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Why continue with floristic checklists in Mexico? The case of the Tacaná-Boquerón Priority Terrestrial Region, in the Mexican State of Chiapas

¿Por qué continuar realizando listados florísticos en México? El caso de la Región Terrestre Prioritaria Tacaná-Boquerón, Chiapas

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Abstract
Background: Some regions of Mexico have been relatively well explored floristically and estimates of the vascular plant richness they contain have been obtained. However, there are still regions that require effort to obtain the most appropriate lists of flora possible that consider both systemization of the information and that benefit from recent botanical explorations.
Questions: What is the species richness of vascular plants in the Tacaná-Boquerón Priority Terrestrial Region? What proportion of the species are endemic or included in risk categories?
Study sites and dates: Tacaná-Boquerón Priority Terrestrial Region, Chiapas State, Mexico. This region is on the Guatemala border and covers an area of 57,400 ha. Between 1920 and 2015.
Methods: A database of 14,487 vascular plant records was integrated. Two sources of information were compared: systematization of databases, and recent botanic expeditions.
Results: We found 2,485 native species belonging to 185 families. Both data sources were complementary in order to obtain a more complete floristic checklist (systematization of database: 1,774 spp., recent botanic expeditions: 1,514 spp.). As novelties, we found three new species and seven new reports for Mexico. Approximately 14 % of the species documented are included in risk categories or are endemic to the study site.
Conclusions: Our checklist is one of the largest in the region (Mexico and Central America) in terms of species count. Our study shows the importance of conducting botanical explorations to complement the information on vascular plant richness in relatively well-explored areas of Mexico.
Key words: Endemic species, plant distribution, Sierra Madre de Chiapas, threatened species.

Resumen
Antecedentes: Algunas regiones de México han sido relativamente bien explorados florísticamente y se han obtenido estimaciones de la riqueza de plantas vasculares que albergan. Sin embargo, aún quedan regiones que requieren esfuerzos para obtener listados florísticos lo más apropiado posible, que consideren tanto la sistematización de la información y se beneficien de exploraciones botánicas recientes.
Preguntas: ¿Cuál es la riqueza de especies de plantas vasculares en la Región Terrestre Prioritaria Tacaná-Boquerón? ¿Cuál es la proporción de especies endémicas e incluidas en categorías de riesgo?
Sitios y años de estudio: Región Terrestre Prioritaria Tacaná-Boquerón, Chiapas, México. Esta región está en los límites con Guatemala y tiene una extensión de 57,400 ha. De 1920 a 2015.
Métodos: Integramos una base de datos con 14,487 registros de plantas vasculares. Dos fuentes de información fueron comparadas: sistematización de bases de datos y exploraciones botánicas recientes.
Resultados: Se encontraron 2,485 especies nativas pertenecientes a 185 familias. Ambas fuentes de información fueron complementarias para obtener una lista florística más completa (sistematización de bases de datos: 1,774 spp., exploraciones botánicas recientes: 1,514 spp.). Entre las novedades, encontramos tres especies nuevas y siete reportes nuevos para México. Aproximadamente 14 % de las especies se encuentran en categorías de riesgo o son endémicas al área de estudio.
Conclusiones: La lista provee uno de los conteos más altos de especies para la región (México y Centroamérica). Nuestro estudio demuestra la importancia de realizar exploraciones botánicas recientes para complementar la información sobre la riqueza de plantas vasculares en áreas relativamente bien exploradas de México.
Palabras clave: Distribución de plantas, especies amenazadas, especies endémicas, Sierra Madre de Chiapas.

Floristic inventories are important because they provide information about species richness of specific regions and contribute to knowledge of total biodiversity (Villaseñor 2016, Ulloa-Ulloa *et al*. 2017). They also aim to increase the stock of specimens in scientific collections and discover new species. In Chiapas, botanical expeditions began in 1796 by the botanist José Mariano Mociño (Breedlove 1981). After more than two centuries of floristic inventories, some areas remain unexplored or require greater exploration effort (González-Espinosa *et al*. 2005). The plant compilation initially proposed by Breedlove (1981) lists 8,248 species, which later increased to 8,790 species (Villaseñor 2016). Of the seven physiographic regions proposed in Chiapas by Müllerried (1957), the Sierra Madre de Chiapas (SMC) is considered the most biodiverse in the Western Neotropics (northwest South America, southern Central America, and northern Central America, Distler *et al*. 2009). For this reason, three Biosphere Reserves (El Triunfo, La Sepultura and Volcán Tacaná), an Area for Flora and Fauna Protection (La Frailescana) and a State Reserve (Pico de Loro-Paxtal) have been decreed. Together these reserves cover more than half of the SMC (Martínez-Camilo *et al*. 2018).

Several studies have recorded the plant vascular species richness in SMC: in Mt. Ovando (Matuda 1950a, 751 species), Soconusco and Mariscal (Matuda 1950b, 2,628 species), El Triunfo (Long & Heath 1991, 751 species), Cerro Cebú (Martínez-Meléndez *et al*. 2008, 502 species), Cerro Quetzál (Pérez-Farrera *et al*. 2012, 795 species), as well as in La Sepultura (Reyes-García 2008, 1,798 species). Other studies have focused on specific taxonomic groups such as vascular epiphytes in El Triunfo (Martínez-Meléndez *et al*. 2009, 465 species) and orchids in the Tacaná-Boquerón region (Solano-Gómez *et al*. 2016, 325 species). In addition to studying vascular plant richness of the region, it is also important to determine the number of endemic species. Endemic species have a narrow distribution or are restricted to a specific geographic area due to different factors related with the species' environment or intrinsic properties (Dirzo & Raven 2003). Documenting endemism is substantial; the quantification of this component of biodiversity contributes to understanding and underlines the importance of a region as a center of diversity and conservation (Dirzo & Raven 2003).

The Tacaná Volcano, which is the highest peak (4,060 m) in southeastern Mexico (SEMARNAT 2013), and the Boquerón Mountain are located in the southeastern portion of the SMC, on the Guatemalan border. These areas have long been the subject of botanists' interest because of their plant richness and endemism (Breedlove 1981). The German botanist Carl Albert Purpus was the first to visit the region in 1914, followed by the explorations of Eizi Matuda (during the twenties and thirties of the twentieth century), Dennis E. Breedlove (during the seventies) as part of the "Flora de Chiapas" project, and Esteban Martínez (during the eighties and nineties) as part of the "Flora Mesoamericana" project (López-Cruz *et al*. 2017). Since then, several botanists have visited the Tacaná Volcano and the Boquerón Mountain, and thus this portion of the SMC may have the most complete collection of botanical specimens (*e.g*., Matuda 1950b, Solano-Gómez *et al*. 2016). Currently, the Tacaná Volcano and Boquerón Mountain are included in a Tacaná-Boquerón Priority Terrestrial Region (Tacaná-Boquerón, hereafter), a regionalization proposal which aims to identify areas of high biodiversity in the country (Arriaga *et al*. 2000). However, few floristic studies have been conducted in the Tacaná-Boquerón. A floristic checklist for the Soconusco region compiled by Matuda (1950b) can be found; this list includes some locations of the Tacaná-Boquerón (*e.g*., Tacaná Volcano, Boquerón Mountain, Aguacaliente and Niquivil). There is also a description of the dominant vegetation (principally of the tropical rain forest) of the upper part of the Tacaná Volcano, in the municipality of Tapachula written by Miranda (1942), a list of orchids for the Tacaná-Boquerón region by Solano-Gómez *et al*. (2016), who catalogued 325 orchid species (one of the highest figures in Mexico for a region), and one study by Damon *et al*. (2015) that highlights the importance of ravines as refuges for conservation of orchid richness. The recent description of new plant species found in the region (Solano-Gómez 2011) is also important, as well as that of newly reported plants of Chiapas and Mexico (Solano-Gómez *et al*. 2011, Martínez-Meléndez *et al*. 2017).

The most threatened plant communities in Mexico, the montane rain forests (or cloud forests) and the tropical rain forest (Rzedowski 1978), are present in the Tacaná-Boquerón. In this region, deforestation and land use change have reduced the original vegetation cover. There are no direct estimations of deforestation in the Tacaná-Boquerón, but the trends must be similar to other reports of deforestation in the SMC. For instance, Navarrete *et al*. (2010) report high loss and fragmentation of montane rain forests, placing this ecosystem's deforestation rate as the highest in the period 1995-2000, in comparison with other plant communities in Chiapas. Similarly, Challenger *et al*. (2010) pointed out that on the Tacaná Volcano, the montane rain forests undergoes greater loss and fragmentation than other forest types in the SMC. According to Zúñiga *et al*. (2008), in this region there are still approximately 22,579 ha of montane rain and tropical rain forests. Although it is encouraging that part of the Tacaná-Boquerón has been decreed a protected natural area (Tacaná Volcano Biosphere Reserve), this alone does not ensure biodiversity conservation. Therefore, conservation actions are required, especially those that involve agricultural alternatives (Navarrete *et al*. 2010).

For more than a century, the Tacaná-Boquerón region has been explored by botanists. Also, a preliminary review of digital databases reveals approximately 5,000 registers of vascular plants. For these reasons, we considered that the Tacaná-Boquerón had been relatively better-explored than other regions of the SMC and of Chiapas in general. The floristic study conducted recently by Solano-Gómez *et al.* (2016) in the Tacaná-Boquerón region incorporated information derived from the review of databases and from field work on the Orchidaceae family; in total, they documented 325 orchid species, 24 % of the known species in Mexico, an unprecedented figure compared with other regions of

Mexico. This motivated us to generate a broader process of systematization of the disperse collection registers in different herbariums, domestic and international, of all the vascular plants of the Tacaná-Boquerón in order to carry out a more detailed analysis. In addition, we made a recent effort to incorporate a larger quantity of species collected in the region, with new collection sites and with the expectation of also increasing the plant species richness estimations. For this reason, here we integrated data from two different sources in order to obtain the plant species richness in the Tacaná-Boquerón, as follows: (1) systematization of data on specimens, which were collected in the Tacaná-Boquerón between 1920 and 2012 and deposited in Mexican and foreign herbaria and (2) through botanical expeditions carried out in the Tacaná-Boquerón between 2013 and 2015. We started from the following questions. (1) What is the species richness of vascular plants in the Tacaná-Boquerón? (2) What proportion of the species is considered endemic or included in risk categories? These were key questions that helped us to provide evidence of the importance of continuing floristic checklists in relatively well-explored regions, such as the Tacaná-Boquerón.

Material and methods

Study area. The work was conducted in the Tacaná-Boquerón, located in the southeastern portion of the SMC that borders Guatemala (Figure 1), and has an estimated area of 57,400 ha (Arriaga *et al*. 2000) and includes portions of the seven municipalities: Cacahoatán, Mazapa de Madero, Motozintla, Tapachula, Tuxtla Chico, Tuzantán, and Unión Juárez. The Tacaná-Boquerón includes the Tacaná Volcano Biosphere Reserve, which has an estimated area of 6,378 ha (SEMARNAT 2013). The elevation gradient ranges from sea level (the study area begins at 650 m) to the volcano peak (4,092 m). Due to this variation, there are important changes in climate. For instance, the climate at lower elevations is warm and humid, with an average temperature of 27 °C and

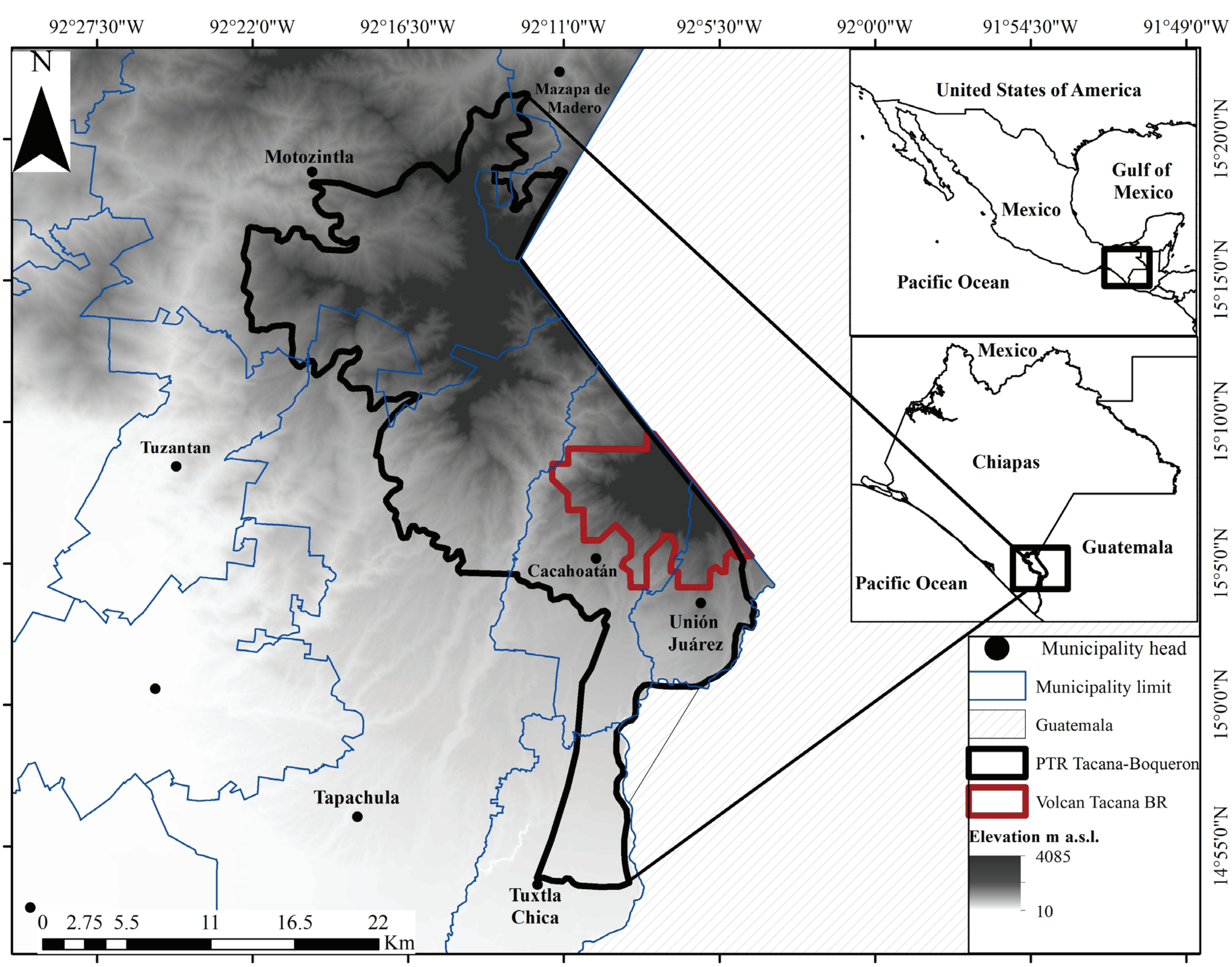

Figure 1. Study area: The Tacaná-Boquerón Priority Terrestrial Region, Mexico.

annual precipitation of 3,500 mm, and at upper elevations, it is temperate and drier, with an average temperature of 8 °C and annual precipitation of 2,500 mm.

Along the elevation gradient, there are at least six plant communities based on Beard's classification (1955). The tropical rain forest (tropical rain forest: Holdridge 1967; bosque tropical perennifolio: Rzedowski 1978), between 200 and 1,700 m, is one of the most reduced and fragmented vegetation types in the region (Navarrete *et al*. 2010), and it is now restricted to ravines and areas of difficult access. The latter was transformed principally into agricultural land, mainly cacao and coffee plantations, the most important economic activities in the region (SEMARNAT 2013). The semi-evergreen seasonal forest (tropical or subtropical premontane, moist forest: Holdridge 1967; bosque tropical subcaducifolio: Rzedowski 1978), between 700 and 1,300 m, has rugged dirt roads that lead to the human settlements of Aguacaliente (Cacahoatán) and Berriozabal (Motozintla). Its presence is uncommon given the high precipitation rate that occurs in the region. This vegetation type is favored by the soil conditions: shallow and rocky on steep slopes. Many trees lose their leaves in a very short period during the driest months (February to Abril). The deciduous seasonal forest (tropical or subtropical dry, very dry forest: Holdridge 1967; bosque tropical caducifolio: Rzedowski 1978), at an elevation of around 1,000 m, seems to be isolated in a small portion of land along the road to Aguacaliente. It shares climate and elevation conditions with the tropical sub-deciduous forest, but the former is characterized by trees with more severe loss of leaves during the dry season. The montane rain forest or cloud forest (tropical montane moist, subtropical montane wet or rain forest: Holdridge 1967; bosque mesófilo de montaña: Rzedowski 1978) found between 1,600 to 3,000 m is one of the most representative vegetation types in the Tacaná-Boquerón, characterized by the presence of mist and humidity almost the entire year. Here, trees are completely covered with epiphytes, and tree ferns and palms are very common in the understory. There are also three subtypes of high mountain forest (in part, subtropical montane moist forest: Holdridge 1967; bosque de coníferas: Rzedowski 1978): (1) *Pinus* forest, the largest extension in the Tacaná-Boquerón occurs at elevations of 2,000 to 4,000 m, where the dominant species are *Pinus tecunumanii* F. Schwerdtf. ex Eguiluz & J.P. Perry, *P. hartwegii* Lindl., and *P. devoniana* Lindl; (2) *Abies* forest, limited to some areas in Aguacaliente, occurs above 3,000 m; this monospecific forest is dominated by *Abies guatemalensis* Rehder, and (3) forests of *Juniperus*, which is a dwarf tree, occur from 3,800 m to the highest part of the Tacaná Volcano. The dominant species is *Juniperus standleyi* Steyerm. The paramo (grasslands or páramo: Rzedowski 1978) occur above 4,000 m in areas exposed to strong winds. It consists of different associations of herbaceous and shrub species, but mainly grasses, present in a patchy distribution and isolated. The plants present in this type of vegetation, such as *Werneria nubigena* Kunth, *Stevia ovata* Willd. (Asteraceae) and the genus *Alchemilla* L. (Rosaceae), are usually very small (some of them of a few centimeters high), are tolerant to low temperatures and grow in shallow rocky soils. Also, there are isolated *J. standleyi* and *P. hartwegii* trees.

The floristic checklist was integrated considering two sources of information. Initially, we compiled and systematized information on herbarium specimens deposited in AMO, CAS, CHIP, ECOSUR, HEM, MEXU, MO and XAL, and records of the CONABIO database. Then, we incorporated information derived from 22 field expeditions carried out between February 2013 and June 2015. The collection sites were at elevations from 650 to 4,060 m in conserved forest, secondary vegetation, and coffee plantations of Cacahoatán, Motozintla, Tapachula and Unión Juárez. The authors, as well as national and foreign specialists, supported taxonomic determination (see Acknowledgements). The floristic checklist was arranged according to APG (2009), Christenhusz *et al.* (2011) and Christenhusz & Chase (2014) for angiosperms, gymnosperms and ferns, respectively. The collected specimens were deposited in the Eizi Matuda Herbarium (HEM) of the Universidad de Ciencias y Artes de Chiapas. We excluded 162 morphospecies determined only to genus level, accounting for 514 records (3.6 % of the total). The main reason was the difficulty of identifying samples that lacked reproductive structures or those belonging to taxonomically complex families (*e.g*., Asteraceae, Fabaceae, Rubiaceae). Aspects regarding nomenclature, such as scientific names (valid names and synonyms), were verified using an on-line database (www.theplantlist.org). We also standardized the information regarding collector names, and we completed the geographic information (latitude and longitude) for those registers that lacked them. Of the total number of species, 99 were obtained directly from the floristic checklist of Solano-Gómez *et al*. (2016), and it was not possible to assign them coordinates. To complete missing geographic information, we employed Google Earth© software.

To compare the sampling effort of the two sources (systematization of databases and recent botanical expeditions), species accumulation curves were constructed. Bootstrap techniques were used on the curves to generate confidence intervals (95 % confidence) and to determine visually whether there were differences between the two sources. To obtain the species richness values used in the species accumulation curves, we located all of the registers (separated by source) on a map. We then generated a grid with 4 × 4 km cells (total of 54 cells), and we obtained the richness for each cell (Villaseñor *et al.* 2018). In addition, for each source, the distribution maps of the registers were generated to visualize the distribution. The generation of maps and the procedure for generating the richness by cell were performed using ESRI software (2016). For the species accumulation curves, the vegan library (Oksanen *et al*. 2019) was used in R Software (R Core Team 2019). We opted for this approach of generating richness values by cell because of the impossibility of comparing the two sources used. For example, the collection period differed notably between the sources (more than a century *vs* three years). We completed the comparison of the two sources to determine the number of species, genera and families that were not found in both sources, using a Venn diagram.

Finally, to determine the conservation status of each species, we consulted the Risk List of the Norma Oficial Mexicana (SEMARNAT 2018) and the Red List of the International Union for Conservation of Nature (IUCN) (González-Espinosa *et al*. 2011, IUCN 2017). Additionally, we defined endemism levels based on geographic distributions. This approach has been used in recent floristic studies (*e.g*., Martínez-Camilo *et al*. 2012, Villaseñor 2016). We consider three levels of endemism: species for which their known distribution is only the state of Chiapas, those that are found in Chiapas and in the neighboring country of Guatemala, and those that are found in Chiapas and in the state of Oaxaca. This was supported with the database of the Missouri Botanical Garden (www.tropicos.org) and the plant list of Villaseñor (2016). Although we use a geopolitical approach, there are biogeographic arguments that are expressed in this delimitation. For example, the great floristic affinity between Chiapas and Guatemala is due to several factors, some related to (1) a common geological origin of what is today the territory of Chiapas, Guatemala and other Central American countries (Arroyo-Cabrales *et al.* 2008, Graham 2010), and (2) similar processes of biotic conformation; for example, Chiapas and Guatemala have an important quantity of floristic elements from South America and floristic elements that are native to both territories, many of which are endemic to the region (Rzedowski 1978, Breedlove 1981). The floristic affinity of Chiapas and Oaxaca is much less, mainly because they have different geological origins (Arroyo-Cabrales *et al.* 2008) and because the Isthmus of Tehuantepec is an important biogeographic barrier that has interrupted the flow of floristic elements from the north toward a portion of Chiapas and Central America and *vice versa* (Graham 2010).

Results

Species richness. We obtained 6,350 records from databases of herbaria and 8,137 records from field expeditions, for a total of 14,487 records (Figure S1). Of the total, we documented 2,485 species of vascular plants, distributed among 884 genera, and 185 taxonomic families (Table 1, Table S1). The main group, the Eudicots, had 1,485 species, followed by the Monocots with 588, and the group of Pteridophyta with 263 species (Table 1). The taxonomic families with the highest number of species were Orchidaceae (326), followed by Asteraceae (239) and Rubiaceae (104); together with 12 other families, they group more than 52 % of the total number of species (Figure 2, Table S2). The genera with the highest number of species were *Epidendrum* L. (37), *Solanum* L. (36), and *Peperomia* Ruiz & Pav. (35). Figure 3 shows the 17 genera with the highest number of species, together representing 15.8 % of all the species.

Table 1. Species number per plant group in Tacaná-Boquerón Priority Terrestrial Region, Mexico.

Main group	Families	Genera	Species
Lycopodiophyta	2	4	26
Pteridophyta	29	67	263
Gymnosperms	3	5	12
Magnoliidae	9	19	111
Eudicots	118	600	1,485
Monocots	24	189	588
Total	**185**	**884**	**2,485**

During field expeditions, we found floristic novelties: three new species, two of them belonging to the genus *Chamaedorea* Willd. (Arecaceae; Donald R. Hodel & Miguel Ángel Pérez-Farrera, pers. comm.) and one belonging to the genus *Magnolia* L. (Magnoliaceae; Antonio Vázquez & Miguel Ángel Pérez-Farrera, pers. comm.). The descriptions are in process of publication. Also, we found seven new reports for Mexico (*Chamaedorea pachecoana* Standl. & Steyerm. [Arecaceae], *C. volcanensis* Hodel & Cast.Mont, *Drymonia guatemalensis* (C.V. Morton) D.N. Gibson [Gesneriaceae], *Hillia triflora* (Oerst.) C.M. Taylor var. *triflora* [Rubiaceae], *Ilex ampla* I.M. Johnst. [Aquifoliaceae], *Pitcairnia wilburiana* Utley in L.B.Sm. & Read [Bromeliaceae], and *Ocotea oblongifolia* van der Werff [Lauraceae]), a new report for Chiapas (*Asplenium hallbergii* Mickel & Beitel [Aspleniaceae]) and rediscovery of *Ocotea subalata* Lundell (Lauraceae), collected only by Eizi Matuda in 1939 and 1945.

Data sources. With the distribution maps of the records for each information source (Figure S2), it can be seen that there are differences in the number of sites where collections were carried out. The number of sites referred to in recent botanic expeditions (2013-2015) is smaller than in the systematized database (1920-2012). For this reason, in the species accumulation curve for the phase of recent expeditions, there are fewer 4 × 4 km cells (see Methods) than in the period 1920-2012. Despite this, both trends in the generated curves are similar in terms of total species richness (Figure 4).

We found that the species number derived from herbarium databases was higher than the species number derived from field expeditions (1,774 and 1,514, respectively, Figure 5). This trend was also detected at the genus level (745 and 612, respectively) and family level (166 and 164, respectively). The counts at each taxonomic level reveal that the data sources are complementary for the Tacaná-Boquerón floristic checklist. That is, of the 1,774 species listed in the 1920-2012 period, 970 species were not found in recent expeditions. Nevertheless, we found a lower -but not less important- number of species, 710, that were not found previously (Figure 5). At the genus level, 272 were not found in recent expeditions, but we added 139 new genera. Finally, at the family level, 21 and 19 families were not found in each source (recent expeditions and systematization of database, respectively).

Species in at risk categories and endemic species. Regarding conservation status, of all the species in our checklist, we found 232 that have been evaluated and listed in risk categories (Table 2, Table S1). According to the Norma Oficial Mexicana, 10 species are categorized as Endangered

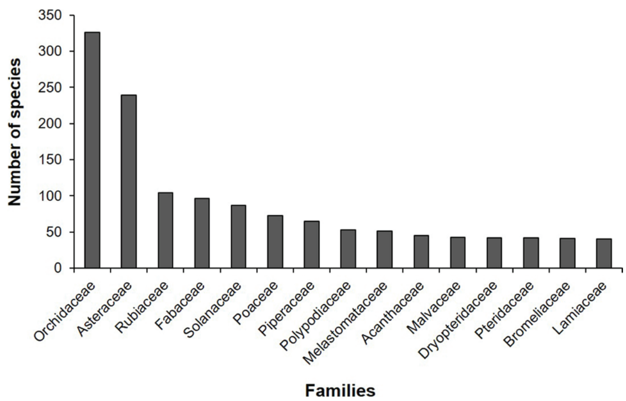

Figure 2. Main plant families ordered from highest to lowest species richness in the Tacaná-Boquerón Priority Terrestrial Region, Mexico.

(P), another 38 species are categorized as Threatened (A) and 31 as Protected (Pr). The IUCN Red List increases the number to 165 species. Specifically, one species of Lauraceae (*Ocotea subalata*) is considered Extinct (EX), 16 other species are considered Critically Endangered (CR), 60 Endangered (EN), 56 Vulnerable (VU), and 32 are placed in two Lower Risk categories (Least Concern and Near Threatened, Table 2, Table S1).

Of the total species, 38 species have to date been reported exclusively (endemics) in Chiapas, and of these, the type locality of 15 species is found in the Tacaná-Boquerón. The following species have limited distribution and are known exclusively in the study area: *Arachnothryx sousae* Borhidi (Rubiaceae), *Ctenardisia purpusii* (Brandegee) Lundell (Primulaceae), *Dahlia purpusii* Brandegee (Asteraceae), *Eizia mexicana* Standl. (Rubiaceae), *Furcraea niquivilensis* Matuda ex García-Mend. (Asparagaceae), *Ocotea subalata* (Lauraceae), *Passiflora tacanensis* Port.-Utl. (Passifloraceae), *Rhipidocladum martinezii* Davidse & R.W.Pohl (Poaceae), *Schultesianthus uniflorus* (Lundell) S. Knapp (Solanaceae), *Stelis soconuscana* Solano (Orchidaceae), *Stenostephanus purpusii* (Brandegee) T.F. Daniel (Acanthaceae), and *Symplocos tacanensis* Lundell (Symplocaceae). Most of the species with restricted distribution occur in Chiapas and Guatemala (98 species, Table S1), suggesting high flora affinity in this region. We found only ten species of Chiapas and Oaxaca that have known distribution (Table S1).

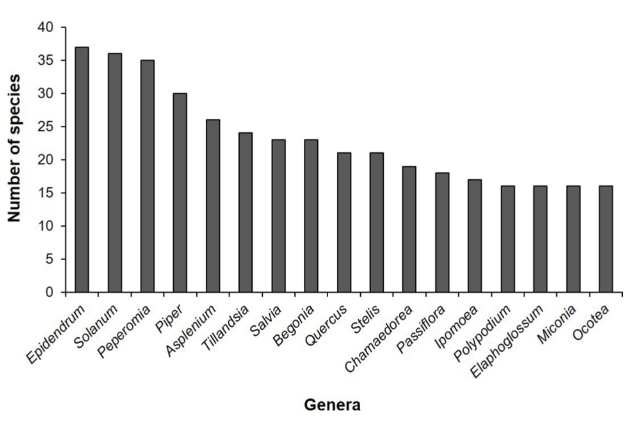

Figure 3. Main plant genera ordered from highest to lowest species richness in the Tacaná-Boquerón Priority Terrestrial Region, Mexico.

Discussion

Species richness. The reported flora of the Tacaná-Boquerón accounts for approximately 28.4, 10.7, and 2 % of that of Chiapas, Mexico (Villaseñor 2016), and America (Ulloa-Ulloa *et al*. 2017), respectively. The latter estimations are important considering that the study area represents less than 1 % of the state's territory. The area of the Tacaná-Boquerón is smaller than other areas in Mexico where plant species richness is high (see Table 3), such as the Selva Lacandona (Martínez *et al*. 1994), Sierra de Manantlán (Vázquez & Cuevas 1995), Tehuacán-Cuicatlán Valley (Dávila *et al*. 2002), La Amistad International Park (Monro *et al*. 2017), and Los Tuxtlas (Villaseñor *et al*. 2018).

Except for some variations, the order of importance of taxonomic families (Orchidaceae, Asteraceae, Rubiaceae, and Fabaceae) matches reports of other mountain areas in Mexico (Villaseñor 2016) and Mesoamerica (Martínez-Meléndez *et al*. 2008, Pérez-Farrera *et al*. 2012, Monro *et al*. 2017). We report 326 species of Orchidaceae. It is noteworthy that orchid species richness accounts for 21 % of the total orchids listed for Mexico (Soto-Arenas *et al*. 2007). Orchidaceae is the most important taxonomic family in the list of Monro *et al.* (2017) for mountain forests of Costa Rica and Panama. In mountain systems, orchids as well as other taxonomic families with epiphyte habit (*e.g*., Bromeliaceae, Polypodiaceae, Piperaceae) develop well because of suitable conditions (*e.g.,* high precipitation rates, constant humidity, in a wide elevation gradient), which also favor high speciation rates (Givnish *et al.* 2015). It is important to mention that in the Tacaná-Boquerón, orchids have been better inventoried by Solano-Gómez *et al*. (2016) than other taxonomic families. These authors report 55 more species, which we could not find in the study area. However, the study area used by Solano-Gómez *et al.* (2016) is larger than ours (Arriaga *et al*. 2000). Other well-inventoried taxonomic families in the study area were Asteraceae, with 7.8 % of species, it is the richest family in Mexico according to Villaseñor (2018), followed by other widely diverse groups in mountain systems such as Rubiaceae with 15.8 % (Borhidi 2006), Bromeliaceae with 10.2 % (Espejo-Serna *et al.* 2017), Piperaceae with 26.5 %, and Melastomataceae with 25 % (Villaseñor 2016).

We added a modest number of species that are new reports for Mexico (seven species) and Chiapas (one species). The new reports for Mexico (except for *Hillia triflora* (Oerst.) C.M. Taylor var. *triflora*), previously known only in Guatemala, were from only a few locations and have been poorly collected (http://www.tropicos.org/ accessed March 20, 2019). These are endemic species whose distribution is

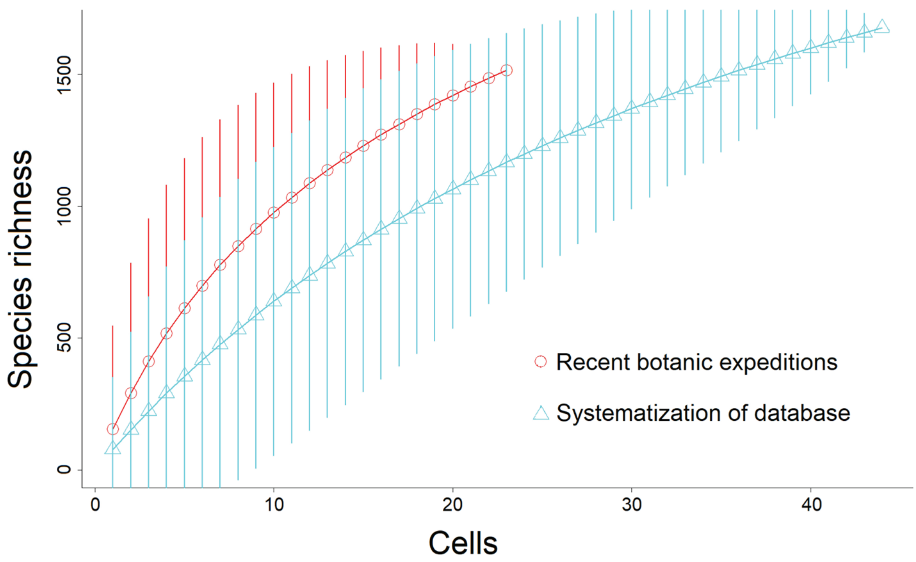

Figure 4. Comparison of plant species richness obtained from two sources of information (systematization of databases and recent botanic expeditions) using species accumulation curves in the Tacaná-Boquerón Priority Terrestrial Region, Mexico.

restricted to Chiapas and Guatemala (except for *Diastema racemiferum*, which was previously reported in Guatemala and Honduras). Also, we collected a new report for Chiapas; *Asplenium hallbergii*, a fern species whose description is based on a specimen from Oaxaca, is widely distributed throughout central and northern Mexico (Villaseñor 2016) and is also reported in Guatemala (Missouri Botanical Garden 2018). Although *Hillia triflora* var. *triflora* (Rubiaceae) was mentioned in the plant list of Villaseñor (2016), according to Lorence & Taylor (2012), its occurrence in Mexico is derived from an erroneous determination. However, here we present a reliable record of the species in tropical deciduous forest at an elevation of 1,389 m.

The species *Ocotea subalata* is an important rediscovery. It was collected by Eizi Matuda in 1939 and 1945 (three specimens, including type) and was considered extinct in the wild by The Red List of Mexican Cloud Forest Trees (González-Espinosa *et al*. 2011). Hence, its rediscovery is very important, and we add a new collection locality. Recent publications include the rediscovery of *Eizia mexicana* (Rubiaceae), with five collected specimens including duplicates (Martínez-Camilo *et al*. 2015); *Dahlia purpusii* (Asteraceae) with just one known specimen and its duplicates, collected by Carl Albert Purpus in 1914 and rediscovered in 2011 (Reyes-Santiago *et al.* 2013); and a new register for Mexico of the orchid *Lockhartia hercodonta* Rchb. f. ex Kraenzl. (Martínez-Meléndez *et al.* 2017).

In this study, we highlight a floristic checklist with a larger number of species than other inventories carried out in Mexico and Central America. Table 3 shows a list of studies with more than 1,000 species records. Species richness in the Tacaná-Boquerón is lower than that reported by Vázquez & Cuevas (1995) in the Sierra de Manantlán Biosphere Reserve (Jalisco and Colima), by Martínez *et al*. (1994) in the Selva Lacandona (Chiapas), both in Mexico, and by Monro *et al*. (2017) in La Amistad International Park (Costa Rica and Panama). However, it is slightly higher than the species richness reported by Dávila *et al*. (2002) in the Cuicatlán-Tehuacán Valley (Puebla and Oaxaca) and by Villaseñor *et al*. (2018) in Los Tuxtlas (Veracruz). Nevertheless, the extension of our study area is smaller than any of these areas mentioned, but this should be considered with much caution. We used estimations of the number of species per unit of area (*e.g*., quotient of the number of species over the area of the study sites; see Dávila *et al*. 2002, Villaseñor 2018), the values generated for the Tacaná-Boquerón would be of the highest if compared with the calculations in Table 3 and with Dávila *et al*. (2002) and Villaseñor (2018). An exception is the Biological Station Los Tuxtlas, with an area of 70 km^2,

Table 2. Species recorded in Tacaná-Boquerón Priority Terrestrial Region, which are included in the NOM-ECOL-059 Extinction Risk List (SEMARNAT 2010) and IUCN Red List (González-Espinosa *et al*. 2011).

Source	Conservation status	Species number
IUCN Red List	Least Concern (LC)	10
	Near Threatened (NT)	22
	Vulnerable (VU)	56
	Endangered (EN)	60
	Critically endangered (CR)	16
	Extinct (EX)	1
NOM-ECOL-059	Protected (Pr)	31
	Threatened (A)	38
	Endangered (P)	10

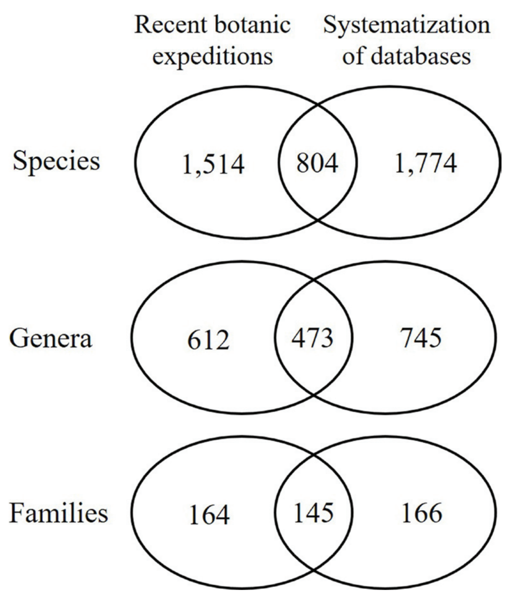

Figure 5. Number of species, genera and families obtained from two data sources (systematization of databases and recent botanic expeditions), integrating the floristic checklist of the Tacaná-Boquerón Priority Terrestrial Region, Mexico. Each data source displays the number of species, genera and families, as well as the values in the overlap zone, which correspond to the number of species, genera and families that were found in both data sources.

where 818 species were documented (Ibarra & Sinaca 1987). We suggest that good collection effort and botanical explorations would notably increase knowledge of the site. Although most of the studies do not offer information on the number of collections, Table 3 shows that some with high species richness also have a considerable number of collections. We must not lose sight of the importance of the factors of short (*e.g.*, topographic complexity, climate) and long temporal scope (*e.g.*, evolutionary and geological history, processes of conformation of the biota) that determine or explain the high species richness for a given site.

Data sources. We believe that the generated information (6,350 specimens) derived from twentieth century expeditions is notable, relative to other study areas in Chiapas or to other floristic inventories of southeastern Mexico (*e.g.*, Martínez-Meléndez *et al*. 2008, Pérez-Farrera *et al*. 2012, Meave *et al*. 2017). Incorporation of the information derived from recent botanical expeditions (carried out between 2013 and 2015) complements knowledge of the flora in the Tacaná-Boquerón. Even though we carried out more field expeditions, we did not find 970 species, but we were able to contribute 710 other species to the final list (28.6 %). Rare and uncommon species could explain this tendency, since they are less likely to be collected or found with reproductive structures. In the present study, 882 and 445 species are represented by one or two collected specimens, respectively, indicating that half the species have been poorly collected over more than a century of botanical explorations in the Tacaná-Boquerón.

Our collection sites prioritized conserved areas, principally emblematic sites such as the Boquerón Mountain and some of the Tacaná Volcano foothills (frequently mentioned in the database information). Currently, forests with variable degrees of conservation are located above 1,700 m, and below this elevation it becomes more difficult to detect forested areas. Decades ago, Miranda (1942) and Breedlove (1981) pointed out the severe transformation of forests at the lower and middle elevation parts of the Tacaná volcano. Moreover, recent field expeditions did not include some localities in the study area (Figure S1) because their complex topography made access difficult and serious social problems in some localities made botanical exploration unsafe. Mainly, in the

Table 3. Comparison of the vascular plant species richness in Tacaná-Boquerón Priority Terrestrial Region with other floristic inventories containing more than 1,000 species in Mexico and Central America. ND = Non data.

Region or natural area protected	Area (ha)	Species number	Species/ha (x100)	Collection number	Endemic species	Threatened species	Source
La Lacandona, Mexico	2,000,000	3,400	0.17	ND	ND	ND	Martínez *et al*. 1994
Valle de Tehuacán-Cuicatlán, Mexico	1,000,000	2,564	0.26	ND	ND	ND	Dávila *et al*. 2002
La Amistad International Park, Costa Rica-Panamá	401,000	3,046	0.76	19,466	73	ND	Monro *et al*. 2017
Los Tuxtlas, Mexico	330,000	2,548	0.77	29,373	307	ND	Villaseñor *et al*. 2018
Chiquibul Forest, Belize	177,000	1,355	0.77	7,047	ND	ND	Bridgewater *et al*. 2006
RB La Sepultura, Mexico	167,309	1,798	1.07	5,808	ND	ND	Reyes-García 2008
RB Sierra de Manantlán, Mexico	140,000	2,997	2.14	ND	90	71	Vázquez & Cuevas 1995
Tacaná-Boquerón Priority Terrestrial Region, Mexico	57,400	2,485	4.33	14,487	146	79*/165**	This work
San Cristóbal de Las Casas, Mexico	48,400	1,260	2.6	ND	ND	9	Beutelspacher *et al*. 2017
La Chinantla, Mexico	26,500	1,021	3.85	2,653	39	123**	Meave *et al*. 2017

* According to the Norma Oficial Mexicana (NOM) (SEMARNAT 2018). ** According to González-Espinosa *et al*. (2011)

central part of the Tacaná-Boquerón, using the localities of Pavencul, Pinabete and Toquián Grande (municipality of Tapachula) as reference, and toward the northern part of the Boquerón-Tacaná, in the municipality of Motozintla. These same gaps in the information can be seen in the registers of the databases (Figure 1, Figure S1, S2). The species checklist presented here is an important baseline of information for the Tacaná-Boquerón, although it is possible that the number of species will increase in the coming years as a result of taxonomic studies and the review of specimens that may have been incorrectly determined. Taxonomic determination is a continuous and long-term process, which benefits from taxonomic, systematic and phylogenetic studies (Villaseñor 2016).

Species in risk and endemic species. To highlight the biological value of certain areas and regions, it is important to identify the species that are included in risk categories or are endemic (Martínez-Camilo *et al*. 2012). In this study, we report that approximately 14 % of the species are included in risk categories or have restricted distribution. This estimation is relevant and suggests the importance of the Tacaná-Boquerón, but the considerably high number of species listed in risk categories confirms and underlines its importance. The most outstanding cases are *Ocotea subulata* (Lauraceae) and *Eizia mexicana* (Rubiaceae). The former was considered extinct in the wild in The Red List of Mexican Cloud Forest Trees (González-Espinosa *et al*. 2011), and the latter was declared extinct by a group of specialists (Lorence & Taylor 2012, Martínez-Camilo *et al*. 2015). Both species were known only from type specimens and were collected decades ago by Eizi Matuda at intermediate elevations on the Tacaná Volcano (between 1,000 and 2,100 m). During the field expeditions carried out in 2013-2015, the collected specimens of the two species revealed the persistence of populations, despite their growing near corn and coffee plantations.

The number of species restricted to the Tacaná-Boquerón, in addition to those occurring only in Chiapas, Chiapas and Guatemala, and Chiapas and Oaxaca, should encourage the creation of conservation programs not only within the study area, but in the surrounding areas. For example, *Litsea glaucescens* Kunth is catalogued as endangered (SEMARNAT 2018) and vulnerable (González-Espinosa *et al*. 2011). Its leaves are used as a condiment, and today its use involves complete pruning of the tree in the forests and extraction of juvenile individuals (<1 m) to be planted in the patios of houses in some communities (Manuel Martínez-Meléndez, pers. comm.). Although we did not evaluate in what type of vegetation most of the at risk or endemic species occur, we did observe that a large proportion occur in the altitudinal belt corresponding to the cloud forest, which we consider to be one of the most fragmented and highly reduced vegetation types in the study area. Although there are no studies that have assessed forest loss and fragmentation rates in the Tacaná-Boquerón, it seems that here these processes have been much more severe than in the rest of the SMC (Toledo-Aceves *et al*. 2011). Among the many causes, we can mention the following: forest conversion to crops (mainly coffee, cacao, and corn plantations), the large number of human settlements, and lumber and firewood extraction.

This study, like others carried out in the Tacaná-Boquerón, have acknowledged the high biodiversity of the area (Damon *et al*. 2015, Solano-Gómez *et al*. 2016). However, only 6,378 ha are protected as a Biosphere Reserve (11.11 % of the total area of the Tacaná-Boquerón; SEMARNAT 2013), which encompasses the lower and middle elevation parts of the Tacaná Volcano. Nevertheless, this protection category excludes a large extension, primarily the areas surrounding the Boquerón Mountain, a part near Niquivil (above 3,000 m), and the lower and middle parts of the Tacaná-Boquerón, which hold the few remnants of tropical rain forest (from 100 to 1,800 m). In recent years, the government has aimed to expand the Tacaná-Boquerón Biosphere Reserve boundaries (CONANP 2011); this goal is still pending but must be achieved as soon as possible. Legal actions are necessary to protect forest fragments and should be complementary to natural resources conservation, exploitation and sustainable management programs for the parts of the reserve held by human communities and landowners inside the Tacaná-Boquerón.

The study area, as well as the Selva Lacandona, exhibits strong floristic affinities with Central and South America (Miranda 1942). Therefore, the northern distribution limits of many mountain forest species from Central and South America are situated in the Tacaná-Boquerón, or extend a little more to the northwest, within the El Triunfo and La Sepultura Biosphere Reserves (*e.g*., species of the genus *Chamaedorea* [Arecaceae], *Arachnothryx* [Rubiaceae], *Symplocos* [Symplocaceae]). This is evident when evaluating species distribution; for instance, there is an increase in the proportion of Tacaná-Boquerón species restricted to Chiapas and Guatemala. This proportion is much higher than that of the species shared by Chiapas and Oaxaca. A similar trend was found by Martínez-Camilo *et al.* (2012) in the El Triunfo Biosphere Reserve.

Finally, the Tacaná-Boquerón can be considered one of the areas with the richest flora in Mexico. Its floristic elements are distinctive, mainly due to their affinity with those of Central and South America. The region has experienced many volcanic events in the last thousands of years, unlike the rest of the SMC (Arroyo-Cabrales *et al.* 2008). These events have influenced floristic composition and its particularities among the rest of the southeastern Mexican forests, which need to be assessed by floristic studies, incorporating a huge amount of information from Mexico and Central America forests. Studies that thoroughly evaluate the biological, geological and biogeographic processes that have given rise to the development and conformation of the biota in the Tacaná-Boquerón are still required. We hope that the information presented here will motivate the scientific community and society to make greater effort in natural resources management and conservation of the Tacaná-Boquerón, one of the most biodiverse regions in Mexico. We urge continuing the task of floristic documentation in highly biodiverse regions, regardless of whether or not they have been relatively well-explored.

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Supplementary data

Supplementary material for this article can be accessed here: http://doi.org/10.17129/botsci.2174.

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