by camera traps in the same ecosystem: tropical rainforest. (Source: SNMB)

availability in the medium or long term (Stern et al. 2002; Schieltz and Rubenstein 2016; Öllerer et al. 2019; Schulz et al. 2019). This can lead to malnutrition in wild individuals (Chaikina and Ruckstuhl 2006) and eventually to lowering population numbers or to cause human wildlife conflicts if, for example, when deer seek to forage on crops (Nyhus 2016; Flores-Armilla et al. 2020). Furthermore, if local populations of deer are reduced and high numbers of cows remain on a particular site, a different human-wildlife conflict can arise if local large predators are forced to prey on human-induced livestock. Such human-wildlife conflicts tend to not end well for native big carnivores (Nyhus 2016).

Fig. 23.4 Two ruminant species, white-tailed deer (*Odocoileus virginianus*, above) and a cow (*Bos taurus*, below), co-occurring in the same camera trap in a sampling site in temperate forest. (Source: SNMB)

In the case of dogs, even if they are considered alone as a functional group, they can still have negative impacts on native species since dogs have been reported to consume many native prey species, largely affecting their local abundance (Gompper 2013). Therefore, dogs can compete for food resources, in various degrees, with many native predators and, therefore, also negatively impact them. Importantly, dogs can severely impact native carnivores through spillover of diseases not found locally or present or those normally found at a much lower prevalence (Gompper 2013; Nyhus 2016; Guedes et al. 2021).

23.5 Conclusions

- Biomass is an indicator that allows evaluating the state and condition of natural animal communities, whereas considering only at the number of records by species will result in an incomplete picture. We therefore recommend the use of body mass together with species identification of both wild and domesticated animals, as presented herein, to better describe the condition of a site or ecosystem.
- Comparing temperate and tropical forests of Mexico, we found less than one-fifth of the total biomass of mammals to be represented by wild species. As dire as this sounds, it is still a higher value than previous studies reported recently at a global scale (Bar-On et al. 2018). Yet it is hardly a cause for celebration and more a wake-up call to reduce habitat conversion and forest fragmentation and to reduce livestock invasion into forested ecosystems.
- We propose a much more rigorous employment of spatial planning and a revision of agricultural subsidies to stop these nefarious practices if only for the sake of public health by reducing wildlife-domestic-human contact interfaces which have led to the current pandemic and undoubtedly will lead to many more.
- Land cover loss in Mexico is highest in tropical forests (CONABIO 2006). Yet, this loss only represents land cover conversion. Taking into account the findings of our study, one has to surmise that the effects of ecosystem degradation by massive livestock invasion are grossly underestimated, and as Mexico is not an exception, this underestimation occurs at a global scale.
- The much higher share of observed biomass of cattle in Mexican forests when compared to wild mammals in this work shall serve as evidence of the underestimation of human impact derived from current satellite-derived assessments (CONABIO 2006 and Global Forest Watch data) because they do not detect the presence of livestock and thus probably do not account for the real loss in wild mammal biomass.
- The presence of large domestic mammals such as cattle in wild areas represents a great extraction of energy out of these systems, not only based on their foraging habits but also the other negative impacts, as described in this chapter. This has severe far-reaching consequences for the integrity and the health of the ecosystems which are impacted.
- Previous studies indicate that the presence of domestic fauna in ecosystems alters biotic interactions directly and indirectly by extirpation of selected mammal species and by causing negative interactions between introduced and native fauna.
- Cattle management strategies should be revised, reconsidered, and modified at the very least to substantially diminish the stocking density (head/ha) of cattle particularly in natural protected areas and other forested and preserved areas.

Acknowledgments We acknowledge the support of the United Nations Development Program (UNDP), the Comisión Nacional de Areas Naturales Protegidas (CONANP), and the Global Environmental Fundation (GEF), as well as the Fondo Mexicano para la Conservación de la Naturaleza (FMCN) and Comisión Nacional Forestal (CONAFOR) that participate in the monitoring program at national scale.

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Chapter 24
Pollination by Wild and Managed Animal Vectors

Lislie Solís-Montero, María del Coro Arizmendi, Alejandra Martínez de Castro Dubernard, Carlos H. Vergara, Miguel Ángel Guzmán Díaz, and Rémy Vandame

Contents

L. Solís-Montero (✉) · M. Á. G. Díaz
Departamento de Agricultura Sociedad y Ambiente, El Colegio de la Frontera Sur, Tapachula, Chiapas, México
e-mail: lsolis@ecosur.mx

M. del Coro Arizmendi
Laboratorio de Ecología, UBIPRO, FES Iztacala, Universidad Nacional Autónoma de México, Ciudad de México, México

A. M. de Castro Dubernard · R. Vandame
Departamento de Agricultura Sociedad y Ambiente, El Colegio de la Frontera Sur, San Cristóbal, Chiapas, México

C. H. Vergara
Departamento Química y Biología, Universidad de las Américas, Puebla, México

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_24

24.1 Introduction

Pollination is one of the essential ecological services that assures sexual plant reproduction. By this process, pollen grains are transferred (i.e., pollen containing male gamete) from anthers to the stigma of conspecific plants to reach ovules (i.e., female gamete) followed by fertilization, which results in seed production. Pollination in most flowering plants involves mutualistic interactions among plants and animals (Ollerton et al. 2011). In such plant-pollinator interactions, plants reward pollinators by providing principally nectar, pollen, and oil. In return, pollinators, such as insects, mammals, and birds, transfer their pollen grains favoring self- or cross-pollination, which makes it a crucial process in the maintenance of natural vegetation and crop production (Abrol 2012).

It is estimated that worldwide, a large percentage of wild plants (80–85%) and principle crops (70%) depend on animal pollination (Klein et al. 2007; Gallai et al. 2009; Potts et al. 2010; Ollerton et al. 2011). Similar percentages are reported in Mexico, where 85% of crops rely on pollinators for fruit or seed set (Ashworth et al. 2009). However, of this percentage, the level of pollinator dependence is only known for 37% of plant species, and only for 20% of species has the pollinator been identified (Sosenski and Dominguez 2018). As for wild plants in Mexico, there is no precise estimate of the percentage of plants pollinated by animals. Potential pollinators include species of insects (e.g., 1800 species of Apoidea; Ayala et al. 1996), mammals (e.g., 12 species of nectar feeding bats; Arita and Santos 1999), and birds (e.g., 58 species of hummingbirds; Arizmendi and Berlanga, 2014). The wide diversity of flowering plants (21,841 species; Villaseñor and Ortiz 2014) and potential pollinators involves a large number of complex plant-pollinator interactions. Yet, few studies have focused on pollination biology and ecology of wild plants in Mexico.

24.2 Present Knowledge of Wild and Managed Pollinators in Mexico

24.2.1 Wild Pollinators

We reviewed literature of wild pollinators contributing to wild plant reproduction in Mexico (n = 100 plant species in 21 families). Only the studies (n = 50) that described either efficiency (i.e., flower exposition to pollinator that result in fruit and seed production) or effectiveness (i.e., pollen transfer on pollinator's bodies, contact with sexual flower organs, pollen deposition) of pollination performance were considered. And the studies which only reported floral visitors were excluded.

Pollination dependence was determined following the methods employed by Klein et al. (2007) and Ashworth et al. (2009). We considered plant floral morphologies (e.g., polymorphisms, poricidal anthers, etc.), reproductive systems (e.g.,

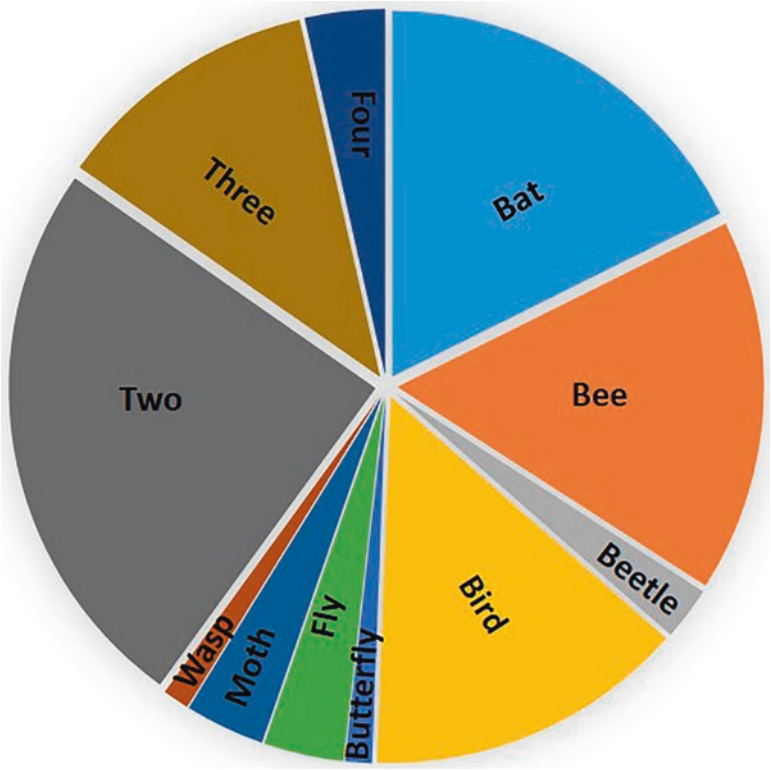

Fig. 24.1 Percentage of wild plant species (n = 85) pollinated by one to four types of pollinators in Mexico

self-compatibility, autonomous autogamy, agamospermy), or vegetative reproduction ($n = 71$ plant species). We classified the level of dependence only in studies that conducted a pollinator exclusion treatment and quantified natural pollination. Then, we calculated the reduction of fruit production in the absence of pollinators. The following categorization previously used by these authors was applied: (1) essential dependence, if reduction of fruit or seed set where >90% in absence of pollinators; (2) high dependence, when reduction were between 40% and 90%; (3) modest dependence, when reduction reported were between 10% and <40%; and (4) little dependence, >0–10% of reduction.

We found that 76% of studied wild plant species depend on pollinators for reproduction. Of these species, 54.7% were essential pollinator-dependent for fruit production; 9.3% was highly dependent; 11% was modestly dependent; 9.3% was little dependent; and 13% was unknown (n = 54 plant species). As reported, the main pollinators of wild plants were bats that pollinated 18% of plants species, followed by bees (16%) and birds (14%, Fig. 24.1). Bats were the most frequently reported pollinators probably because most of the studies reviewed here described the pollination ecology of plants belonging to Asparagaceae and Cactaceae families (n = 43 plant species). Both plant families have many species mainly pollinated by bats (Eguiarte et al. 2000; Valiente-Banuet 2002), some of which are wild species of economic and alimentary importance in Mexico (Ashworth et al. 2009). Most plants (60%) were pollinated only by one type of pollinator, 25% of the plants by two types of pollinators, and the rest by three or four types of pollinators (Fig. 24.1).

24.3 Managed Pollinators

24.3.1 Meliponiculture

Stingless bees (Meliponini) are important organisms in tropical and subtropical regions (Nogueira 1997). They have their center of distribution in the Neotropical America (Velthuis 1997; Michener 2000) where more than 400 species have been described, 46 species of which are reported in Mexico (Ayala 1999). Stingless bees have a highly reduced, nonfunctional stinger; hence, they have developed other defense mechanisms such as biting with mandibles, hiding inside nest, and entangling in hair (Martínez et al. 1993; Guzmán et al. 2004; González 2008).

Stingless bees have an essential role in pollination of wild and cultivated plants which promotes fruit and seed production (Roubik 1989; Martínez et al. 1993). In fact, bees pollinate more than a half of cultivated plants in tropics (Bawa 1990). Stingless bees pollinate around 250 plants species (Heard 1999); moreover, the pollination effectiveness of stingless bees is higher than that of other insects due to their floral constancy (Roubik 1995).

Stingless bees are managed for pollination of crops (Nogueira 1997; Guzmán 2002; Quezada 2005), such as coffee (Rincón et al. 1995, 2002), rambutan (Guzmán 2002), and macadamia (Heard 1988, 1994). This practice has been found to remarkably increase the production of these crops. However, the ecological and economical importance of stingless bees is being threated due to land-use changes and forest fragmentation, which affect floral resources and nest-site availability (Chacoff and Morales 2007; Guzmán et al. 2011).

Meliponiculture, the management and rearing of stingless bees, has been a tradition that dates from pre-Hispanic times in some regions of Mexico (Labougle and Zozaya 1986; Arnold et al. 2018), and it represents an important biocultural patrimony. The Maya culture, for instance, had a strong relation with stingless bees, and their products influenced the economic, cultural, cosmogonic, and pharmaceutical activities (González and De Araujo 2005; González 2008). Stingless bee honey was used by women after childbirth; it was also used to cure injuries, eye infections, asthma, and cough as well as to prepare balché, a revitalizing beverage of honey and pollen. In addition, wax produced by stingless bees (commonly called "Campeche wax") was used to make candles and figures that served as offerings to their gods (González 2008; Guerrero 2011; Vásquez and Hipólito 2011).

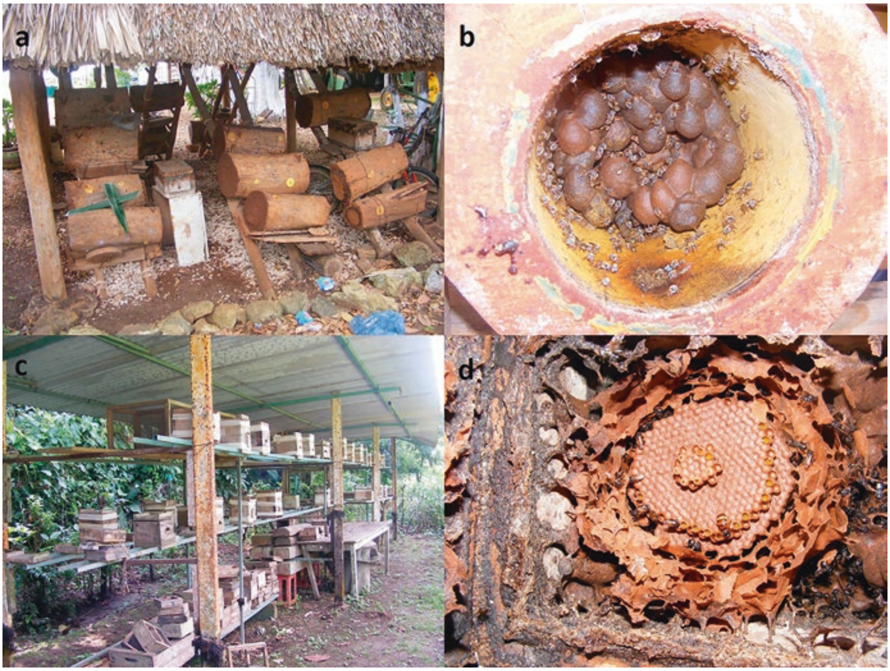

Fig. 24.2 (**a**) Traditional meliponary with (**b**) colonies of *Melipona beecheii* in trunks "jobones." (**c**) Technified meliponary with (**d**) colonies of *Scaptotrigona mexicana* in specialized boxes

After the Spanish conquest, breeding and culture of *Melipona beecheii*, a native stingless bee domesticated by Mayan culture, was continued. A meliponary often had from 100 to 200 modified tree trunks, in which this stingless bee was cultured. Bee rearing was based mainly on meliponiculture from the sixteenth to the eighteenth centuries, despite the Spanish imposition of high taxes for stingless bee honey and wax. However, this activity gradually started to decline after the introduction of the honey bee, *Apis mellifera*, by the Spanish in the sixteenth century (Brand 1988; González 2008).

Originally, it is believed that meliponiculture involved the harvest of honey directly from wild nests located in tree trunks. In the first stage of its development, the wild colonies found in trunks were placed together nearby people's dwellings to make it easier for them to obtain the products of bee colonies. Following this, Mayans built the first meliponaries, which were hollow tree trunks containing stingless bee colonies stacked horizontally. Later, meliponaries were constructed using branches in pyramidal structure, where trunks were placed on both sides; these later designs were covered by palm ceiling (Fig. 24.2a; González and De Araujo 2005; González 2008). Since 1975, people in Yucatan, Mexico, began to replace "jobones," the traditional colonies in trunks (Fig. 24.2b) by wood boxes (Fig. 24.2c, d; González 2008).

Currently, meliponiculture is still being practiced in various Mexican States such as Campeche, Quintana Roo, Yucatán, Puebla (González and De Araujo 2005; Quezada 2005), Veracruz (Domínguez and Rojas 1999), Tabasco (Murillo 1984), Guerrero, Oaxaca, and Chiapas (González 2008; Guzmán et al. 2009; Arnold et al. 2018). It has been found that 18 stingless bee species are used in this activity, the most common of those are from the genera *Melipona* (Fig. 24.2b) and *Scaptotrigona* (Fig. 24.2d), followed by species from the genera *Nannotrigona*, *Tetragonisca*, and *Cephalotrigona* (González 2008; Guzmán et al. 2009; Arnold et al. 2018).

Unfortunately, traditional meliponiculture is now in decline because stingless beekeepers are mostly elderly people and because young generations are not getting involved in this activity. This portends the loss of not only local indigenous knowledge but also a sustainable productive activity (Quezada 2005; González 2008). In addition, wild and managed colonies are being threatened by extensive agriculture, cattle ranching, pesticide use, and colony theft (Guzmán et al. 2011, 2016).

In order to maintain the continuity of meliponiculture, conservation of stingless bee's habitat is essential. Likewise, more research is needed to understand stingless bee biology and colony function (Quezada 2005). We suggest not only the rescue of traditional meliponiculture as a biocultural legacy but also the modernization of techniques for rearing bees as well as for obtaining and processing products. For instance, the utilization of specially designed nest boxes permits efficient management (Toto 2008) and a better control of stingless bee's natural enemies through manageable and periodical revisions of colonies (González 2008; Guzmán et al. 2011).

The commercialization of colony products (e.g., honey, pollen, wax, and propolis) has a high market potential. Stingless bee honey costs from four to ten times more than *Apis mellifera* honey because of its medicinal properties (Grajales et al. 2018). Also, other derived products such as syrup, capsules, cream, soap, and shampoo are being produced and sold. However, these products are only commercialized in local and regional markets, and their prices are not standardized (e.g., the cost of a liter of honey ranges from 25 to 76 USD).

Meliponiculture has recently been promoted in some regions of Mexico (González 2008; Arnold et al. 2018). It involves the rescue of traditional knowledge and the introduction of new production practices. It also requires the formation of specialist working groups and tight collaboration of stingless beekeeper communities that contribute to improvements in the management of colonies, habitat conservation, and reduction of pesticide use. By including meliponiculture as an economic activity in communities, its continuity can be assured, as well as the pollination of wild and cultivated plants around meliponaries.

Given the present decline of pollinators and its impact on food reduction, meliponiculture could be a viable alternative to increase pollination services in some tropical crops. For example, farmers have rented colonies of *Scaptotrigona mexicana* (from 4.2 to 5.4 colonies per ha) to increase fruit production of rambutan crops in the southeast of Mexico (Metapa municipality, Chiapas) since 2006. As a result, they have produced an average ± standard error (SE) 16.41 ± 0.99 ton/ha per year ($n = 15$ years). This converts to two times more production of rambutan compared with the production obtained before stingless bees were introduced in these crops (8.73 ± 0.16 ton/ha, two years), indicating that the use of stingless bees may favor rambutan production. Therefore, promoting meliponiculture to increase pollinator service and fruit production in some tropical crops could be a feasible alternative to increase the economical income of stingless beekeepers and farmers in Mexico.

24.3.2 Bombiculture

Bombiculture refers to the activity of raising bees of the genus *Bombus*, known as bumble bees. The primary aim of this activity is to produce colonies of bumble bees to pollinate some crops, mainly of the Solanaceae family, such as tomato and eggplant. These plants have flowers which display a complex morphology, which requires high-frequency vibrations to release pollen from the anthers (Buchmann 1983; Vallejo-Marín 2019). Bumble bees produce such vibrations to remove and collect pollen grains from the flowers and, consequently, transfer these grains to stigma of the same or other flowers and fertilize them in a process called "buzz pollination."

Commercialization of bumble bee pollination has expanded globally. Bumble bees are used to pollinate more than 26 crops. For instance, it is estimated that 95% of commercialized colonies are used for tomato pollination (Velthuis 2002; Velthuis and van Doorn 2006). This came after the discovery by Dr. De Jonghe of the economic value of the European bumble bee, *Bombus terrestris*. Commercial rearing became popular as bumble bee pollination was more efficient and economical than manual and mechanical pollination in greenhouse crops (Velthius 2002). As a result, *B. terrestris* was introduced to some countries, including Mexico in 1995 (Winter et al. 2006). Later, this bumble bee was replaced by the North American bumble bee *B. impatiens*, a native bumble bee of the eastern United States but still an exotic bumble bee in Mexico. Most colonies of *B. impatiens* have been imported to Mexico since 2001 (Kimberly et al. 2006). Currently, there are five species traded worldwide (Table 24.1), being the exotic species *B. impatiens* mostly used in Mexico.

Table 24.1 (Sub)species of bumble bees commercially traded for crop pollination

Species	Origin	Where it is used
B. terrestris L.	Europe, North of Africa, and West of Asia	Europa, North of Africa, Asia, Australasia, and South America
B. terrestris canariensis Pérez	Canary Islands	Canary Islands
B. lucorum L.	Europe and Asia	East Asia
B. ignitus Smith	East Asia	East Asia
B. occidentalis Greene	West of North America	West of North America
B. impatiens Cresson	East of North America	North America and Mexico

Taken and modified from Velthuis and Van Doorn (2006)

However, relying on exotic species is of concern for the conservation of native species. There are different threats associated with the use of exotic bumble bees (see Sect. 24.4.4), which can be dealt with by finding local pollination alternatives. This has led researchers to study the use and breeding of native Mexican bumble bees for crop pollination.

24.3.2.1 Potential Use of Native Bumble Bees for Pollination

The diversity of bumble bees in Mexico provides alternatives for replacement of exotic bumble bee colonies. One of these alternatives is *B. ephippiatus*, which has been extensively studied and is among the most common bumble bees found in this country. Another species that has been also considered for commercialization is *Bombus huntii*, distributed in Canada, the United Sates, and Mexico.

Studies with *B. ephippiatus* have focused on the biology (Fuentes Montemayor and Madrid Cuevas 2003; Llorente Torres 2005) and on the pollination efficiency of this species (Vergara and Fonseca-Buendía 2012; Torres Ruiz 2013). Other research works have tried to understand its reproduction and rearing under controlled conditions (Martínez de Castro Dubernard 2019). Regarding pollination efficiency of *B. ephippiatus*, Vergara and Fonseca-Buendía (2012) demonstrated that tomatoes (*Solanum lycopersicum* L.) pollinated by *B. ephippiatus* had higher number of seeds than those tomatoes mechanically or manually pollinated. In addition, the fresh weight and sugar content were also significantly higher in those tomatoes pollinated by this bumble bee species than in tomatoes produced by any other type of pollination.

In another study, it was found that *B. ephippiatus* is as efficient as *B. impatiens* in pollinating tomatoes in greenhouse (Torres-Ruiz and Jones 2012). Regarding its rearing, *B. ephippiatus* has been successfully reared under laboratory conditions, and there are ongoing efforts to achieve large-scale production. Today, the existing Mexican Association of Native Bumble Bee Breeders (Asociación Mexicana de Criadores de Abejorros Nativos, AMCAN), whose main goal is to achieve the breeding of native bumble bees for their future use in agriculture, is considering *B. ephippiatus* as the preferred candidate bee for this purpose (Secretaría de Agricultura y Desarrollo Rural 2015; López Fábila 2017).

Accordingly, *B. ephippiatus* is thought to be a valuable crop pollinator species because of its pollination efficiency and its successful rearing. Nonetheless, it is important to ensure private sector's engagement as well as collaboration between scientists and farmers to achieve the utilization of this bumble bee as a crop pollinator. Some guidelines have been already proposed to the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO; Vandame et al. 2019), so that the existing differences of genetic populations in bumble bees distributed in different areas of the country are maintained (Duennes et al. 2012). Duennes et al. (2012, 2017) have proposed four taxonomic units, which are distributed in Costa Rica and in Mexico the northern of the Isthmus of Tehuantepec (IT); two sympatric taxonomic units are located from south of the IT to Honduras.

In light of the above discussion, it is necessary to ensure a proper balance between the conservation of native bumble bees and their commercialization, in which management for food production does not pose a threat of harm to bee populations. To achieve this, the guidelines suggested in Vandame et al. (2019) include the following: (1) the exclusive utilization of local bumble bee species; (2) classifying as a different or a new bumble bee species, when there is enough evidence that population of bumble bees present in a region constitute a separate genetic lineage; (3) bearing in mind that relocating possible infected colonies of bumble bees may pose risk to local bumble bees and applying protocols for the identification and control of pathogens as well as for the removal of infected hives; and (4) standardization of practices to avoid risk to bumble bee populations, such as the collection of queens and the release of queens and males from managed colonies, even in the case of native species.

24.3.3 Biovectoring

Entomovectoring is a set of techniques aimed at spreading substances used in the biological control of plant pests and diseases by means of an insect vector. The insect is usually a honey bee, bumble bee, or mason bee, but it may also be any other insect that spreads pollen among plants. Bees are well-known vectors of not only pollen but also fungi and bacterial spores (Batra et al. 1973; Harrison et al. 1980; Sandhu and Waraich 1985; Thomson et al. 1992; Free 1993). The concept of bee vectoring was pioneered by Peng et al. (1992) in Canada, and it subsequently expanded to the use of other vectors and control agents (Smagghe et al. 2012).

The choice of vector species is decided by a combination of conditions such as the variety of insect species available in the area with the plants to be pollinated, the plant species to be treated, and the ease of care of the vector species. The vectored substance is typically a powdered material containing a virus, bacterium, or fungus to be used in order to protect the host plant from a given disease or pest. The insect, or vector, is exposed to this material by placing a tray containing the powder at the hive exit or nest congregation site or by using fans to blow it into the hive.

A critical step in the vectoring of a biocontrol organism (BCO) by pollinators is to load the vector in an efficient manner to ensure a sufficient loading. To achieve this, designing an appropriate dispenser is essential. The main goal of the dispensers is to load the vectors (the bees) with the powdery product (the pollen and/or formulated BCO product) as they walk through it on their way out of the hive so that they can disperse it to the target crops. An efficient dispenser should not only optimize the loading of the vector but also have a low dispenser reloading interval, enabling easy mounting on the hive. The dispenser also needs to have no influence on the vector's foraging behavior (Mommaerts and Smagghe 2011).

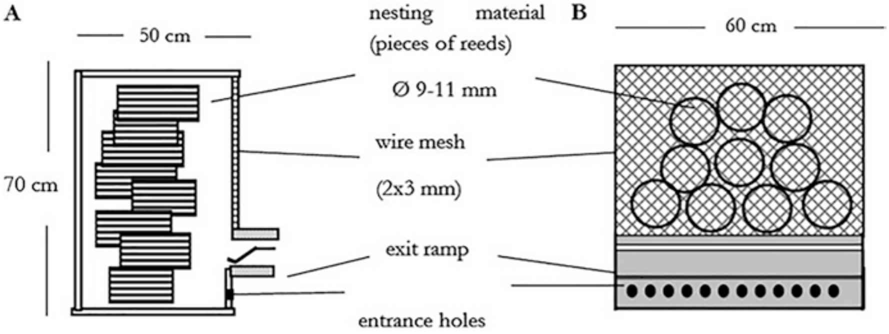

Fig. 24.3 Side (**a**) and front (**b**) views of the dispenser for *Osmia cornuta* mounted on nesting shelter (from Maccagnani et al. (2020))

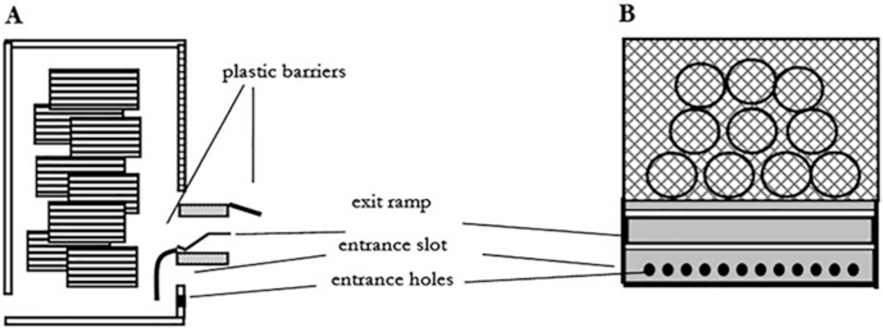

Fig. 24.4 Side (**a**) and front (**b**) views of the modified dispenser for *Osmia cornuta* (from Maccagnani et al. (2020))

Entomovectoring using native species in Mexico has not been attempted to the date. Currently, only honey bees and the exotic bumble bee *Bombus impatiens* are used as entomovectors in Mexico. However, stingless bees are potential entomovectors, yet dispensers for these species need to be designed. Efficient dispensers have been developed in Europe for *Osmia cornuta*, a nonsocial bee species showing gregarious behavior. These dispensers could be adapted for its utilization with stingless bees. To do so, the dispenser must be integrated into the nesting material and have a two-way design: outgoing bees must be obliged to walk on the BCO and returning bees must avoid getting in contact with it. This dispenser consists of a simple wooden box in which a plastic ramp is inserted. It could be positioned in the lower part of the shelter, and a metal mesh function is to close the remaining portion of the front side of the shelter. The BCO powder formulation is placed in a channel at the base of the ramp. Outgoing bees are expected to fly from their nest toward the mesh and walk downward to get to the first available entrance provided by the dispenser ramp. Thus, bees are obliged to pass through the channel with the powder formulation before climbing up the ramp to exit the dispenser. Returning bees enter the shelter through a series of holes drilled below the dispenser to avoid contact with the powder formulation (Figs. 24.3a, b and 24.4a, b; Maccagnani et al. 2020).

Several species of native Mexican bumble bees are suitable pollinators for potential commercial use as explained above. *Bombus ephippiatus* and *Bombus huntii* (Torres-Ruiz and Jones 2012) are the most promising species and could also be used for entomovectoring purposes by implementing the technology already designed for other bumble bee species.

24.4 Pollinator Crisis and Main Threats

24.4.1 Habitat Loss

Anthropogenic disturbances such as logging, habitat fragmentation through agricultural activities, cattle ranching, and urban development affect plant-pollinator interactions. This in turns alters the availability of resources and densities of native pollinators (Aizen and Feinsinger 1994; Kearns et al. 1998). Particularly, in tropical regions, the transformation of original forests to secondary forest, pasture, or urban areas threatens biodiversity (Díaz Infante et al. 2020) and associated biological interactions.

Habitat fragmentation can drive species with highly restricted ranges to extinction. A good example of this is the short-crested coquette (*Lophornis brachylophus*), a hummingbird inhabiting 40 km^2 of cloud and pine-oak forest in the Sierra Madre del Sur at Guerrero, Mexico (Arizmendi et al. 2021). Any change in the habitat within its distribution may have further negative effects on its declining population (Arizmendi et al. 2021). Another four hummingbird species are also threatened in spite of having larger distribution areas. However, other generalist pollinators such as some hummingbirds and some native or exotic bees are favored under a moderate human-disturbed habitat probably due to abundant and diverse floral resources (Cairns et al. 2005; Díaz Infante et al. 2020). Yet, it has been reported that some native bees present a greater diversity in protected areas compared with that of bees in disturbed areas (Cairns et al. 2005; Razo-León et al. 2018).

Specialist and/or migratory pollinators are also vulnerable to habitat loss. For example, monarch butterflies (*Danaus plexippus*), which travel from Canada to Mexico, depend on nectar availability, roosting locations, and water sources along the migration route to survive (Moreno-Sanchéz et al. 2019; Chap. 3, this volume). However, generalist migratory bats in the North of Mexico are less vulnerable to human perturbations in comparison with specialist local bats found in the center of Mexico (Valiente-Banuet 2002).

Pollinators in urban areas also contribute to plant reproduction of gardens and in food produced by urban agriculture (Ramírez-Segura and Jones 2016; Marín et al. 2020). Besides home gardens may function as pollinator refuges in urban areas (Marín et al. 2020). The effect of urbanization on pollinators varies according to the city studied and the pollinator type evaluated (Ramírez-Segura and Jones 2016). For example, some cities with abundant flowering resources present higher abundance of some floral visitor types than that in natural areas (Ramírez-Restrepo and Halffter 2013; Razo-León et al. 2018; Marín et al. 2020).

24.4.2 Pesticides

In agricultural landscapes, pesticides (e.g., fungicides, herbicides, and insecticides) are used for crop protection against pests and diseases. These pesticides have the potential to affect wild pollinators, and they can contaminate pastures, soil, water, and other vegetations (Aktar et al. 2009). In Mexico, the introduction and use of chemical pesticides result from the technological paradigm of capitalist modernization, known as the Green Revolution. Currently, 183 active ingredients are allowed for sale in Mexico (Bejarano González 2017). The development of various chemicals used as pesticides has had a significant negative impact, and they have affected not only pest organisms but also nontarget organisms, such as birds, bats, beneficial insects, and plants (Aktar et al. 2009).

Wild pollinators are exposed to pesticides through different routes: (i) by direct contact with aerosols and particles suspended in the air or by contact with treated plant surfaces; (ii) by ingestion of pollen, nectar, and pest molecules found water; and (iii) by inhalation of volatile pesticides. The route of exposure depends on the method of pesticide application, its physical-chemical properties and persistence, the weather conditions, and the behavior and foraging preferences of the different pollinators (Botías and Sánchez-Bayo 2018). Pesticide exposure may affect pollinator life cycles, diversity, and abundance.

The use of pesticides in Mexico and their effects on pollinators have been addressed in several studies. For example, in a study that evaluated bee biodiversity in cropping systems (i.e., polycultures, pastures, and monocultures) in Campeche, Mexico, a greater diversity and abundance of bee species was reported in polycultures than in monocultures (Vides-Borrell et al. 2019). It was found that many variables had an effect on these results, one of which was the presence of pesticides in intensive cultivation areas.

In another study on stingless bees, the toxicity of pesticides (neonicotinoids, permethrin, diazinon, and methomyl) on *Melipona beecheii*, *Trigona nigra*, and *Nannotrigona perilampoides* was evaluated. Findings revealed that all species were highly susceptible to pesticides (Valdovinos-Núñez et al. 2009). In 2018, the effects of the Gf-120 aerial sprays (spinosad) applied in the Municipality of Mazatan, Chiapas, Mexico, were investigated. The study reported that exposure to this pesticide reduced colony strength in *S. mexicana* colonies (Gómez-Escobar et al. 2018).

As for vertebrate pollinators, little research has been carried out on the effects of pesticides. However, recent studies have described how the presence of pesticides on visited plant species can cause detrimental effects in hummingbirds (Bishop et al. 2018, English et al. 2021). Also, genotoxic effects were found in bats with a great exposure to pesticides related to agricultural activity as they presented a higher incidence of micronuclei (Sandoval-Herrera et al. 2021).

24.4.3 Climate Change

Climate change can disrupt animal-plant interactions by causing temporal mismatch (phenological shifts), demographic mismatch (changes in population densities), or spatial mismatch (distribution changes). Climate warming and its associated effects can impact the phenology of both plant and pollinators. In some insects, climate warming has changed the timing of peak abundances and the duration of their activity periods (Memmott et al. 2007; Scranton and Amarasekare 2017). Likewise, plant flowering time and duration may be altered (Memmott et al. 2007; Hegland et al. 2009). These temporal mismatches may cause reduction of food supplies from 15 to 50% for pollinators (Memmott et al. 2007) or result in novel plant-pollinator interactions (Hegland et al. 2009).

Climate change has an impact on plant or animal local abundances (Hegland et al. 2009). For some insects, warm temperature decreases birth rate and increases mortality affecting growth rate and their abundances (Scranton and Amarasekare 2017). Regarding plants, temperature drives changes on floral abundance and affects plant reproduction success as well as food availability to pollinators (Hegland et al. 2009). When pollinators have to reduce their diet, they are likely to suffer a population decline (Memmott et al. 2007).

Also, climatic change affects distribution of species due to modifications in the distribution of suitable areas for survival and reproduction. For example, in endangered migratory bat species, such as *Leptonycteris nivalis*, which pollinate *Agave* spp., climate models under various scenarios predict that an overlap between plants and their pollinators will be reduced by at least 75% (Gómez-Ruiz and Lacher 2019). These changes in distribution could reduce available foraging resources and threaten both bat and *Agave* populations (Gómez-Ruiz and Lacher 2019).

24.4.4 Exotic Pollinator Introductions

The introduction of an exotic pollinator in new habitats can have negative effects on native pollinators and can also favor exotic plant reproduction because an exotic pollinator may prefer to visit these plants (Goulson 2003). In the particular case of bees in Mexico, many colonies of *Bombus impatiens* were imported to Mexico for commercial pollination (Kimberly et al. 2006). The continued use of this exotic bumble bee is of concern because it threatens the health of native bumble bee species and because it may result in interspecific hybridization (Duennes et al. 2017). As 45% of sampled colonies in greenhouse were positive for one or more pathogens such as *Apicystis bombi*, *Locustacarus buchneri*, *Nosema bombi*, *Crithidia bombi*, or other viral pathogens that are associated with colony collapse disorder (Sachman-Ruiz et al. 2015), the possibility of emerging infectious diseases transmitted by *B. impatiens* to wild bumble bees is a latent risk. In fact, it was found that *Crithidia* and *Nosema* infected several species of endemic bumble bees in Mexico (Gallot-Lavallée et al. 2016).

Another example is that of *Apis mellifera* (Apidae), which was introduced in Mexico from Europe to increase honey and wax production in the sixteenth century (Brand 1988). The current status of this species as crop pollinators and honey-producing bees (67,657 honey tons in 2020) contributes to Mexican economy (SIAP 2021). However, it has been reported that introduced honey bees have negative effects in different parts of the world, which include competition with native bees for floral resources or nest sites, on transmission of parasites or pathogens to native species, on pollination that favors the reproduction of invasive plant species, and on seed production of native plants (Goulson 2003).

Honey bees in Mexico pose several threats to native bees. The transmission of two viruses (deformed wing virus and black queen cell virus) from honey bees to native stingless bees (*S. mexicana*) poses a potential risk for native bees. This transmission probably occurs by physical contact or through pollen in commonly visited plants (Ramirez-Arriaga and Martinez-Hernandez 2007; Guzman-Novoa et al. 2015). In addition, honey bees have been shown to displace native bees for floral resources in squash and watermelon crops (Pinkus-Rendon et al. 2005). Moreover, Africanized honey bees (AHB) competed with solitary bees for floral resources and alter their floral preferences (Roubik and Villanueva 2009). And for AHB, an aggressive competitive behavior (e.g., physical attacks) against stingless bees for floral and water resources has been reported (Cairns et al. 2005).

24.4.5 Cultural Traditions

Hummingbirds are closely associated with many American cultures representing love, good luck, and the link between two worlds, the living and the dead. In some cultures, they also represent war. However, cultural traditions can be harmful to hummingbird's populations. For example, during the 1960s, wearing feathers in hats was considered luxurious, so thousands of birds were killed to create a beautiful hat. Fortunately, this is now out of fashion, but other peculiar practices threaten hummingbirds such as the "amarres" divination ritual common in some regions of Mexico (UNAM global, 2019). Two dead hummingbirds wrapped in a plastic bag filled with a honey-like infusion can supposedly prognosticate the possibility of finding a wife or a husband. If the bills are tied together, the "amarre" is for marriage, whereas if the bills are in opposition foretells of a divorce. This practice guarantees 90% efficiency, and hummingbirds are sold for this purpose on the Internet (Arizmendi, personal communication). Although this practice is against the law, it remains a real problem for hummingbird conservation.

Another popular Mexican tradition is the consumption of tequila, one of the most important Mexican exports. However, its production endangers nectar-feeding bats because *Agave* plants are harvested before they flower, a time when plants have the highest sugar concentration (Trejo-Salazar et al. 2016). The impact of this on bats is significant as it diminishes their populations and decreases the genetic diversity of *Agave* that is provided through bat pollination (Trejo-Salazar et al. 2016; see also Chap. 14, this volume).

24.5 Pollinator Conservation

24.5.1 Conservation Status

The impact of threats on pollinators depends on the type of pollinator and on the magnitude of disturbance. In this section, we document the conservation status of main groups of pollinators. For instance, hummingbirds face a number of threats that can be challenging for their conservation. In Mexico, there are 58 species, including all North American hummingbird species, 13 species of which are endemic to Mexico. According to reports, five of these species are threatened, and the remaining species have been included in the "least concern" category by IUCN (International Union for Conservation of Nature) (Table 24.2), whereas the Official Mexican Norm (NOM-059-SEMARNAT-2019) considers 20 hummingbird species in a risk category. In the case of nectar-feeding bats (Tribe Glossophagini), 12 species are distributed in Mexico, 2 of which are endemic species (Arita and Santos 1999). Four species of nectar-feeding bats are considered threated, and the remaining species have categorized as "least concern" by IUCN (Table 24.2), while the Official Mexican Norm includes only four species.

The drastic decline of insect populations in the Anthropocene is a global phenomenon that is placing at risk many ecosystem functions, one of which is pollination (Goulson 2019; van der Sluijis 2020). However, the Official Mexican Norm that lists endangered species includes only nine species of insects. One of these species is regarded as a pollinator, the charismatic monarch butterfly (*Danaus plexippus*), whose populations fell by 80% over the last decade until 2016 (Semmens et al. 2016; Chap. 3, this volume). Lastly, Vandame et al. (2017) evaluated 21 species of Mesoamerican bumble bees. Six species of those are regarded as threated, and four species belong to the "least concern" category by IUCN (Table 24.2). These ten species are distributed in Mexico, yet they have not been included in Official Mexican Norm list of threatened species.

Table 24.2 Species of pollinator included in the International Union for Conservation of Nature (IUCN) and Official Mexican Norm (NOM-059-SEMARNAT-2019)

Pollinator type	Species	IUCN category	Category Nom-059-2019
Bat	*Anoura geoffroyi*	LC	
Bat	*Choeroniscus godmani*	LC	
Bat	*Choeronycteris mexicana*	NT	A
Bat	*Glossophaga commissarisi*	LC	
Bat	*Glossophaga leachii*	LC	
Bat	*Glossophaga morenoi*	LC	
Bat	*Glossophaga soricina*	LC	
Bat	*Hylonycteris underwoodi*	LC	
Bat	*Leptonycteris yerbabuenae*	NT	Pr
Bat	*Leptonycteris nivalis*	EN	A
Bat	*Lichonycteris obscura*	LC	
Bat	*Musonycteris harrisoni*	VU	P
Bees	*Bombus brachycephalus*	EN	
Bees	*Bombus diligens*	NT	
Bees	*Bombus ephippiatus*	LC	
Bees	*Bombus haueri*	EN	
Bees	*Bombus macgregori*	LC	
Bees	*Bombus medius*	VU	
Bees	*Bombus mexicanus*	VU	
Bees	*Bombus steindachneri*	EN	
Bees	*Bombus trinominatus*	LC	
Bees	*Bombus weisi*	LC	
Bird	*Abeillia abeillei*	LC	Pr
Bird	*Amazilia rutila*	LC	Pr
Bird	*Amazilia viridifrons*	LC	A
Bird	*Atthis ellioti*	LC	A
Bird	*Campylopterus excellens*	LC	Pr
Bird	*Campylopterus rufus*	LC	Pr
Bird	*Cynanthus latirostris*	LC	Pr
Bird	*Doricha eliza*	NT	P
Bird	*Doricha enicura*	LC	A
Bird	*Eupherusa cyanophrys*	EN	P
Bird	*Eupherusa poliocerca*	VU	A
Bird	*Heliomaster longirostris*	LC	Pr
Bird	*Heliothryx barroti*	LC	A
Bird	*Lampornis viridipallens*	LC	Pr
Bird	*Lamprolaima rhami*	LC	A
Bird	*Lophornis brachylophus*	CR	P
Bird	*Lophornis helenae*	LC	A
Bird	*Phaethornis striigularis*	LC	Pr
Bird	*Thalurania ridgwayi*	VU	A
Bird	*Tilmatura dupontii*	LC	A
Butterfly	*Danaus plexippus*	LC	Pr

IUCN: *LC* least concern; *NT* near threatened; *V* vulnerable; *EN* endangered; *CR* critical endangered. NOM-059-2019: risk of extinction (P), threatened (A), and subject to special protection (Pr)

24.5.2 Conservation Strategies

Despite scientific evidence about insect decline and scientist's calls to prioritize insect conservation, pollinator conservation policies have been neglected or are not adequate (van der Sluijis 2020). Particularly in Mexico, efforts are focused on developing guidelines for policy makers according to scientific research evidence on different types of pollinators. With regard to bees, the work of different scientific groups has integrated a large database which includes around 400,000 bee records, of which an estimated 32,039 records are about bumble bees. Researchers at El Colegio de la Frontera Sur in Chiapas have studied *Bombus ephippiatus* rearing and developed protocols to reach high levels of reproduction (Martínez de Castro Dubernard personal communication; Williams et al. 2020). In addition, researchers from Central America and Mexico have suggested pertinent recommendations to policy makers on the possible risk of trading exotic bumble bees (Vandame et al. 2019).

One of the main threats pollinators face is pesticide pollution mainly associated with the cultivation of crops (Dicks et al. 2016). Agroecological practices offer alternative ways to reduce the use of pesticides in food production. An example of this is the organic coffee production in Chiapas, Mexico, that includes thousands of indigenous peasants who integrate sustainable, nonchemical agroecological practices (Mier y Terán Giménez Cacho et al. 2018). However, many agrochemicals are still being used in Mexico and efforts to ban them are incipient. For instance, the herbicide glyphosate has been banned by Mexican government, but the agrochemical industry has legally opposed this initiative.

Although urban settlements can cause habitat destruction, they can also provide conditions for environmental education and conservation-oriented programs. Moreover, strategies for the conservation of pollinators can be developed and implemented. For instance, the creation of pollinator gardens that promote both communal and private gardens to maintain pollinator populations and get people close to nature is a strategy that has been pursued in many countries including Mexico (Arizmendi et al. 2020). The creation of gardens using native plants can be considered also a restoration activity.

Finally, an action plan of the National Autonomous University of Mexico and the Tequila Interchange Project encourages tequila farmers to allow flowering of 5% of agaves per hectare in their tequila plantations. This action sustains approximately two million bats per month (Trejo-Salazar et al. 2016). To encourage this practice, the project has an official certification process for tequila labeling as bat-friendly, a certification that promotes bats and agave conservation together with its mutualistic interaction.

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Chapter 25

Origins and Coadaptation of Insect Pests from Wild to Domesticated Host Plants: Examples from Maize, Cotton, and Prickly Pear Cactus

Robert W. Jones, Julio S. Bernal, Ek del Val de Gortari, and Uriel J. Sánchez-Reyes

Contents

R. W. Jones (✉)
Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro,
Juriquilla, Queretaro, Mexico
e-mail: rjones@uaq.mx

J. S. Bernal
Department of Entomology, Texas A&M University, College Station, TX, USA

E. del Val de Gortari
Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional
Autónoma de México, Morelia, Michoacan, Mexico

U. J. Sánchez-Reyes
Instituto Tecnológico de Ciudad Victoria, Ciudad Victoria, Tamaulipas, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_25

25.1 The Processes in the Emergence of Insect Pests on Cultivated Plants

One of the earliest human impacts on environments of the Anthropocene is land transformation to favor domesticated plant species (Ellis et al. 2002). As one of a handful of primary centers of plant domestication (Vavilov et al. 1992; Sarukhán et al. 2017), agriculture (farming) as a form of land transformation began in Mexico at least 8700 years before present. This process probably began as a complement to hunting-gathering activities and was intensified beginning ~7000 years before present, as indicated by increased abundance of weedy plant species and *Zea* pollen and increasing levels of carbon deposits apparently from brush and forest burning (Zizumbo-Villarreal et al. 2016).

The selection and planting of incipient crop lineages that accompanied the land transformation also favored specific guilds of herbivorous insect species and their predaceous and parasitic associates that had long histories of coadaptation with crop ancestors and wild relatives (Chen et al. 2015). Prior to domestication, these herbivores had to overcome the direct and indirect defenses of their host plants in order to survive and reproduce. With domestication and the spread of agriculture, their host plants gradually became superabundant and were grown under resource-rich conditions that favored their growth and reproduction but often weakened their herbivore defenses (Maag et al. 2015; Bernal and Medina 2018). Presumably through drift, selection, and inbreeding, these long associated herbivores of maize, beans, squash, cotton, chili pepper, and numerous other Mesoamerican domesticates quickly adapted to their newly exuberant and poorly defended crop hosts and became pests in the Americas and more recently in other parts of the world (Bernal and Medina 2018).

Crop wild ancestors and relatives have long been acknowledged as important natural resources critical for development of sustainable options for world agriculture (Frankel 1970; Meilleur and Hodgkin 2004; Maxted et al. 2012; Goettsch et al. 2021). Preservation of crop ancestors and relatives can be divided in ex situ and in situ conservation. The former includes storage of plant taxa apart from where they were collected (e.g., in germplasm or seed banks), whereas in situ attempts to conserve taxa in the places where they are encountered (Engelmann and Engels 2002). In situ conservation is most appropriate for crop ancestors and wild relatives and is carried out in protected areas or in on-farm and home garden settings (Engelmann and Engels 2002), though in situ conservation is increasingly relevant to crop landraces (Gepts 2006; Bellon and van Etten 2014). Although in situ efforts are mainly directed at conserving the genetic diversity of crop ancestors, wild relatives, and landraces, such efforts also lead to the preservation of other organisms directly and indirectly linked to those plant species and native habitats. In particular, in situ conservation of crop landraces, ancestors, and wild relatives also preserves ancestral insect pest lineages and invariably sustains a greater diversity of their natural enemies than on domesticated cultivars (Chen et al. 2015). Wild hosts also are usually better defended against insect herbivores and maintain tri-trophic interactions

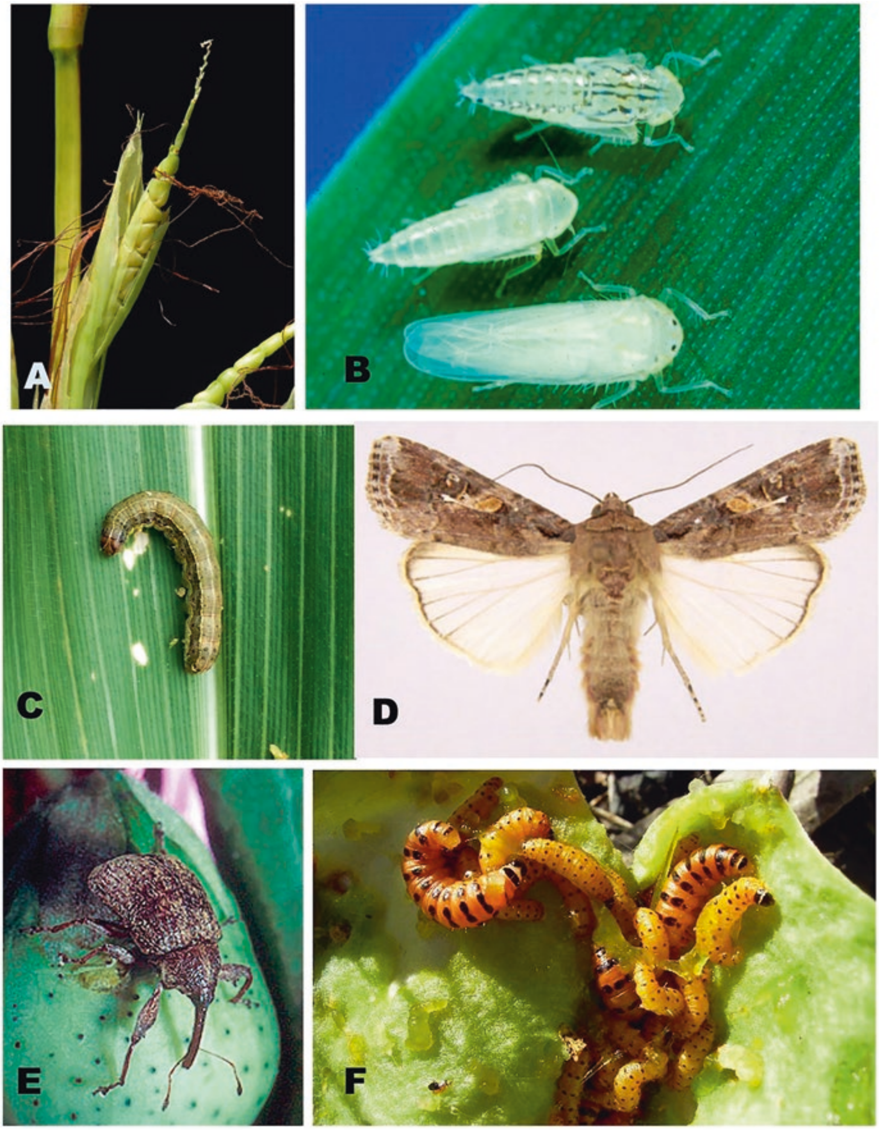

Fig. 25.1 (**a**) Balsas teocintle, *Z. mays* L. ssp. *parviglumis* Iltis & Doebley, female fruiting body (Photo Pedro Tenorio Lezama CONABIO 2022). (**b**) Adult and late instar nymphs of the corn leafhopper, *Dalbulus maidis* Delong & Wolcott (Photo Lowell R. Nault). (**c**) Larva and (**d**) adult of fall armyworm, "cogollero," *Spodoptera frugiperda* J. E. Smith (Larval photo, Juan Fornoni; adult, Canadian Biodiversity Information Facility, http://www.cbif.gc.ca). (**e**) Boll weevil, *Anthonomus grandis* Boheman (USDA, US Department of Agriculture, ID K2742–6). (**f**) Cactus moth larvae within *Opuntia* cactus pad. (Photo Fernando Bahena)

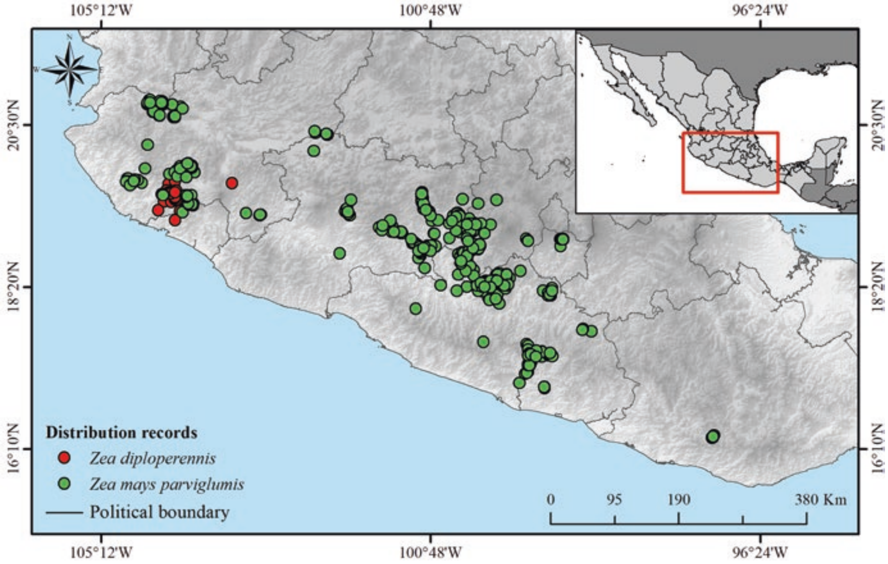

Fig. 25.2 Distribution records of Balsas teosinte, *Zea mays parviglumis* Iltis & Doebley, and perennial teosinte, *Zea diploperennis* Iltis, Doebley & Guzman in Central Mexico. (Data obtained from Global Biodiversity Information Facility site (GBIF.org 2022))

(plant-herbivore-natural enemy) that augment the impact of natural enemies against their herbivores (Dávila-Flores et al. 2013; Whitehead et al. 2017; Fontes-Puebla and Bernal 2020). These coevolved plant-herbivore systems provide windows into the evolutionary processes and associated organisms that have shaped both the plant and its herbivores, and their study can lead to novel options for sustainable management of insect pests (Chen et al. 2015, 2018; Bernal and Medina 2018; Fontes-Puebla and Bernal 2020).

25.2 Origin and Coevolution of Maize and the Corn Leafhopper

Maize (*Z. mays* L. ssp. *mays*) was domesticated from Balsas teosinte (*Z. mays* ssp. *parviglumis* Iltis & Doebley) (Fig. 25.1a) beginning ~9.2 K years before present (ybp) (Piperno et al. 2009). Presently, Balsas teosinte is a lowland species that grows along the Mexican Central Pacific coast, from near sea level to ~1960 m above sea level (asl; Fig. 25.2), and maize domestication likely occurred in the Balsas River drainage (~700 m asl) on the slopes of the Western Sierra Madre (Matsuoka et al. 2002; Hufford et al. 2012; Sánchez-González et al. 2018). From its area of domestication, maize rapidly spread in the Americas in every direction. Near contemporaneously, maize spread eastward to Mexico's Gulf coast by 7.3 K ybp and southward to Panama by ~7.5 K ybp, reaching coastal Peru, the Andes, and lowland Bolivian Amazon by ~6.5–6.3 K ybp and Atlantic South America, including Argentina, by 2–4 K ybp via an eastern, lowland route; northward, maize reached the southwestern United States and the Colorado Plateau by ~4 K ybp (Piperno and Flannery 2001; Gil et al. 2006; Pohl et al. 2007; Kistler et al. 2018).

Prior studies hypothesized that the chronology and geography of maize domestication and early spread are relevant to the emergence of maize pests in the Americas (Nault 1990; Medina et al. 2012; Bernal and Medina 2018; Bernal et al. 2019). Those studies focused on corn leafhopper (hereafter CLH; *Dalbulus maidis* Delong & Wolcott; Hemiptera: Cicadellidae; Fig. 25.1b), a *Zea* specialist and phloem feeder that is widespread in the Americas from the southern United States and California to northern Argentina and the Caribbean (Nault 1990). The leafhopper genus *Dalbulus* includes at least 11 species, including CLH (Nault 1990; Dietrich et al. 1998), although among those species only CLH is a maize pest. Nault (1990) postulated that at least another six species were potential maize pests. Dietrich et al. (1998) identified five *Dalbulus* species as specialists on *Zea* or specialists on *Zea* and *Tripsacum*, a genus of perennial grasses closely related to *Zea*. *Zea* specialists included CLH and *D. elimatus*, and *Zea-Tripsacum* specialists included *D. gelbus*, *D. guevarai*, and *D. longulus*. The geographic and elevational distributions of these five species were described by Nault (1990), who showed that while the geographical distributions of the non-CLH species overlap with that of CLH, there is considerably less overlap in their elevational distributions. While CLH is most abundant at elevations below 750 m asl, the elevational distributions of the remaining four species ranged higher from 735 to 2400 m asl, with average distributions ranging from 1188 to 1792 m asl. The elevational and geographic distributions of the *Dalbulus* species are relevant to the emergence of *Dalbulus* species pestiferous on maize because the maize ancestor, Balsas teosinte, grows only along the Mexican central Pacific coast below 1960 m asl (average 1058 m asl), a distributional range broadly overlapping with that of CLH but overlapping partially and only with those of *D. elimatus* and *D. guevarai* (Nault 1990; Hufford et al. 2012; Sánchez-González et al. 2018). Plausibly, the broad distributional overlap between Balsas teosinte and CLH likely played a significant role in the emergence of CLH as a pest of maize.

In addition to CLH's greater distributional overlap with Balsas teosinte compared to other *Dalbulus* species with potential for becoming maize pests (*D. elimatus*, *D. gelbus*, *D. guevarai*, *D. longulus*), a number of life history or performance variables likely are relevant to its emergence as a maize pest. For example, compared to potentially pestiferous species of *Dalbulus*, CLH developed faster; had higher fecundity and survival, especially at warmer, lowland-like temperatures; and completed two full generations, while showing population growth in the second compared to first generation (Madden and Nault 1983; Nault 1990). The overwintering ecologies of CLH and potentially pestiferous *Dalbulus* are relevant as well. The rainy season extends from ~June to ~September in the area where Balsas teosinte occurs, and this defines the growing season for rain-fed maize, which is planted beginning in late June and harvested beginning in November. Maize crops begin senescing in ~October, which forces CLH and potentially pestiferous *Dalbulus* on maize to seek overwintering hosts, usually in the form of perennial grasses, vegetation in the vicinity of permanent bodies of water, or “winter” irrigated maize or rain-fed maize where the winter climate allows maize cultivation. On those overwintering hosts, CLH and potentially pestiferous *Dalbulus* may overwinter as adults either nonreproducing (e.g., CLH, *D. elimatus*) or those that continue reproducing (e.g., *D. gelbus*). However, the overwintering ecologies of potentially pestiferous *D. longulus* and *D. guevarai* are unknown, though they may overwinter in the egg stage (Nault 1990; Larsen et al. 1992). At the beginning of the rainy season, CLH and potentially pestiferous *Dalbulus* take flight searching for hosts, and CLH is the first to colonize maize crops and occupy the whorl, which offers nutritional benefits and partial protection from natural enemies. Put together, the opportunity to exploit the maize ancestor Balsas teosinte, the enhanced performance on maize, and the overwintering ecology suited for exploiting rain-fed maize crops – the locally dominant host plant – were bases for hypothesizing that CLH, unlike the other potentially pestiferous *Dalbulus* species, had comparatively superior adaptations (“pre-adapted”) for successfully colonizing and exploiting maize upon its domestication (Nault 1990; Dávila-Flores et al. 2013; Medina et al. 2012; Bernal and Medina 2018). This hypothesis was bolstered by the genetic results of AFLP- and mitochondrial DNA-based studies showing that a CLH population on perennial teosinte (*Zea diploperennis* Iltis, Doebley & Guzman), the basal species of *Zea*, is genetically discrete and ostensibly ancestral to the pestiferous CLH population on maize and Balsas teosinte, *Z. m. parviglumis*) (Medina et al. 2012; Bernal et al. 2019). In contrast to Balsas teosinte, perennial teosinte has a more restricted attitudinal and geographic distribution, found in cloud forests of the uplands of the Pacific coast of the states of Colima and Jalisco (Fig. 25.2).

As noted, the results of earlier studies led to the hypothesis that after evolving on Balsas teosinte, CLH was better able to expand its host range and colonize domesticated maize, when compared to similar *Dalbulus* species (Nault 1990; Medina et al. 2012). This hypothesis was expanded by Medina et al. (2012) who suggested the following scenarios of adoption of maize as a host: (i) CLH spread upland with maize farming and colonized the upland host perennial teosinte, *Z. diploperennis* (Fig. 25.2), (ii) colonization of this perennial teosinte led to genetic structuring in which CLH in Mexico included a “pestiferous” population on maize and Balsas teosinte and a wild population on perennial teosinte, and (iii) the wild CLH population on perennial teosinte represented ancient genetic variation present at the time that this upland host plant was colonized. These hypotheses were consistent with shifts in the intensity of maize farming in the vicinity of perennial teosinte habitat during the last ~7 K years, as documented in archaeological and ethnohistoric studies, and recent proscription (since the mid-1980s) of maize cultivation within perennial teosinte habitat (Medina et al. 2012).

Subsequent studies by Bernal et al. (2019) and Ramirez-Romero et al. (2019) tested these hypotheses and predictions derived from them. Using larger sample sizes than that of Medina et al. (2012), including sample sequences from Argentina, Bernal et al. (2019) confirmed via AFLP and mitochondrial DNA (COI) sequence data that indeed CLH consisted of two distinct pestiferous populations, one on maize and Balsas teosinte and another wild population on perennial teosinte, *Z. diploperennis* (Fig. 25.2). Additionally, they used COI sequences to reconstruct the evolutionary history of the pestiferous and wild CLH populations, calibrated per the known chronology with the spread of maize to Argentina. Specifically, calibration was based on the presumed maximum age of a COI haplotype found in Argentina and absent in Mexico, which was assumed could not exceed 4000 years, the longest plausible presence of maize in Argentina. At ages below 2000 years for the Argentinian haplotype, the pestiferous and wild CLH populations were estimated to have diverged consistent with the timings of widespread maize farming in the area surrounding perennial teosinte habitat at 7 K ybp and intensified maize farming in the perennial teosinte habitat at 1200–800 ybp. With these results, Bernal et al. (2019) concluded that the wild CLH population on perennial teosinte represented ancient genetic variation present at the time that this upland host plant was colonized and that the wild population is ancestral to the pestiferous population. These and later results (Ramirez-Romero et al. 2019) indicated that wild CLH easily colonized and performed well on maize compared to perennial teosinte, thus supporting the hypothesis that CLH had fortuitous traits to better exploit maize, and as such, it readily became a pest of this domesticated crop (Nault 1990; Medina et al. 2012).

We believe that the research described above clearly illustrates how human activity, in this case in the form of crop domestication and spread of agriculture, creates new genetic variation and population structuring in insects. Thus, with maize domestication, a well-adapted CLH to the maize ancestor, Balsas teosinte, colonized the newly domesticated crop and became a pest. Moreover, the emergence of CLH as a pest was facilitated by human activities, such as the spread of maize farming beyond the distributional range of CLH's ancestral host (Balsas teosinte), artificial (crop) selection for yield by early farmers, and breeding for yield by agricultural scientists in the last ~100 years (Dávila-Flores et al. 2013; Bellota et al. 2013; Bernal and Medina 2018). CLH's emergence as a pest with maize domestication likely represents only an example within a broader phenomenon in which crop domestication, agricultural spread, breeding, and agricultural intensification, among other processes, lead to the emergence and increasing aggravation of insect pests (Bernal and Medina 2018; Chen et al. 2018; Fontes-Puebla and Bernal 2020). Overall, we believe that CLH and other insect pests that have been shown to be products of past anthropogenic activities represent valuable case studies for analyses and design of anthropogenic activities, such as food production among many others, in the face of a global climate change and ensuing rapidly changing environments.

25.3 The Fall Armyworm, *Spodoptera frugiperda* (J. E. Smith): The Emergence of a Superpest

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (hereafter FAW, Fig. 25.1c, d), is a particularly significant Mexican herbivorous insect that has become a worldwide agricultural pest in recent years (Day et al. 2017; Sharanabasappa et al. 2018; Yan et al. 2021). This noctuid species is distributed widely in the Americas and has considerable dispersal capacity (Johnson 1987). In Mexico, the FAW is the most significant pest of maize, particularly in intensive farming systems in tropical and subtropical areas (Sifuentes 1967; Bautista Martinez 2006; Blanco et al. 2014).

The FAW was assuredly part of the maize pest complex in pre-Hispanic societies. Indeed FAW is seemingly depicted in the fifteenth-century Borgia Codex, which shows spotted caterpillars with the face of the wind god (*Ehecatl*), occurring at the beginning of the rainy season in the months of May and June (Bricker and Milbrath 2011), an early-season pest whose larvae are dispersed by the wind and frequently reach outbreak densities (e.g., Luginbill (1928), Andrews (1980)). Given the extended coevolutionary history, FAW has many natural enemies in Mexico, and the pest's populations are often held in check by diseases, parasitoids, and predators. In some locations, dozens of species of Hymenopteran parasitoids have been reported, and overall, ca. 400 species of FAW natural enemies have been documented in Mexico, including 263 parasitoids, 88 predators, and 39 pathogens, from fungi, bacteria, and protozoans to nematodes (Molina-Ochoa et al. 2004; Hoballah et al. 2004; Bahena et al. 2010; Ordóñez-García et al. 2015; Bahena-Juárez and Cortez-Mondaca 2015).

In 2014, the "corn strain" lineage of FAW initiated an unparalleled worldwide expansion reaching many countries of Africa, Asia, and even Australia and causing significant losses in agriculture (Nagoshi et al. 2018; Wan et al. 2021). Presently, Wan et al. (2021) reported invasions of 47 African, 18 Asian, and 2 Oceanian countries since the first detection of FAW in Nigeria and Ghana in 2016 (Wan et al. 2021). Concurrent with its expansion, its importance as a pest has increased due to the expansion of its host range to at least 353 host plants, its ability to survive in a wide range of new habitats, and its strong migration ability, high fecundity, and rapid development of resistance to insecticides and viruses (Wan et al. 2021).

The recent expansion of FAW's distribution and incidence has been attributed to several factors. Within Mexico, increasing temperatures in mountainous areas related to climate change as well as agricultural simplification are linked with its expansion within the country (Díaz-Álvarez et al. 2020). However, relevant to invasion in Africa and Asia, studies have found that since FAW was subject to intensive artificial selection due to extensive insecticide and biocontrol measures in the Americas (Leibee and Capinera 1995; Blanco et al. 2014; Gutierrez-Moreno et al. 2020), the resulting FAW populations are highly resistant to insecticides, increasingly polyphagous, with high fecundity rates and migration abilities that enable them to invade entire countries in less than a year (Wan et al. 2021). Importantly, though, studies in Mexico and Central America suggest that FAW's significance as a pest is lesser in traditional maize agriculture compared to intensive maize agriculture (Carrillo Sanchez 1993; Bernal et al. 2015; Wyckhuys and O'Neil 2006). Some studies in Mexico suggested that FAW suppression in traditional maize systems may be due to the activity of natural enemies, from parasitoids and predators to endophytic bacteria, and that such suppression is increasingly weaker from maize's wild and landrace ancestors to modern, highly improved varieties (Takahashi et al. 2012; Bernal et al. 2015).

The challenge to control FAW in newly invaded areas is urgent since it has proven to be able to feed upon the main staple crops in many impoverished areas, such as maize, rice, and sorghum. Researchers around the world are working to develop management technologies, from chemical control to environmental and genetic manipulations to searches for host plant resistance, and biological control to manage FAW populations (Koffi et al. 2020; Tendeng et al. 2019; Abang et al. 2021; Nagoshi et al. 2018, 2019; Zhan et al. 2020; Chen and Palli 2021). It is clear that FAW management is a realistic objective, but not eradication, given the current extent of the pest's distribution, abundance, and dispersal capabilities. In this context, it will likely prove fruitful for researchers to look to Mexico and Central America where FAW is a long-standing, but often infrequent pest in traditional maize agriculture to understand the ecological mechanisms by which its populations are typically maintained at tolerable levels (Carrillo Sanchez 1993; Wyckhuys and O'Neil 2006).

25.4 Importance of Ancestral Pest Lineages as a Source of Natural Enemies and Phylogenetic History: An Example of the Cotton Boll Weevil

Cotton is the most widely grown and important fiber crop in the world (Khan et al. 2020). The most extensively planted species of cotton is *Gossypium hirsutum* L. or upland cotton, of which Mexico is considered one of its centers of domestication (Wendel et al. 1992; d'Eeckenbrugge and Lacape 2014). In contrast to maize, where domestication is evidenced by marked morphological transformations confirmed by archeological evidence, the processes and timing of domestication cotton in Mexico are largely unknown (Smith and Stephens 1971; Fryxell 1979; d'Eeckenbrugge and Lacape 2014). The oldest archeological remains of cotton are from the Tehuacán Valley, dated at 5500–4300 ybp, but consist of remains from fully domesticated plants (Smith and Stephens 1971). By the time of the Spanish conquest, cotton was widely cultivated by indigenous societies in Central, Southern, and Western Mexico and cotton cloth a highly prized commodity (Rodríguez Vallejo 1986; McCafferty and McCafferty 2000). Based on calculations of the quantity of tributes in cotton cloth and clothing received by the Mexicas (aka Aztecs) from their aligned city-states, 77,000 hectares would have had to be dedicated to the cultivation of cotton in Central Mexico (Rodríguez Vallejo 1986).

A variety of insect herbivores are found associated with wild and domesticated *Gossypium.* Of these, the cotton boll weevil, *Anthonomus grandis* Boheman (Coleoptera: Curculionidae), is one of the most important pests of cotton in the Americas (Fig. 25.1e). Historical, morphological, and genetic evidence indicate that the boll weevil that is presently a pest of cultivated cotton, *Gossypium hirsutum* L., originated in Southern Mexico and northern Central America (Burke et al. 1986; Jones 2001; Kuester et al. 2012; Alvarado et al. 2017). The boll weevil was apparently an established pest of cotton cultivated by indigenous pre-Hispanic populations as evidenced by the presence of a boll weevil in a dried cotton boll (fruit) in an archeological site in Oaxaca that dated to 900 AD by Warner and Smith (1968). However, the insect was only recognized as a pest at the end of the nineteenth century, when it first entered the United Sates and subsequently displayed its destructive potential throughout the cotton-producing areas of the south. It has subsequently invaded most cotton-producing areas of South America during the latter part of the twentieth century. More recently, a highly successful boll weevil eradication program with joint support from the federal government and cotton growers culminated in 2009 with the eradication of the boll from nearly all cotton-growing areas of the United States, except for a small region in extreme Southern Texas (Raszick 2021). However, the boll weevil is still a key pest of cotton in Mexico and Central and South America.

The boll weevil is not restricted to reproducing on *G. hirsutum* and has 11 reported wild host plants in Mexico (Sánchez-Reyes et al. 2022), including species from other members of the cotton tribe (Gossypieae) in the genera *Gossypium*, *Hampea*, and *Cienfuegosia* (Burke et al. 1986). Of these, the genus *Hampea*, and not *Gossypium*, is postulated to be the ancestral host plant of the boll weevil based on ecological and phylogenetic analysis of closely related weevil species (Fryxell and Lukefahr 1967; Burke et al. 1986; Jones 2001). Various morphological and phenological characteristics of species of *Hampea* may have led adaptations of the boll weevil that favored the exploitation of cultivated cotton. These include high flower bud production per trees which offers many oviposition and larval feeding sites but are limited to only 3 months of the year requiring survival of adults in a nonreproductive state during the remaining months of the year (Stansly 1985; Jones and Baro-Peruyero 2002). These conditions are comparable to that of cotton grown as an annual in monoculture.

Importantly, as expected of ancestral host plant lineages, more species of parasitoids of the boll weevil have been reported from wild host plants, in particular *Hampea* spp., than from all species of wild or cultivated cotton (Cate et al. 1990). The parasitoid, *Jalisco* (*Catolaccus*) *grandis* (Burks), a species collected from boll weevils on *H. nutricia* Fryxell and *Cienfuegosia rosei* Fryxell in Southern Mexico, showed promise as an effective control agent of the boll weevil in commercial cotton with several reported rearing techniques (Greenberg et al. 1995; Rojas et al. 1996). This species was also released in Brazil and has become part of the parasitoid guild attacking the boll weevil on cultivated cotton there (Ramalho et al. 2000). In addition, the association of *Hampea* with the boll weevil and other pests may have apparently resulted in the evolution of characters that effectively enhance the plant's resistance to herbivores, although these have received little attention (Cate et al. 1990; Jones and Baro-Peruyero 2002).

Wild host populations from Mexico have provided valuable genetic information concerning the population structure, migration history, and possible sources of colonization of the boll weevil in the United States, Mexico, and South America (Scataglini et al. 2006; Martins et al. 2007; Kuester et al. 2012; Alvarado et al. 2017; Marquesini et al. 2021; Raszick et al. 2021). The boll weevil consists of two distinct and diverse genetic lineages corresponding to distinct wild and domesticated host plants: the "eastern" and "western" lineages (Sánchez-Reyes et al. 2022). The "eastern lineage" includes populations known as the "cotton boll weevil" and is an economic pest of cotton in Northeastern Mexico, the United States, and South America. This lineage also reproduces on three genera of wild hosts, *Hampea* (*H. latifolia* Standley, *H. nutricia* Fryxell, *H. rovirosae* Standley; *Cienfuegosia* (*C. rosei* Fryxell, *C. drummondii* A. Gray) Lewton and wild *Gossypium* (*G. aridum* (Rose & Standley ex Rose) Skovsted*, G. hirsutum* L.) is found from southern Chiapas and the Isthmus of Tehuantepec north along the Gulf Coast of Mexico to Southern Texas (Sánchez-Reyes et al. 2022). The wild hosts of the "western lineage" are found exclusively on diploid species of cotton, *Gossypium* (*G. aridum* (Rose & Standley ex Rose) Skovsted, *G. hirsutum* L.) Skovsted. The *G. davidsonii* Kellogg, *G. harknessii* Brandegee, *G. hirsutum* L., *G. laxum* G. Phillips, *G. lobatum* H. Gentry, *G. thurberi* Todara, *G. turneri* Fryxell occur along the western Pacific Coast into Arizona and Baja California Sur (Sánchez-Reyes et al. 2022). This lineage was originally thought to only utilize the wild host, *G. thurberi* as a host plant in Northern Arizona and Northern Sonora, but recent genetic studies of populations from various host plants in Mexico and Arizona indicate that there are not sufficient genetic differences between those on wild and cultivated cottons (Alvarado et al. 2017; Raszick et al. 2021). Both the eastern and western lineages of *A. grandis* display higher genetic diversity and strong population structure within each lineage on wild host than when compared to populations of cultivated cotton (Alvarado et al. 2017). Genetic studies have confirmed the expected sources and diversity of the relatively recent mid- to late twentieth-century spread in the continent. As expected, South American populations have very low genetic diversity, as would be predicted from a recent founder event (Martins et al. 2007; Marquesini et al. 2021). Importantly, haplotypes in Brazil were found to be closely related to boll weevil populations from Northeastern Mexico and Southern Texas, the site of the original founder event of the expansion into the southeastern United States (Marquesini et al. 2021).

While the idea of conserving "pests" may seem counterintuitive, the preceding examples highlight how ancestral pest lineages on wild host plants can provide important information of how and why certain insects become pests, the diversity and ecology of their original natural enemies, and the genetic diversity that arose with and differentiated on wild and cultivated host plants. The most practical approach to preservation of these important ancestral insect lineages and their associates is through in situ conservation of their host plants. In the case of the boll weevil, all wild species of their *Gossypium* host plants and one species of *Hampea* (*H. montebellensis*) are officially listed within a protection category by the Mexican government (Jones et al. 2018; CONABIO 2021; SEMARNAT 2010). One important conservation initiative of wild cottons is through the Commission for the Knowledge and Use of Biodiversity (CONABIO 2021), which leads the "Cotton genetic diversity and conservation program" and finances various research and conservation projects (Wegier et al. 2009; CONABIO 2021). Also, in situ conservation is sustained by both indigenous groups and through government programs. Semidomesticated populations of *G. hirsutum* and *G. barbadense* are maintained by several Huichol indigenous groups in Nayarit and other local groups in Oaxaca (Pérez-Mendoza et al. 2016). A number of botanical gardens in Mexico preserve accessions of the *Gossypium* sp. in Southern Mexico, in particular a government-maintained garden located in Iguala, Guerrero State, which has the largest collection of living native wild cottons (Pérez-Mendoza et al. 2016). There are presently no conservation initiatives for species of *Hampea* or *Cienfuegosia rosei*.

25.5 From Biological Control Agent to Insect Pest: The Cactus Moth, *Cactoblastis cactorum*, a Potential Exotic Invasive of Prickly Pear Cactus on the US-Mexico Border

Mexico is the center of origin and diversification of prickly pear cacti "nopal" (*Opuntia* spp.). The country has 93 species of *Opuntia*, of which 62 are endemic (Scheinvar et al. 2020). Opuntias are tightly linked with Mexican culture given a prominent place at the center of the origin mythology of the Mexican people and even depicted on the Mexican national flag and government seal. These cacti are often a dominant species and provide an important habitat for hundreds of species in arid and semiarid lands, which cover ~three million hectares in the country (Soberón et al. 2001). Also, since their fruits (prickly pears or "tunas") and cladodes ("nopalitos") are widely consumed, there were ~13,000 cultivated hectares in 2019. As for all native crops, Opuntias have evolved with a variety of herbivores that each year consume some of their tissues. There are >30 herbivores associated with Mexican *Opuntia*, but only a few are regarded as pests, particularly in cultivated conditions (Rocha-Flores et al. 2017). The prickly pear weevil, *Cactophagus spinolae*, and cactus webworm, *Loxomorpha flavidissimalis* (Grote), are considered to cause agricultural losses (López-Martínez et al. 2016; González-Hernández et al. 2019).

A new cactus pest has appeared in North America, an erstwhile beneficial insect converted to an insect pest through human error. This is the cactus moth, *Cactoblastis cactorum* (Berg) (Fig. 25.1f), which is endemic to South America (Argentina, Brazil, Paraguay, and Uruguay) where it feeds on native species of *Opuntia*. It was introduced to many countries as a biocontrol agent of exotic invasive species of *Opuntia*. The outcomes of such introductions were clear successes in biological control, as *C. cactorum* is a voracious herbivore and reduced the abundance of invasive species of *Opuntia* in Australia and South Africa to levels that they are no longer problematic (Raghu and Walton 2007). Because of these initial successes, *C. cactorum* was introduced for control of *Opuntia* to the island of Nevis in the Caribbean in the 1950s. Probably because of hurricane activity in the region, it subsequently invaded most of the adjacent islands (Andraca-Gómez et al. 2015) and in 1989 was later found in Florida (Pemberton 1995; Johnson and Stiling 1998).

With the report of the cactus moth in Florida, alarms were raised in the United States, and especially in Mexico, given its 2000 km shared border with the United States. A bilateral strategy was put in place to stop *C. cactorum* from invading the southern United States beyond Florida. This included constant field surveillance in the Southern United States and the use of Sterile Insect Technique (SIT) technology (Hight et al. 2005; Carpenter et al. 2001). This strategy slowed the pace of invasion for several years, but production and release of sterile insects were recently suspended, and *C. cactorum* larvae were subsequently spread westward and found in four counties south of Houston, Texas, in 2021 (Texas Entomology 2021). Additionally, *C. cactorum* was recorded on *Opuntia* on Isla Mujeres, off the coast from Cancún in 2008, and considerable effort was made to successfully eradicate it from the island.

The occurrence of the prickly pear moth near the northern Mexican border and in the Caribbean is ominous. In the north, it continues to spread southward through Texas, which suggests that an invasion of Northern Mexico is imminent. Additionally, the likelihood of future *C. cactorum* invasions along Mexico's southeastern coast from populations in the Caribbean is also high, due to the current increased hurricane activity of the region (Andraca-Gómez et al. 2015). In response, the Mexican government established a surveillance network of traps along the coasts of the states of Yucatan and Quintana Roo in order to have an early alert system in place when *C. cactorum* arrives, though a more aggressive plan is needed in order to stop any invasion once the moth arrives. The repercussions of a *C. cactorum* invasion of inland Mexico could be devastating since, as noted above, *Opuntia* represents a fundamental component of the biodiversity of arid ecosystems of Mexico and an important cultivated food resource that is intricately linked with Mexican culture.

25.6 Conclusions

The "New Pangea" is a metaphor that compares past geological events to the present to conceptualize the global processes occurring in the Anthropocene (Rosenzweig 2001; McKinney 2005). This metaphor promotes the idea that the present biosphere is comparable to the time when Pangea was the single massive continent of the Earth more than 250 million years ago. The difference now is that the biological connections within "New Pangea" are not geographical but the result of human transport of organisms which has broken down the barriers among the present distinct biogeographic realms of the world. The consequence of this loss of barriers is an increasing worldwide homogenization of the biosphere composed of a reduced number of favored species, adapted to similar and simplified human-dominated habitats (McKinney 2005).

The process of homogenization had its earliest beginnings in the regional centers of crop domestication when a select few plants were favored and cultivated. In the examples presented herein are insects associated with the plants under domestication in the Mexican region and were those favored and genetically adapted in tandem with the genetic modifications of the cultivated plant. They also followed the population expansions of their hosts to new regions in the New World. For the corn leafhopper, this process allowed for a highly specific plant herbivore previously restricted in its distribution to that of its native host plant, teocintle, but with important favorable adaptations, favoring its expansion of its range and populations on teocintle's descendent, maize, which has been cultivated far beyond the insect's prior distribution. For the fall armyworm, its dispersal capabilities combined with its adaptation to crops grown increasingly in monoculture, particularly maize, set the stage for a twenty-first-century invasion of vast areas of Africa, Asia, and Australia in a mere 5 years. Hopefully this scenario will not play out with introduction of the cactus moth, *Cactoblastis cactorum*, into North America. In this case, its present spread is one of blatant human errors and lack of understanding of the reproductive potential of an insect herbivore. The importance of this pending disaster to arid ecosystems of North America needs to be prioritized again, and control measures increased after the initial alarms were sounded during that start of the twenty-first century. Finally, the scenario of the corn leaf hopper and the boll weevil and their ancestral host plants highlight the value of preserving ancestral pest-host plant lineages in situ in order to better understand the origin and evolution of crop pests and also to preserve possible innovative-, biological-based management options in the future.

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Chapter 26
The Potential of the Parasite Fauna as an Indicator of Ecosystem Health in the Anthropized Environments of Mexico

Norma Hernández-Camacho and Salvador Zamora-Ledesma

Contents

26.1 Introduction: Parasites Are Important to Ecosystems

Before discussing the potential of parasite fauna as possible indicators of environmental quality in Mexican ecosystems, it is necessary to understand the importance of this ecological relationship. Considering that, for each species of free-living organism that exists in a community, there must be at least one species of parasite, that all living beings have been parasitized at some time during our life cycle and that the oldest evidence of parasitized organisms date back to the Middle-Upper Devonian (Poulin 1999; Lucševics et al. 2009; Goater et al. 2014), it can be established that parasitism is one of the most abundant and oldest forms of life history strategies on the planet. Parasitism is a complex ecological relationship characterized by tolerance and often cospeciation between both parasite and host.

Parasites are relevant to the biodiversity of ecosystems, and adequate faunal inventories targeting the identification of these organisms could increase the species richness of communities globally by more than 50% compared to current data. Such

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N. Hernández-Camacho (✉) · S. Zamora-Ledesma
Universidad Autónoma de Querétaro, Faculty of Natural Sciences, Queretaro, Mexico
e-mail: norma.hernandez@uaq.mx

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_26

an effort would have a direct effect on the tally of global species richness but would invariably vary depending on the characteristics of the area and the ecological and biogeographical variables of the biological communities of the region, as well as the human activities that take place there (Lafferty 2012).

Unfortunately, parasites have been underestimated in ecological studies of biological diversity and ecosystem functioning at the global level (Poulin 1999; Lafferty et al. 2006; Lafferty 2012). Parasites, by definition, are organisms that survive at the expense of another, normally without causing their death (Poulin 1998; Goater et al. 2014), since, for parasites, the host is the main habitat. To understand the parasites integrally, it is essential to know the biological and ecological history of its hosts. Diverse and interacting host characteristics, such as body size, life cycles, types of feeding, or width in the distribution areas, can modulate the colonization-extinction rates of parasites, which can result in an increase or decrease in the diversity of these organisms at different spatial scales (Watve and Sukumar 1995; Poulin 1999; Poulin and Morand 2000; Buckling and Rainey 2002; Poulin 2004; Harris and Nunn 2010; Rudolf and Lafferty 2011).

Parasites are considered as regulators of the populations of their hosts, and they have a direct effect on the composition and structure of biological communities (Dobson and Hudson 1986; Frank 1993; Combes 1996; Thomas et al. 2000; Moritsen and Poulin 2005). Parasites influence all levels of the food web of the communities where they are found, often exceeding the regulatory effect and biomass of top predators. They are capable of modifying the behavior of their hosts in order to continue their life cycle through various strategies. These include encouraging predation of intermediate hosts by definitive hosts, either by physical limitations caused by the parasites themselves such as injuries that modify their movement, which increases the probability of predation, or by hormonal and neurological modifications that cause a loss of fear and attraction toward predators or definitive hosts. They can also intervene in affecting the evolution and variation in mating and reproductive systems as some may increase host reproductive rates prior to host castration, to mention a few examples (Lafferty 1999; Poulin 1999; Poulin and Morand 2000; Lafferty et al. 2006, 2008; Lindenfors et al. 2007; Barber and Dingemanse 2010; Harris and Nunn 2010; Patterson and Piertney 2011; Goater et al. 2014).

However, the hosts, in turn, have developed intra- and interspecific strategies for population control of their parasites, which can cause a dilution effect of the presence of parasites in the communities, which, collaterally, creates the illusion that parasites do not play a relevant role in ecosystems. However, they are present, and their effect is quite important. An example of this is observed in the transmission process of parasites, which can be complicated because of the physical distribution, the relative abundance, and the physical state of the hosts. Therefore, the parasites can only be found in certain age ranges of their hosts. This results in a proportion of the hosts, mainly those with a weakened immune system, having a more diverse and abundant parasitic load when compared with other hosts of the same species, which, due to the characteristics of their spatial ecology, may present a less diverse and less abundant parasite load (Smith 1996; Goater et al. 2014). These contrasts in parasite loads occur as a response to the ecological adaptation of the hosts to the environment, which will be reflected in the strength of their immune system, which constitutes an important barrier for the establishment of parasites in this habitat-host. This situation occurs at different stages of their life cycle, involving different types of hosts, which has a direct effect on the composition of the community where they are found (Smith 1996; Goater et al. 2014).

One of the most important anthropogenic disturbances of the parasite-host systems is the introduction of invasive hosts and parasite species, which affects both parasite and hosts. In the case of exotic invasive parasites, native parasites must compete with the new parasite species and can often end up eliminated from the system. This extirpation is especially true for specialist parasites, which results in only generalist parasite species with simple life cycles surviving within the community, often being dominated by the exotic species (Dobson and Hudson 1986; Watve and Sukumar 1995; Poulin 1999; Lafferty 1999; Thomas et al. 2000; Buckling and Rainey 2002; Moritsen and Poulin 2005; Rudolf and Lafferty 2011; Lafferty 2012).

Thus, the introduction of exotic parasite species usually causes a decrease in the parasitic diversity of the community. In the case of hosts, the introduction of a new parasite can be catastrophic because the host population has not had previous exposure to development sufficient immune defenses to the novel parasite population. This situation has the potential to produce an epizootic (a term synonymous with epidemic in humans), increasing the mortality rate of the hosts, which can put the trophic stability of the entire ecosystem at risk. There are several historical cases of such occurrences including the extinction of endemic birds in Hawaii due to the introduction of birds carrying avian malaria or the decrease in lion populations in the Serengeti due to infection with distemper from domesticated dogs. In this latter case, this decrease resulted in a trophic cascade leading to an increase in the populations of hyenas (*Crocuta* sp.) and wildebeest (*Connochaetes* spp.), causing further impacts in other animals and plants within the trophic structure (Dobson and Hudson 1986; Watve and Sukumar 1995; Poulin 1999; Lafferty 1999; Thomas et al. 2000; Buckling and Rainey 2002; Moritsen and Poulin 2005; Rudolf and Lafferty 2011; Lafferty 2012).

For a certain parasite species to exist, it is necessary that the environmental conditions and specific intermediate hosts exist to fulfill the life cycles of the parasites, ensuring the permanence of these species within the system. Therefore, if any part of the parasite's life cycle is disturbed due to habitat loss and/or fragmentation, then the possibility of extinction of this parasite species would increase, having a negative effect on the ecosystem functionality (Pence 1990; Hudson et al. 2006; Palm and Rückert 2009; Goater et al. 2014). This situation is quite common in ecosystems at a global level as a consequence of the high degree of human disturbance, which has caused a decrease in parasitic diversity. This decrease as generalist species of parasites is mainly being recorded, which have direct life cycles with a great variety of paratenic (transport) hosts that allow them to ensure their passage between the trophic levels of the ecosystem to reach their definitive host (Poulin and Morand 2000; Luque 2008; Lafferty 2012).

26.2 Discovering the Indicator Potential of Parasites for the Health of Ecosystems

The concept of sentinel species of the health of ecosystems forms the basis for one of the methodological proposals to identify, quantify, prevent, and mitigate the negative effect of habitat and biodiversity loss due to human activities in natural environments. Depending on the user's objective in using the methodology, it is possible to select the aspects to be evaluated, which can be of a biological or ecological nature that indicates and identifies types of human impact (Rapport et al. 1998; Kremen 2005; Burger 2006; Alonso-Aguirre 2009; Müller and Burkhard 2012).

A wide variety of studies on sentinel species have been used to assess the health status of ecosystems. Some of these are capable of efficiently signaling the presence of toxic substances in the air and on the ground and in marine and inland waters (Mussali-Galante et al. 2012; Tovar-Sánchez et al. 2012; Bossart 2006; Rombouts et al. 2013) or to give an alarm signal in the case of epizootics in wildlife or possible zoonosis of risk to human health (Alonso-Aguirre 2009; Alvarado-Esquivel et al. 2012).

The indicators established for monitoring the health of ecosystems, including sentinel species, must meet three characteristics to be considered efficient (Burger 2006): (1) biological relevance, which gives early warning, with rapid response to stress, with measurable changes both at the level of organisms and through the food web; (2) methodological relevance, being easy to measure in the field and to analyze and interpret which can be tested in a short time at low cost; and (3) social relevance, of interest to the general public due to their cost-efficiency or complementary to other indicators, especially public health. If any of these three aspects are not fulfilled, this possible indicator would not serve as such (Bauler 2012).

Species of specialist parasites with complex life cycles have the greatest potential of meeting the three requisites of a sentinel species. This is because they have different and complex life cycles which put them in contact with different trophic levels of the system and in different physical environments (Fig. 26.1). Therefore, the presence of these specialist species in an ecosystem can serve as indicators of the state of both abiotic variables (e.g., physicochemical parameters of the habitats where the intermediate hosts are located) and biotic variables (abundance of intermediate hosts). Likewise, when ecosystems present a certain degree of disturbance, this, in turn, will be reflected in the composition of the parasitic communities. This leads to the next question: what is then the relationship of parasites with the health of ecosystems?

A healthy ecosystem will be defined in this study as one that presents a stable and diverse parasitic community, made up of species with both simple and complex life cycles that involve several species of intermediate, paratenic, and vector hosts, which, in turn, are directly related to the biological diversity of the ecosystem at the different trophic levels. In contrast, an unhealthy ecosystem is one whose parasitic community is impoverished, mainly with direct cycle, generalist species, which may be at risk of causing epizootics or zoonoses. Because these generalist species

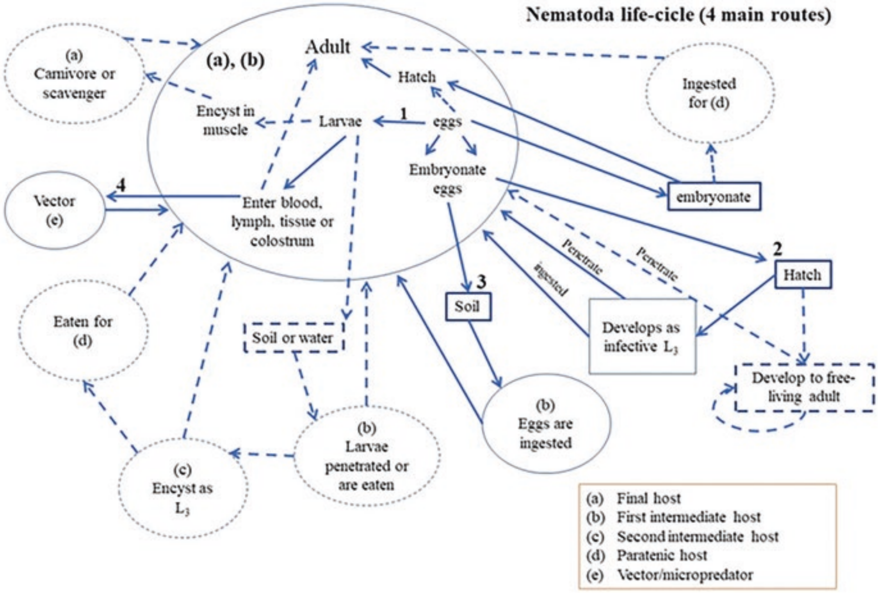

Fig. 26.1 A generalized example of the life cycle of a nematode, including different stages in water or soil, with first and second intermediate host and with vector/micropredator (based on Goater et al. (2014))

have a wide range of definitive hosts, often including humans, this will allow them to survive in disturbed environments and also present greater risk of zoonosis for the human population given the greater probability of contact between humans and these parasites. This last aspect is important for the concept of health of the ecosystems where the well-being of humans is considered an integral part of the overall system (Pence 1990; Lafferty 1992, 2012; Combes 1996; Daszak et al. 2000; Hudson et al. 2006; Palm and Rückert 2009; Goater et al. 2014; Vidal-Martínez et al. 2009; Costa et al. 2012; Merlo et al. 2010; Shea et al. 2012).

26.3 What Remains to Be Done?

The study of terrestrial vertebrate metazoan parasite fauna in Mexico has a history of almost a century; however, it is estimated that only 21% of the total number of vertebrate species in the country have been studied so far (1145 recorded species out of 5488), with the mammalian group being one of the least studied with 121 host species out of 535 species recorded (Pérez-Ponce de León 2001; Pérez-Ponce de León and García-Prieto 2001; Pérez-Ponce de León et al. 2011). Unfortunately, these data reflect the trend in the information obtained on terrestrial vertebrate parasite fauna worldwide, because of the bias between the interest in such studies, the biological properties of each host taxa, the type of habitat and its accessibility, and the conservation status and legal access of the species to be studied (Poulin 2014), to name a few.

This information gap for a megadiverse country like Mexico not only has importance for purely biological data, such as the richness and diversity of parasite species and their hosts, but also has relevance to human health and strategic decision-making in Mexico considering the potential risk of vertebrate to human transmission of parasites (Bush et al. 2001; Poulin and Morand 2000; Sarukhán et al. 2009; García-Prieto et al. 2012; Hernández-Camacho et al. 2012). It is essential to have a formal, intensive, and comprehensive monitoring of the parasitic communities of wildlife in the country, from simple and rapid fauna lists and indirect methods, such as coprological analysis. These in turn can serve as the basis of more complex and long-term ecological studies that evaluate the consequences of habitat fragmentation in the changes occurring in the natural role of diseases and parasites as regulatory factors of wildlife populations. Critical to these studies is the inclusion of the role of feral and domestic animals in the disease transmission at the wildlife-human interface. Such studies will help understand the ecological dynamics of parasites in the medium and long term and develop and apply a series of strategies of ecological preventive measures and in the identification of important zoonotic risk areas.

One of the most relevant environments for the medium- and long-term study of parasitic communities in wildlife and their interrelation with humans and domestic animals is the immediate area surrounding cities, called the metropolitan area. Due to the physical characteristics of the conurbation, such as the presence of means of communication and infrastructure, it is considered as a functional continuum that connects the main urban settlement, the city, with areas in different degrees of development located in its periphery. These may present fragments of the natural habitat in different degrees of fragmentation due to human activities (GEO 2008). With its physical heterogeneity, the metropolitan area has the potential to host a great diversity of wild mammals and species that are tolerant to habitat fragmentation and human presence, which, together with their parasitic load, will therefore have a greater probability of encountering humans and their domestic animals (Daszak et al. 2000).

In Mexico, principally in the rural areas that are in the conurbation of cities, domestic animals, mainly dogs and cats, may have greater freedom of movement than their urban counterparts. In extreme cases, they may return partially to the wild and not depend on a human for their maintenance. When this happens, domestic dogs and cats become feral animals and resume their predatory behavior, producing a phenomenon called intra-guild competition, where these domestic carnivore species compete for the same food and cover resources as wild carnivores. Feral populations may become so large as to result in the extirpation of one or more competing wild carnivore species, generally meso-predators of smaller size, such as the gray fox (*Urocyon cinereoargenteus*), the wildcat (*Lynx rufus*), the raccoon (*Procyon lotor*), or the ringtail (*Bassariscus astutus*). These meso-predators play a very important role in the regulation of these ecosystems disturbed by human activities, due to the historical extirpation of larger apex predators (Lenth et al. 2008; Vanak and Gompper 2009; Reed and Merenlender 2011; Young et al. 2011; Hughes and MacDonald 2013).

Meso-predators such as gray fox (*Urocyon cinereoargenteus*), coyote (*Canis latrans*), skunks (*Mephitis* spp.), or ringtails (*Bassariscus astutus*) participate in maintaining the functionality of ecosystems since they are involved in various ecological processes such as seed dispersal and regulation of the demography of prey species or in the distribution and abundance of other meso-predators. Likewise, they participate in the nutrient cycle by feeding on decomposing organic matter and in the cycles of parasites of other animals, including humans (Morrison et al. 1992; Bender et al. 1998; Buskirk 1999; Miller et al. 1999; Woodroffe 1999; Sunquist and Sunquist 2001; Crooks 2002; Gehring and Swihart 2003; Alonso-Aguirre 2009; Prough et al. 2009). The competition of wild carnivores with domestic and feral species has a negative effect on the survival of these meso-predators, which will increase the probability of parasite transmission to domestic and feral fauna as a consequence of the loss of richness and abundance of potential hosts, since it is precisely the greater diversity of wildlife that creates a "dilution effect" and decreases the possibility of dangerous zoonotic events occurring in humans (Hudson et al. 2006; Johnson et al. 2008; Tompkins et al. 2010).

In Mexico, case studies of zoonotic diseases have generally been approached from the epidemiological point of view, mainly in the human-domestic animal sphere (Nava-Cortés et al. 2015; Rubio-Robles et al. 2015), whereas for wildlife parasitofauna, studies of ecology are relatively scarcer (Suzán-Azpiri and Ceballos-González 2005; Hernández-Camacho et al. 2012). In the last decade, studies by Hernández-Camacho and López-González (2009), Hernández-Camacho and Pineda López (2012), Hernández-Camacho et al. (2011, 2012) with parasites of wild canids in the fragments of low deciduous forest located south of the metropolitan area of the City of Querétaro have generated information that differs notably from what is mentioned in the international literature on the parasite fauna of two species of wild carnivores, the gray fox and the coyote. In these fragments, the presence of generalist species of parasites is constant in both species of canids with a notorious absence of certain groups of parasites with complex life cycles such as trematodes or acanthocephalans. This situation has not been reported in Canada and the United States, even in populations of metropolitan areas (Hernández-Camacho et al. 2016). Considering this, it is possible to establish sentinel ecosystem health monitoring programs using parasite-host systems for early detection of alterations in ecosystems.

This situation with the parasite fauna of wild canids in Querétaro raises more questions of a biological nature: why is the diversity of parasites of these carnivores so low in a megadiverse country like Mexico? Although the coyote (*Canis latrans*) is considered the species of carnivore with the greatest diversity of parasites in the United States, with more than 100 registered species (Harris and Nunn 2010) here in Mexico, it only has 2 species of parasites formally registered so far (Hernández-Camacho and Pineda López (2012); García-Prieto et al. 2012). Why is there greater diversity in a more temperate northern environment, than one located in the tropics which contradicts the general notion of a latitudinal gradient in biodiversity (Pianka

1966; Willig et al. 2003)? This is a key question in medium- and long-term studies with the parasite fauna of wildlife, mainly because we live in a changing world, due to the effect of climate change, which has a direct effect on the presence, absence, aggressiveness, dispersion, transmission, and host specificity of the parasites (Brooks and Hoberg 2007). If action is not taken promptly, important zoonotic epidemics could occur that could have been prevented in advance if the characterization of the parasitic communities of wild and domestic-feral fauna was more thoroughly known. The training of human resources dedicated to working with the parasitofauna of Mexico is a necessity and a very urgent one. We need basic information on the richness and abundance of parasites as well as applied studies regarding where and when we can expect the next pandemic. Hopefully, we have learned from the experience through the impact of COVID-19.

26.4 Conclusions

The formal study of parasitic communities in a megadiverse country like Mexico should form part of the country's National Strategic Programs of the National Commission of Science and Technology (*Los Programas Nacionales Estratégicos del Conacyt*), since knowledge of these species and their communities are basic for understanding the functioning of Mexico's diverse ecosystems and the development of future prevention, control, and eradication strategies of emerging diseases. At present, there is not enough information to be able to do so. Furthermore, this should be approached in a multidisciplinary way, both in the field and in the laboratory, to obtain as much information as possible from the biological, ecological, veterinary, and human points of view, before it is too late.

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Chapter 27
Citizen Science for Deep Ocean Biodiversity: A Crowdsourcing Tool in Support of Conservation

Elva Escobar-Briones and León Felipe Álvarez-Sánchez

Contents

27.1 Introduction

Engagement of students, stakeholders, and the public allows collection of data with more geographic coverage, to document ecological patterns and address ecological questions relevant to shifts and trends in species from stressors (Chandler et al. 2017). Citizen science contributes to science by collecting data on distribution and abundance of species and biodiversity monitoring among other activities. This volunteer work helps to inform the policymakers and significantly expands the spatial and temporal scale of knowledge (Consoli et al. 2020).

E. Escobar-Briones (✉)
Laboratorio de Biodiversidad y Macroecología, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: escobri@cmarl.unam.mx

L. F. Álvarez-Sánchez
Unidad de Informática Marina, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

R. W. Jones et al. (eds.), *Mexican Fauna in the Anthropocene*,
https://doi.org/10.1007/978-3-031-17277-9_27

Citizen science strengths have been recognized by Earp and Liconti (2020) who mention that these extend across the scientific and human science frontiers. They cite the "many eyes hypothesis" related to the effectiveness of producing biodiversity data across time and space scales. Community engagement may promote advocacy of conservation actions and policies and advancement of science instead of opposing to them. They recall how participants connect and increase their understanding with nature and how their opinions on anthropogenic threats to marine life and on research and policy grow with an enriched literacy and enhanced awareness.

Marine citizen science has grown popular over the past decades. Earp and Liconti (2020) recognized in their survey on citizen science initiatives that national marine programs represent 53.3%, which select mainly coastal ecosystems, usually focusing on fish, and training is provided in 64.2% of the projects among many other activities. Monitoring through engagement with the public with increased social acceptance may lead to conservation in the long term.

27.2 Generalities of Citizen Science for Deep Ocean Biodiversity

The advancement of scientific knowledge has recognized that biodiversity plays an important role in providing ecosystem services (Luypaert et al. 2020) although those which humans derive from the deep ocean are less understood. The increasing activities and use of the ocean in the Anthropocene, distant from the coastal ocean and deeper from the ocean surface, have generated stressors leading to changes and loss of the marine diversity and the destruction of habitats. How to assess and monitor these changes in the vastness of the deep ocean poses challenges to scientists and defies innovation on how to stop this trend of devastation and in turn, renovate and conserve these critical ecosystems. Better understanding of the marine biodiversity is needed to recognize these changes early (Scholes et al. 2017).

"Community engagement," "citizen science," and "participatory science" are terms used to define the involvement of an extended observing community of stakeholders, students, or public in scientific research relying on these as observers, data collectors, and contributors and monitoring ocean processes, ecosystems, and its biodiversity (Chandler et al. 2017). Involving citizens to opportunities of doing science has proven valuable. Engaging traditional knowledge to science is still a challenge for conservation and its decision-making (Escobar et al. 2021). Integrating research and exploration to citizen science through well-planned strategies and commitment may contribute to literacy, prosperity, and well-being of the communities (Levin et al. 2019). Not only science is benefited with an early involvement of citizen science but also monitoring key ecosystem services preferred by societies and meaningful indicators to support decision-making that allows for speedier adoption of conservation frameworks in practice (Balvanera et al. 2017).

Biodiversity monitoring has had a tradition of citizen observers that have expanded the knowledge in coastal ocean biodiversity. This is not the case for the deep ocean.

Real-time documenting of habitats and its diversity has accelerated with the advent of cabled ocean observatories, the use of remote observing technology, and the involvement of nonprofessionals in scientific research. Stakeholders have become an important voluntary, conventional approach for collecting data on marine ecosystems' key species in a standardized manner. Their participation may increase the understanding of the effects of stressors on marine life and ecosystems in the next decades. Among the activities that citizen science and crowdsourcing have contributed to deep ocean biodiversity is by having public access and engagement with the ocean sciences community through annotations of video, images, and sound from recorded materials in cruises or broadcasted live through telepresence with the use of remote observation vehicles or with cabled observatories (Hoeberechts et al. 2015).

27.3 Trends of Recent Change in the Context of Mexico

The Workshop on Biodiversity Citizen Science in Latin America organized by CONABIO and held in Mexico City in 2018 communicated basic information on biodiversity citizen science initiatives and described progress, challenges, and opportunities of the existing initiatives (Tello 2018). The citizen science initiatives in support of the deep ocean biodiversity are missing in the report creating a gap that should be considered in future workshops.

The citizen science programs and initiatives are absent in the structure of consortia that carry our long-term projects such as the multi-institutional CIGoM CONACyT-SENER consortium that despite its multidisciplinary and multiyear coverage reported technical descriptive information from the deep Gulf of Mexico. This basin has been studied for decades by international collaborative cruises in the Mexican Exclusive Economic Zone (EEZ), by both foreign and national scientists. The deep ocean ecosystems are only referred in peer-reviewed publications, reports, and outreach webinars; however, the citizen science programs are a pending action.

The Ocean Exploration Trust, the Schmidt Ocean Institute, and the NOAA's telepresence live broadcast have engaged scientists, students, and the public in a real-time exploration experience of the deep ocean ecosystems and biodiversity (Gallaudet et al. 2020). Telepresence has a global-scale coverage and impact. The Revillagigedo Archipelago exploration was live broadcasted to the public (Raineault et al. 2018).

An exception to all other collaborative cruises to National Parks and Biosphere Reserves is that a wiki educational tool, the Morphotype Atlas of the Abyssal Megafauna in the Revillagigedo Archipelago in the Eastern Tropical Pacific, offers a citizen science initiative (Álvarez-Sánchez et al. 2019). This platform is available at UNAM's UNINMAR open access site (http://uninmar.icmyl.unam.mx/mmaar/index.php/P%C3%A1gina_principal); citizens need to contact UNINMAR coordinator directly for access. Its growth relies on volunteer work, fundamental for identifying the seafloor habitats and taxonomic diversity. The ongoing wiki platform offers advantages to traditional science. The wiki platform is defined as a collaborative tool with an open-editing system, allowing to contribute and modify the

Fig. 27.1 Deep ocean pelagic and benthic specimens and seafloor habitats from Mexican locations. From left to right, top row: jellyfish; Siboglinidae tubeworm, genus *Riftia*; and brittle star on deep water coral. Bottom row: sponge, subclass Hexasterophora; sea urchin, class Echinoidea; and Siboglinidae tubeworm, genus *Oasisia*. (Source: Ocean Exploration Trust, Inc. https://nautiluslive.org/)

contents facilitating citizen science contributions (Parker and Chao 2007). One of these is the larger involvement of expertise in generating biodiversity records across phyla and the habitats where they occur. It offers capacity development and student training by integrating the scope of other disciplines in biology, ecology, and oceanography in addition to general knowledge. We implemented the use of the wiki platform to develop a crowdsourcing and a citizen science tool with an illustrated guide to recognize the morphotype diversity of megafauna occurring in abyssal habitats in the National Park and Biosphere Reserve Revillagigedo Archipelago by using the free software and information and communication technologies, MediaWiki (MediaWiki 2018). This wiki platform grew the interest of undergraduate students that annotate the geomorphology of the deep seafloor in Revillagigedo, habitats to many deep ocean benthic taxa (Álvarez-Sánchez et al. 2019).

The Morphotype Atlas of the Abyssal Megafauna in the Revillagigedo Archipelago uses video data as a tool obtained from the live video recording from ROV cameras on the seafloor (Fig. 27.1). During the telepresence live broadcast, audience participation in the deep ocean expedition engaged high school, undergraduate, and graduate students, teachers, scientists, and the general public with the deep ocean ecosystem extending the interactions from the ship and the seafloor directly into the classrooms. This initiative pursued public interest in scientific discovery. Asynchronous learning materials were shared with the educational audiences. The archived digital video offers advantages to the Morphotype Atlas of the Abyssal Megafauna in the Revillagigedo Archipelago initiative of being readily accessible and editable at distance from the personal computers (http://uninmar.icmyl.unam.mx/mmaar/index.php/P%C3%A1gina_principal). It was an excellent project during the COVID-19 restriction providing students incomparable possibilities to explore the deep ocean biodiversity in a poorly documented National Park and Biosphere Reserve of Mexico.

27.4 Analytical Tools and Methods that Allow Its Evaluation

The deep ocean remains as the one of the least studied environments due to its vastness, remoteness, costly accessibility, and lack of scientific knowledge. The many decades of exploration and research have generated large deep ocean environmental data, image, and video databases and recently sound recordings. However, very few are available online for crowdsourcing. The identification of deep ocean organisms has been an obstacle as it is difficult and requires the participation of experts, with support of genetic tools, the availability of guides, and capacity development. Many are new species to science and endemic to particular habitats.

Telepresence is among the tools and methods used in citizen science initiatives with outreach events and ocean literacy material that help increase the knowledge of the deep ocean biodiversity, attract the attention of school children and local communities and emphasize its importance to the well-being of the society.

New Artificial Intelligence and Machine Learning tools and platforms under development by the Challenger 150 UN Ocean Decade program (https://challenger150.world/) seek to make identification quicker, easier, and automatic while working at sea. It is here that virtual citizen scientists' initiatives are timely. The help needed to educate computers/software from a distant office, classroom, or home with counting, identifying, and validating the diverse taxa on videos was exemplified through the Zooniverse volunteer's efforts in the Seafloor Explorer international initiative in a fishery program (Earp and Liconti 2020).

Wiki-like platforms such as the Atlas of Morphotypes of the Abyssal Megafauna of the Revillagigedo Archipelago are widely used in teaching poorly known topics or absent in the educational curricula, for their ability to collaborate and interact with multiple users while learning. Wiki platforms have not been used to disseminate the exploration of the deep ocean. The platform allows to enter, identify, and share material that will be classified by experts and can work as an educational prototype tool. The video and image material, obtained along exploration transects with a ROV, was shared by the Ocean Exploration Trust from a joint exploration cruise with UNAM carried out in 2017 (Raineault et al. 2018). This participatory science initiative is a first step to increase the inclusion, equitability, and accessibility, as it allows participants to contribute by identifying and classifying abyssal fauna in this virtual platform and to deep ocean literacy. This program has inspired the general public, helping them understand what lives in the 95% of the vastness of the distant, dark deep ocean which is virtually inaccessible to humans. This is especially important for people living in high altitude cities, the desert, or even those along small coastal communities where access to specialized education is difficult.

Among the crowdsourcing and citizen science initiatives, the iNaturalist offers volunteers to find projects (Mazumdar et al. 2018) and to use Machine Learning Assisted Image Annotation methods (Zurowietz et al. 2018) that could be of great support to the underwater image training database for ocean exploration and discovery of FathomNet (Boulais et al. 2020). Crowdsourcing has benefited from the wiki pages, web apps, or social media that have enabled data analysis by online contributors, which is in the initial stages for the deep ocean (Matabos et al. 2017).

Citizen science through the Atlas of Morphotypes along with other initiatives such as the iNaturalist in CONABIO can change these educational breeches and understanding gaps in Mexico. The ROVs and the telepresence efforts are people's eyes of the twenty-first-century and the next explorers sharing globally in real time. UNINMAR and CONABIO are currently working on a deep ocean immersive virtual reality initiative that depicts the hydrothermal vents in the Guaymas Basin, another deep ocean protected area in an ecologically and biologically significant marine area in Mexico.

Volunteer citizen science activities can support researchers and decision-makers. Investment, efforts, and resources required for building the national biodiversity repositories have been made that are related to the deep ocean are in process with a bias pattern linked to their collection methods (Hughes et al. 2021). This is evident not only in the national repositories but in the Ocean Biodiversity Information System (OBIS). A search in OBIS allows the recognition of the sampling effort that has been conducted in the northern hemisphere ocean regions and in coastal environments and recognizes that the open ocean, deep ocean off developing countries and small islands requires further sampling efforts.

In the same way, there are preferences in taxonomic knowledge that is being generated by citizen science. For example, marine vertebrates are more commonly recorded. Online crowdsourcing digital high-definition video and images of the deep ocean can be benefited from the use of machine learning, artificial intelligence and the new automated software. In contrast, identifying invertebrates is complex (Costello et al. 2017). Participants that are more experienced help to improve the annotations, engage in quality control, and help to build capacity in distinguishing the taxonomic characters. Well-illustrated guides for nonexpert are the most useful regional documents for crowdsourcing and biodiversity monitoring, especially if these are available in multiple languages (Chandler et al. 2017).

An additional tool used in citizen science initiatives for the deep ocean is the immersive virtual reality technology that facilitates understanding of the ecosystem through a virtual spatial presence (Burke and Crocker 2020). The immersive virtual reality is evolving as a tool for generating ocean digital twins or virtual representations of the real-world environments to evaluate scenarios of change during the experience of immersive presence in a virtual geo-habitat (Hruby et al. 2020).

27.5 Citizen Science for Deep Ocean Biodiversity Conservation Actions

27.5.1 Examples of Deep Ocean Conservation and Its Importance

Deep ocean species can be long lived, up to 17,000 years in some species of corals (Wagner and Opreski 2015), sponges (Jochum et al. 2017), tubeworms (Durkin et al. 2017) and fish (Cailliet et al. 2001, Nielsen et al. 2016) and they can be unique, rare, or endemic. The deep ocean and seafloor remain in complete darkness, under high pressure, low temperature, and limited in food supply, and with high water transparency; conditions that have been responsible for their high diversity. The recovery times to perturbations may exceed hundreds to millions of years. The importance of this biodiversity relies on the value of the ecosystem services provided and potential biotechnological use.

Some habitats are unique or vulnerable or recognized as essential habitats, breeding sites, or host high biodiversity. At the global scale, these have been identified as ecologically or biologically significant marine areas (Johnson et al. 2021), areas of particular environmental interest (Jones et al. 2021), with local- and national-scale national parks, natural World Heritage sites, and nature reserves, among others. What is important to note is that the deep ocean biodiversity subject to conservation is distant, rarely studied, and poorly understood; however, it is critically fundamental to the planet (DOSI 2022). Assessing and monitoring the biological diversity and recording the changes from anthropogenic activities and climate change are important.

27.5.2 The Contributions of Citizen Science to Conservation

The reason that the deep ocean biodiversity is unexplored and that conservation actions are slow is its inaccessibility and high cost. These limitations prevent scientists, institutions, and some countries from benefiting from the exploration findings. Citizen science appropriating digital technologies expand the new ways of engaging with scientific discoveries (Morais et al. 2022). Many citizen science initiatives are motivated by local conservation contributing to effective decision-making (Newman et al. 2017). Additionally, conservation areas that are successfully managed and governed are recognized with the IUCN Green List of Protected and Conserved Areas (https://www.iucn.org/theme/protected-areas/our-work/iucn-green-list-protected-and-conserved-areas) standard of best practices.

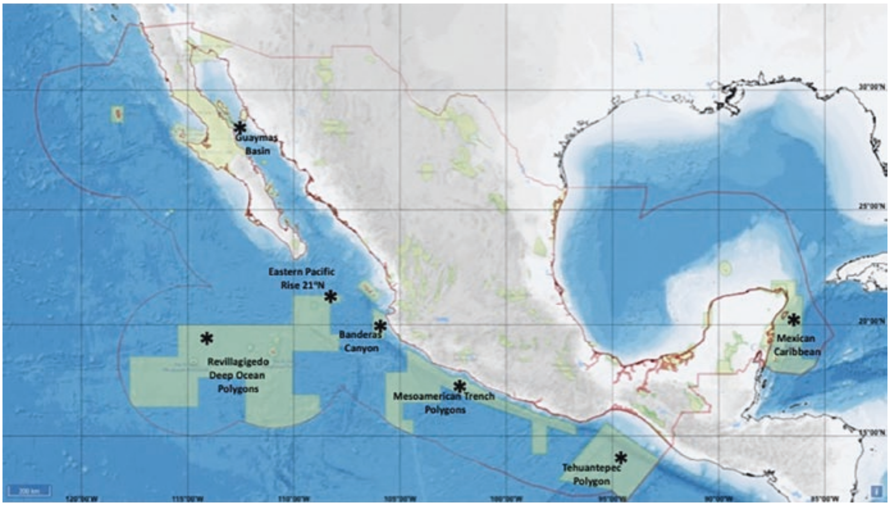

Fig. 27.2 The deep ocean conservation areas (green shaded with an asterisk) in the Mexican Exclusive Economic Zone (solid red line). (Image generated from UNINMAR. http://uninmar.icmyl.unam.mx/geoportal#zoom=5.6002197265625&lat=-11454020.52&lon=2790995.99&layers=cnsr_mxc1:anp_enero_2017;cnm1_psc1:contdv250_zeemgw)

27.6 Current Conservation Status of Major Fauna Groups in Mexico and Their Habitats

The ocean represents 65% of the Mexican territory, and below 200 m, it represents between 95 and 97% of the space where marine life evolves. Conservation in Mexico includes deep ocean national protected areas covering diverse habitats and ecosystems where unexplored, undescribed biodiversity occurs. The deep ocean conservation areas are limited to the Pacific and the Caribbean Ocean (Fig. 27.2). In Mexico, deep ocean locations with important biodiversity and uniqueness have been nominated as ecologically or biologically significant marine areas and as national protected areas with different degrees of protection. These locations are summarized in Tables 27.1 and 27.2. Some of these are entirely deep ocean habitats; in other cases, the national nomination is based on the emerged features in open ocean waters with deep seafloor below.

Crowdsourcing as a form of citizen science still needs to be developed for the deep Mexican conservation areas. The public participates in activities and committees in the national protected areas but seldom in the scientific research projects or acquiring and/or processing data. Citizens have the potential to contribute to crowdsourcing of videos (Hoeberechts et al. 2015); however, more efforts are required from the scientific community to make the deep seafloor and biodiversity accessible to the public.

Table 27.1 Summary of the Mexican deep ocean national protected areas. All columns are according to the Protected Areas Catalogue

Num	Name	Management category	EBSA region	Coordinates	Land surface (ha)	Marine surface (ha)	COP decision date
1	Guaymas Basin Hydrothermal Vents Sanctuary	Uniqueness, diverse biological processes, relatively pristine devoted to scientific research, and subject to potential resource use led to rapid decline	Eastern Tropical and Temperate Pacific ETTP_3_ EBSA.geojson	Latitude N max 27°05′49.54″ – latitude N min 26°57′20.43″; longitude W max 111°27′53.01″ – longitude W min 111°19′24.88”	0.00	Depth below 500 m in the water column and on the seafloor	Dec-COP-12-EC-22
2	Alijos Islands	High biological productivity, diversity, and naturalness	North Pacific NP_10_EBSA. geojson	24° 57.5′ latitude N and 115° 45.0′ longitude W	Volcanic peaks	Open Ocean and deep seafloor	DEC-COP-12-DEC-22
3	Coronado Island	High biological productivity and diversity	North Pacific NP_11_EBSA. geojson	Polygon 32°28’N, 117°18’O32° 25’N, 117°16’O;32°25’N, 117°16’O; 32°25’N, 117°15’O	Archipelago of four small islands (252 ha) surrounded by open ocean and deep seafloor	Continental margin, 13.6 km off the northwest coast of Baja California	DEC-COP-12-DEC-22
4	Guadalupe Island	High biological productivity and diversity and Special importance for life history stages of species	North Pacific NP_12_EBSA. geojson	29°2’N and 118°16.6’W	Oceanic island of volcanic origin, 241 km to the west of the Baja California Peninsula	Open ocean and deep-sea floor surround the island	DEC-COP-12-DEC-22

Num number; name in brackets the characteristics of the natural protected area; *ha* hectares. *COP* Conference of Parties

Table 27.2 Summary of the deep Mexican ecologically or biologically significant marine areas (EBSAs). All follow information of the CBD EBSA webpage

Num	Name	Management category	Region	Surface (ha)	Land surface (ha)	Marine surface (ha)	Decree date
7	Loreto Bay (mostly shallow, recently extended on the slope)	National Park	Baja California Peninsula and Northern Pacific	206,580.75	21,692.08	184,888.67	19/07/96
18	Cabo Pulmo (mostly shallow)	National Park	Baja California Peninsula and Northern Pacific	7111.01	38.86	7072.15	06/06/95
19	Cabo San Lucas (peaks surrounded by open and deep water)	Protection Area for Flora and Fauna	Baja California Peninsula and Northern Pacific	3996.05	208.05	3788.00	29/11/73
26	Caribe Mexicano (mostly deep ocean)	Biosphere Reserve	Yucatan Peninsula and Northern Caribbean	5,754,055.36	28,589.50	5,725,465.87	07/12/16
73	Isla Guadalupe (island surrounded by open and deep water)	Biosphere Reserve	Baja California Peninsula and Northern Pacific	476,971.20	26,276.97	450,694.23	25/04/05
117	Pacífico Mexicano Profundo (fully deep open and deep water)	Biosphere Reserve	Baja California Peninsula and Northern Pacific, Eastern and Central Pacific, Western and Southern Pacific Border and Tehuantepec Isthmus	43,614,120.19	0.00	43,614,120.19	07/12/16
140	Revillagigedo island and mostly open and deep water	National Park	Baja California Peninsula and Northern Pacific	14,808,780.12	15,518.22	14,793,261.90	27/11/17
170	Ventilas Hidrotermales de la Cuenca de Guaymas y de la Dorsal del Pacífico Oriental (all in deep water)	Sanctuary	Baja California Peninsula and Northern Pacific	145,564.81	0.00	145,564.81	05/06/09

Source: Johnson et al. (2021)
Num number; *ha* hectares

27.7 Opportunities and Future Challenges in Citizen Science for Deep Ocean Biodiversity

The growing engagement of online participants in deep ocean research can contribute to literacy and informed citizen input to policy (Matabos et al. 2017) and decision-making in the benefit of biodiversity conservation.

Among the opportunities that this engagement can bring to citizen science are the following:

1. The fundamental role to future funding for ocean science and infrastructure.
2. Integrating citizen science programs in the intersection of science, conservation, and restoration.
3. Expanding telepresence experiences as an extended, deep ocean biodiversity observing community.
4. An optimal reuse of data, imagery, and video for conservation.
5. Production of education materials to disseminate scientific knowledge from national protected areas.
6. Creating a national clearing house on marine biodiversity for science, conservation, and sustainable development to map events and citizen science initiatives with institutions, scientists, and cruises.

Among the challenges in citizen science for the deep ocean are the following:

1. Defining low-cost/no cost programs for times of financial hardship and not leaving anyone behind.
2. Assessing and monitoring the biodiversity changes in the deep ocean vastness.
3. Growing socioeconomic and security concerns from ocean resources use and climate change risks.
4. Data types and quality for future conservation and biodiversity forecasting.
5. Partnering with ocean observation initiatives increasing crowdsourcing and new knowledge.
6. Tool development to annotate and visualize data collection for visually impaired and other lifelong, developmental disabilities, including communication.
7. The unique physical, ecological, and cultural aspects of the Mexican society and its changes.

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Index

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