

# Biogeography and conservation assessments of the species of *Lamourouxia* (Orobanchaceae)

# Biogeografía y evaluaciones de conservación de las especies de *Lamourouxia* (Orobanchaceae)

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## Abstract:

**Background and Aims:** Parasitic plants represent approximately 1% of the world's angiosperm diversity. The highest richness of parasitic plant species among angiosperms belongs to Orobanchaceae, the only family with three main nutritional stages: autotrophic, hemiparasitic, and holoparasitic. Hemiparasitic genera are the most diverse, unstudied, and sometimes neglected within Orobanchaceae. Pedicularideae, the largest tribe of hemiparasitic taxa in Orobanchaceae, contains several poorly known genera. One of these is *Lamourouxia*, a genus of 30 species distributed throughout the Americas, but mostly endemic to Mexico. Due to the lack of knowledge about the biogeographic patterns, endemism, and conservation status of *Lamourouxia* species, the objectives of this study were to estimate their species richness and endemism, determine the areas of endemism in the Americas, and assess their conservation status.

Methods: Applying a taxonomic revision of physical and digitized herbaria specimens, citizen science observations, and scientific open access databases, we conducted biogeographic analyses for the whole genus. Moreover, the conservation status of all Lamourouxia species was assessed following the IUCN Red List guidelines.

Key results: The highest species richness, highest weighted endemism, and corrected weighted endemism values occurred in southern Mexico. Three areas of endemicity were distributed throughout western Mexico. Four species were classified as Endangered (EN), and three as Critically Endangered (CR) according to the IUCN risk categories. Endemic and rarely recorded *Lamourouxia* species were mostly distributed in unprotected areas in the Sierra Madre del Sur, Mexico.

**Conclusions:** The Mexican Transition Zone is the center of diversification of *Lamourouxia*, and one third of the genus is endemic to this region. It is strongly encouraged to carry out actions to conserve threatened species of *Lamourouxia*, which are distributed in the Sierra Madre del Sur, the biogeographic province with the highest number of endemic species in Mexico.

Key words: Americas, endemic species, hemiparasitic species, IUCN, Mexico, Pedicularideae.

## Resumen:

Antecedentes y Objetivos: Las plantas parásitas representan aproximadamente 1% de la diversidad mundial de angiospermas. La mayor riqueza de especies de plantas parásitas pertenece a Orobanchaceae, la única familia con tres principales niveles nutricionales: autótrofo, hemiparásito y holoparásito. Los géneros hemiparásitos son los más diversos, desconocidos y olvidados dentro de Orobanchaceae. Pedicularideae, la tribu más grande de taxones hemiparásitos, contiene varios géneros escasamente estudiados. Uno de esos es *Lamourouxia*, con 30 especies distribuidas en América y mayormente endémicas de México. Debido al vacío de conocimiento de los patrones biogeográficos, endemismo y estado de conservación de sus especies, los objetivos de este estudio fueron estimar la riqueza de especies y endemismo, determinar las áreas de endemismo en América y evaluar su estado de conservación.

Métodos: Con la revisión taxonómica de ejemplares de herbario físicos y digitalizados, observaciones de ciencia ciudadana y bases de datos científicas de acceso libre, realizamos análisis biogeográficos para Lamourouxia. También evaluamos el estado de conservación de sus especies siguiendo los lineamientos de la Lista Roja de la UICN.

Resultados clave: Los más altos valores de riqueza de especies, endemismo ponderado y endemismo ponderado corregido se encontraron en el sur de México. Tres áreas de endemismo se distribuyen en el occidente de México. Cuatro especies fueron clasificadas en la categoría de riesgo de la UICN "amenazada" y tres como "críticamente amenazada". Las especies endémicas y raramente registradas de *Lamourouxia* se encuentran distribuidas principalmente en áreas sin protección de la Sierra Madre del Sur, México.

Conclusiones: La Zona Mexicana de Transición es el centro de diversificación de Lamourouxia y un tercio del género es endémico de esta región. Se recomienda implementar acciones para conservar las especies amenazadas de Lamourouxia que se distribuyen en la Sierra Madre del Sur, la provincia biogeográfica con el mayor número de especies endémicas de México.

Palabras clave: América, especies endémicas, especies hemiparásitas, UICN, México, Pedicularideae.

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## Introduction

Parasitic plants are angiosperms that attach to host plants by means of specialized structures known as haustoria, to obtain carbon, nutrients, and water (Press and Phoenix, 2005; Nickrent, 2020). They represent about 1% of flowering plant diversity with ca. 4750 species (Heide-Jørgensen, 2013; Nickrent, 2020; Cai, 2023). Based on phylogenetic studies, it has been proposed that they evolved independently at least 12 times in equal number of orders and 27 families among angiosperms (Westwood et al., 2010; Nickrent, 2020; Krasylenko et al., 2021). The most diverse family of parasitic plants is Orobanchaceae with 102 genera and 2163 species, containing 49.3% of total parasitic plant diversity among angiosperms (Nickrent, 2020; Teixeira-Costa and Davis, 2021). Also, it is the only family with several levels of photosynthetic activity and dependence on its hosts (Westwood et al., 2010). Orobanchaceae contains photosynthetic, hemiparasitic, and holoparasitic species and varieties or subspecies (Heide-Jørgensen, 2013; Schneider et al., 2016). Hemiparasitic taxa partially obtain their needs of water and nutrients from their hosts, while the rest of their nutrients are generated by photosynthesis. Hemiparasites can sometimes survive without haustorial connections to a host, but their development is poorer than with a host, and they are known as facultative hemiparasites. There are also cases where a parasitic plant parasitizes another parasitic plant attached to a non-parasitic host. This interaction is called hyperparasitism. On the other hand, holoparasitic taxa have reduced or no photosynthetic activity, so all or most of their nutritional requirements are obtained from their hosts. Contrary to hemiparasites, holoparasites are necessarily dependent on a host, and sometimes they form self-parasitic haustoria in the presence of a non-parasitic host, a phenomenon termed autoparasitism (Heide-Jørgensen, 2013; Goyet et al., 2019; Krasylenko et al., 2021).

Recently, studies in Orobanchaceae have focused on genome evolution in hemi- and holoparasites (Yoshida et al., 2019; Zhou et al., 2019), horizontal gene transfer from the host to the parasite (Yang et al., 2016; Schneider et al., 2018), absorption of toxic metals by holoparasites (Turnau et al., 2018), alternative edible broomrapes (Renna et al., 2018), and taxonomic determination based on volatile organic compounds (Tóth et al., 2016), among other examples. Most of the leading studies have focused on the genomics and phylogenetics of holoparasitic genera (Schneeweiss et al., 2004; Weiss-Schneeweiss et al., 2006; Li et al., 2013; McNeal et al., 2013), while hemiparasitic genera have been addressed only in topics like phylogenetics and taxonomy (Tank and Olmstead, 2009; Tank et al., 2009; Morawetz et al., 2010; Robart et al., 2015; Uribe-Convers and Tank, 2016; Freeman et al., 2020). Therefore, many hemiparasitic genera remain unstudied and poorly known, such as *Lamourouxia* Kunth.

Lamourouxia belongs to Pedicularideae, the most diverse tribe of Orobanchaceae, with 21 genera and 1033 species. It is a monophyletic clade of root hemiparasitic plants, mainly distributed in the Americas and Asia (McNeal et al., 2013; Fu et al., 2017; Nickrent, 2020; Teixeira-Costa and Davis, 2021). Lamourouxia comprises 30 species endemic to the Americas, which are distributed from Mexico to Peru, with 19 species endemic to Mexico (Ernst, 1972; Francisco-Gutiérrez et al., 2022; 2023). Because most Lamourouxia species are endemic and distributed in Mexico, it was considered one of the representative genera of the flora for this country (Rzedowski, 2019). The Mexican species of Lamourouxia were studied by Paray (1950), but then forgotten during half a century, from the generic treatment of Ernst (1972) until the taxonomic revision by Francisco-Gutiérrez et al. (2023). Ernst (1972) classified the genus into three sections based on floral morphology: Adelphidion W.R. Ernst, Hemispadon Benth., and Lamourouxia. On a global scale, none of the genera of Orobanchaceae have been studied concerning their richness, endemism, or biogeographic patterns. Regarding the environmental legislation of the countries of the Americas, only L. barbata (Bertol.) MacVean, Cristof., T.F Daniel & Baldini (formerly named L. lanceolata Benth.) is included in the list of threatened species of Guatemala (CONAP, 2009). None of the Lamourouxia species have had their conservation status evaluated according to the IUCN Red List guidelines (IUCN, 2023).

In a previous taxonomic treatment of the Mexican species of *Lamourouxia* (Francisco-Gutiérrez et al., 2023), it was found that 26 of 30 species of the genus in the Americas were distributed in southern Mexico, particularly in the Mexican Transition Zone (MTZ), a complex area where Neotropical and Nearctic floras and faunas overlap (Halffter, 1976, 1987; Halffter and Morrone, 2017). The MTZ has a rich biological diversity and has been studied in more than 130 biogeographic and endemicity analyses (López-García and Morrone, 2023). The biogeographic regionalization that best fits the conceptualization of Halffter (1987) is the one proposed by Morrone (2014; 2020), where, besides classifying the complexity of biomes of the MTZ, biogeographic provinces and subprovinces for the rest of the Americas are included as well.

To know the biogeographic patterns and the risk categories of each species of *Lamourouxia*, this study aimed to 1) estimate the species richness and endemism of *Lamourouxia* by biogeographic regionalization and grid cells, 2) determine the areas of endemism of *Lamourouxia* in the Americas, and 3) assess the conservation status of all species of *Lamourouxia*.

## Material and Methods

## Taxonomic determination of *Lamourouxia* species

A taxonomic revision of herbarium specimens housed in the four main Mexican herbaria was undertaken: ENCB, IBUG, MEXU, and XAL. Also, digitized specimens of the following herbaria were revised: A, AAU, ARIZ, ASU, BR, BRU, CAS, CLEMS, CM, COLO, CR, DES, E, F, G, GBH, GH, GOET, HAO, JE, K, L, M, MICH, MO, NY, OBI, P, RSA, TEX, UNM, US, UTC, W (all acronyms according to Thiers, 2023). All digitized specimens were obtained from the databases of the Red de Herbarios del Noroeste de México (Red de Herbarios del Noroeste de México, 2022), the Portal de Datos Abiertos de Colecciones Biológicas (Portal de Datos Abiertos UNAM, 2022), TROPICOS (TROPICOS, 2022), the virtual herbarium of the New York Botanical Garden (NYBG Steere Herbarium, 2022), and the Global Biodiversity Information Facility (GBIF, 2021a).

For all the recognized species in the classification of Ernst (1972), the digitized types of the *Lamourouxia* species stored in the JSTOR Plants database (JSTOR, 2021) were consulted. Many of these species from Mexico and Central America were lectotypified in the monograph of the Mexican *Lamourouxia* by Francisco-Gutiérrez et al. (2023). Dichotomous keys and descriptions provided by Ernst (1972),

Turner (1993), and Francisco-Gutiérrez et al. (2022) were used for taxonomic determination of herbarium specimens, as well as photographs of living plants of *Lamourouxia* from the iNaturalist node Mexico database (Naturalista, 2021). For this study, only observations from iNaturalist of species with poor representation in herbaria and records outside the known distribution of widespread species were used. The herbarium specimens and observations of citizen science taxonomically determined for this study are available in Appendix 1 (see supplementary material).

Due to the morphological similitude and diversity of the species, all the specimens from Mexico and several from Central America were personally determined when possible. Data of species distributed in Central and South America of which there are no digitized herbarium specimens (Lamourouxia gutierrezii Oerst., L. multifida Kunth, L. sylvatica Kunth, L. virgata Kunth, L. viscosa Kunth, and L. xalapensis Kunth) were downloaded from the Global Biodiversity Information Facility (GBIF, 2021b, c, d, e, f, g, respectively). Only specimens determined by authorities in Orobanchaceae (N.H. Holmgren, J.L. Fernández-Alonso, K. Barringer, U. Molau, and M.J.M. Christenhusz) were used for this study (records from BM, CONN, CR, DUKE, E, INB, IND, ITIC, KANU, KU, LAGU, MO, TEFH, UCR, UNA, US, and USF herbaria). A database of the Lamourouxia specimens of the CIIDIR herbarium was provided by Arturo-Castro-Castro.

Also, botanical expeditions to find rare species *Lamourouxia colimae* W.R. Ernst & Baad, *L. dispar* W.R. Ernst, *L. jaliscana* W.R. Ernst & Baad, *L. gracilis* B.L. Rob. & Greenm., *L. parayana* W.R. Ernst (with two to five specimens in literature and herbaria) were carried out in 2019 in the type localities and surrounding municipalities in the states of Colima (24-27 October), Jalisco (22-25 February, 18-23 November), Mexico and Morelos (18-23 November), Puebla (10 December), and Veracruz (19 October, 7 November).

#### Geographic data

Geographic coordinates were used when indicated on the herbarium specimen labels. When localities were not specified but without geographic coordinates, they were georeferenced using Google Earth Pro v. 7.3.4 (Google, 2021).



Duplicated, unlocated or doubtful localities were excluded. Also, spatial data from taxonomically determined Naturalista (2021) observations were included. Maps of biogeographic analyses were designed in QGIS v. 2.18.15 (QGIS Development Team, 2016), using the digital elevation model (30 s resolution) provided by Fick and Hijmans (2017) and the shapefiles of the biogeographic regions and provinces for the Americas provided by Lowenberg-Neto (2014), based on the regionalization of Morrone for the Americas (Morrone, 2014) and Mexico (Morrone et al., 2017).

#### Species richness and endemism

Species richness and endemism were estimated by different area criteria: 1) biogeographic regionalization proposed by Morrone (Morrone, 2014; Morrone et al., 2017), and 2) grid cells of 0.5 × 0.5 degrees for comparison purposes. To analyze the patterns of biodiversity of Lamourouxia, we estimated the species richness, weighted endemism (WE), and corrected weighted endemism (CWE). Species richness is a measure of species diversity and is a count of the number of species inhabiting a given area or habitat (Kiester, 2013). WE is the species richness weighted by the inverse of the range size of each species, so species occurring over smaller ranges will have higher scores. CWE is the weighted endemism index divided by the species richness (Crisp et al., 2001; Guerin et al., 2015). These analyses were performed with Biodiverse v. 3.1 (Laffan et al., 2010). All indexes were calculated in the software with origin in 0° latitude and longitude. The resulting files were processed with the tool "Calculate Statistics" of ArcCatalog in ArcMap v. 10.5 (ESRI, 1999-2010).

#### Areas of endemism

Areas of endemism were obtained employing the Endemicity Analysis, with the method established by Szumik et al. (2002) and Szumik and Goloboff (2004), available in the software NDM/VNDM v. 2.5 (Goloboff, 2004). Geographic coordinates of all *Lamourouxia* records were included in a xyd file (Appendix 2, see supplementary material), generated with the tool GeX (Santos and Fuhlendorf, 2018) available at UFABC (2023). The file xyd was edited with TextEdit v. 1.15 (Apple, 1995-2019), and can be opened with Note-Pad v. 11.2302 (Microsoft, 2023). Cell size was adjusted to 0.5 for "X" and "Y", and the grid origin was established automatically by the program at X= -111.283, Y= 32.143. The parameters used in the program were: 1) scores equal to or higher than 2.0 and two or more defining species, 2) 1000 replicates of search with overlapping subsets if 98% of species were unique, 3) edge proportions for each search, and 4) "Set minimum species score" value of 0.6. The most frequent area in the replicates estimated by the program was selected. The files generated were transformed into polygons in DIVA-GIS v. 4.2 (Hijmans et al., 2004).

#### Conservation status assessments

Conservation assessments for each Lamourouxia species followed the Guidelines for Using the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee, 2022). Geographic ranges of the Extension of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using the Geospatial Conservation Assessment Tool (GeoCAT, 2015) based on Bachman et al. (2011). This tool employs the default scale of  $2 \times 2$  km grid cells suggested in the guidelines for the calculation of geographic ranges. Records of verified herbarium specimens and determined observations from Naturalista (2021) were used. Studies containing information on threats in the geographic range of each species were included to determine the risk category they belong (Aguilar-Tomasini et al., 2020; Alcocer et al., 2018; Almazán-Núñez et al., 2016; Bax and Francesconi, 2018; Cruz-Romero et al., 2020; Escalante and Aguilar-Ortega, 2021; Eva et al., 2012; Hernández-Flores et al., 2017; Munroe et al., 2007; Novo-Fernández et al., 2018; Olivera-Lozano, 2018; Pérez-González et al., 2017; Ponce-Reyes et al., 2012; Robalino et al., 2017; Rosete-Vergés, 2014; Soto-Molina and Delgado-Granados, 2020; Tapia-Armijos et al., 2015). Protected areas where species are distributed were obtained from the layer of government and private protected areas in Latin America and the Caribbean provided by the UNEP-WCMC and IUCN (2022).

## Results

#### Databases and temporality of collections

This study is the result of the revision of 2075 physical and digitized specimens from 48 herbaria and 49 selected observations from Naturalista (2021) (which illustrate the spe-



cies diversity in Fig. 1). The total number of records was 2116. Of these, 1583 were georeferenced (74.81%). The georeferenced records occur in Belize (2), Colombia (41), Costa Rica (44), Ecuador (229), El Salvador (23), Guatemala (46), Honduras (26), Mexico (1088), Nicaragua (35), Panama (16), and Peru (33). Except for the type specimens, 24 of 2071 herbarium specimens (1.15%) were collected before 1900; 1617 specimens (78.07%) in the 20th century, mostly in the 1970s to 1990s; and 430 (20.76%) after the year 2000 (Fig. 2A).

#### Species richness

#### Species richness by biogeographic regionalization

Lamourouxia is distributed across 21 biogeographic provinces from three regions in the Americas. The richest region is the MTZ with 25 species (11 of which are endemic), followed by the Neotropics with 18 (five endemic), and the Nearctic with five (no endemisms) (Table 1, Fig. 2B). The richest province is the Sierra Madre del Sur (SMS) with 18 species, followed by the Trans-Mexican Volcanic Belt (TMVB) with 15, and the Balsas Basin (BB) with ten, all of them in Mexico. The province with the largest number of endemic species is the SMS with three species, followed by the Sierra Madre Occidental (SMOC) with two. Finally, the Chiapas Highlands (CH), Pacific Lowlands (PL), TMVB, and Puntarenas-Chiriquí (PC, located between Costa Rica and Panama) provinces possess one endemic species each (Table 1, Fig. 2C).

#### Species richness by grid cells

The study area was divided into 6952 cells of 0.5 × 0.5 degrees. The species richness was homogeneous along most Nearctic and Neotropical regions with cells of one to three species. Most of the richest cells were found in the MTZ region (Fig. 3): A) a cell with ten species in a zone of very rugged orography in the eastern SMS; B) a cell with nine species along the TMVB and Veracruzan provinces including three biodiversity conservation zones (Pico de Orizaba National Park, which includes the country's highest peak; part of the Tehuacán-Cuicatlán Biosphere Reserve (TCBR) and Cañón del Rio Blanco National Park, CRBNP); C) a cell with nine species in the PL; and D) close to the richest one, a couple of cells with eight species in the SMS which includes the Sierra de Juárez and part of the TCBR (Fig. 3A). Many other cells containing five to seven species are found along the CH, SMS, and Sierra Madre Oriental (SMOR). Three species were registered in only one cell across the Americas: *L. colimae*, *L. jaliscana*, *L. parayana*, followed by *L. gracilis* within two cells.

#### Endemism

#### Weighted endemism (WE)

Weighted endemism values were low and homogeneous along Nearctic and Neotropical regions. Weighted endemism analysis retrieved six main cells with high and moderate values (Fig. 3): A) the highest value was found in the PL (Central Guerrero), followed by B and C) cells in the PL (Sierra de Cuale in Jalisco, and northeastern Colima, respectively), D) a cell in the eastern TMVB, and E and F) located in the SMS (Fig. 3B).

#### Corrected Weighted endemism (CWE)

Corrected Weighted endemism analysis recovered almost all the cells across the American continent with low values. The cell with the highest value was found in A) the PL (northeastern Colima), whereas cells with low values were B) in the PL (Sierra de Cuale, Jalisco), C) in the south-central TMVB, D) the PL (south-central Oaxaca) (Fig. 3C).

#### Areas of endemism

The endemicity analysis estimated three areas of endemism of *L*. in the Americas, all of them in Mexico (Fig. 3D). The first and largest encompasses the SMS, TMVB, and PL provinces. This area was distinguished by very restricted species: *Lamourouxia colimae* (microendemic to Colima state), *L. jaliscana* (microendemic to Jalisco state), and the recently described *L. avendanoi* Franc. Gut. endemic to the SMOC. The second and third areas covered the SMOC and PL, and a small surface of the Sonoran province. The last two areas of endemism were characterized by the species *L. avendanoi*, *L. pacifica* Franc. Gut. & Ruiz-Sanchez, and *L. longiflora* Benth. (the latter endemic to the SMOC) (Fig. 3D).



Figure 1: Diversity of the Lamourouxia Kunth species. Section Adelphidion W.R. Ernst: A. Lamourouxia brachyantha Greenm. (Naturalista, 2023a); B. Lamourouxia dasyantha (Cham. & Schltdl.) W.R. Ernst (Naturalista, 2023b); C. Lamourouxia sylvatica Kunth (Naturalista, 2023c); D. Lamourouxia virgata Kunth (Naturalista, 2023d). Section Hemispadon Benth.: E. Lamourouxia avendanoi Franc.Gut. (Naturalista, 2023e); F. Lamourouxia barbata (Bertol.) MacVean, Cristof., T.F. Daniel & Baldini (Naturalista, 2023f); G. Lamourouxia dispar W.R. Ernst (Naturalista, 2023g); H. Lamourouxia gracilis B.L. Rob.; I) Lamourouxia gutierrezii Oerst. (Naturalista, 2023i); J. Lamourouxia integerrima Donn.Sm. (Naturalista, 2023j); K. Lamourouxia nelsonii B.L. Rob & Greenm. (Naturalista, 2023k); L. Lamourouxia pacifica Franc.Gut.; M. Lamourouxia rhinanthifolia Kunth (Naturalista, 2023m); N. Lamourouxia smithii B.L. Rob. & Greenm. (Naturalista, 2023n); O. Lamourouxia viscosa Kunth (Naturalista, 2023o). Section Lamourouxia: P. Lamourouxia longiflora Benth. (Naturalista, 2023p); Q. Lamourouxia macrantha M. Martens & Galeotti; R. Lamourouxia ovata M. Martens & Galeotti (Naturalista, 2023r); S. Lamourouxia xalapensis Kunth (Naturalista, 2023s); T. Lamourouxia multifida Kunth (Naturalista, 2023t); U. Lamourouxia pringlei B.L. Rob. & Greenm. (Naturalista, 2023u); V. Lamourouxia zimapana B.L. Turner (Naturalista, 2023v) (Photographic credits: Table S1).





Figure 2: Temporality and biogeographic distribution of the records of the *Lamourouxia* Kunth species in the Americas. A. records of *Lamourouxia* Kunth by decade analyzed in this study; B. species richness of *Lamourouxia* by biogeographic regions; C. species richness by biogeographic provinces *sensu* Morrone (2014), and Morrone et al. (2017). TS: Total species, ESR: Endemic species to the region, ESP: Endemic species to the province. Biogeographic regions: MTZ: Mexican Transition Zone. Biogeographic provinces: BB: Balsas Basin, CAU: Cauca, CD: Chihuahuan Desert, CH: Chiapas Highlands, D: Desert, GT: Guatuso-Talamanca, MAG: Magdalena, MOS: Mosquito, PAR: Páramo, PC: Puntarenas-Chiriquí, PL: Pacific Lowlands, PUN: Puna, R: Rôndonia, SMS: Sierra Madre del Sur, SMOC: Sierra Madre Occidental, SMOR: Sierra Madre Oriental, TAM: Tamaulipas, TMVB: Trans-Mexican Volcanic Belt, V: Veracruzan, WE: Western Ecuador, Y: Yungas.

#### Conservation assessments

According to the criteria of the IUCN Red List (IUCN Standards and Petitions Committee, 2022), *Lamourouxia* species were classified in the following categories: Least Concern (LC), nine species; Near Threatened (NT), two; Vulnerable (VU), 12; Endangered (EN), four; and Critically Endangered (CR), three (Table 2). Nineteen species were distributed within protected areas in nine countries.

### Discussion

#### Temporality of collections

The reduction in the number of recent collections of *Lamourouxia* in the late 20st century in Mexico, where most species inhabit and where most records are from, can be attributed to the increasing insecurity conditions (García-Jiménez and Vargas-Rodríguez, 2021) for students and researchers during fieldwork in areas of high species richness and endemism (i.e., Guerrero, Michoacán, and Sinaloa

states), and the continuous deforestation of preserved forests (Ponce-Reyes et al., 2012; Rosete-Vergés et al., 2014). An increasing number of citizen science records can be a useful tool for precisely locating observed specimens and collecting them for deposition in scientific collections.

#### Species richness

The species richness obtained in this study shows a similar pattern with the American genera *Echeandia* Ortega (Ortiz-Brunel et al., 2021), *Dahlia* Cav. (Carrasco-Ortiz et al., 2019) and *Cosmos* Cav. (Vargas-Amado et al., 2020), in which areas of highest richness were distributed in the MTZ. We also obtained the same distribution of the cells with the highest values of species richness of *Lamourouxia* as in the analysis of species richness for the SMS with 9524 species of vascular plants. This similarity in the distribution of richest cells is due to the complex orography and volcanic activity of the MTZ, temperature fluctuations Table 1: Species richness, infrageneric classification (sensu Ernst, 1972), and continental distribution of Lamourouxia Kunth species by politicaldivision and biogeographic regionalization (sensu Morrone, 2014; Morrone et al., 2017). Biogeographic regions: MTZ: Mexican Transition Zone,NA: Nearctic, NT: Neotropics. Biogeographic provinces: BB: Balsas Basin, CAU: Cauca, CD: Chihuahuan Desert, CH: Chiapas Highlands, D: Desert,GT: Guatuso-Talamanca, MAG: Magdalena, MOS: Mosquito, PAR: Páramo, PC: Puntarenas-Chiriquí, PL: Pacific Lowlands, PUN: Puna, R: Rôndonia,SMS: Sierra Madre del Sur, SMOC: Sierra Madre Occidental, SMOR: Sierra Madre Oriental, TAM: Tamaulipas, TMVB: Trans-Mexican Volcanic Belt, V:Veracruzan, WE: Western Ecuador, Y: Yungas. \*: Endemic species of the Mexican Transition Zone; +: Endemic species of the Neotropics.

Species	Biogeographic Region:
	Biogeographic Provinces
Lamourouxia avendanoi Franc. Gut.*	MTZ: SMOC.
Lamourouxia barbata (Bertol.) MacVean, Cristof., T.F Daniel & Baldini*	MTZ: CH, PL, V.
Lamourouxia brachyantha Greenm.	MTZ: TMVB. NT: CD.
Lamourouxia colimae W.R. Ernst +	NT: PL.
Lamourouxia dasyantha (Cham. & Schltdl.) W.R. Ernst	MTZ: SMOR, SMS, TMVB. NA: CD, TAM. NT: BB, V.
Lamourouxia dependens Benth. +	NT: CH.
Lamourouxia dispar W.R. Ernst *	MTZ: SMS, TMVB.
Lamourouxia gracilis B.L. Rob. & Greenm.	MTZ: TMVB. NT: BB.
Lamourouxia gutierrezii Oerst. +	NT: PC.
Lamourouxia integerrima Donn. Sm. *	MTZ: CH, SMS.
Lamourouxia jaliscana W.R. Ernst & Baad *	MTZ: SMS.
Lamourouxia longiflora Benth. *	MTZ: SMOC.
Lamourouxia macrantha M. Martens & Galeotti *	MTZ: CD, CH, SMOC, SMOR, SMS, TMVB.
Lamourouxia microphylla M. Martens & Galeotti *	MTZ: SMS.
Lamourouxia multifida Kunth	MTZ: CH, SMOC, SMOR, SMS, TMVB. NA: CD. NT: BB, PL, V.
Lamourouxia nelsonii B.L. Rob. & Greenm.	MTZ: SMOR, SMS, TMVB. NT: BB.
Lamourouxia ovata M. Martens & Galeotti *	MTZ: CH, SMS, TMVB.
Lamourouxia pacifica Franc. Gut. & Ruiz-Sanchez	MTZ: SMOC, SMS, TMVB. NT: PL.
Lamourouxia paneroi B.L. Turner	MTZ: SMS. NT: BB.
Lamourouxia parayana W.R. Ernst *	MTZ: TMVB.
Lamourouxia pringlei B.L. Rob. & Greenm.	MTZ: SMS, TMVB. NT: BB.
Lamourouxia rhinanthifolia Kunth	MTZ: SMOC, SMOR, SMS, TMVB. NA: CD.
Lamourouxia smithii B.L. Rob. & Greenm.	MTZ: SMS. NT: BB.
Lamourouxia stenoglossa Hunnewell & L.B. Sm.	MTZ: CH, SMS. NT: PL.
Lamourouxia sylvatica Kunth +	NT: CAU, D, PUN, R, Y.
Lamourouxia tenuifolia M. Martens & Galeotti *	MTZ: SMS.
Lamourouxia virgata Kunth +	NT: CAU, MAG, PAR, WE.
Lamourouxia viscosa Kunth	MTZ: CH, SMOC, SMOR, SMS, TMVB. NA: CD. NT: BB, GT, MOS, PC, PL, V.
Lamourouxia xalapensis Kunth	MTZ: CH, SMOR, SMS, TMVB. NA: CD. NT: BB.
Lamourouxia zimapana B.L. Turner	MTZ: SMOR, TMVB. NT: BB.

(Mastretta-Yanes et al., 2015), high levels of speciation, and accumulation of lineages from the Nearctic and Neotropics (Aragón-Parada et al., 2023).

The MTZ region is the center of diversification of *Lamourouxia* with 25 of 30 species of the genus. Data obtained in this study allow us to establish that *Lamourouxia* probably originated in Mexico with later southward dispersal. Wolfe et al. (2005) hypothesized that dispersal from North to South America is one of the possible paths for radiating taxa in Orobanchaceae. This pathway has been confirmed in

other amphitropical genera, i.e., *Castilleja* Mutis ex L.f. (Pedicularideae; Tank and Olmstead, 2009), and *Aphyllon* Mitch. (Orobancheae; Schneider and Moore, 2017). The MTZ is an important region where a biotic interchange between the Nearctic and Neotropical regions occurs (Morrone, 2014; 2020). The MTZ harbors 323 genera of flowering plants distributed either in North or South America, or in both (Villaseñor et al., 2020). The MTZ also harbors other endemic and rare genera of Orobanchaceae, such as *Silviella* Pennell (Wolfe et al., 2005), the holoparasitic and monotypic *Eremitilla* Yatsk.



Figure 3: Maps of *Lamourouxia* Kunth species richness and endemism areas based on the biogeographic regionalization of Morrone (2014). A. species richness; B. weighted Endemism: C. corrected Weighted Endemism; D. areas of endemism. Biogeographic provinces with *Lamourouxia* Kunth species: 0) Nearctic region (it includes Tamaulipan and Chihuahuan Desert of Mexican regionalization of Morrone et al., 2017), 1) Sierra Madre Occidental, 2) Sierra Madre Oriental, 3) Trans-Mexican Volcanic Belt, 4) Sierra Madre del Sur, 5) Chiapas Highlands, 13) Pacific Lowlands, 14) Balsas Basin, 15) Veracruzan, 17) Mosquito, 18) Guatuso-Talamanca, 19) Puntarenas-Chiriquí, 24) Magdalena, 26) Cauca, 28) Western Ecuador, 39) Yungas, 48) Páramo, 49) Desert, 50) Puna.

& J.L. Contr. (Yatskievych and Contreras-Jiménez, 2009), as well as *Escobedia* Ruiz & Pav. and *Seymeria* Pursh (Rzedowski, 2019). According to the taxonomic revision of the *Lamourouxia* species of Mexico (Francisco-Gutiérrez et al., 2023), no hosts were reported in literature, herbarium specimens, and citizen science observations. Therefore, the identity and influence of the hosts in the richness and dispersal of the species is still unknown. Table 2: Conservation status assessments of *Lamourouxia* Kunth species. Criteria based on the IUCN Standards and Petitions Committee (2022). NR: number of records, GR: geographic range, EOO: Extent of Occurrence, AOO: Area of Occupancy, LC: Least Concern, NT: Near Threatened, VU: Vulnerable, EN: Endangered, CR: Critically Endangered. Biogeographic regions abbreviated: Sierra Madre Occidental (SMOC), Sierra Madre del Sur (SMS), Tehuacán-Cuicatlán Biosphere Reserve (TCBR), Trans-Mexican Volcanic Belt (TMVB).

Species	Risk category	Number of	EOO	A00	Criteria
		records	(Km²)	(кт-)	
Lamourouxia avendanoi Franc.Gut.	VU B2ab(III)	8	15,644	32	axon restricted to the SMOC. Locations ≤10 (Francisco-Gutierrez et al., 2022). Continuing decline observed in habitat quality (González- Elizondo et al., 2013; Novo-Fernández et al., 2018). Distributed in Cuenca Alimentadora del Distrito Nacional de Riego 043 Nayarit protected area.
<i>Lamourouxia barbata</i> (Bertol.) MacVean, Cristof., T.F. Daniel & Baldini	VU B2ab(ii,iii)	48	13,130	88	Several specimens distributed on volcanoes (Tacaná, Mexico; Acatenango, Guatemala; San Salvador, El Salvador), and protected areas (Cañón del Sumidero, Mexico; Cuenca del Lago Atitlán, Guatemala; Celaque, Honduras; Los Quetzales, Costa Rica). AOO<500 km <sup>2</sup> . Threatened by habitat fragmentation (Munroe et al., 2007).
Lamourouxia brachyantha Greenm.	NT	24	44,334	96	Distributed near Mexico City, possibly threatened by urbanization (Hernández-Flores et al., 2017). Distributed in protected areas Sierra de Guadalupe, Mexico State; El Tángano, Querétaro, Mexico.
<i>Lamourouxia colimae</i> W.R. Ernst & Baad	CR B1ab(ii,iii) + B2ab(ii,iii)	2	0	8	Taxon was searched at type locality and potential localities, but not found. EOO<100 km <sup>2</sup> , AOO<10 km <sup>2</sup> . Threatened by demographic growth and land use change in the metropolitan area of Colima City (Pérez-González et al., 2017). Last collection: 1984.
<i>Lamourouxia dasyantha</i> (Cham. & Schltdl.)	LC	179	328,704	700	Widespread species in semiarid environments and pine forests. Possibly threatened by deforestation of Mexican forests in recent decades (Rosete-Vergés et al., 2014). Distributed in 16 protected areas.
<i>Lamourouxia dependens</i> Benth.	VU B1a(iii)	9	5,474	36	EOO<20,000 km <sup>2</sup> , locations ≤10. Most specimens are distributed in protected areas (Quetzaltenango-Saqbé, Cuenca del Lago Atitlán, Volcán de Fuego, Volcán de Agua, Guatemala). Continuing decline observed in habitat quality (Eva et al., 2012; Sesnie et al., 2017).
<i>Lamourouxia dispar</i> W.R. Ernst	EN B2ab(ii, iii)	5	34,668	20	AOO<500 km <sup>2</sup> , locations ≤5, severely fragmented. Some specimens distributed in Lagunas de Zempoala National Park (Mexico). Threatened by modifications in land use in the SMS (Almazán-Núñez et al., 2016). Last collection: 1988.
<i>Lamourouxia gracilis</i> B.L. Rob.	EN B1ab(ii, iii)	5	760	20	Very rare in the field. AOO<500 km <sup>2</sup> and locations ≤5. Threatened by urbanization of Cuernavaca, Mexico (Olivera-Lozano, 2018), where most collections were made.
<i>Lamourouxia gutierrezii</i> Oerst.	LC	25	10,972	84	Distributed in Costa Rica and Panama. Most specimens collected in protected areas (Cerros de Escazú, Las Tablas, Braulio Carrillo, Volcán Barú, Chirripó, Talamanca Range-La Amistad National Park, Costa Rica-Panama). Low risk of deforestation in protected areas of Costa Rica (Robalino et al., 2017).
Lamourouxia integerrima Donn.Sm.	VU B2ab(ii, iii)	10	44,089	36	Specimens distributed in the protected area Lagunas de Montebello, Mexico. Taxon restricted to humid forests. AOO<500 km <sup>2</sup> . Continuing decline observed in habitat quality (Eva et al., 2012; Alcocer et al., 2018; Sesnie et al., 2017).
<i>Lamourouxia jaliscana</i> W.R. Ernst.	CR B2ab(ii, iii)	2	0	8	Taxon was searched at type locality and potential localities in conserved areas, but not found. Species restricted to Talpa, Jalisco, Mexico. AOO<10 km <sup>2</sup> and locations severely fragmented by urbanization and crop fields (Cruz-Romero et al., 2020). Last collection: 1960.

#### Table 2: Continuation.

Species	Risk category	Number of	EOO	A00	Criteria
		records	(km²)	(km²)	
Lamourouxia longiflora Benth.	VU B2ab(ii, iii)	23	51,341	88	This taxon is restricted to the SMOC. AOO<500 km <sup>2</sup> . Continuing decline observed in habitat quality (González-Elizondo et al., 2013; Novo-Fernández et al., 2018).
<i>Lamourouxia macrantha</i> M. Martens & Galeotti	VU B2ab(ii, iii)	22	414,375	72	This taxon has AOO<500 km <sup>2</sup> . Species distributed in protected areas from Mexico (Pico de Orizaba, Volcán Tacaná, Nevado de Toluca National Parks). Observed decline in habitat quality in national parks (Agramont et al., 2012; Soto-Molina and Delgado-Granados, 2020).
Lamourouxia microphylla M. Martens & Galeotti	VU B2ab(ii, iii)	7	15,967	28	Taxon restricted to the SMS. AOO<500 km <sup>2</sup> and observed decline of habitat quality (Almazán-Núñez et al., 2016). Last collection: 1998.
<i>Lamourouxia multifida</i> Kunth	LC	239	827,634	932	Widespread species from Mexico to Guatemala. Distributed in 24 protected areas.
<i>Lamourouxia nelsonii</i> B.L. Rob. & Greenm.	LC	43	64,380	172	Species distributed in protected areas (Iztaccíhuatl-Popocatépetl National Park, Sierra Gorda and Tehuacán-Cuicatlán Biosphere Reserves).
Lamourouxia ovata M. Martens & Galeotti	EN B2ab(iii)	5	62,157	20	This taxon is restricted mostly to the SMS. AOO<500 km <sup>2</sup> and locations ≤5, severely fragmented. Continuing observed decline of habitat quality (Almazán-Núñez et al., 2016). Last collection: 1990.
<i>Lamourouxia pacifica</i> Franc.Gut. & Ruiz- Sanchez	VU B1ab(ii,iii) + B2ab(ii,iii)	9	88,839	36	Species distributed throughout the SMOC. AOO<500 km <sup>2</sup> . Only distributed in the protected area Cuenca Abastecedora del Distrito Nacional de Riego 043 Nayarit.
<i>Lamourouxia paneroi</i> B.L. Turner	VU B1ab(ii,iii)	12	14,169	48	EOO<500 km <sup>2</sup> . Taxon mostly distributed in the SMS. Continuing observed decline of habitat quality (Almazán-Núñez et al., 2016).
Lamourouxia parayana W.R. Ernst	CR B1ab(i,ii,iii) + B2ab(i,ii,iii)	2	0	8	Taxon was searched at type locality and potential localities in conserved areas, but not found. Restricted to Sultepec, Mexico State, Mexico. AOO<10 km <sup>2</sup> . Threatened by land cover change in the TMVB (Aguilar-Tomasini et al., 2020). Last collection: 1970.
<i>Lamourouxia pringlei</i> B.L. Rob. & Greenm.	NT	24	27,289	96	Species mostly distributed in the SMS. AOO<500 km <sup>2</sup> . Threatened by modifications in land use in the SMS (Almazán-Núñez et al., 2016).
Lamourouxia rhinanthifolia Kunth	LC	101	549,813	400	Widespread species from Mexico. Distributed in 12 protected areas.
<i>Lamourouxia smithii</i> B.L. Rob. & Greenm.	VU B2ab(ii,iii)	9	29,378	36	Taxon mostly distributed in the SMS. AOO<500 km <sup>2</sup> , severely fragmented. Continuing observed decline of habitat quality (Almazán-Núñez et al., 2016). One specimen recorded in the TCBR.
Lamourouxia stenoglossa Hunnewell & L.B. Sm.	EN B2ab(iii)	16	102,970	60	AOO<500 km <sup>2</sup> . Severely fragmented. Observed decline of area and quality of habitat (Eva et al., 2012; Almazán-Núñez et al., 2016; Sesnie et al., 2017). Distributed in five protected areas.
<i>Lamourouxia sylvatica</i> Kunth	LC	56	233,019	164	Species fragmented and distributed in two protected areas (Podocarpus, Ecuador and Cutervo, Peru, National Parks). AOO<500 km <sup>2</sup> . Observed and estimated decline in area and quality of habitat due to deforestation and fragmentation (Tapia-Armijos et al., 2015; Bax and Francesconi, 2018).
Lamourouxia tenuifolia M. Martens & Galeotti	VU B2ab(ii,iii)	10	24,290	40	AOO<500 km <sup>2</sup> . Taxon restricted to the SMS. Continuing observed decline of habitat quality (Almazán-Núñez et al., 2016).
<i>Lamourouxia virgata</i> Kunth	LC	247	202,216	596	Widespread species from Colombia to Peru. Distributed in 11 protected areas.
<i>Lamourouxia viscosa</i> Kunth	LC	343	1,956,536	1,172	Widespread species from Mexico to Panama. Distributed in 32 protected areas.

#### Table 2: Continuation.

Species	Risk category	Number of records	EOO (km²)	AOO (km²)	Criteria
<i>Lamourouxia xalapensis</i> Kunth	LC	89	420,625	336	AOO<500 km <sup>2</sup> . Taxon mostly distributed in cloud forests, endangered by deforestation and projected decline in quality of area (Ponce- Reyes et al., 2012). Inhabiting 12 protected areas.
Lamourouxia zimapana B.L. Turner	VU B2ab(ii,iii)	9	30,469	32	Taxon severely fragmented, AOO<500 km <sup>2</sup> . Distributed in Sierra Gorda Biosphere Reserve and Los Mármoles National Park, Mexico. Endemic taxa threatened by deforestation in the TMVB (Escalante and Aguilar-Ortega, 2021).

## Weighted endemism and corrected weighted endemism

The WE analysis recovered cells with similar geographic locations and moderate to high values like those obtained by Ortiz-Brunel et al. (2021) for Echeandia, and the vascular plants of the SMS (Aragón-Parada et al., 2023). CWE analysis showed only one cell with the highest value in the state of Colima. CWE obtains values of per-species endemism, while WE retrieves richness-based endemism. The differences between the number of cells in both analyses can be explained by the masking effect of the per-species endemism metrics, where absolute concentrations of range-restricted species can be hidden by non-restricted species occurring simultaneously (Guerin et al., 2015). The only cell with high value in the CWE analysis is because of the presence of Lamourouxia colimae, which is the only species occurring in its own grid, biologically meaningful by being distributed in a different type of vegetation regarded to the other species in Lamourouxia (tropical deciduous forests vs. pine-oak and cloud forests), low elevation (450-500 m vs. >1500 m), and different soil (calcareous vs. volcanic substrates).

#### Areas of endemism

The endemicity analysis recovered three areas of endemism. Most of the surface of these areas belongs to the MTZ (SMS, SMOC, TMVB provinces). The same pattern occurs in the Mexican woody bamboos (Ruiz-Sanchez et al., 2020). The largest area of endemism of *Lamourouxia* matches with that obtained for Mexican endemic epiphytic bromeliads and orchids (Estrada-Sánchez et al., 2019). The smaller endemism areas of *Lamourouxia* include El Salto, Durango and Sierra de Quila, Jalisco, which are areas of endemism of Mexican angiosperms (Sosa and De-Nova, 2012). Also, it is coterminous with the area of endemism of many Mexican angiosperms (Rodríguez et al., 2018) located in western Jalisco. The MTZ is an extensive area with complex orography, Neotropic and Nearctic biotic exchange, and climatic stability zones, which has led to endemicity, diversification, and radiation of various lineages since the Miocene (Pinilla-Buitrago et al., 2018; Sosa et al., 2018; Morrone, 2020; Aragón-Parada et al., 2023).

#### Conservation assessments

Previously, Lamourouxia brachyantha Greenm., L. macrantha M. Martens & Galeotti, and L. nelsonii B.L. Rob. & Greenm. were considered microendemic species. This category was assigned to species recorded in a single cell of one degree per side throughout Mexico by Sosa and De-Nova (2012). In this study, with cells of 0.5 degrees per side, three species were registered as microendemics in only one cell across the Americas: L. colimae, L. jaliscana, L. parayana, followed by L. gracilis in two cells. According to the Red List of threatened species (IUCN, 2023), Orobanchaceae has 72 species evaluated but no single genus as a whole. Forty species are evaluated in the category LC, five in NT, nine in VU, six in EN, three CR, and one extinct (EX). With the evaluations given in this study, the potential three CR, four EN, 12 VU, two NT, and nine LC species to be included in the IUCN Red List, would duplicate the number of the evaluated species in Orobanchaceae. This information could address efforts in conservation, and inclusion of threatened species in the protection laws, specifically the NOM-059-SEMARNAT-2010 (SEMARNAT, 2010) from Mexico, where most Lamourouxia species are endemic.





Figure 4: Map of protected areas in the Sierra Madre del Sur biogeographic province in southern Mexico and *Lamourouxia* Kunth species richness. A. cuenca Abastecedora del Distrito Nacional de Riego 043 Nayari; B Sierra de Manantlán Biosphere Reserve; C. Tehuacán-Cuicatlán Biosphere Reserve; D. Cañón del Río Blanco National Park. Protected areas obtained from the layer of the government and private protected areas in Latin America and the Caribbean provided by the UNEP-WCMC and IUCN (2022).

According to our conservation assessments, most species populations are fragmented and threatened by human activities throughout the Americas. Surprisingly, the SMS with the highest number of endemic species in Mexico (Aragón-Parada et al., 2021) only has two small, protected areas in the western portion (Cuenca Abastecedora del Distrito Nacional de Riego 043 Nayarit, Sierra de Manantlán Biosphere Reserve) and two little areas at the eastern portion (TCBR and CRBNP) (Fig. 4). Specimens of most species were not collected within protected areas, including the species evaluated in the categories CR. Considering the evidence obtained with this study and the comprehensive evaluation of the endemism of vascular plants in the SMS, it is suggested to include most threatened *Lamourouxia* species distributed in Mexico in the conservation law NOM- 059-SEMARNAT-2010 (SEMARNAT, 2010), and increase the protection in the eastern portion of this province relevant to the flora of Mexico. This kind of studies evaluating endemism and conservation status can be replicated particularly with holoparasitic genera, which have a high extinction rate because of the specificity of their host (Cai, 2023; Schneider and Moore, 2017), being threatened by multiple biotic, abiotic and anthropogenic pressures.

## Conclusion

The MTZ is the center of diversification of *Lamourouxia*, and one third of the species of this genus is endemic to this region. Twenty-two of 30 species are classified in IUCN Red List categories. Fieldwork is necessary to rediscover microendemic species. Most *Lamourouxia* species are threatened and should be included in the protection laws in several countries of the Americas to ensure their protection.

## Author contributions

AFG wrote the manuscript, performed the taxonomic revision and analyses, and designed the figures. ERS designed the study, supervised the analyses, and wrote the manuscript. ALN revised and commented on the manuscript. All authors approved the final version of the manuscript.

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## Supplementary information

**Table S1:** Photographic credits and accession addresses.

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Appendix 1: Database with georeferenced herbaria specimens and observations of citizen science with accessions addresses of *Lamourouxia* Kunth species in the Americas.

Appendix 2: XYD file with georeferenced occurrence data of Lamourouxia Kunth species.

