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The rarest of rarities in the flora of Mexico

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Abstract:
Background: Endemism can originate from multiple biogeographic and evolutionary processes that promote the formation or persistence of species with restricted distributions (rare species). Understanding rare species' distributions is a central question in biogeography and is crucial for biodiversity conservation.
Questions: What are the rarest plant species in Mexico? How are they distributed? Under what risk categories should they be classified?
Studied species: Vascular species considered rare in the flora of Mexico.
Study site: Mexico.
Methods: "Rare species" were defined as species endemic to Mexico whose distribution is restricted to a single 1 × 1° cell. We analyzed rare species' distributions and proposed the risk category for each according to IUCN criteria. For some of the species distributed in the cell with the highest number of rare species, we compared the proposed category with published evaluations.
Results: We identified 2,705 rare species. The richest cells in terms of rare species are in southern Mexico. Only 302 species had been previously evaluated under IUCN criteria. The remaining 2,403 qualify for the Near Threatened (NT) category or higher. The cell with the highest rare species richness, located in the Sierra Norte of Oaxaca, contained only 10 species with an existing IUCN risk category; for another 81 species, the categories of Vulnerable (VU), Endangered (EN) or Critically Endangered (CR) are indicated.
Conclusions: Recognizing the rarity of these 2,705 species will increase attention on them, allowing more precise appraisal of their extinction risk and possible strategies for their conservation.
Keywords: Alpha diversity, Area of Occupancy, Endemism, Extent of occurrence, IUCN, Species threatened.

Resumen:
Antecedentes: El endemismo puede originarse a partir de múltiples procesos biogeográficos y evolutivos que promueven la formación o persistencia de especies de distribución restringida o raras. Entender su distribución es una cuestión central en biogeografía y crucial para la conservación de la biodiversidad.
Preguntas: ¿Cuáles son las especies de plantas raras en México? ¿Cómo se distribuyen? ¿Bajo qué categorías de riesgo son clasificadas?
Especies de estudio: Especies vasculares consideradas raras en la flora de México.
Sitio: México.
Métodos: Se identificaron las especies endémicas de México cuya distribución se restringe a una sola celda de 1 × 1°, llamadas especies raras. Se analizó su distribución y se propuso una categoría de riesgo de acuerdo con la IUCN; para algunas de ellas incluidas en la celda con mayor número de especies raras se comparó contra evaluaciones publicadas.
Resultados: Se identificaron como raras 2,705 especies. Las celdas más ricas se encuentran en el sur del país. Sólo 302 especies han sido evaluadas con los criterios de la IUCN, las restantes 2,403 al menos deberían de tener la categoría de Casi amenazadas (NT). Una celda en la Sierra Norte de Oaxaca contó con la mayor diversidad alfa; sin embargo, sólo 10 de ellas tienen una evaluación por la IUCN, para otras 81 especies se determinaron categorías como Vulnerable (VU), En peligro (EN) y En peligro crítico (CR).
Conclusiones: El reconocimiento de 2,705 especies raras permitirá ahora prestarles más atención, definiendo con más detalle su riesgo de extinción y las posibles estrategias para su conservación.
Palabras clave: Área de ocupación, Diversidad alfa, Endemismo, Especies amenazadas, Extensión de ocurrencia, IUCN.

Some species are found across multiple hemispheres, while others are only known from a few localities; this enormous variation in species' range size has long intrigued scientists. Recently, Enquist *et al.* (2019) revealed that more than a third of the world's flora should be considered rare. Meanwhile, when Villaseñor & Meave (2022) tabulated the number of grid cells (1° latitude and longitude size) occupied by 25,077 species in Mexico; they documented 4,633 species that have been recorded in only one grid square (singletons) and 3,943 species found in two grid squares (doubletons). Thus, the number of species with restricted distribution comprise an important proportion of Mexico's flora (Villaseñor & Meave 2022).

Small geographic range sizes are among the most important predictors for assessing species' risk of extinction (Purvis *et al.* 2000). The International Union for Conservation of Nature (IUCN) proposes a series of criteria to classify species by their potential risk of extinction (IUCN 2022); most of the species that meet these criteria are considered rare and more likely to become extinct. Some of the most important criteria are the populations' estimated size reduction, the decline in habitat quality, extent of occurrence (EOO), and area of occupancy (AOO). For example, to assign a species to the Near Threatened category (NT) under Criterion B (excluding population numbers or their fragmentation) requires an EOO less than 20,000-30,000 km^2 or AOO less than 2,000-3,000 km^2 (IUCN 2022).

During the last three decades, an effort has been made to document the geographic distribution of the species that make up the flora of Mexico at the national level. Due to the country's large surface area and paucity of data, a grid network of 1° latitude and longitude has been used to estimate the AOO of species and subspecific taxa (Figure 1) based on current information obtained from published literature and online databases. These data now make it possible to establish the number of grid cells occupied by most taxa of the Mexican flora, which can in turn be used to define as a rare species any species recorded in a single grid cell (*i.e.*, "singletons").

The numbers of singletons and doubletons considered by Villaseñor & Meave (2022) represent 34.2 % of the total Mexican flora known to date, comparable to the worldwide percentage determined by Enquist *et al.* (2019). At the latitude of the country, the 1° latitude and longitude grid cells used to assess the geographic distribution of species measure approximately 11,638 km^2. This area is smaller than the lower bound IUCN Criterion B to determine NT species based on EOO. Therefore, singletons (especially endemic ones) should be included in the Red List of species.

Because the levels of endemism in the flora of Mexico are now better understood, in this paper we perform a spatial analysis of the geographic distribution of the rarest set of endemic species in the flora of Mexico (hereafter referred to interchangeably as singletons or rare species). Since the level of risk is unknown for a high percentage of them given their rarity, we postulate that evaluating their distribution will substantially enrich the number of species that should be considered in future conservation strategies. As indicated above, in addition to population size and habitat degradation, the species' range is an important parameter to determine its potential risk of extinction. Determining the alpha diversity of grid cells in terms of the rarest species allows further analyses aimed at estimating patterns of diversity.

Materials and methods

We performed a literature review and the examination of public databases to gather information on the specific distribution sites of rare species. The databases consulted were the two most important Mexican internet-accessed databases, the SNIB of the *Comisión Nacional para el Conocimiento y Uso de la Biodiversidad* (CONABIO: www.conabio.gob.mx) and IBData from the *Instituto de Biología, Universidad Nacional Autónoma de México* (UNAM) (www.ibdata.ib.unam.mx).

First, we verified the distribution in 1° degree latitude and longitude grid cells for all rare endemic species. Then, as a case of study, we used the georeferenced data for the rarest species within the grid cell that was richest in rare species to estimate the EOO and AOO of each species with higher precision. This latter process was performed using the R package ConR (Dauby *et al.* 2017). Although there are native non-endemics and introduced species that are only known from a single grid square (singletons), in this study we considered only species endemic to Mexico, since they constitute the main group of species considered in red lists, for example, the Norma Oficial Mexicana 059 (SEMARNAT 2010) or the IUCN (IUCN 2022, 2023).

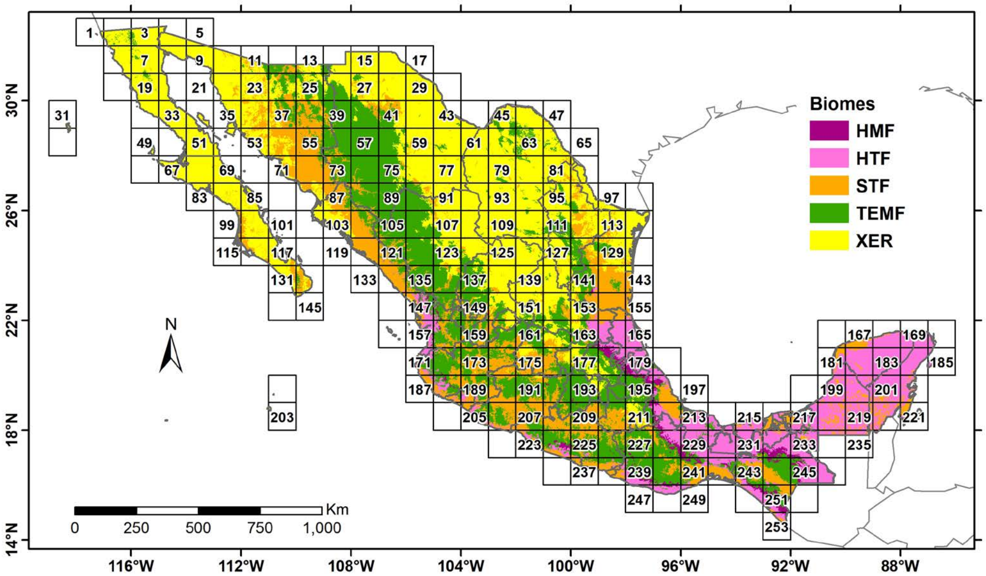

Figure 1. Mexico divided into 1° latitude and longitude grid cells. The numbering was used to locate each species in its respective grid square. The biomes correspond to the regional classification for Mexico by Villaseñor & Ortiz (2014). HMF = Humid Montane Forest, HTF = Humid Tropical Forest, TEMF = Temperate Forest, STF = Seasonally Dry Tropical Forest, XER = Xerophytic Scrub.

The known distribution of endemic Mexican singletons was first determined by state distribution and mapped on the grid cell size used to determine patterns of alpha diversity. This made it possible to detect areas of high concentration of rare species throughout the Mexican territory. In addition, we determined the biome(s) in which species occurred by overlapping the species' occurrences with the shapefile of the main biomes of Mexico (Villaseñor & Ortiz 2014). We used this information to calculate the incidence of rare species by biome for each grid cell.

It has been discussed that site-level environmental conditions change at approximately 5 km (Graham *et al.* 2008). Therefore, records of rare species from sites at least 5 km apart were considered to show sufficient environmental variation to be considered members of distinct populations. The number of records selected with this procedure was considered equivalent to the global species abundance distribution (gSAD) as defined by Enquist *et al.* (2019), and was therefore used to assess the number of observations or samples for each species.

Results

The rarest vascular flora of Mexico (singletons) comprises 2,705 species, distributed among 51 orders, 140 families, and 722 genera (Table 1). There were rare species from all major taxonomic groups except for the basal angiosperms. The Asterids, Rosids, and Monocots had especially large numbers of rare species, while the Ferns and allies, Eudicots and Gymnosperms had the lowest numbers.

Table 2 includes the families and genera with the highest number of rare species. The three families with the highest numbers of rare species were Asteraceae, Fabaceae, and Crassulaceae; at the genus level, the highest number of rare species were from *Salvia* (Lamiaceae), *Tillandsia* (Bromeliaceae), and *Echeveria* (Crassulaceae). The 15 families listed in Table 2 (10.6 % of the total families with rare species) accounted for 62.3 % of all rare species, while the 15 genera in Table 2 account for 18.8 % of all rare species.

Distribution of rare species by grid cell. Figure 2 shows the grid cells with the rarest endemic species. Of the 253 grid cells into which the country is divided, 66 did not contain rare species; most of them cover only a small portion of the mainland territory (*i.e.*, a large portion of the grid square area was water or shared with foreign countries). The other grid cells (N = 169) contained between one species (34 grid cells) to a maximum of 138 (grid cell 228), with a median of six species and a mode of one.

Table 1. Taxonomic distribution of the rare endemic species (recorded in one grid square) in the flora of Mexico. Angiosperms were subdivided into their six major phylogenetic groups according to APG IV (2016).

Plant group	Orders	Families	Genera	Species
Ferns and Monilophytes	5	12	18	39
Gymnosperms	2	2	4	21
Basal Angiosperms	-	-	-	-
Magnoliids	3	6	12	111
Monocots	9	18	125	599
Eudicots	3	5	7	13
Rosids	16	48	193	725
Asterids	13	49	363	1,195
	51	140	722	2,705

Table 2. The 15 families and genera in Mexico with the highest number of rarest species.

Family	Species	Genus	Species
Asteraceae	373	*Salvia*	82
Fabaceae	191	*Tillandsia*	66
Crassulaceae	147	*Echeveria*	58
Bromeliaceae	146	*Hechtia*	50
Orchidaceae	145	*Sedum*	44
Rubiaceae	128	*Ageratina*	40
Lamiaceae	118	*Agave*	37
Asparagaceae	102	*Verbesina*	37
Euphorbiaceae	85	*Carex*	30
Cactaceae	81	*Pinguicula*	29
Acanthaceae	60	*Piper*	27
Poaceae	53	*Begonia*	25
Apocynaceae	52	*Euphorbia*	25
Piperaceae	51	*Lobelia*	25
Cyperaceae	45	*Peperomia*	24

A total of 85 grid cells (Table 3) had more than the median of six rare species. The five grid cells with the largest number of rare species were cells 228 (138 species), 227 (102), 225 (89), 211(85), and 240 (85). Three of these five richest grid cells were contained within the state of Oaxaca (227, 228, and 240), one was contained within the state of Guerrero (225), and one was mostly in Puebla with some extension into Oaxaca and Veracruz (211; Table 3, Figure 2).

Distribution of rare species by state. All the Mexican states include at least one rare species (Table 4); however, two states (Aguascalientes and Tlaxcala) had no rare species that were exclusively distributed in that state since all of the rare species present were in grid cells that included the area from a neighboring state. For example, of the 10 rare species recorded in the grid cells including territory in Aguascalientes, five are shared with Jalisco, four with Zacatecas and one is shared in the grid cell that contains areas of Aguascalientes, Jalisco, and Zacatecas (grid cell 160).

The states with the highest total numbers of rare species were Oaxaca (615), Jalisco (296), Guerrero (270), Chiapas (248), and Veracruz (240). When considering only the rare species that are state endemics (*i.e.*, all known occurrences are within a single state), Chiapas moves to second place (228) and Jalisco to fourth (200), while the other states maintain the same order. In total, the known distribution of 75.5 % of all rare species is restricted to a single state.

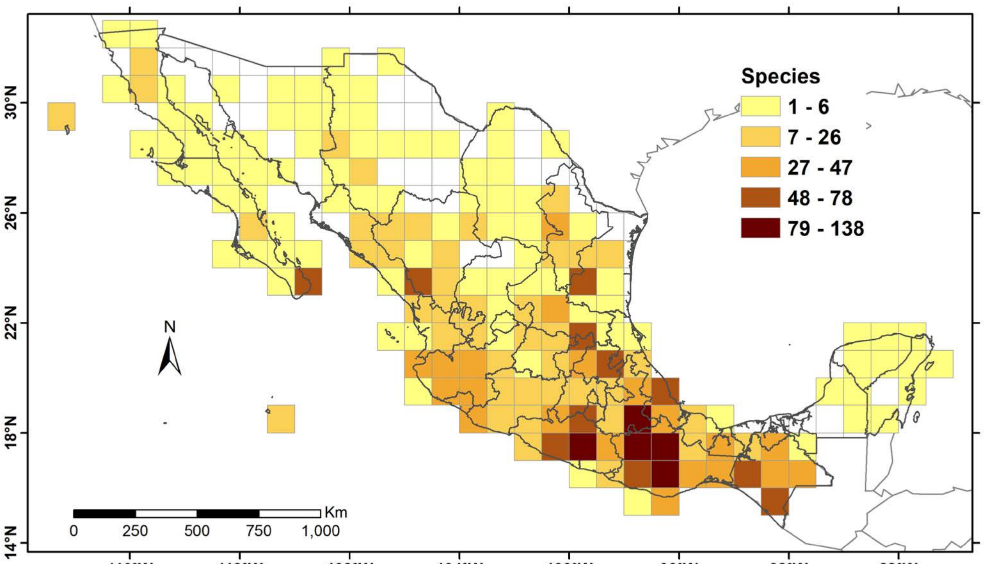

Figure 2. Frequency of the 2,705 rare Mexican endemic species in each of the grid cells used to subdivide the territory (1° latitude and longitude; see Figure 1). The first class shows values less than or equal to the median (six).

Distribution of rare species by biome. Table 5 indicates the occurrence of rare endemic species among the five major biomes considered by Villaseñor & Ortiz (2014). Not all the major plant groups are found in a single biome, although several include representative species (known only in that biome, Table 5). Ferns and Monilophytes as well as Eudicots and Magnoliids are better represented in humid environments, either in humid lowlands (HTF) or humid montane areas (HMF). Gymnosperms predominate in montane biomes (HMF and TEMF), although an equivalent number is present in the HTF, mostly characterized by Zamiaceae species. The most derived lineages (Monocots, Rosids, and Asterids) are in general more homogeneously distributed among the biomes. Temperate forests (TEMF) had the largest number of species of both Asterids and Rosids, Asterids are equally represented in HMF and XER, Monocots are second in Humid mountain forests (HMF) and Rosids in Seasonally dry tropical forests (STF).

Rare species and their status according to the IUCN criteria. Only 302 species recorded any risk status agreeing to IUCN standards (Supplementary material); this number represents 11.1 % of the total rare species. From least to the greatest threat, 37 species are listed as Data Deficient (DD), 21 as Least Concern (LC), six as Near Threatened (NT), 24 as Vulnerable (VU), 115 as Endangered (EN), and 98 as Critically Endangered (CR). One species is considered extinct (EX, *Faramea chiapensis* Borh.).

The state of Oaxaca, in addition to concentrating the greatest richness of species, contained the three grid cells with the greatest numbers of rare species. Grid cell 228, which had the greatest number of rare species, was selected to develop a case study aimed at evaluating the species' potential risk category according to IUCN criterion B. We selected a total of 91 species (out of 138) recorded in the grid cell that had occurrence records in the analyzed database. Table 6 provides the EOO and AOO surface area estimated, as well as the corresponding threat category; the number of localities per species and the unique localities after applying a filter of 5 km distance between all known localities are also indicated. Based on the calculation of the EOO, from lowest to highest risk, one species qualifies as Vulnerable (VU), 20 Endangered (EN), and 70 Critically Endangered (CR). Considering the AOO value, 30 species qualify as Endangered (EN) and 61 as Critically Endangered (CR). The number of localities per species ranged from one (35 species) to 30 (one species) when considering all known locations; after applying the 5 km distance filter, the number of unique localities ranged from one (41 species) to 17 (one species).

Discussion

Villaseñor & Meave (2022) in the most recent listing of the vascular plants of Mexico, considered 25,077 species (native and exotic), which accounts for 7 % of all the vascular flora in the world (Murguía-Romero *et al.* 2023). These authors reported 4,633 singletons in total; here we consider only the 2,705 that are also endemic to Mexico. Thus, there are 1,928 additional singletons representing native non-endemic (as well as several exotic) species. Thus, 10.7 % of the flora of Mexico constitute the rarest endemic elements.

Table 3. Number of rare Mexican endemic species recorded in the grid cells with more than six species (median or above of total grid cells).

Grid cell	Species	Grid cell	Species
228	138	158	20
227	102	031	19
225	89	213	19
211	85	207	18
240	85	210	18
251	78	127	15
141	72	193	15
163	68	128	14
243	68	136	13
224	64	019	12
196	61	95	12
209	57	194	12
135	54	149	11
132	53	159	11
178	51	206	11
239	51	056	10
189	47	074	10
111	45	176	10
173	45	108	9
188	45	123	9
241	45	147	9
172	41	174	9
226	39	179	9
248	39	100	8
171	38	105	8
177	37	121	8
195	37	223	8
208	36	229	8
245	35	007	7
242	34	106	7
230	33	120	7
205	31	129	7

Grid cell	Species	Grid cell	Species
232	31	151	7
244	31	161	7
212	30	231	7
152	29	238	7
192	27	109	6
191	24	137	6
190	23	153	6
203	23	160	6
104	21	187	6
148	21	219	6
162	21		

Table 4. Number of rare Mexican endemic vascular plant species by state in Mexico.

State	Species	Species exclusive to the state
Aguascalientes	10	-
Baja California	68	62
Baja California Sur	86	80
Campeche	11	3
Chiapas	248	228
Chihuahua	47	30
Ciudad de México	3	1
Coahuila	79	28
Colima	42	26 (7 in Revillagigedo Archipelago)
Durango	132	47
Guanajuato	47	10
Guerrero	270	204
Hidalgo	89	19
Jalisco	296	200
México	89	34
Michoacán	142	80
Morelos	30	19
Nayarit	66	14 (4 in Marias Islands)
Nuevo León	108	36
Oaxaca	615	534
Puebla	132	58
Querétaro	107	21
Quintana Roo	12	3
San Luis Potosí	119	31
Sinaloa	99	45
Sonora	33	17
Tabasco	23	8

State	Species	Species exclusive to the state
Tamaulipas	106	60
Tlaxcala	1	-
Veracruz	240	131
Yucatán	13	7
Zacatecas	52	6
	2,705	2,042

The taxonomic dispersion of rare species is wide; they included 51 of the 77 orders (66.2 %) recognized for Mexico by Villaseñor (2016), 140 of the 297 families (47.1 %), and 722 of the 2,854 genera (25.3 %). Therefore, rare species represent almost the entire evolutionary spectrum of vascular plants. Only the most basal group of the flowering plant phylogeny (Basal Angiosperms) had no rare endemic species, although some of its representatives with a greater distribution (non-singletons) will surely be included in some risk category when they are properly evaluated. Among the oldest rare species of the flora of Mexico, the genus *Ceratozamia* Brongn. merits special mention: this genus of gymnosperms originated a little more than 50 million years ago (Lu *et al.* 2014). It contains about 36 species (Martínez-Domínguez *et al.* 2022) distributed in Mesoamerica (Mexico to Honduras), 35 of them native to Mexico and 12 considered rare in this work. Rare species from this genus were found in ten grid cells (163, 178, 196, 228, 232, 238, 241, 242, 243, 248), making these locations potential centers of paleo-endemism, especially grid cell 196, which contained three of the rare species.

Among the rare species considered, some of hybrid origin also deserve special mention. The species list (Supplementary material) includes 18 species (nothospecies) and two genera (nothogenera: × *Pacherocactus*, and × *Patrocereus*, Cactaceae). These taxa represent examples of evolutionary events by hybridization (and probably introgression) that shaped the great floristic diversity in the country. These phenomena will surely reveal the possible hybrid origin of many species of our flora (*e.g.*, Weiss-Schneeweiss *et al*. 2012).

Asteraceae and Fabaceae stand out as the most important families in terms of their number of rare species. They likewise occupy the two first places when considering total Mexican floristic richness (Villaseñor 2016). In third place is Crassulaceae, showing a relevant number of rare species, despite being in sixteenth place in terms of its total number of species in the country (Villaseñor 2016). Orchidaceae and Poaceae, which are the third and fourth richest families in terms of total species, are positioned in fifth and twelfth place, respectively, when considering rare endemic species. Other families that are notable for their number of rare species, although not for their total number of species in Mexico, are Bromeliaceae (fourth place), Asparagaceae (eighth), or Acanthaceae (eleventh).

It is interesting to highlight that for ten families, more than a quarter of their total species in Mexico are rare species; these include Amaryllidaceae (25.6 %), Bromeliaceae (31.3 %), and Crassulaceae (34.9 %). Only Lecythidaceae, a monospecific family, is considered a rare family following the criteria applied in this work. For 40 genera, 100 % of their species are rare; these were monospecific genera, except *Cotinus* and *Petronymphe* (with two species), and *Cremnophila* (with three species). Based on figures proposed by Villaseñor (2016), 22.7 % of vascular plant genera in Mexico contain rare species.

Although the number of rare species is greater in the tropical region of Mexico (2,139 species), a substantial number (566 species) is recorded from the extratropical region (above the Tropic of Cancer). The number of species recorded in the extratropical region of Mexico is strongly related to the prevailing biomes in this region; the largest number corresponds to the TEMF (240 species) and the XER (161), with low numbers in STF (62), HMF (34) and HTF (7).

Centers of endemism represent areas of special evolutionary history, and probably centers of diversification. To date, efforts have been made to identify areas of floristic endemism at the national level (*e.g.*, Rzedowski 1991, Villaseñor & Meave 2022), at more local scales (*e.g.*, Ibarra-Manríquez *et al.* 1995, Vega-Aviña *et al.* 2000, Méndez-Larios *et al.* 2004, Salinas-Rodríguez *et al*. 2017, Villarreal-Quintanilla *et al*. 2017, Estrada-Márquez *et al.* 2020, Aragón-Parada *et al.* 2021), and even for specific taxonomic groups (*e.g.*, Villaseñor 1990, 1991, Lira *et al.* 2002, Villarreal-Quintanilla *et al.* 2005, 2017, Suárez-Mota & Villaseñor 2011, Salinas-Rodríguez *et al.* 2017, Delgadillo-Moya *et al.* 2003, 2019). However, mapping full sets of vascular plant species richness, especially endemic and/or rare species has been poorly done in Mexico. Few projects are focused on these topics or aimed at identifying species at risk. In addition, species' EOO or AOO have been estimated only in single-species studies or considering groups of species (*e.g.*, Vázquez-García *et al.* 2013, Redonda-Martínez *et al.* 2021, Samain *et al.* 2022), rarely considering the full set of endemic species. This is the first attempt to analyze the entire set of endemic species with restricted geographical distribution.

Rare species considered in this study mostly fall into one of the three types of rare species discussed by Drury (1974). Although little is known about the size of their populations, they are species known from a few localities in a narrow geographic area. Likewise, they constitute part of the set of species defined as rare by Rabinowitz (1986) due to their restricted range of distribution. Taking this criterion of restricted geographic distribution as a first step toward a more precise definition of the rarity concept will lead to this concept becoming clearer, justifiable, and refutable. Thus, the restricted distribution to a single grid cell of 2,705 endemic species, meets the rarity criteria as defined based on restricted distribution.

Table 5. Number of rare Mexican endemic species distributed in major taxonomic groups and their occurrence in the five major biomes in the country (Villaseñor & Ortiz 2014). The number of species recorded exclusively in each biome is indicated in parentheses. HMF = Humid Montane Forest, HTF = Humid Tropical Forest, TEMF = Temperate Forest, STF = Seasonally Dry Tropical Forest, XER = Xerophytic Scrub.

Plant group	HMF	HTF	STF	TEMF	XER
Ferns and Monilophytes	15 (9)	5 (1)	3 (3)	13 (11)	2
Gymnosperms	6 (2)	7 (6)	3 (1)	7 (3)	1
Basal Angiosperms	-	-	-	-	-
Magnoliids	41 (22)	32 (25)	14 (7)	25 (10)	2 (1)
Monocots	124 (46)	75 (34)	126 (70)	283 (181)	71 (44)
Eudicots	3 (3)	-	1 (1)	2 (2)	2 (2)
Rosids	87 (36)	83 (50)	182 (118)	260 (166)	104 (80)
Asterids	231 (82)	130 (70)	184 (108)	561 (371)	225 (167)
	507 (200)	332 (186)	513 (308)	1,152 (745)	408 (295)

Distribution of rare species by state. Species conservation strategies are carried out at different government levels. The numbers of rare species found in this study (Table 1) put into perspective the importance of national-level strategies in protecting this important component of their biodiversity. However, almost all states showed significant numbers of rare species (Table 4), and a high percentage of rare species were restricted to a single state's political territory. Consequently, state and municipal governments should commit to their conservation, considering information of this type in addition to previously published evaluations of species' risk levels (*e.g.*, Vázquez-García *et al.* 2013, Redonda-Martínez *et al.* 2021, Samain *et al.* 2022).

The importance of documenting lists like the one included in Supplementary material, even at the coarsest scale of state political divisions, allows for subsequent evaluations of species that would otherwise go unnoticed. Without a doubt, many species listed here will be documented in additional states or grid cells in the future, which will change their status from rarer to more widely distributed. An example is the orchid *Anathallis oblanceolata* (L.O. Williams) R. Solano & Soto Arenas. This species was initially considered micro-endemic to the state of Oaxaca and defined as a singleton, but recent studies have expanded its distribution to at least five additional states, now occupying a total of nine grid cells (Solano & Licona 2023). However, despite the species showing a broader distribution than initially documented, this orchid is known from no more than 13 herbarium specimens or observations, highlighting its small number of populations.

Distribution of rare species by biome. It is important to underline the ecological fidelity of rare species to one or two contiguous biomes (Table 5); 1,734 species are reported from a single biome, while 510 have been documented from two biomes and only 50 species have been recorded in three biomes.

The biomes with the highest number of species showing ecological fidelity are the temperate forests (TEMF), with 745 species known only from that biome. Seasonally dry tropical forests (STF, 308 species), and the Xeric scrublands (295) follow, and the Humid mountain forests (HMF) and Humid tropical forests (HTF) have fewer rare endemic species, although their numbers are not negligible (200 and 183 respectively). A smaller number of species (971) was distributed in two or more biomes, showing adaptations to a slightly greater ecological variation, as an adaptive response to the biomes where they occur.

Distribution of rare species by grid cell. Strategies for the conservation of the documented rare species should lead to commitments at the federal level considering all rare species at the national level, at the state level considering the grid cells comprising their territory (for example five grid cells in Oaxaca, three in Guerrero, or two in Durango), or concerted actions among states that share territory with important concentrations of rare species (Table 3). The Island of Guadalupe (grid cell 31) or the Revillagigedo archipelago (summarized in grid cell 203) also deserve special mention; they represent the most important island component in addition to the conterminous country and display important numbers of rare species.

Future work will provide a better understanding of the biotic or abiotic factors that determine the sympatric occurrence of rare species. For example, what are the factors that promoted the evolution of the 138 species known only from grid cell 228? This grid cell includes the central valleys of the state of Oaxaca (including part of the Tehuacán-Cuicatlán valley), as well as an important mountain range, known as the Sierra Norte or Sierra de Juárez, characterized by an unusual richness of flora and endemism (Torres-Colín *et al.* 2009, Suárez-Mota *et al.* 2018). Each of the 85 grid cells included in Table 3 merits its own study since they constitute centers of endemism that surely have historical and ecological components that, once known, will improve our understanding of the enormous floristic diversification that has taken place in the country.

Rare species and their status according to the IUCN criteria. In addition to geographic restrictions, population size, and ecological constraints are parameters used to assess risk status. The 302 species that already had an assigned IUCN risk category share a low population density, represented by the small number of observations in the field. As shown in Table 6, the other 2,403 rare species recorded in this study that have not yet been specifically evaluated also contain few records of occurrences, with many of them known only by the type specimen with which they were described. In addition, as shown in Table 5, they show ecological fidelity to one or two biomes.

Primary vegetation in Mexico faces significant risks from land use change. For example, in a cartographic evaluation of the land use and vegetation done by INEGI in 2005, 28 % of the national territory was surface without natural vegetation (Villaseñor 2015). Specifically, the analysis revealed that practically all states have more than 30 % of their surface transformed, with especially high proportions in Chiapas (45 %), Guerrero (33 %), Jalisco (37 %), Michoacán (39 %), and Oaxaca (33 %), and in most extreme case, Veracruz, in which 80 % the state's area was without primary vegetation. In the two decades since then, much more primary vegetation territory has surely been lost. Therefore, it is urgent to determine the risk level of most species, especially the rarest ones that show the strongest ecological fidelity, restricting their occurrences to one or two biomes (Table 5, Supplementary material).

The identification of only 302 species in some risk category based on the IUCN criteria prior to this study highlights the deficiencies in this aspect. For example, Samain *et al.* (2022) evaluated 1,474 tree species that are endemic or nearly endemic to Mexico and determined their IUCN risk status; among them, 119 are listed as rare in this paper, and 66 additional rare tree species here included were not considered in their evaluation. More than 88 % of rare species have not been formally categorized according to the IUCN classification, although our findings show that all of them should be classified at least as NT, based on their restricted geographical distribution.

Among the 91 species analyzed specifically for grid 228, only 10 of them are currently registered on the IUCN Red List (Table 6); the remaining 81 species, based on Criterion B for EOO (IUCN 2022), all qualify for (at least) the Near Threatened (NT) category. Based on species records obtained from the online databases, we found here that some species fulfill the EOO and AOO criteria for inclusion in higher-risk categories, such as Vulnerable (VU), Endangered (EN), and Critically Endangered (CR) (see Table 6). If the study case with the 91 species in grid cell 228 is extrapolated to the 2,403 rare species in Mexico that have not yet been evaluated, it is likely most of them will also be classified in categories of greater risk of extinction. In addition, for the 10 species evaluated following the IUCN Red List criteria, the estimated AOO in this study raises the risk category in half of the cases (Table 6) -two species classified as Least Concern would become Endangered, one Vulnerable species would become Endangered, two Endangered species would be Critically Endangered.

Table 6. A selected list of 91 rare Mexican endemic species (out of 138) occurring in grid cell 228 in Oaxaca, their EOO and AOO values estimated with updated information, and their cited threat category according to IUCN (IUCN 2022). The number of filtered localities was obtained after applying the threshold distance of 5 km among all known localities. In the Red List column, the species' currently recognized risk category on the IUCN Red List is indicated (IUCN 2023); empty cells indicate that the species has not been formally evaluated.

Family / Species	EOO Km²	EOO Category	AOO Km²	AOO Category	Localities	Localities filtered	Red List
Acanthaceae							
Justicia angustiflora	4	CR	4	CR	1	1	
Justicia torresii	4	CR	4	CR	1	1	
Stenostephanus oaxacanus	4	CR	4	CR	1	1	
Apocynaceae							
Matelea gracilis	4	CR	4	CR	1	1	
Matelea oaxacana	8	CR	8	CR	2	2	
Araceae							
Anthurium cerropelonense	537.5	EN	24	EN	8	6	
Anthurium subovatum	1,153.8	EN	40	EN	13	10	
Anthurium yetlense	8	CR	8	CR	2	2	
Arecaceae							
Chamaedorea queroana	8	CR	8	CR	2	2	
Asparagaceae							
Echeandia llanicola	4	CR	4	CR	2	1	
Maianthemum comaltepecense	4	CR	4	CR	1	1	
Aspleniaceae							
Asplenium stolonipes	4	CR	4	CR	1	1	
Asplenium yelagagense	4	CR	4	CR	1	1	
Asteraceae							
Achyrocline oaxacana	8	CR	8	CR	2	1	

Family / Species	EOO Km²	EOO Category	AOO Km²	AOO Category	Localities	Localities filtered	Red List
Ageratina etlana	4	CR	4	CR	1	1	
Ageratina humochica	4	CR	4	CR	1	1	
Ageratina megaphylla	4	CR	4	CR	1	1	
Ageratina soejimana	4	CR	4	CR	1	1	
Ageratina tejalapana	4	CR	4	CR	1	1	
Bartlettina calderonii	5.75	CR	12	EN	3	3	
Chionolaena eleagnoides	1,049	EN	40	EN	13	9	
Mikania pooleana	4	CR	4	CR	1	1	
Oxylobus subglabrus	262.3	EN	16	EN	5	4	
Psacalium beamanii	4	CR	4	CR	3	1	
Stachycephalum mexicanum	4	CR	4	CR	1	1	
Stramentopappus congestiflorus	33.4	CR	12	EN	5	4	
Telanthophora liebmannii	2,096.1	EN	76	EN	23	15	
Bromeliaceae							
Tillandsia lagunaensis	8	CR	8	CR	2	2	
Cactaceae							
Opuntia chiangiana	4	CR	4	CR	2	1	
Caricaceae							
Horovitzia cnidoscoloides	1,486.3	EN	68	EN	27	14	VU
Clethraceae							
Clethra luzmariae	2,092.4	EN	36	EN	20	8	EN
Crassulaceae							
Echeveria brachetii	4	CR	4	CR	1	1	
Echeveria juarezensis	9,085.5	VU	40	EN	10	9	
Echeveria zorzaniana	8	CR	8	CR	2	2	
Sedum porphyranthes	4	CR	4	CR	1	1	
Sedum pulvinatum	8	CR	8	CR	2	2	
Thompsonella spathulata	4	CR	4	CR	1	1	
Villadia imbricata	1,708.8	EN	12	EN	3	3	
Cyperaceae							
Carex austromexicana	8	CR	8	CR	2	2	CR
Carex flexirostris	8	CR	8	CR	2	2	
Dennstaedtiaceae							
Hypolepis microchlaena	4	CR	4	CR	1	1	
Dryopteridaceae							

Family / Species	EOO Km²	EOO Category	AOO Km²	AOO Category	Localities	Localities filtered	Red List
Elaphoglossum leonardii	4	CR	4	CR	1	1	
Ericaceae							
Orthaea stipitata	8	CR	8	CR	2	2	
Euphorbiaceae							
Euphorbia xylopoda	17.2	CR	12	EN	3	2	
Plukenetia carabiasiae	3.95	CR	12	EN	4	3	
Fabaceae							
Dalea rubrolutea	8	CR	8	CR	2	2	
Gesneriaceae							
Corytoplectus oaxacensis	73.3	CR	12	EN	7	4	
Moussonia hirsutissima	675.5	EN	52	EN	19	9	
Smithiantha laui	8	CR	8	CR	2	2	
Solenophora coccinea	8	CR	8	CR	2	2	
Iridaceae							
Sisyrinchium planicola	4	CR	4	CR	1	1	
Lamiaceae							
Condea mixta	4	CR	4	CR	1	1	
Stachys torresii	4	CR	4	CR	1	1	
Lauraceae							
Licaria chinanteca	77.3	CR	16	EN	8	4	LC
Ocotea sauroderma	942.9	EN	24	EN	8	5	LC
Lentibulariaceae							
Pinguicula hemiepiphytica	420.9	EN	64	EN	20	11	
Loranthaceae							
Struthanthus alnii	8	CR	8	CR	2	2	
Malvaceae							
Triumfetta martinezalfaroi	8	CR	8	CR	3	1	
Melanthiaceae							
Schoenocaulon conzattii	8	CR	8	CR	2	2	
Melastomataceae							
Miconia erythrantha	8	CR	8	CR	2	2	
Miconia liebmannii	1,527.9	EN	88	EN	30	17	
Miconia phaeotricha	4	CR	4	CR	1	1	
Monimiaceae							
Mollinedia torresiorum	98.2	CR	20	EN	6	5	

Family / Species	EOO Km²	EOO Category	AOO Km²	AOO Category	Localities	Localities filtered	Red List
Onagraceae							
Lopezia smithii	4	CR	4	CR	2	1	
Orchidaceae							
Epidendrum costatum	4	CR	4	CR	1	1	
Habenaria felipensis	4	CR	4	CR	1	1	
Habenaria ixtlanensis	8	CR	8	CR	2	2	
Lepanthes aprica	4	CR	4	CR	1	1	
Lepanthes catlingii	4	CR	4	CR	1	1	
Lepanthes chiangii	337.7	EN	12	EN	3	3	
Lepanthes galeottiana	160.3	EN	28	EN	8	6	
Lepanthes schultesii	8	CR	8	CR	2	2	
Oncidium iricolor	8	CR	8	CR	2	2	
Orobanchaceae							
Castilleja dendridion	4	CR	4	CR	1	1	
Passifloraceae							
Passiflora complanata	2,254.8	EN	44	EN	13	9	
Pentaphylacaceae							
Cleyera cernua	145.9	EN	12	EN	3	3	EN
Primulaceae							
Parathesis cuspidata	372.2	EN	24	EN	6	5	
Parathesis gracilis	4	CR	4	CR	1	1	
Ranunculaceae							
Thalictrum nelsonii	4	CR	4	CR	1	1	
Rubiaceae							
Arachnothryx ginetteae	8	CR	8	CR	2	2	
Deppea arachnipoda	4	CR	4	CR	1	1	
Deppea keniae	4	CR	4	CR	1	1	EN
Deppea martinez-calderonii	112.4	EN	16	EN	4	3	
Didymaea ixtepejiensis	4	CR	4	CR	1	1	
Mexotis kingii	73.6	CR	20	EN	5	4	
Randia nodifolia	4	CR	4	CR	1	1	
Sabiaceae							
Meliosma starkii	9.84	CR	12	EN	5	3	EN
Selaginellaceae							
Selaginella cuneata	46.6	CR	8	CR	3	2	

Family / Species	EOO Km²	EOO Category	AOO Km²	AOO Category	Localities	Localities filtered	Red List
Selaginella subrugosa	353.7	EN	20	EN	9	5	
Thymelaeaceae							
Daphnopsis liebmannii	4	CR	4	CR	1	1	EN
Zamiaceae							
Ceratozamia whitelockiana	1,003.6	EN	16	EN	4	4	EN

Conservation biology relies on a good knowledge of species richness, endemism, and rarity. Data on Mexican richness and endemism have already been published using grid cells (*e.g.*, Cruz-Cárdenas *et al.* 2013, Rodríguez *et al.* 2018, Villaseñor 2016, Villaseñor & Meave 2022). However, rarity as a concept has been poorly discussed in the Mexican botanical literature. In this study, we found that the rarest species endemic to Mexico, characterized by their restricted geographic distribution, accounted for 10.7 % of the total vascular flora. Identifying these species is a fundamental first step toward determining their risk status and selecting better sites for the conservation of the rarest elements of the flora of Mexico.

Rare species probably show low tolerance to several abiotic conditions and exploit a limited range of resources. In addition, it is not known how many of them are species of incipient evolution or which have reduced their distribution area due to changes in climate or stochastic fluctuations in the environment. It will be interesting to analyze the causes of their reduced distributions, both from a historical point of view (*e.g.*, species' position in the phylogeny) and from an ecological point of view (*e.g.*, which environmental variables are most influential in explaining small geographical distributions).

As demonstrated in this work, despite the coarse scale of grid cells used, mapping species' occurrences reveals patterns of geographical distribution (Figure 2). Here the concept of rarity used was based on the species' limited range. Although not fully demonstrated, the few examples used and the literature dealing with the assessment of the risk level of some species suggest that many of the species that are considered rare also have low abundances. Although population data are absent for most species, the number of records selected with the 5 km filtering of localities may help to consider the number of unique localities as equivalent to the global species abundance distribution (gSAD) as defined by Enquist *et al.* (2019). Future studies on this topic will help to clarify the relationship between the number of localities (equivalent to populations) and the abundance of species using herbarium records. This information can be the starting point for future studies that more rigorously evaluate the level of risk of this important percentage of Mexico's flora. For the time being, all the species that have not undergone previous critical evaluations, should be considered at least under the Near Threatened (NT) category due to their restricted area of occupation.

The 2,705 rare species identified will be especially vulnerable to the climate changes that are occurring and the anthropogenic pressures that reduce the natural spaces where they thrive. Their recognition will now increase attention on them, allowing a more precise appraisal of their extinction risk and possible strategies for their conservation. Similarly, the identification of grid cells that are particularly rich in rare species (Figure 2, Table 3), as suggested by Brown (1995), will allow explorations to identify the causes of such a concentration of rare species. For many of the species considered here as singletons, future fieldwork will likely document additional populations outside the current known grid cell; however, their status as rare and possibly under some threat criteria will not change substantially.

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Supplementary material

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