Evolutionary history of the flora of Mexico: Dry forests cradles and museums of endemism

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Abstract  Mexico is considered an exceptional biogeographic area with a varied endemic flora, however spatial phylogenetic measures of biodiversity have not yet been estimated to understand how its flora assembled to form the current vegetation. Patterns of species richness, endemism, phylogenetic diversity, phylogenetic endemism and centers of neo- and paleo-endemism were determined to examine differences and congruence among these measures, and their implications for conservation. Of 24 360 vascular plant species 10 235 (42%) are endemic. Areas of endemism and phylogenetic endemism were associated with dry forests in zones of topographic complexity in mountain systems, in deserts, and in isolated xeric vegetation. Every single locality where seasonally tropical dry forests have been reported in Mexico was identified as an area of endemism. Significant phylogenetic diversity was the most restricted and occurred in the Trans-Mexican Volcanic Belt and in the Sierra de Chiapas. Notably, the highest degree of phylogenetic clustering comprising neo-, paleo-, and super-endemism was identified in the most restricted and occurred in the Trans-Mexican Volcanic Belt and the Sierra de Chiapas. Notably, the highest degree of phylogenetic clustering comprising neo-, paleo-, and super-endemism was identified in southernmost Mexico. Most vascular plant lineages diverged in the Miocene (5–20 mya) when arid environments expanded across the world. The location of Mexico between two very large landmasses and the fact that more than fifty percent of its surface is arid favored the establishment of tropical lineages adapted to extreme seasonality and aridity. These lineages were able to migrate from both North and South America across Central America presumably during the Miocene and to diversify, illustrating the signature of the flora of Mexico of areas of endemism with a mixture of neo- and paleo-endemism.

Key words: aridification, dry forest, highlands, phylogenetic endemism, phylogenetic niche conservatism, seasonally tropical dry forest, topographical complexity.

1 Introduction

Advanced biodiversity estimates for understanding the spatial components of evolution are increasingly utilized to identify priority areas for conservation and highly endangered groups of organisms. Analytical methods for these measures coincide in the phylogenetic approximations used to identify evolutionary and ecological patterns in the tree of life from a spatiotemporal perspective (e.g., Kozak & Wiens, 2012; González-Orozco et al., 2015; Laffan et al., 2016). The prevailing means of assessment—i.e., endemism, phylogenetic diversity and phylogenetic endemism—characterize the assembly of evolutionary history in geographical space. Similarly, lineage differentiation, lineage subsistence through time and confinement to certain areas, whether attributable to biotic or abiotic factors, are the main mechanisms contributing to patterns of endemism and phylogenetic diversity (Carnaval et al., 2014; Veron et al., 2017). Furthermore, estimating these measures helps to determine whether conservation areas are actually protecting the different aspects of biodiversity or not (Tucker & Cadotte, 2013; González-Orozco et al., 2016).

Endemism, phylogenetic diversity and phylogenetic endemism have been assessed in a number of regions around the world and for different lineages of organisms (e.g., Laffan et al., 2013; Pyron & Wiens, 2013; González-Orozco et al., 2015; Irl et al., 2015; Mráz et al., 2016; Zhang et al., 2016; Baldwin et al., 2017; Heenan et al., 2017; Scherson et al., 2017). Methods for identifying areas of endemism seek geographic spaces that include at least two endemic taxa with non-random spatial congruence (see criteria for areas of endemism in Harold & Mooi, 1994). Diverse methods have been proposed to assess areas taking into account the extent of the distribution of endemic species such as weighted endemism (Linder, 2001). Phylogenetic diversity identifies the parts of a phylogenetic tree that are restricted to a certain geographic area (Faith, 1992; Faith et al., 2004), while weighted phylogenetic endemism combines phylogenetic diversity and weighted endemism measures to identify the geographic areas to which considerable phylogenetic diversity is confined, thus the latter emphasizes the spatial restriction of phylogenetic diversity (Rosauer et al., 2009). Furthermore, categorical analyses based on these measures allow us to identify centers...
of neo- and paleo-endemism based on inferred branch lengths in a phylogram (Mishler et al., 2014). Neo-endemics, i.e., recently diverged species, are endemic because of their lack of dispersal/migration out of their ancestral area (short branches in the phylogram in terms of amount of genetic change), whereas paleo-endemics are ancient taxa that were perhaps more widespread in the past, but are now restricted to a local region (long branches in the phylogram in terms of genetic change) (Mishler et al., 2014).

Endemic species are distributed unequally across the world (Kier et al., 2009) and among abiotic factors influencing the ecological and evolutionary mechanisms responsible for generating areas of endemism and phylogenetic diversity are climate, geology and topography (Linder, 2008), with historical climate stability having been proposed as one of the most crucial factors (Harrison & Noss, 2017). The historical climate stability hypothesis proposes that taxa have differing abilities to adapt to climate changes and that the areas with a stable climate allow for the persistence of species for long periods of time, decreasing extinction events (Svenning et al., 2015). Another crucial factor mentioned is topographical complexity, which generates heterogeneous environments and facilitates short displacements in elevation and limited expansions making easier for species to survive even with limited migration rates (Fine, 2015 and references therein).

There are evolutionary biodiversity estimates for biogeographic areas with unique floras such as Australia, California, Chile, China, and New Zealand, among others (Weber et al., 2014; Thornhill et al., 2016, 2017; Baldwin et al., 2017; Heenan et al., 2017; Scherson et al., 2017, Lu et al., 2018). Although Mexico is considered another exceptional biogeographic area owing to its highly diverse unique endemic vascular flora, with almost half of the global total of ca. 24,500 species (CONABIO, 2009; Villaseñor, 2016), measures of evolutionary biodiversity have not yet been estimated for the country. Diversity in Mexico and Central America is high because together they form a transition zone between the Nearctic and Neotropical biotas (Halffter, 1987; Marshall & Liebherr, 2000). Furthermore, Mesoamerica and the Madrean pine-oak woodlands are two biodiversity hotspots partially located in Mexico, identified because of their notable number of endemic species (Conservation International, 2004). Additionally, the North American Deserts are considered to be among the last remaining high-biodiversity wilderness areas (Mittermeier et al., 2003) as well as important areas for diversification of xerophytic floras (Wilson & Pitts, 2010) and most of the Chihuahuan Desert and part of the Sonoran Desert are located in Mexico.

The elevated plant diversity of Mexico flourishes in a country with complex geological and climate histories. Mexico is crossed by large mountain systems corresponding to different geological provinces that differ vastly in age. The Baja California Peninsula holds a mosaic of small north-south chains; the Sierra Madre Oriental and the Sierra Madre Occidental are north-south mountain systems; the Trans-Mexican Volcanic Belt is a complex assemblage of hundreds of volcanoes that run west to east; the Sierra Madre del Sur and the Sierra de Chiapas are southern mountain conglomerates (Fig. 1A). These highlands have elevations from 1000 to 1800 m a.s.l. with their highest peaks over 5000 m a.s.l. (Fig. 1B). Two deserts in the north, the Sonoran Desert and the Chihuahuan Desert occupy extensive areas (Fig. 1A). Biogeographic areas in the south include a region drained by the Balsas River, the Balsas River Basin, and a depression in Chiapas, the Chiapas Central Depression (Fig. 1A).

![Fig. 1. A, Main bioregions, mountain systems and deserts of Mexico. B, Elevation map of Mexico. Maps were generated from the GIS website of the Mexican Commission for the Knowledge and Use of Biodiversity (CONABIO) under a CC BY license.](image-url)
Endemism in the Mexican flora has been linked to dry current climates distinctive of xeric vegetation (Rzedowski, 1993; Sosa & De-Nova, 2012). Among the outstanding wild vascular groups distributed in Mexico with exceptional life forms are cacti, copal trees, agaves and agave-like forms, and among the most diverse families in this country (Asteraceae, Fabaceae, Orchidaceae and Poaceae) the Asteraceae are by far the group with the most endemic species (Rzedowski, 1993). Additionally, Setchellanthaceae is the only family comprising the Asteraceae, Orchidaceae and Poaceae) the Asteraceae are by far the group with the most endemic species (Rzedowski, 1993). Additionally, Setchellanthaceae is the only family encompassing cacti, copal trees, agaves and agave-like forms, and a number of studies have focused on patterns of species richness and endemic taxa in certain regions of Mexico (Dávila-Aranda et al., 2004; Contreras-Medina & Luna-Vega, 2007; Riemann & Ezcurra, 2007; Hernández & Gómez-Hinoostrosa, 2011; De-Nova et al., 2012; Gámez et al., 2014; Rodríguez-Correa et al., 2015; Sanginés-Franco et al., 2015; Munguía-Lino et al., 2016; Sosa & Loera, 2017; De-Nova et al., 2018). The majority of these studies identified the southern regions of the Sierra Madre Oriental and Sierra Madre Occidental mountain ranges, the Trans-Mexican Volcanic Belt and the Tehuacán Valley as having high degrees of endemism.

Here, we consider the vascular plant species distributed in Mexico and by assessing their main phylogenetic measures we characterize their assembly and evolutionary history, identifying the spatiotemporal divergence patterns of their lineages. Based on previous research on plant endemism in the country and based on the heterogeneity of habitats that mountains encompass we expect that centers of endemism and phylogenetic diversity will be located in dry forests in the southern mountain chains of the country.

The aims of this study are to: (i) map and identify patterns of endemism, phylogenetic diversity and phylogenetic endemism for the vascular plant species distributed in Mexico; (ii) map and identify areas of neo- and paleo-endemism; and (iii) examine differences and congruence among the centers of phylogenetic diversity and phylogenetic endemism and explore the implications for conservation.

2 Material and Methods

2.1 Spatial data

The vascular plant checklist included ferns and fern allies, gymnosperms and angiosperms distributed all across Mexico based on CONABIO (2009), Villaseñor (2016) and complemented with information from the literature. Taxonomy was standardized using Taxonstand v.2.0 (Taxonomic Standardization of Plant Species Names, Cayuela et al., 2012). Families follow APG (Angiosperm Phylogeny Website version 14, Stevens, 2001). Georeferences were obtained following two approaches. For the vascular non-endemic species we consulted the Global Biodiversity Information Facility (GBIF) (www.gbif.org), and for endemic species, records were supplemented with: (i) our previous research (Sosa & De-Nova, 2012; Gándara & Sosa, 2014; Sosa & Loera, 2017); (ii) consulting specimens from Mexican herbaria (ANSM, ENCB, IBUG, IEB, MEXU, and XAL; acronyms based on Thiers, 2017, sweetgum.nybg.org/science/jih/); and (iii) consulting additional biodiversity databases such as SEINet (swbiodiversity.org/seinet), and Tropicos (www.tropicos.org). The identity of records was verified prior to their inclusion in the database.

2.2 Phylogenetic tree

To estimate phylogenetic diversity and weighted phylogenetic endemism, we constructed a phylogenetic tree for the vascular plant species utilizing the mega-phylogeny PhytoPhylo from S.PhyloMaker (Qian & Jin, 2016). It is based on the phylogeny of Zanne et al. (2014) that was expanded to include all extant families of seed plants comprising 32,223 species of land plants. This was done using R 3.4.0 software (R Development Core Team, 2018). S.PhyloMarker associates plant names of your interest to those in PhytoPhylo and add them to the mega-phylogeny based on three scenarios: as basal polytomies within their families or genera, randomly among existing taxa within their parental taxa, or as polytomies within their parental taxa and assigned with branch lengths using BLADJ. The latter is an application developed by Webb et al. (2008) that takes as its input the phylogeny, with named internal nodes, and a simple table of interior node names and ages returning a new phylogeny with adjusted branch lengths. BLADJ has the advantage that even with only a few nodes dated, the resulting phylogenetic distances are improved (Qian & Jin, 2016). BLADJ scenario was used for constructing the phylogenetic tree of the vascular plants distributed in Mexico.

2.3 Biodiversity indices

A grid with a pixel size of 0.5 decimal degree was overlaid on a map of Mexico (614 grids in total to cover all of Mexico) and records of species were mapped on the grids. Species richness (SR) was estimated directly using the occurrence points considering each species as absent or present on each grid. For endemism, we used the measure of weighted endemism (WE) proposed by Linder (2001), which is “the sum of the reciprocal of the total number of cells in which each species is found” (Linder, 2001). The study area is divided into grid squares georeferenced with their latitude and longitude, and the occurrence points mapped onto each grid. Weighted endemism is divided by grid diversity; every species in each cell is weighted by the inverse of its distribution range such that a species found in only one grid is scored as 1. Weighted endemism emphasizes areas with a higher proportion of species that have restricted ranges (Crisp et al., 2001). Phylogenetic diversity (PD) was estimated as the sum of branch lengths on the spanning path linking a set of taxa to the root of the tree, as a proportion of the total length of the tree (Faith, 1992; Faith et al., 2004). Weighted phylogenetic endemism (WPE) incorporates the ranges of all the branches of the tree connecting the species, not only the terminal branches (Rosauer et al., 2009). WPE takes into account the distribution range size of the taxa occurring in an area along with all taxa in the phylogeny no matter what their distribution range is. WPE takes into account not only the range of each taxon, but also of each branch, and it is the sum of branch length/clade range for each branch on the connecting path linking a set of taxa to the root of the tree (Rosauer et al., 2009). The four measures (species richness,
Fig. 2. Representative endemic vascular plant species of Mexico. A, *Ephedra compacta* (Ephedraceae). B, *Agave gracielae* (Asparagaceae). C, *Agave victoriae-reginae* (Asparagaceae). D, *Laelia gouldiana* (Orchidaceae). E, *Olmeca reflexa* (Poaceae). F, *Setchellanthus caeruleus* (Stechellanthaceae). G, *Echeveria heterosepala* (Crassulaceae). H, *Thompsonella minutiflora* (Crassulaceae). I, *Pachyphytum oviferum* (Crassulaceae). J, *Beiselia mexicana* (Burseraceae). K, *Bursera rupicola* (Burseraceae). L, *Enriquebeltraniana disjuncta* (Euphorbiaceae). M, *Euphorbia (Pedilanthus) coalecanensis* (Euphorbiaceae). N, *Calochortus cernuus* (Liliaceae). O, *Nissolia microptera* (Fabaceae). P, *Coursetia* sp. (Fabaceae). Q, *Lophophora diffusa* (Cactaceae). R, *Ariocarpus kotschoubeyanus* (Cactaceae). S, *Leuchtenbergia principis* (Cactaceae). T, *Aztekium hintonii* (Cactaceae). U, *Fouquieria columnaris* (Fouquieriaceae). V, *Viscainoa geniculata* (Zygophyllaceae). W, *Dahlia sherffii* (Asteraceae). X, *Matelea pilosa* (Apocynaceae). Y, *Stenandrum nanum* (Acanthaceae).
weightsEndemism, phylogenetic diversity and weighted phylogenetic endemism were estimated using Biodiverse v.1.1 software (Laffan et al., 2010). In addition, a Pearson’s correlation coefficient analysis was carried out to assess spatial congruence between patterns of species richness and phylogenetic diversity across grid cells. Since the results indicated spatial autocorrelation ($r = 0.86$), a randomization test was further run to identify grid cells with values significantly different from those expected from a random assemblage of the same number of taxa. Only significant PD values (those that fell in the 2.5% upper tail of the two-tailed test) were mapped. The analyses were run in Biodiverse v.1.1. software as well (Laffan et al., 2010).

### 2.4 Categorical analysis of Neo- and Paleo-endemism

“CANAPE” the categorical analysis of neo- and paleo-endemism that searches for centers of endemism, and classifies them by the branch lengths of the rare taxa within them was performed in this study; it was carried out in a two-step process run in Biodiverse v.1.1 (Laffan et al., 2010, based on Mishler et al., 2014). In the first step, for each grid, relative phylogenetic diversity (RPD) and relative phylogenetic endemism (RPE) were calculated. A two-tailed test was run as both indices might have values significantly higher or significantly lower than the null model. If the observed value fell into the highest 2.5% of the distribution for that grid cell it was judged significantly high; if the observed value fell into the lowest 2.5% of the distribution for that grid cell it was judged significantly low. In the second step, the grids identified with a significantly high $\alpha$ were compared using agglomerative clustering in Biodiverse version 1.1 (Laffan et al., 2010) to identify centers of endemism sharing similar sections of the phylogeny.

### 3 Results

#### 3.1 Endemic taxa and phylogenetic tree

A total of 24,360 vascular plant species was recorded from which 10,235 are endemic to Mexico. Table 1 presents the plant families with the most elevated percentages of endemic species. The database comprised 650,825 georeferences. The phylogenetic tree, utilized to estimate PD and WPE, showed that in the majority of the clades divergence occurred during the Miocene (5–20 mya) (Fig. S1). Time of divergence for the most notable endemic groups of the flora of Mexico is indicated in Table 2. The vascular plant species checklist, database and phylogenetic tree were submitted to the Dryad Digital Repository (doi:10.5061/dryad.c6f7453).

#### 3.2 Observed biodiversity estimates

Maps with estimates of SR, WE, PD and WPE are shown in Fig. 3. The highest species richness lies in the mountain chains located in the south of Mexico, in the northeastern and southernmost parts of the Sierra Madre Occidental, in the southernmost parts of the Sierra Madre Oriental, in the center of the Trans-Mexican Volcanic Belt, in the Sierra Madre del Sur, in Sierra de Juárez and in the northern area of the Sierra de Chiapas; the Tehuacán Valley and the Balsas Basin were also areas rich in species (Fig. 3A). The areas with the highest values of weighted endemism are restricted to the north of the Baja California Peninsula, a limited region in the north of the Sierra Madre Oriental, small areas in the central and eastern Trans-Mexican Volcanic Belt, the Tehuacán Valley and the Sierra of Chiapas (Fig. 3B). Significant phylogenetic diversity is confined to limited areas in the north of the Sierra Madre Oriental, the center and eastern parts of the Trans-Mexican Volcanic Belt, the Tehuacán Valley, the Central Depression of Chiapas and the Sierra Madre of Chiapas (Fig. 3C). The regions with high values for the indices of weighted phylogenetic endemism follow a pattern similar to that of weighted endemism, however areas are smaller (Fig. 3D).

#### 3.3 Areas of Paleo- and Neo-endemism

The result of the first step of CANAPE analysis is displayed in Fig. 4 as areas of paleo- and neo-endemism. The majority of areas displayed mixed neo- and paleo-endemism. Paleo-endemic areas were identified in the north and south of the Baja California Peninsula, in the Sonoran Desert, in the north of the Chihuahuan Desert, in a restricted area of the Sierra Madre Oriental, in the westernmost area of the Trans-Mexican Volcanic Belt, in the Tehuacán Valley, in the Balsas River Basin, Sierra Madre del Sur and Sierra Madre de Chiapas. Neo-endemic areas were restricted to the Sonoran Desert (Fig. 4). Areas with super-endemism were the northern part of the Baja California Peninsula, isolated areas in the Chihuahuan and Sonoran Deserts, regions in the Mexican Plateau, Sierra Madre Oriental, Trans-Mexican Volcanic Belt and Balsas River Basin, the Sierra de Chiapas, the Chiapas Central Depression, and the northeastern part of the Yucatan Peninsula (Fig. 4). The result of the second step of CANAPE, the agglomerative clustering showed that neo- and paleo-lineages were not grouped into the same cluster (Fig. S2).

Genera and families with abundant endemic species such as Agave, Bursera, Amaryllidaceae and Asparagaceae are present in either neo- or paleo-endemic zones. Arid adapted groups

| Vascular plant families with the most elevated percentages of endemic species to Mexico | Species (total) | % Endemic |
|---------------------------------|---------------|-----------|
| Setchellanthaceae | 1 | 100 |
| Zamiaceae | 57 | 86 |
| Fouquieriaceae | 11 | 82 |
| Burseraceae | 102 | 77 |
| Crassulaceae | 377 | 74 |
| Asparagaceae | 455 | 67 |
| Amaryllidaceae | 116 | 66 |
| Cactaceae | 689 | 61 |
| Lamiastrum | 763 | 59 |
| Dioscoraceae | 80 | 59 |
| Asteraceae | 3129 | 53 |
| Euphorbiaceae | 722 | 51 |
| Acanthaceae | 381 | 50 |
| Orchidaceae | 1347 | 49 |
| Zygophyllaceae | 31 | 48 |
| Fabaceae | 1969 | 45 |
| Apocynaceae | 444 | 43 |
with elevated percentages of endemism are located particularly in the areas of the Sonoran and Chihuahuan Deserts and in the Tehuacán Valley, such as Cactaceae, Yucca, and ferns in the Anemiaceae and Dryopteridaceae. Agave, a speciose endemic genus is present in several areas of endemism (neo-, paleo-, mixed and super endemism) as are monocots such as Calochortus, Hymenocallis and Milla. Most of the endemic Fabaceae are distinctive of the seasonally tropical dry forests (Fig. 4).

Areas of super endemism and paleo-endemism in the Sonoran and Chihuahuan Deserts, and in the limit of the Baja California Peninsula, in the Cape Region, share lineages in monocots such as Asparagaceae (Dichelostemma, Brodiaea), Amaryllidaceae (Habranthus), Liliaceae (Calochortus) as well as in Bursera (Burseraceae), and Viscainoa and Sericodes (Zygophyllaceae). Notable genera in the Cactaceae such as Aztekium, Ariocarpus, Leuchtenbergia or genera in Acanthaceae such as Holographis, Mirandea and Justicia, many Agave species, Asteraceae representatives in Dahlia, Cosmos and Coulterella were identified in areas of mixed endemism and super-endemism in the Mexican Plateau in the Chihuahuan Desert, and in restricted areas of the Sierra Madre Oriental. The small paleo-endemic area in the western extreme of the Trans-Mexican Volcanic Belt included orchid genera such as Bletia, and Asparagaceae species in genera like Agave, Yucca, Bessera, Milla and abundant representatives in the Asteraceae belonging to Aztecaster, Bolanosa, Digitacalia, Jaliscoa, Dahlia, Mexerion, and species in Dalea, Crotalaria and Mimoso in the Fabaceae.

The largest area of super-endemism was identified close to Guatemala, in the Sierra de Chiapas, Sierra Madre del Sur and the Central Depression of Chiapas. Here many endemic taxa coincided, some found in seasonally tropical dry forests and pine-oak forests, with many ferns in the Dryopteridaceae (Thelipteris, Phanerophlebia), and dominated by endemic Asteraceae (Digitacalia, Henricksonia, Iostephane, Loxothysanus, Villasenoria), Burseraceae, Fabaceae (Cannavalia, Coursetia, Dalea, Mimoso, Phaseolus, Piptadenia), coinciding with monocots like Nothoscordum, Zepyrhanthes, Milla, Agave, Calochortus, and some orchids (Govenia, Bletia).

| Table 2 | Approximate time of divergence of the most important Mexican endemic groups of vascular plants |
|---------|----------------------------------|
| **This study** | **Previous** | **Reference** |
| (mya) | (mya) | |
| Dryopteridaceae | 41.05 | 14 | Gutiérrez-Ortega et al., 2017 |
| Polypodiaceae | 29.41 | 11.5 | Good-Avila et al., 2006 |
| Zamiaceae | 18.14 | 15.8 | Gándara et al., 2014 |
| Asparagaceae | 24.5 | 13.5 | Good-Avila et al., 2006 |
| Agave | 35.4 | 11.5 | Gutiérrez-Ortega et al., 2017 |
| Milla | 14.86 | 15.8 | Good-Avila et al., 2006 |
| Yucca | 15.8 | 13.5 | Good-Avila et al., 2006 |
| Orchidaceae | 44.6 | 40 | Sosa et al., 2016 |
| Bletia | 2.51 | 4.17 | Angulo et al., 2012 |
| Barkeria skinneri | 49.89 | 15 | Panero & Crozier, 2016 |
| Magnoliaceae | 53.75 | 11.94 | Hernández-Hernández et al., 2014 |
| Magnolia | 45.83 | 62.4 | De-Nova et al., 2012 |
| Asteraceae | 48.55 | 17.5 | De-Nova et al., 2012 |
| Dahlia | 30.59 | 11.54 | Hernández-Hernández et al., 2014 |
| Biesella | 4.98 | 5.47 | De-Nova et al., 2012 |
| Burkera microphylla | 48.55 | 12 | Cervantes et al., 2016 |
| Bursera | 48.55 | 14.71 | Enriquebeltrania |
| Cactaceae | 46.19 | 70.36 | Hernández-Hernández et al., 2014 |
| Aztekium | 62.95–57.67 | 11.94 | Hernández-Hernández et al., 2014 |
| Astrophytum | 5.54 | 63 | Magallón et al., 2015 |
| Crassulaceae | 5.54 | 5.47 | Hernández-Hernández et al., 2014 |
| Euphorbiaceae | 18.52 | 12 | Cervantes et al., 2016 |
| Fouquieriaceae | 15.46 | 12 | Tripp & McDade, 2014 |
| Fabaceae | 46.19 | 63 | Magallón et al., 2015 |
| Lamiaceae | 46.19 | 63 | Magallón et al., 2015 |
| Setchellantaceae | 77.52 | 78 | Hernández-Hernández et al., 2013 |
| Acanthaceae | 77.52 | 78 | Hernández-Hernández et al., 2013 |
| Ruellia | 2.39 | 12 | Tripp & McDade, 2014 |

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4 Discussion

4.1 Patterns of weighted endemism and weighted phylogenetic endemism

Patterns of WE and WPE were similar, and particularly for endemism are consistent with earlier research on a number of taxonomic groups: (i) ferns, in which species richness was identified in the SE and in Chiapas, and weighted endemism in several areas in the Sierra Madre Oriental, in the Trans-Mexican Volcanic Belt and Sierra Madre del Sur (Sanginés-Franco et al., 2015); (ii) gymnosperms, for which areas of endemism coincided in the Sierra Madre Oriental and a small area in Oaxaca (Contreras-Medina & Luna-Vega, 2007); (iii) the monocot tribe Tigridieae (Iridaceae), for which endemism coincided in the eastern part of the Trans-Mexican Volcanic Belt and the Sierra Madre Oriental, as well as in the Tehuacán Valley (Munguía-Lino et al., 2016); (iv) oaks, Quercus spp., for which areas of endemism were identified in the Sierra Madre Occidental and in the Trans-Mexican Volcanic Belt (Rodríguez-Correa et al. 2015); (v) the genus Bursera in which three areas of endemism were identified on the Central Mexican Pacific Coast, in the western Balsas River Basin and in the Tehuacán Valley (De-Nova et al., 2012; Gámez et al., 2014); and (vi) cacti from the Chihuahuan Desert where high degrees of endemism were identified on the Mexican Plateau, as well as in the southern area of the Sierra Madre Oriental (Hernández & Gómez-Hinostrrosa, 2011). In addition, for one functional group, the monocot geophytes, significant areas of endemism were identified in the Trans-Mexican Volcanic Belt, the Sierra Madre Oriental, and in the Tehuacán Valley, which also agrees with our results (Sosa & Loera, 2017). Moreover, the southernmost mountainous area in the Baja California peninsula was identified as having high degree of endemism (Riemann & Ezcurra, 2007).

In summary, the most important areas of endemism and phylogenetic endemism for the Mexican vascular plants are located in the main mountain systems (mountain chains in the Baja California Peninsula, Sierra Madre Oriental, Sierra Madre Occidental, Sierra Madre del Sur, Sierra de Chiapas and the Trans-Mexican Volcanic Belt), in desert areas (Chihuahuan and Sonoran Deserts, Tehuacán Valley), in the Balsas River Basin and in the Central Depression of Chiapas.

Thus, areas of endemism and phylogenetic endemism in the Mexican flora are associated with zones of topographical complexity as found for other floristic provinces across tropical and sub-tropical regions (e.g., Irl et al., 2015; Mráz et al., 2016; Steinbauer et al., 2016; Zhang et al., 2016; Thornhill et al., 2017). Our findings support the idea that tropical mountains are hotspots of biodiversity and endemism as a result of local and regional extinction, long-distance colonization, and local recruitment (Merckx et al., 2015).

With regard to areas of phylogenetic diversity, they were the most restricted compared with our assessments of endemism and phylogenetic endemism and occurred in dry forests of the Trans-Mexican Volcanic Belt and of the Sierra de Chiapas. It has been suggested that, with their complex climatic and geological history, the Mexican highlands represent focal areas that have driven diversification and
allowed for the persistence of Mexican biodiversity in a skylan pattern (Mastretta-Yanes et al., 2015). Vascular plant lineages accumulate in these areas of the mountains and survive climatic oscillations through short distance dispersal and by moving to different elevations (Mastretta-Yanes et al., 2015).

4.2 Neo- and paleo-endemism

Most areas identified by our analyses were found to have mixed neo- and paleo-endemism, and without exception (neo-, paleo-endemism, mixed endemism, and super areas of endemism) they occurred in dry forests (Fig. 4B) such as: (i) thorn forests of the Chihuahuan and Sonoran Deserts; (ii) dry xeric shrublands on the Baja California Peninsula; (iii) dry pine-oak forests in northern Baja California, the Trans-Mexican Volcanic Belt and western slopes of the Sierra Madre Oriental and Occidental; and (iv) in seasonally tropical dry forests (STDF). Remarkably, every single place that STDFs have been reported in Mexico (Lott & Atkinson, 2006) was identified as an area of endemism.

Figure 5 displays the landscapes of some of these forests.

With regard to the time of divergence for the Mexican lineages of vascular plants estimated here, the majority originated in the Miocene, corroborating divergence time estimates established for either certain important groups such as Bursera (De-Nova et al., 2012), groups of monocots (Gándara et al., 2014), cacti (Hernández-Hernández et al., 2014), Fouquieria (De-Nova et al., 2018) or for microfossil floras (Graham, 1987) (See Table 2). Mixed endemism was identified because lineages of recent and ancient divergence coincided in the same areas of endemism. Some of the most ancient lineages in the flora of Mexico such as fern taxa in the Dryopteridaceae, the monotypic dicot family Setchellanthaceae, the genus Beiselia (Burseraceae), and some Apiaceae such as Coulterophytum, for example, occurred in areas of mixed endemism.

In summary, the areas of endemism and weighted phylogenetic endemism identified here confirm what previous research had hypothesized, i.e., that endemism in the Mexican flora is associated with drylands (Rzedowski, 1993). Our study also corroborated that most of the Neotropical flora originated in the Miocene (Graham, 1987). Furthermore, time of divergence of the endemic flora of Mexico supports the conclusions of a radiation of the major succulent plant lineages and arid-adapted gymnosperms in the Miocene when arid environments expanded across the world (Arakaki et al., 2011; Hernández-Hernández et al., 2014; Gutiérrez-Ortega et al., 2017; De-Nova et al., 2018). More than fifty percent of the Mexican territory consists of super-arid, arid and semi-arid regions formed in the Miocene when thus offered many suitable areas for colonization by arid-adapted plants that later diversified in these areas (Fig. 4).

4.3 Implications for conservation

A number of methods have been established recently for estimating phylogenetic diversity and phylogenetic endemism (e.g., Rosauer et al., 2009; Guerin & Lowe, 2015), some based on the presence of taxa in grid cells (e.g., Laffan et al., 2013) and others based on overlapping distribution ranges (e.g., Oliveira et al., 2015). We followed the method based on the presence of taxa in grids because it assesses endemism consistently, independently of taxonomic status level and of previously defined political or biological regions. These results can be directly compared between areas because they are based on equivalent spatial units and thus any congruence in endemism, phylogenetic diversity and phylogenetic endemism can be singled out (Rosauer et al., 2009). Following this approach these biodiversity measures can be used to see whether highly important areas or taxonomic groups are under conservation in protected areas. Figure 6 shows the centers of neo- and paleo-endemism overlaid on the map of the protected natural areas of Mexico (CONANP, 2017). The majority of these centers are within protected areas with the
following exceptions that need attention: (i) areas in the Sonoran and Chihuahuan Deserts; (ii) areas in the Sierra Madre del Sur and Sierra de Chiapas; and (iii) the western part of the Yucatan Peninsula.

4.4 Areas of endemism, dispersal directionality and diversification
The most substantial areas of endemism identified by our study are located at the northern and southern extremes of the Mexican territory. In some way the establishment of the northernmost and the southernmost areas might be linked with the directionality of dispersal of vascular plant lineages.

Axelrod (1975) proposed that especially warm-adapted woody taxa of the Madro-Tertiary Geoflora, a fossil flora from the southwestern United States and northern Mexico, migrated to the south and remained isolated in dry areas. A number of taxa have been reported following this migration pattern (e.g., Boraginaceae: Moore & Jansen, 2006; Rosaceae: Vásquez-Cruz & Sosa, 2016; Asteraceae: Soto-Trejo et al., 2017). Moreover it has been demonstrated in lineages that migrated from the north such like Fouquieria, that vicariance was a crucial driver of speciation (De-Nova et al., 2018). Speciation of this tropical lineage was driven by tectonic events during the Miocene related to the early
development of the North American deserts, to the formation of the Gulf of California that isolated the Baja California peninsula, to the uplifting of the Sierra Madre Oriental and the Trans-Mexican Volcanic Belt (De-Nova et al., 2018). These migrations and vicariant speciation events might explain the important areas of neo-endemism in the Sonoran Desert and the paleo-endemic and super-endemic areas in the Chihuahuan Desert.

Regarding directionality from the south, there are examples showing that during the Mid-Miocene, dispersal rates between South America and Mexico increased and that Central America was an important corridor for migration for certain angiosperms from seasonally tropical dry forests such like the Malpighiaceae (Willis et al., 2014). Furthermore, migration of one of the most important elements of these forests, the genus *Bursera* from South America to Mexico and its posterior diversification has been established (De-Nova et al., 2012).

Migration of certain lineages from South America across Central America might explain the most important area of super-endemism in southern Mexico at the border with Guatemala. This area is very complex, with mountain systems such as the Sierra Madre del Sur, the Sierra Madre de Chiapas and an isolated dry area flanked by these mountain chains, the Central Depression of Chiapas. Thus, it is likely that plants pre-adapted to dry climates and extreme seasonality were able to subsist and diversify associated with tectonic events in the Miocene in the Sierra Madre de Chiapas linked with uplifting of the Trans-Mexican Volcanic Belt (Morán-Zenteno et al., 1999; Ferrari et al., 2012). Furthermore, the presence of this super-endemic area coincides with the findings of Steinbauer et al. (2016); they determined that endemism around the world consistently increased with elevation and suggested that isolation caused by topography maximizes speciation rates in the highlands, across all elevations and progressively towards the equator.

**4.5 Dry forests as cradles and museums of endemism and phylogenetic diversity**

For some groups, like ants and beetles, it has been suggested that Neotropical forests have acted as both museums (paleo-endemic areas) and cradles (neo-endemic areas) of diversity (McKenna & Farrell, 2006; Moreau & Bell, 2013). For the vascular flora of Mexico not every type of tropical forest has acted as a cradle or museum for endemic taxa, but our findings suggest that it is dry forests that have played this role. Furthermore, among dry forests, seasonally tropical dry forests have the highest degree of endemism, neo-, paleo-, and super-endemism. Seasonally tropical dry forests are said to be composed of plant lineages that were pre-adapted to precipitation seasonality and that had high rates of dispersal, thus migration accounts for the elevated phylogenetic diversity in these forests to a greater extent than in situ diversification does (Pennington & Lavin, 2016). Moreover, it has been pointed out that it is difficult for new lineages to immigrate to these forests because the resident lineages persisted and are adapted to a stable, seasonally dry ecology (Pennington et al., 2009). This explanation may apply to the other dry forests, scrublands, thorn forests and dry pine-oak forests, where lineages of plants pre-adapted to xeric conditions migrated and remained in these forests supporting the hypothesis of niche conservatism. Niche conservatism refers to the tendency of related species to occupy similar habitats implying that adaptations to major climate changes were not easily accomplished in all vascular plant lineages (Donoghue, 2008). In this case, it is possible that endemic vascular species and lineages maintained their adaptation to seasonal or dry conditions just as their ancestors did.

Spatial phylogenetics of flora of Chile and China recognized areas of neo-endemism or paleo-endemism concentrated in certain geographic areas (Scherson et al., 2017; Lu et al., 2018).
In contrast, our spatial phylogenetic analyses identified mixed areas of endemism containing significant concentrations of both neo- and paleo-endemism in many geographic areas of Mexico. We suggest that the location of Mexico between two very large landmasses and the fact that more than fifty percent of its surface is arid or semi-arid favored the establishment and diversification of tropical lineages adapted to extreme seasonality and aridity, and were able to migrate from both North and South America across Central America during the Miocene contributing to the signature of the flora of Mexico of mixed endemism.

In this paper we identified the areas with elevated diversity, endemism and phylogenetic diversity for the flora of Mexico and we anticipate that our findings should be of broad interest to evolutionary and conservation biologists and serve to stimulate better-informed conservation planning and research.

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Supplementary Material
The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12416/suppinfo:

**Fig. S1.** Phylogenetic tree of the vascular plants distributed in Mexico. The tree was generated pruning the mega-phylogeny PhytoPhylo from S.PhyloMaker (Qian & Jin, 2016) that uses the phylogeny of Zanne et al. (2014).

**Fig. S2.** Cluster displaying phylogenetic similarity among centres of neo- and paleo-endemism of the vascular plants in Mexico. The cluster analysis used PD-dissimilarity and a phylo-Jaccard metric with link-average linkage. Areas that cluster together indicate that they share many branches of their phylogenetic subtrees, and they are displayed in the same color.

**Data S1.** The vascular plant species checklist, database and phylogenetic tree, available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.c6f7453