

Diversity patterns of monocotyledonous geophytes in Mexico

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Abstract

Background: Geophytes, plants with underground perennating organs that lose their aerial organs annually, are able to survive in harsh habitats. This life form is common in the monocots that inhabit Mediterranean climates around the world. In Mexico only the northern area of Baja California has this type of climate.

Hypothesis: In this study, we recorded the species and distribution of Mexican geophyte monocots to pinpoint diversity hotspots. Our hypothesis is that the highest diversity of geophytes will be found in biogeographic areas with complex topography and seasonal climate not only in the north of the Baja California Peninsula.

Data description: Records of geophytes were taken from different sources, collections, taxonomic references and diversity databases. Geophyte locations were mapped in the context of biogeographic and protected areas. Climate preferences were estimated using bioclimatic variables and by a Principal Component Analysis we identified the most significant variables explaining distribution of geophytes.

Results: The Mexican geophyte flora is composed of 476 species, approximately 10 % of the total diversity of monocots. *Echeandia* and *Tigridia* were the two most diverse genera. This flora is dominated by the taxa of Orchidaceae, Asparagaceae and Iridaceae, and ten small endemic genera were recorded. Geophyte diversity was highest in two biogeographic provinces: the Trans-Mexican Volcanic Belt and the Sierra Madre del Sur, in dry forests such as oak-pine, seasonally dry tropical forests and semi-arid shrubby vegetation. Three bioclimatic variables: temperature seasonality, annual precipitation and precipitation of the wettest quarter resulted significant for understanding distribution of geophytes.

Conclusions: Areas sustaining a high diversity and endemism of geophytes are located in the Mesoamerican Biodiversity Hotspot, in unprotected and threatened areas. Our results suggest that geophytes are able to grow in different climates but in areas with marked temperature seasonality and variation of annual precipitation.

Keywords: Balsas River Basin, Chiapas Depression, *Echeandia*, endemism, *Tigridia*, Tehuacán Valley, Trans-Mexican Volcanic Belt

Patrones de diversidad de geofitas monocotiledóneas en México

Resumen

Antecedentes: Las geofitas son plantas que poseen órganos de perennación subterráneos, las cuales pierden sus hojas anualmente y son capaces de sobrevivir en ecosistemas inhóspitos. Esta forma de vida es común en las monocotiledóneas que habitan en áreas con clima Mediterráneo en todo el mundo. En México únicamente el área norte de Baja California tiene este tipo de clima.

Hipótesis: En este estudio se registra la diversidad y endemismo de las geofitas monocotiledóneas en México para identificar áreas con alta diversidad. Nuestra hipótesis plantea que la más alta diversidad de geofitas monocotiledóneas se encontrará en provincias biogeográficas con topografía compleja y variados tipos de climas y no solamente en Baja California.

Descripción de Datos: Se elaboró una lista de geofitas monocotiledóneas con sus georeferencias con base en colecciones, publicaciones taxonómicas y bases de datos electrónicas. Se construyó una base de datos de geofitas con sus georeferencias tomando en cuenta las provincias biogeográficas y las áreas protegidas. Se identificaron sus preferencias climáticas con base en las variables bioclimáticas y mediante un Análisis de Componentes Principales se establecieron las más importantes para explicar la distribución de estas plantas en México.

Resultados: La flora mexicana de geofitas comprende 476 especies, aproximadamente el 10 % del total de la diversidad de monocotiledóneas registradas para el país. *Echeandia* y *Tigridia* son los géneros con más especies. La flora de geofitas está dominada por Orchidaceae, Asparagaceae e Iridaceae y se identificaron diez géneros endémicos con unas cuantas especies. La diversidad más alta de geofitas se detectó en dos provincias biogeográficas: en el Eje Neovolcánico Transversal y en la Sierra Madre del Sur, en bosques secos de pino-encino, en bosques tropicales caducifolios y en vegetación arbustiva semi-árida. Se identificaron tres variables bioclimáticas importantes: estacionalidad de la temperatura, precipitación anual y precipitación del período más húmedo.

Conclusiones: Las zonas con mayor diversidad y endemismo de geofitas se encuentran en el denominado “Hotspot de Biodiversidad Mesoamericano” en zonas sin protección ambiental y enfrentando amenazas a la destrucción de la biodiversidad. Nuestros resultados sugieren que las geofitas son capaces de crecer en climas muy diferentes pero siempre en áreas con marcada estacionalidad de temperatura y con gran variación de precipitación anual.

Palabras clave: Cuenca del Río Balsas, Depresión de Chiapas, *Echeandia*, Eje Neovolcánico Transversal, endemismo, *Tigridia*, Valle de Tehuacán.

Author Contributions

Manuel Cuéllar-Martínez constructed databases, performed analyses and wrote the paper
Victoria Sosa conceived the project, constructed databases and wrote the paper

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The diversity of life forms in angiosperms has been identified as an important factor that enabled flowering plants to become dominant in terrestrial habitats (Ricklefs & Renner 1994, Tiffney & Mazer 1995). Among noteworthy terrestrial life forms are the geophytes, plants with underground perennating organs like bulbs, corms, tubers or rhizomes that lose their aerial parts annually (Hamrick & Godt 1996, Parsons 2000, Proches *et al.* 2005, Proches *et al.* 2006, Kamenetsky 2013). Perennial belowground elements allow plants to survive periods of severe climate conditions (Dafni *et al.* 1981, Parsons 2000, Kamenetsky 2013). Furthermore, it is known that species of geophytes in different lineages of angiosperms have increased their genome size, facilitating the production of larger cells in the underground perennating organs, which is advantageous for fast growth in seasonal habitats (Vesely *et al.* 2012).

Geophytes are often conspicuous components of vegetation after burning (Doussi & Thanos 2002, Verboom *et al.* 2002, Tyler & Borchert 2003, Koniak *et al.* 2009). This life form is more common in monocots, in families like Iridaceae, Orchidaceae, Hyacinthaceae, Amaryllidaceae and Anthericaceae and only occurs in very few dicot taxa (Meerow 2013). There has been great interest in plants with this life form because many geophyte monocot species in genera like *Allium*, *Hyacinthus*, *Iris*, *Narcissus* and *Tulipa* are widely cultivated as ornamentals (Kamenetsky 2013).

Regions with a Mediterranean climate sustain outstanding geophyte diversity and this has been documented for California, Chile, the Mediterranean Basin, Cape Province in South Africa, Australia and Turkey (Rundel 1996, Parsons 2000, Goldblatt & Manning 2002, Parsons & Hopper 2003, Çelik *et al.* 2004, Proches *et al.* 2006). Different genera dominate in certain regions: *Allium* and *Calochortus* in California (Rundel 1996) and *Disa*, *Gladiolus* and *Moraea* in South Africa (Proches *et al.* 2006), for example. A comparison of California, Chile, South Africa, Mediterranean Basin and Australia showed that Orchidaceae has the highest number of monocot geophytes, followed by Amaryllidaceae (Parsons 2000). Endemic geophytes vary as well and the most remarkable example is in Chile, where 70 % of the geophyte flora is endemic (Hoffmann *et al.* 1998). In South Africa, geophyte diversity has been found to be dependent on climate, mainly on the amount and reliability of precipitation (Proches *et al.* 2005). In the New World, geophytes have been recorded from regions with a Mediterranean climate such as California, the northern region of Baja California and central Chile (Rundel 1996, Hoffman *et al.* 1998).

Furthermore, while the most studied regions for geophyte diversity are Mediterranean, this functional group of plants is present as well in areas with seasonal climate and have been accounted in mountainous regions like in the north of Iran where 124 species of geophytes were recorded as one of the dominant life forms (Naqinezhad *et al.* 2014); or in the north of Venezuela in which geophytes are in zones with seven months of rain (Wikander 1984). In Burkina Faso a few geophytes have remained in modified dry landscapes (Madsen *et al.* 2008); or in the Pyrenees an elevated number of 250 geophyte species have been scored (Grau *et al.* 2012). In Peru, in Prepuna plant communities more than 50 geophytes have been documented, among them are some neotropical genera such like *Nothoscordum* and *Sisyrinchium* (Montesinos *et al.* 2012). In Mexico there are also areas that have a marked seasonal climate with suitable areas for geophytes (Peel *et al.* 2007, Kottek *et al.* 2006). Moreover, Mexico is crossed by several mountain chains and has ample differences in climate types that might provide a considerable number of terrestrial ecosystems where geophytes can establish (Marshall & Liebherr 2000).

In this paper we identify geophyte diversity in the biogeographic regions of Mexico. According to Morrone (2014) the Mexican Transition Zone is one of the biogeographical regions in the country, comprising the provinces: Sierra Madre Oriental, Sierra Madre Occidental, Trans-Mexican Volcanic Belt, Sierra Madre del Sur and Chiapas Highlands. These mountain areas have been identified as biodiversity hotspots for temperate taxa (Myers *et al.* 2000). Among them, the Trans-Mexican Volcanic Belt is a complex mountain chain formed by thousands of volcanic structures that originated in four episodes (Gómez-Tuena *et al.*, 2007). This chain crosses Mexico from east to west and its influence on the Mexican highland biodiversity has been amply discussed, either harboring high biodiversity or promoting its diversification (reviewed in Mastretta-Yanes *et al.* 2015). Elevated diversity of several angiosperm groups of Mexico has been identified in the Trans-Mexican Volcanic Belt. For example, the highest diversity of Asteraceae, the largest angiosperm family in Mexico is found mainly in the Trans-Mexican Volcanic Belt (Cruz-Cárdenas *et al.* 2013, Vargas-Amado *et al.* 2013). The Brazilian subregion in the Meso-

american Dominion is an additional biogeographic area identified for Mexico and comprises lowland vegetation in the Pacific slopes, in the Yucatan Peninsula and in the Balsas Basin (Morrone 2014). This biogeographic area also provides suitable habitats for geophytes.

With regard to diversity and endemism of geophytes in Mexico, it is known that most species of tribe Tigridaeae, a geophyte clade in the Iridaceae are distributed in the Trans-Mexican Volcanic Belt (Munguía-Lino *et al.* 2015). The *Milla* clade (Asparagaceae) comprises six geophyte genera endemic to Mexico and it was suggested that a number of areas in the Trans-Mexican Volcanic Belt acted as refugia to this group (Gándara *et al.* 2009, 2014). In the orchid geophyte genus *Bletia*, many Mexican endemic species are distributed in the Trans-Mexican Volcanic Belt and in the Sierra Madre Occidental (Sosa *et al.* 2016).

Here we focus on monocots because the majority of geophytes have been recorded for this lineage and because the monocot flora is well known for Mexico, with approximately 4500 species recorded, of which approximately half are endemic, including groups such as *Polianthes*, *Milla*, *Bletia*, *Tigridia*, *Echeandia*, *Malaxis*, and *Schiedeella* with geophyte life forms (Espejo-Serna 2012). We concentrate on monocot geophytes to gain new insights into diversity patterns for the flora of Mexico, not only in species from the single region of Mediterranean climate in Mexico, in Baja California, in the nearctic California Floristic Province, but also in the rest of the biogeographic provinces identified for the country. We expect the highest diversity of geophytes in the Trans-Mexican Volcanic Belt and in the Sierra Madre del Sur provinces, where seasonal climate has been reported, similar to Mediterranean climate.

The objectives of this paper are: 1) to document monocot geophyte diversity in Mexico, 2) to identify the biogeographic areas with the highest geophyte diversity, and 3) discuss their conservation.

Material and methods

Checklist. We compiled a checklist of the Mexican monocots geophyte species based on checklists, floras and monographs (Correll 1941, Williams 1946, Henrich & Goldblatt 1987, Rzedowski & Calderón de Rzedowski 1985, Salazar 1990, Lascurain-Rangel 1995, López-Ferrari & Espejo-Serna 2002, Croat & Carlsen 2003, Espejo-Serna & López-Ferrari 2003, Rodríguez *et al.* 2003, Rodríguez & Ortiz-Catedral 2003a,b, Espejo-Serna *et al.* 2005, Rodríguez & Ortiz-Catedral 2005, 2006, 2013, Téllez-Valdés & Geeta 2007, Alvarado-Cárdenas & García-Mendoza 2008, Espejo-Serna *et al.* 2009, Gándara *et al.* 2009, Espejo-Serna *et al.* 2010, Flagg *et al.* 2010, Sánchez-Ken 2010, Salazar *et al.* 2011, Barba-González *et al.* 2012, Tapia-Campos *et al.* 2012, 2013, Gándara *et al.* 2014) and in databases such as “eMonocot” (<http://e-monocot.org/>). Plant families follow the APG III classification (<http://www.mobot.org/MOBOT/research/APweb/>).

Database. Distribution records were obtained from the literature cited above and complemented with databases such as the Mexican Biodiversity Database (REMIB) (www.conabio.org), TROPICOS (www.tropicos.org) and the Global Biodiversity Information Facility (www.gbif.org). Records from *Bletia* and *Hexalectris* (Orchidaceae), *Behria*, *Bessera*, *Jaimehintonia*, *Dandya*, *Milla* and *Petronymphe* (Asparagaceae) were based on our collections (Sosa 2009, Sosa *et al.* 2016, Gándara *et al.* 2014). A total of 2593 records were compiled. The distribution of every species was mapped using ArcView (ESRI 1999) in 1 Km² quadrats in which we divided the Mexican territory. Quadrats were then superposed in the biogeographic provinces to identify the most diverse.

Climate variables. To identify the most significant environmental variables related to distribution of geophytes in Mexico, 19 bioclimatic variables derived from temperature and precipitation data were obtained from WorldClim 1.4 (Hijmans *et al.* 2005) at a resolution of 1 km². The bioclimatic variables were extracted using the software R programming language using the packages Raster (Hijmans *et al.* 2016) and rgdal (Bivand *et al.* 2016) considering the 2593 records of our database. A correlation analysis was performed to eliminate correlated environmental variables using the program PAST v3.06 (Hammer *et al.* 2011) and only the fifteen least correlated variables (Pearson ≤ 0.8 based on all sample locations) were utilized. A Principal Component

Analysis was subsequently performed with PAST v.3.06 (Hammer *et al.* 2011) to establish the bioclimatic variables with the highest component scores that explain most variation in the PC axes.

Results

Diversity. The Mexican monocot geophyte checklist comprised 476 species belonging to ten families and 76 genera, the majority in the order Asparagales (Table 1). The families with the

Table 1. Monocotyledonous geophyte species in Mexico recorded in this study.

Taxon	Number of species	Taxon	Number of species
Alismatales		Iridaceae	
Araceae		<i>Cypella</i> Herb.	1
<i>Arisaema</i> Mart.	1	<i>Eleutherine</i> Herb.	2
Asparagales		<i>Fosteria</i> Molseed.	1
Amaryllidaceae		<i>Iris</i> L.	1
<i>Allium</i> L.	28	<i>Nemastylis</i> Nutt.	1
<i>Crinum</i> L.	1	<i>Orthrosanthus</i> Sweet.	2
<i>Habranthus</i> Herb.	9	<i>Rigidella</i> Lindl.	1
<i>Hymenocallis</i> Salisb.	32	<i>Sessilanthra</i> Molseed & Cruden	3
<i>Nothoscordum</i> Kunth	2	<i>Tigridia</i> Juss.	39
<i>Sprekelia</i> Heist.	2	<i>Trimezia</i> Salisb. ex Herb.	2
<i>Zephyranthes</i> Herb.	32	Orchidaceae	
Asparagaceae		<i>Aulosepalum</i> Garay	3
<i>Behria</i> Greene	1	<i>Beloglottis</i> Schltr.	1
<i>Bessera</i> Schult.f.	1	<i>Bletia</i> Ruiz & Pav.	20
<i>Bloomeria</i> Kellog.	2	<i>Brachystele</i> Schltr.	3
<i>Brodiaea</i> Sm.	1	<i>Corallorhiza</i> Gagnebin	10
<i>Chlorogalum</i> Kunth.	1	<i>Cyclopogon</i> C. Presl.	5
<i>Dandya</i> H.E. Moore	4	<i>Cypripedium</i> L.	3
<i>Dichelostemma</i> Kunth.	1	<i>Deiregyne</i> Schltr.	12
<i>Echeandia</i> Ortega	66	<i>Dichromanthus</i> Garay	3
<i>Hesperocallis</i> A. Gray	1	<i>Funkiella</i> Schltr.	9
<i>Jaimehintonia</i> B.L. Turner	1	<i>Galeoglossum</i> A.Rich. & Galeotti	3
<i>Milla</i> Cav.	10	<i>Galeottiella</i> Schltr.	1
<i>Muilla</i> S. Watson	1	<i>Govenia</i> Lindl.	15
<i>Petronympe</i> H.E. Moore	1	<i>Habenaria</i> Willd.	7
<i>Polianthes</i> L.	20	<i>Hexalectris</i> Raf.	7
<i>Prochnyanthes</i> S.Watson	1	<i>Liparis</i> Rich.	5
<i>Triteleia</i> Douglas ex Lindl.	1	<i>Malaxis</i> Sol. ex Sw.	9
<i>Triteleopsis</i> Hoover	1	<i>Mesadenus</i> Schltr.	1
Hypoxidaceae		<i>Pelexia</i> Rich.	1
<i>Hypoxis</i> L.	8	<i>Physogyne</i> Garay	2
Iridaceae		<i>Ponthieva</i> R.Br.	3
<i>Ainea</i> Ravenna	1	<i>Pteroglossa</i> Schltr.	1
<i>Alophia</i> Herb.	4	<i>Sacoila</i> Raf.	1
<i>Cardiostigma</i> Baker	3	<i>Sarcoglottis</i> C.Presl	5
<i>Cipura</i> Aubl.	2	<i>Schiedeella</i> Schltr.	17
<i>Colima</i> (Ravenna) Aarón	2	<i>Sotoa</i> Salazar	1
Rodr. & Ortiz-Cat.		<i>Stenorrhynchos</i> Rich. ex Spreng.	1
Commelinales	1	<i>Triphora</i> Nutt.	4
Commelinaceae		<i>Wulfschlaegelia</i> Rchb.f.	1
<i>Weldenia</i> Schult.f.		Liliales	
Dioscoreales		Liliaceae	
Dioscoreaceae		<i>Calochortus</i> Pursh.	23
<i>Dioscorea</i> L.	1	<i>Diphalangium</i> S.Schauerer	1
		<i>Lilium</i> L.	1
		Zingiberales	
		Marantaceae	
		<i>Maranta</i> L.	1
		Total	476

Table 2. Diversity of monocotyledonous geophytes in the Mexican biogeographic provinces.

Biogeographic region		Number of species	Total number of species	Biogeographic region		Number of species	Total number of species		
California Floristic Province	Amaryllidaceae	11	33	Balsas Basin	Amaryllidaceae	12	77		
	Asparagaceae	8			Araceae	1			
	Liliaceae	5			Asparagaceae	19			
	Orchidaceae	9			Dioscoreaceae	1			
Mexican Plateau	Amaryllidaceae	20	86		Hypoxidaceae	1			
	Asparagaceae	15			Iridaceae	9			
	Hypoxidaceae	2			Liliaceae	4			
	Iridaceae	11			Orchidaceae	30			
	Liliaceae	9			Pacific Lowlands	Amaryllidaceae		9	72
	Orchidaceae	29				Araceae		1	
Sierra Madre Occidental	Amaryllidaceae	10	81		Asparagaceae	24			
	Araceae	1			Dioscoreaceae	1			
	Asparagaceae	18			Iridaceae	3			
	Hypoxidaceae	3			Liliaceae	3			
	Iridaceae	7			Orchidaceae	31			
	Liliaceae	7			Veracruzán	Amaryllidaceae		17	109
Orchidaceae	35	Araceae	1						
Sierra Madre Oriental	Amaryllidaceae	23	107			Asparagaceae	9		
	Araceae	2				Hypoxidaceae	3		
	Asparagaceae	16				Iridaceae	21		
	Hypoxidaceae	5				Liliaceae	2		
	Iridaceae	17			Marantaceae	1			
	Liliaceae	5			Orchidaceae	33			
Sierra Madre del Sur	Orchidaceae	39	119	Yucatán Peninsula	Amaryllidaceae	6	22		
	Amaryllidaceae	13			Asparagaceae	3			
	Araceae	1			Iridaceae	4			
	Asparagaceae	28			Marantaceae	1			
	Commelinaceae	1			Orchidaceae	8			
	Hypoxidaceae	2			Chiapas Highlands	Amaryllidaceae		5	55
Iridaceae	20	Asparagaceae	5						
Liliaceae	2	Commelinaceae	1						
Orchidaceae	52	Hypoxidaceae	1						
Trans-Mexican Volcanic Belt	Amaryllidaceae	21	159			Iridaceae	4		
	Araceae	1				Liliaceae	1		
	Asparagaceae	36			Orchidaceae	38			
	Commelinaceae	1							
	Hypoxidaceae	4							
	Iridaceae	20							
	Liliaceae	11							
	Orchidaceae	65							

largest number of species were the Orchidaceae (181 species), Asparagaceae (114 species), Amaryllidaceae (106 species) and Iridaceae (92 species); the rest included less than 50 species in families such as Araceae, Hypoxidaceae, Commelinaceae, Dioscoreaceae, Liliaceae and Marantaceae (Table 1). The genus with most species was *Echeandia* (66 species) followed by *Tigridia* (39 species), *Hymenocallis* and *Zephyranthes* (32 species each), *Allium* (28 species) and *Calochortus* (23 species) (Table 1). Ten genera, each with only a few species, are endemic (*Ainea*, *Behria*, *Bessera*, *Colima*, *Dandya*, *Fosteria*, *Jaimehintonia*, *Petronymphe*, *Prochnyanthes*, *Polianthes*) to Mexico, as are 344 species of geophytes. The greatest diversity of geophytes lies in the Trans-Mexican Volcanic Belt (170 species), followed by the Sierra Madre del Sur (119 species) (Table 2, Figure 1).

Of the 476 monocot geophyte species, 34 are classified as being at some risk of extinction (SEMARNAT 2010), with Orchidaceae and Iridaceae having the majority of at-risk species (10 and 9 species respectively) (Table 3).

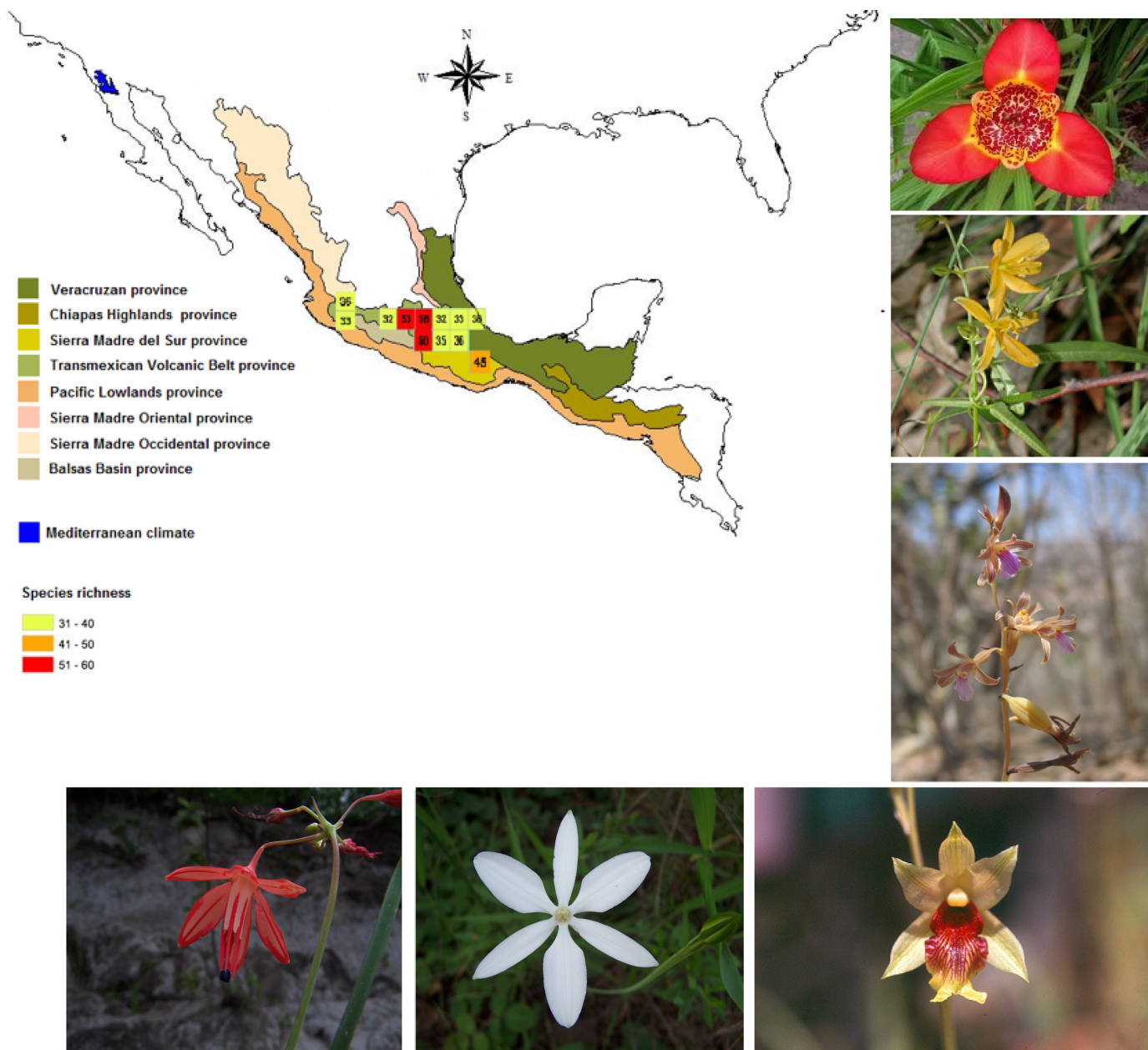


Figure 1. Highest diversity of Mexican monocot geophytes in biogeographic provinces. Representative monocotyledonous geophytes: from top to bottom and right to left: *Tigridia pavonia*, *Echeandia flavescens*, *Hexalectris spicata*, *Bletia roezlii*, *Milla biflora*, *Bessera elegans*.

Climate variables. From the 19 climate variables our analysis of correlation identified four correlated variables (1, 2, 7, 11) that were not considered for the subsequent PCA analysis. PC1 and PC2 explained 81 % of variability, and based on their scores, the most significant climate variables were: BIO4 Temperature seasonality (standard deviation $\times$ 100), BIO12 Annual Precipitation and BIO 16 Precipitation of Wettest Quarter (Table 4).

Discussion

Our records document the noteworthy diversity of geophytes in the Mexican flora; species with this life form represent 2.0 % of the approximately 23,500 vascular plants and 10.4 % of the 4,500 species of monocots. Amaryllidaceae, Asparagaceae, Iridaceae and Orchidaceae are the

Table 3. Geophyte species currently assigned to some risk of extinction category based on NOM-059-SEMARNAT (2010). P: in danger of extinction, A: threatened, Pr: special protection.

Species	Category	Species	Category
<i>Ainea konzattii</i> (R.C. Foster) Ravenna	A	<i>Physogyne gonzalesii</i> (L.O. Williams)	Pr
<i>Bletia urbana</i> Dressler	A	Garay	
<i>Calochortus foliosus</i> Ownbey	Pr	<i>Polianthes densiflora</i> (B.L.Rob.	Pr
<i>Calochortus nigrescens</i> Ownbey	Pr	& Fernald) hinners	
<i>Corallorhiza macrantha</i> Schlr.	Pr	<i>Polianthes howardii</i> Verh.-Will.	Pr
<i>Cypripedium dickinsonianum</i> Hágsater	Pr	<i>Polianthes longiflora</i> Rose	Pr
<i>Cypripedium irapeanum</i> La Llave & Lex.	A	<i>Polianthes palustris</i> Rose	Pr
<i>Fosteria oaxacana</i> Molseed	A	<i>Polianthes platyphylla</i> Rose	Pr
<i>Galeottia sarcoglossa</i> Schltr.	Pr	<i>Ponthieva brittonae</i> Ames	Pr
<i>Govenia tequilana</i> Dressler & Hágsater	Pr	<i>Sarcoglottis cerina</i> W.H.Baxter	Pr
<i>Hymenocallis concinna</i> Baker	P	<i>Sessilanthera heliantha</i> (Ravenna) Cruden	Pr
<i>Hymenocallis durangoensis</i> T.M. Howard	P	<i>Tigridia bicolor</i> Molseed	Pr
<i>Hymenocallis guerreroensis</i> T.M. Howard	A	<i>Tigridia flammea</i> (Lindl.) Ravenna	Pr
<i>Hymenocallis leavenworthii</i> (Standl.	A	<i>Tigridia hintonii</i> Molseed	Pr
& Steyerl.) Bauml		<i>Tigridia huajuapense</i> Molseed	Pr
<i>Lilium parryi</i> S.Watson	A	ex Cruden	
<i>Malaxis greenwoodiana</i> Salazar	Pr	<i>Tigridia inusitata</i> (Cruden) Ravenna	Pr
& Soto Arenas		<i>Tigridia orthantha</i> (Lem.) Ravenna	Pr
<i>Malaxis hagsateri</i> Salazar	Pr	<i>Zephyranthes konzattii</i> Greenm.	A
<i>Petronymphe decora</i> H.E. Moore	P		

lineages with the highest diversity of this life form. Two genera stand out owing to their elevated number of species: *Echeandia* and *Tigridia*, both distributed in the New World and with their greatest diversity in Mexico (Rodríguez & Ortiz-Catedral 2013, Munguía-Lino *et al.* 2015).

Of the ten Mexican endemic geophyte genera, five belong to Asparagaceae (*Behria*, *Bessera*, *Dandya*, *Jaimehintonia*, *Petronymphe*) and are members of the *Milla* clade. These taxa have restricted distributions, remarkable distinct floral morphology, few species and are distributed from Arizona to Guatemala, originating in the California Floristic Province (Gándara *et al.* 2014). *Prochnyanthes* is a monotypic genus (*P. mexicana*) and belongs as well to Asparagaceae. The four remaining genera belong to Iridaceae and the best known is *Polianthes* that includes *P. tuberosa*, a cultivated species since prehispanic times, used as an ornamental and its extracts used in perfumery; it is currently cultivated worldwide (Trueblood 1973, Waithaka *et al.* 2001). The remaining genera are monotypic: *Ainea*, *Fosteria* and *Colima* and closely related to *Tigridia* (Ravenna 1979, Molseed 2008, Rodríguez & Ortiz-Catedral 2003b).

The Trans-Mexican Volcanic Belt province has the highest diversity of geophytes, and the combination of its complex geological history, topography, enormous variation in elevation and climate, along with its geographical position in the central part of Mexico provides suitable habitats for multiple organisms (Marshall & Lieberr 2000). Our results show that the highest

Table 4. Significant climate variables related to distribution of Mexican monocotyledonous geophytes identified by the PCA. PCA scores of axes PC1 and PC2 represented 81% of the total variation. BIO4 = Temperature seasonality (standard deviation × 100). BIO12 = Annual Precipitation. BIO16 = Precipitation of the wettest quarter.

	PC1	PC2	Range
Temperature seasonality	0.40	0.60	238 - 8113
Annual precipitation	0.85	0.34	59 - 4017 mm
Precipitation of wettest quarter	0.76	0.30	27 - 2065 mm

number of monocot geophytes lie in this mountain chain, specifically in regions of dry pine-oak forests. This coincides with the richness of species reported for tribe Tigrideae in Mexico, to which most of our reported Iridaceae belong (Munguía-Lino *et al.* 2015). This also agrees with the findings of Marshall & Liebherr (2000) who identified the Trans-Mexican Volcanic Belt as a biogeographic region with a high degree of endemism in insects, fishes, reptiles and plants. Furthermore, Mastretta-Yanes *et al.* (2015) concluded that volcanic activity in the Pleistocene leading to simultaneous climate and topographic changes in the Trans-Mexican Volcanic Belt promoted speciation events as well as long-term continuity of biodiversity. Further research to verify whether this area comprising the three grids acted as a refugium for geophytes should include paleoclimate modeling to identify suitable climates in time and include additional taxa with different plant life forms from the diverse lineages reported for this area.

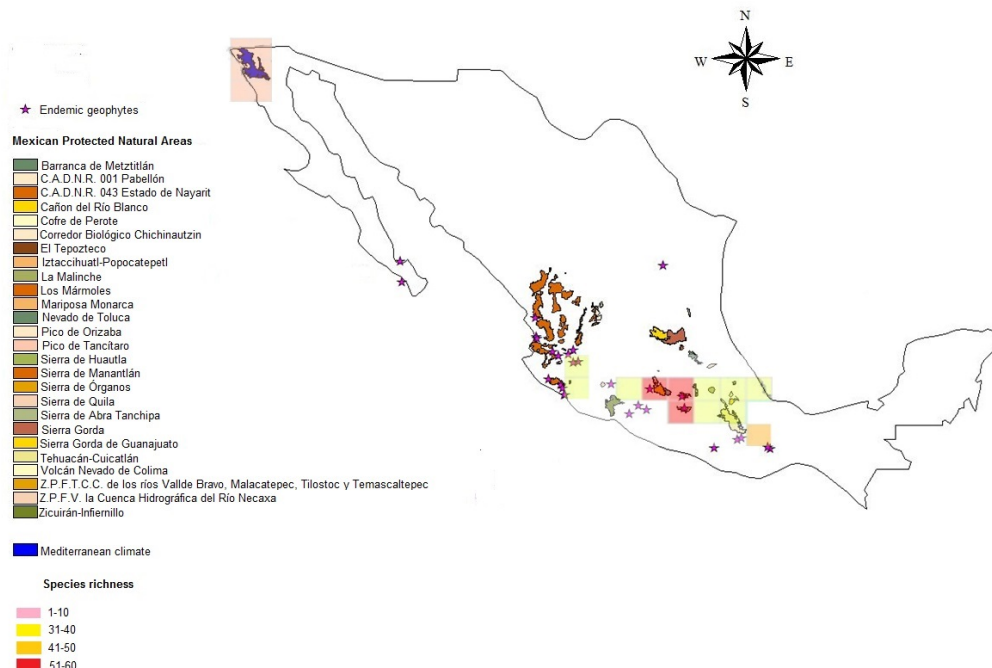
The other biogeographic province with elevated monocot geophyte diversity is the Sierra Madre del Sur. Geophytes were recorded in seasonally dry tropical forests in the Balsas River Basin and in the Chiapas Depression, and in semi-arid shrubby vegetation in the Tehuacán Valley. These zones coincide with areas of endemism reported for Mexican plants (Sosa & de-Nova 2012). One of the quadrats with 50 monocot geophyte species corresponds to the Tehuacán Valley, which was established as a protected area because of its plant diversity and endemism (Méndez-Larios *et al.* 2005). For the Balsas River Basin a high degree of diversity and endemism of woody species of Leguminosae, *Bursera* (Burseraceae) and *Cordia* (Boraginaceae) have been documented (Pineda-García *et al.* 2007). Seasonally dry tropical forests in the Neotropics are a metacommunity of tropical forests that grow on fertile soils in areas with erratic precipitation regimes and with elevated endemisms (Pennington *et al.* 2009).

Winter rainfall was suggested to be the most important climate variable for explaining the diversity of geophytes in Mediterranean-like regions, such as South Africa (Proches *et al.* 2005). In Mexico, the Mediterranean climate only occurs in the north of the Baja California Peninsula (Kassam *et al.* 2012) (see Figure 1). However, our results suggest that the bioclimatic variables temperature seasonality, annual precipitation and precipitation of the wettest quarter resulted significant for distribution of monocotyledonous geophytes in Mexico. Geophytes are thus able to survive in contrasting habitats with scarce to abundant annual precipitation, with large variation in precipitation of the wettest quarter and remarkably, temperature seasonality is high denoting that temperature is not stable during the year. These values correspond to seasonal habitats, which most plant life forms are not able to survive but geophytes remain underground (by perennating organs like bulbs, corms, tubers or rhizomes) in harsh climate conditions and sprout when conditions are favorable.

The two biogeographic provinces with the greatest diversity and endemism of geophytes, the Trans-Mexican Volcanic Belt and the Sierra Madre del Sur, lie within the Mesoamerican Biodiversity Hotspot (Myers *et al.* 2000). Our results suggest that many of the endemic species of monocot geophytes are not located in protected areas and several of them are on the Mexican Red List (Figure 2). Although areas with high diversity of geophytes are located in biosphere reserves such as “Sierra Gorda”, “Tehuacán-Cuicatlán” “Sierra de Huautla” and “Sierra de Manantlán” or in protected areas for flora and fauna like the “Corredor Biológico Chihunautzin” and “Pico de Tancitaro” some regions with high diversity are dispersed in small unprotected zones, mainly in the east end of the Trans-Mexican Volcanic Belt and in the north area of the Balsas Basin (Figure 2). A number of conservation strategies have been proposed for this biodiversity hotspot at different geographic scales, and for different ecosystems and taxa (Harvey *et al.* 2008, DeClerck *et al.* 2010, Golicher *et al.* 2012). All of them agree that it is not possible to manage such large areas parks or reserves, and suggest that it is desirable to adopt an integrative management style that involves human land use while ensuring the continuity of the biodiversity. Specifically for geophytes, it has been suggested that promoting their cultivation by horticultural societies might protect germplasm because many of these species are widely used as ornamentals and others might also be suitable for this type of use (Hoffman *et al.* 1998).

Clearly areas with Mediterranean climate such like California (252 species, Parsons 2000), Chile (250 species, Hoffman *et al.* 1998), Israel (217 species, Fragman & Shmida 1996), South-Western Australia (496 species, Parsons & Hooper 2003) and Victoria, Australia (287 species, Parsons 2000) harbor more geophyte species in smaller areas compared to Mexico. Moreover,

Figure 2. Distribution of geophytes in the context of protected areas in Mexico. The protected areas shown in this map were based on “Áreas Nacionales Protegidas” of the Mexican Government <http://sig.conanp.gob.mx/website/pagsig/anp/nal/inde>.



the Cape Flora of South Africa with 2098 species (Proches *et al.* 2006) is remarkable for geophyte diversity. However, our climate preferences analyses suggest that geophytes are able to grow in different climates located in areas with marked temperature seasonality and variation of annual precipitation.

Further phylogeographic research should be conducted to identify genetic signatures that might establish whether areas in the Trans-Mexican Volcanic Belt or in the Sierra Madre del Sur acted as refugia for geophyte species. In addition, detailed analyses should be conducted to understand whether there are differences in climate preferences in the main groups of geophytes such like Amaryllidaceae, Asparagaceae, Iridaceae or Orchidaceae.

Conclusions

Our records identified an elevated number of geophytes in Mexico, approximately 500 species, representing almost 10 % of the monocots listed for the country. Amaryllidaceae, Asparagaceae, Iridaceae and Orchidaceae are the lineages of this life form with the highest diversity. *Echeandia* and *Tigridia* are the most diverse, and ten other small genera are endemic. Two biogeographic provinces, the Trans-Mexican Volcanic Belt and the Sierra Madre del Sur, have the highest diversity and degree of endemism. Areas sustaining a high degree of geophyte diversity and endemism are located in the Mesoamerican Biodiversity Hotspot, in unprotected and threatened areas. Integrative management of the unprotected areas where these plants have been recorded and promoting their cultivation are probably good strategies for their conservation. Our analyses found that the most significant bioclimatic variables for geophyte distribution were: temperature seasonality, annual precipitation and precipitation of the wettest quarter, indicating that even if geophytes are distributed over an ample range of climates they have their seasonality in common.

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