

Taxonomic richness of lycophytes and ferns of the Mexican beech forest: Highest ever recorded among *Fagus* forests worldwide?



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ABSTRACT

The composition, richness and distribution of fern and lycophyte species were studied in the three largest and most intact stands of the beech *Fagus grandifolia* subsp. *mexicana* in Mexico, located in the Sierra Madre Oriental (SMO) in the state of Hidalgo. During fieldwork, specimens were collected in these stands, and five 60 m² sampling plots were also selected in order to estimate the relative importance value (RIV) of the species at each locality. Floristic similarity between localities was calculated based on species absence/presence data, and richness was estimated as a measure of plant biodiversity. In both analyses, data from previous studies in different regions of the SMO were included. In total, 21 families, 49 genera and 82 species of ferns and lycophytes were recorded for the beech forest of the state of Hidalgo; five of those species fall under a risk category according to Mexican legislation. Most species had either terrestrial or epiphytic habit. The species with high RIV differed among localities, except for *Lophosoria quadripinnata* which was dominant at all three localities. Our results indicate that Mexican *Fagus* forests have a higher richness of lycophyte and fern species per unit area than any other *Fagus*-dominated forests in the world. Thus, conservation and management programs should be implemented in the short term, in view of the limited area occupied by these forests and the constantly increasing levels of human-generated disturbance.

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1. Introduction

The *Fagus* (sensu Rzedowski, 2006) or beech forest, whose canopy is dominated by *Fagus grandifolia* Ehrh. subsp. *mexicana* (Martínez) E. Murray (Valencia and Flores-Franco, 2006), represents a plant association of special interest in the context of the Mexican cloud forest (MCF), since it is a relic of the Pliocene–Miocene. Its current distribution is restricted to the mountainous regions of the Sierra Madre Oriental in the Mexican states of Hidalgo, Puebla, San Luis Potosí, Tamaulipas and Veracruz (Rowden et al., 2004; Williams-Linera et al., 2003). Unlike

other temperate *Fagus* forests of the Americas, Asia or Europe, the Mexican beech forests are subtropical and represent the southern distribution limit of this forest at a latitude of 21°N (Peters, 1995; Ortiz-Quijano et al., 2016).

The *Fagus* forest in the state of Hidalgo covers an area of 106.79 ha, which represents 73% of the known extent of this plant community in the entire country, making it the largest beech forest in Mexico and also the least disturbed (Williams-Linera et al., 2003; Rowden et al., 2004; Rodríguez-Ramírez et al., 2013). Since the forest grows in a narrow elevation band where mist forms, it is highly vulnerable to both climate change and human-caused disturbances (Ortiz-Quijano et al., 2015). In general, ca. 60% of the area presently occupied by the cloud forest (CF) of the state of Hidalgo is disturbed, because of land use change to crop agriculture and cattle ranching, and by logging and habitat fragmentation. These result in changes to the species composition and structure of the forest, the

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magnitude of which depends on the frequency, intensity and size of the disturbance (Ortiz-Quijano et al., 2015; Vargas-Rodríguez et al., 2010).

Knowledge of the identity and biology of plant species coexisting in the *Fagus* forest in Mexico has increased in recent years as a result of several ecological and floristic studies on non-vascular plants (Mejía, 2015) and vascular flowering plants (Alcántara and Luna-Vega, 2001; Chávez, 2014; Ortiz-Quijano et al., 2016; Williams-Linera et al., 2003). Additionally, several studies have contributed quantitative data on the demography and population structure of *Fagus grandifolia* subsp. *mexicana* (Godínez-Ibarra et al., 2007; Ortiz-Quijano et al., 2016). However, the available information on lycophyte and fern species growing in the beech forests of Mexico is limited, although both groups are important structural components of the Mexican cloud forest and actively participate in the regeneration of disturbed sites (Tejero-Díez et al., 2014). Unlike many vascular plants with seeds, lycophytes and ferns require particular environmental conditions—especially high atmospheric humidity—for reproduction and proper physiological functioning (Arcand and Ranker, 2008), which is why they usually serve as indicators of climate conditions (Arcand and Ranker, 2008; Mehlreter, 2008; Mehlreter, 2010; Paciencia and Prado, 2005).

The present study aims to: (1) assess the composition, structure and distribution of lycophyte and fern species in the least disturbed patches of *Fagus grandifolia* subsp. *mexicana* forest in Mexico, and (2) based on species richness and composition, assess whether the patches of this forest represent an oasis or refuge for ferns and lycophytes, given that they are among the cloud forest sites in Mexico with the lowest degree of disturbance, and have relatively homogeneous environmental conditions. The small total area of beech forest in Mexico (less than 150 ha), along with the continuously increasing stress on it because of human activities, justify the effort to conduct floristic and ecological studies to characterize it in detail and to propose appropriate short term management and conservation programs or strategies. Moreover, we contribute to ongoing studies on diversity and ecology of lycopods and ferns in beech forests around the world. Regional data will enable comparative analyses of differences and similarities between these forests on a supra-regional scale.

2. Materials and methods

2.1. Area of study

The patches of *Fagus* forest studied in this work are distributed in the municipalities (county equivalents) of San Bartolo Tututepec, Tenango de Doria and Zacualtipán de Ángeles in the eastern part of the state of Hidalgo, on windward slopes of the Sierra Madre Oriental (Table 1, Fig. 1). This forest grows at an elevation from 1560 to 1987 m, in sites with irregular topography, on slopes of 20° to 42° (Rodríguez-Ramírez et al., 2013). The soils are of ando (originating from volcanic ash), humic and vitric types, following the FAO-UNESCO classification, with a clay loam texture and an acid pH between 4 and 6 (Peters, 1995; Rodríguez-Ramírez et al., 2013). The climate is humid temperate (Cm(f)b), with an annual mean temperature of 12.7 °C and an annual minimum temperature of −10 °C; the summers are long and cool; the precipitation and mist regime is constant throughout the year; and annual cumulative precipitation is 1500 to 2300 mm. Average annual atmospheric humidity ranges between 60 and 85% (García, 1988 Peters, 1995).

The forest canopy is dominated by *Fagus grandifolia* subsp. *mexicana* (Fagaceae); other tree species characteristic of this association are *Quercus corrugata* Hook, *Q. delgadoana* S. Valencia, Nixon & L. M. Kelly, *Q. xalapensis* Humb. & Bonpl., *Clethra macrophylla* M. Martens & Galeotti, *Liquidambar macrophylla* Oerst., *Magno-*

lia schiedeana Schltdl. and *Podocarpus reichei* J. Buchholz & N.E. Gray (Ortiz-Quijano et al., 2016; Villavicencio-Nieto and Pérez-Escandón, 2008; Williams-Linera et al., 2003). Numerous shrubs and herbaceous plant species grow in the understory. The most important species include *Begonia incarnata* Link & Otto, *Cestrum fasciculatum* (Schltdl.) Miers, *Deppea purpurea* Standl., *Epifagus virginiana* (L.) W.P.C. Barton, *Eugenia capuli* (Schltdl. & Cham.) Hook. & Arn., *Miconia glaberrima* (Schltdl.) Naudin and *Rubus pringlei* Rydb. (Chávez, 2014; Godínez-Ibarra et al., 2007).

2.2. Field work

Between December 2011 and May 2014, the municipalities and localities with beech forest in the state of Hidalgo were explored and specimens were collected (Table 1). Lycophytes and ferns were sampled in rectangular plots being 60 m² in size (3 × 20 m) in order to determine the population variables of coverage and density for each species, so as to assess their structural importance (Franco et al., 2001). Five sampling plots at least 20 linear m apart were selected per locality (15 plots in total). This plot size and distribution has been recommended in other studies for sampling the herbaceous layer in plant communities in temperate climates (Franco et al., 2001; Mueller-Dombois and Ellenberg, 1974).

2.3. Laboratory work

The collected lycophyte and fern specimens were identified mainly according to the work of Mickel and Smith (2004) and they were deposited at the HGOM herbarium (Centro de Investigaciones Biológicas) of the Universidad Autónoma del Estado de Hidalgo; 46 duplicates were deposited in the Herbario Nacional (MEXU) at the Instituto de Biología of the Universidad Nacional Autónoma de México.

Using incidence data, the species inventory completeness percentage was calculated by means of two conventional non-parametric species richness estimator; first-order jackknife, and bootstrap (Colwell and Coddington, 1994). EstimateS v. 9.1.0 software (Colwell, 2015) was used for the analysis.

Using the relative values of the structural variables for cover and density, the relative importance value (RIV) of the species was estimated, modified from the RIV proposed by Mueller-Dombois and Ellenberg (1974). Density was defined as the total number of individuals of each species per unit area, and cover (C) was calculated using the formula: $C = \pi * (d_1/2)^2 * (d_2/2)$, where $\pi = 3.1416$, d_1 and d_2 are the major and minor diameters perpendicular to each other of the vertical projection of the crown of the individual; and $RIV = (\text{relative coverage} + \text{relative density})/2$.

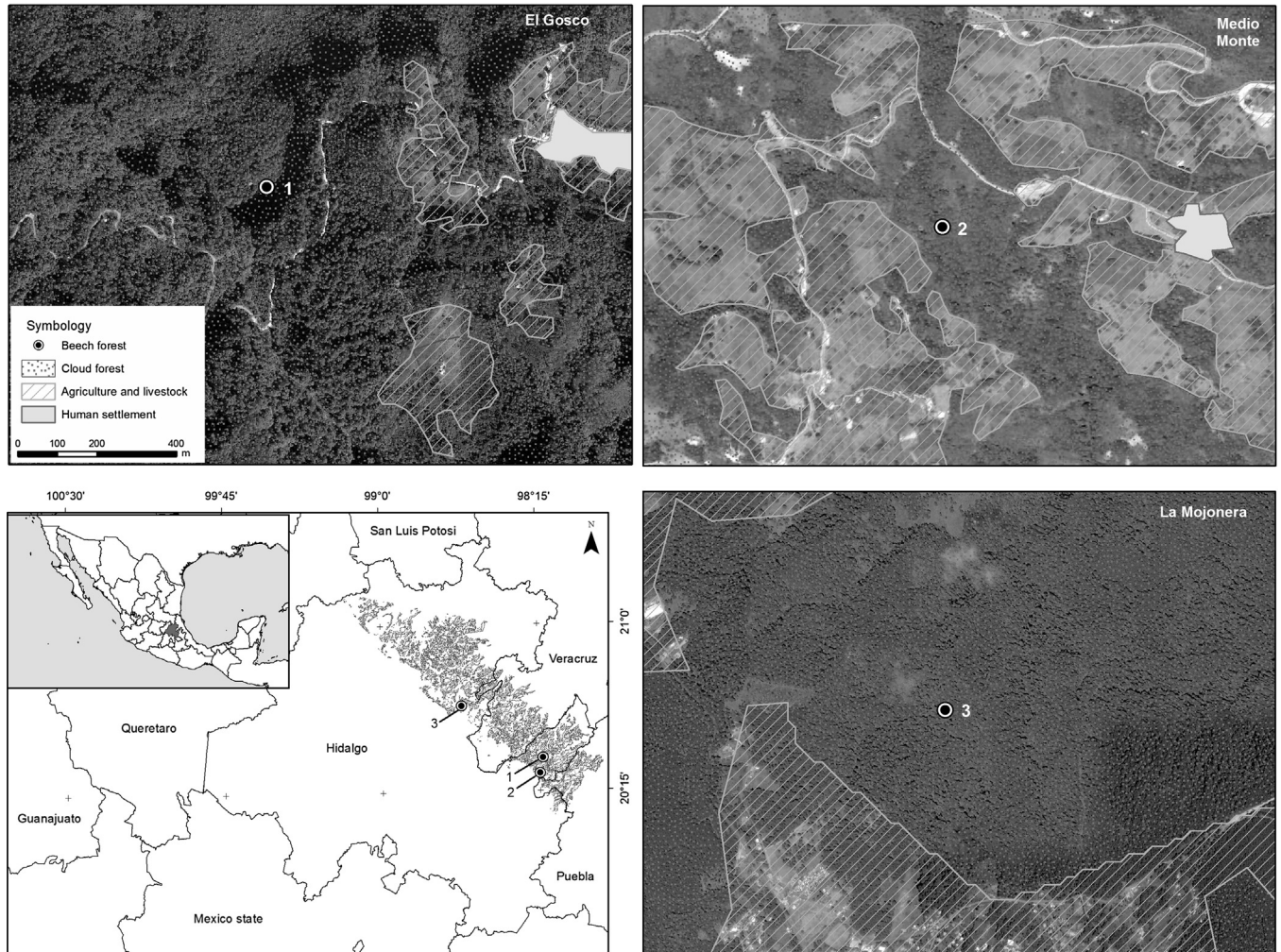
In order to compare the degree of similarity in species composition among the *Fagus* forest localities in the state of Hidalgo, and to compare these to other localities with cloud forest in Mexico (Cartujano et al., 2002; Pérez-Paredes et al., 2012; Vázquez et al., 2006; Williams-Linera et al., 2004), a cluster analysis was carried out. The Jaccard index was chosen as the distance measure for determining the similarity among groups and the group average was used as a linking method (McCune and Grace, 2002). The PC-ORD program (McCune and Mefford, 1999) was used for the analysis.

As a complement, the species richness of the *Fagus* forest was compared with the species richness measured in other studies of lycophytes and ferns in different types of vegetation and other states of Mexico, using the taxonomic biodiversity index (BI): $BI = S/\ln A$, where S = total of recorded species and $\ln A$ = natural logarithm of the size of the area (Squeo et al., 1998).

Table 1

Characteristics of collecting and sampling localities (UTM-NAVD29).

Municipality/Locality	Area (ha)	Elevation (m)	Latitude	Longitude
San Bartolo Tutotepec/Medio Monte	48.24	1800–1944	20°24'39.14"	98°14'24"
Tenango de Doria/El Gosco	4.5	1557–1864	20°19'37.8"	98°14'57.1"
Zacualtipán de Ángeles/La Mojonera	54.05	1780–1987	20°38'05.8"	98°36'51.8"

**Fig. 1.** Area of study, including three municipalities and three localities with *Fagus* forest in the state of Hidalgo, Mexico.

3. Results

3.1. Floristic composition

A total of 214 specimens of lycophytes and ferns were collected, which were identified and their names verified against type specimens in JSTOR Global Plants (access granted by the National University of Mexico, 2016). The specimens belonged to 82 species (10 in Lycopodiopsida), 49 genera (six in Lycopodiopsida) and 21 families (two in Lycopodiopsida; *sensu* Christenhusz et al., 2011 and the Pteridophyte Phylogeny Group: PPG, 2016; Table 2). It is important to note that five of the species found in the *Fagus* forests are protected under Mexican law, since they are included in the *Norma Oficial Mexicana, Secretaría de Medio Ambiente y Recursos Naturales* (NOM-059-SEMARNAT-2010): *Alsophila firma*, *Cyathea fulva*, *Dicksonia sellowiana*, *Marattia weinmannifolia* and *Psilotum complanatum*.

The families with two or more genera were Polypodiaceae (8), Dryopteridaceae (6), Pteridaceae (5), Lycopodiaceae (5), Hymeno-

phyllaceae (4), Blechnaceae (3), Cyatheaceae, Dicksoniaceae and Gleicheniaceae (2), and the remaining families are represented by only one genus. The families with four or more species were Polypodiaceae (17), Dryopteridaceae (11), Hymenophyllaceae (9), Lycopodiaceae (6), Blechnaceae and Pteridaceae (5). The rest of the families are represented by four or fewer species. The most representative genera were *Asplenium* and *Elaphoglossum* (6 species), *Hymenophyllum* (5), *Pleopeltis*, *Polypodium* and *Selaginella* (4). The rest of the genera had between one and three species.

The results from the non-parametric estimators show that further sampling efforts are required to obtain a more complete inventory of the lycophytes and ferns of the *Fagus* forests in the state of Hidalgo. The jackknife and bootstrap estimators indicated that the completeness of the inventory ranged from 79 to 90%, respectively. The bootstrap estimator predicts a potential richness of 91 species, and the jackknife a richness of 104.

Table 2
Distribution of number and percentage (in parenthesis) of fern and lycophyte genera and species in the most diverse families (a), and number of species in the most important genera (b) present in the *Fagus* forest in Hidalgo, México.

Family	No. of Genera/Species (a)	Genus	No. of Species (b)
Polypodiaceae	8 (16)/17 (21)	<i>Asplenium</i>	6 (7)
Dryopteridaceae	7 (14)/11 (13)	<i>Elaphoglossum</i>	6 (7)
Pteridaceae	5 (10)/5 (6)	<i>Hymenophyllum</i>	5 (6)
Lycopodiaceae	5 (10)/6 (7)	<i>Pleopeltis</i>	4 (5)
Hymenophyllaceae	4 (8)/9 (11)	<i>Polypodium</i>	4 (5)
Gleicheniaceae	2 (4)/2 (3)	<i>Selaginella</i>	4 (5)
Blechnaceae	2 (4)/5 (6)	<i>Amauropelta</i>	3 (4)
Cyatheaceae	2 (4)/2 (3)	<i>Woodwardia</i>	3 (4)
Dicksoniaceae	2 (4)/2 (3)		
Others	12 (27)/23 (28)	Others	47 (57)

Table 3
Fern and lycophyte species with greatest relative importance value in the sampling localities.

Sampling locality	El Gosco	La Mojonera	Medio Monte
Species	Relative Importance Value (%)		
<i>Lophosoria quadripinnata</i>	35.4	11.4	19.3
<i>Dryopteris wallichiana</i>	–	19.9	–
<i>Plagiogyria pectinata</i>	–	–	19.6
<i>Ctenitis erinacea</i>	16.5	3.6	–
<i>Dicksonia sellowiana</i>	4.9	7.9	11.8
<i>Woodwardia martinezii</i>	–	2.9	11.4
<i>Polystichum distans</i>	5.2	10.6	0.4
<i>Cyathea fulva</i>	8.6	–	4.7
<i>Elaphoglossum peltatum</i>	7.5	–	3.4
<i>Elaphoglossum seminudum</i>	1.8	6.6	7.3
<i>Lomariopsis mexicana</i>	0.5	–	6.2
<i>Arachnoides denticulata</i>	5.4	2.5	2.1
<i>Dennstaedtia globulifera</i>	–	5	–
<i>Marattia weinmannifolia</i>	0.5	8.5	0.5
<i>Selaginella silvestris</i>	2.8	0.5	3.3
<i>Pteris orizabae</i>	–	3.5	–
<i>Woodwardia semichordata</i>	–	2.8	–
<i>Pleopeltis lepidotricha</i>	2.7	–	–
<i>Adiantum andicola</i>	–	2.5	–
<i>Amauropelta atrovirens</i>	1.4	1.3	2.4
<i>Asplenium sessilifolium</i> var. <i>sessilifolium</i>	0.4	2.2	0.7
<i>Diplazium ternatum</i>	–	–	2.0
<i>Austroblechnum stoloniferum</i>	1.8	0.4	–
<i>Asplenium monanthes</i>	–	1.8	0.3
<i>Hymenophyllum polyanthos</i>	1.1	–	1.6
<i>Pleopeltis plebeia</i>	–	1.2	–
<i>Elaphoglossum obscurum</i>	0.6	0.9	–
<i>Asplenium cuspidatum</i>	–	0.8	0.3
<i>Cystopteris fragilis</i>	0.4	–	–
<i>Selaginella flexuosa</i>	0.4	–	–
<i>Polypodium rodhopleuron</i>	0.4	–	–
<i>Diplazium lonchophyllum</i>	0.4	–	–
<i>Melpomene leptostoma</i>	0.4	–	0.3
<i>Pecluma longepinnulata</i>	–	–	0.4
<i>Phlebodium pseudoaureum</i>	–	–	0.3
<i>Vittaria graminifolia</i>	–	–	0.3

3.2. Growth substrate

Because of the biotope where the *Fagus* forest grows (slopes with deep soils), terrestrial species were the most common, with 42.5% species being of this type, followed by rupicolous-terrestrial (15%) and a smaller percentage (12.5%) of epiphytic or corticolous species. Some species (10%) were generalist, since they were found growing in the three substrates; others in two: epiphytic-terrestrial (7.5%), epiphytic-rupicolous (7.5%), and four were exclusively rupicolous in habit (5%; Fig. 2).

3.3. Relative importance value (RIV)

In the sampling plots, the lycophyte and fern species with the highest structural importance value differed between localities,

except for *Lophosoria quadripinnata*, which was the only species present and dominant at all localities (Table 3). At the El Gosco site, the species with the highest RIV were *Lophosoria quadripinnata* (35.4), *Ctenitis erinacea* (16.5) and *Cyathea fulva* (8.6). At La Mojonera they were *Dryopteris wallichiana* (19.9), *Lophosoria quadripinnata* (11.4) and *Polystichum distans* (10.6). At Medio Monte they were *Lophosoria quadripinnata* (19.3), *Plagiogyria pectinata* (19.6), *Dicksonia sellowiana* (11.8) and *Woodwardia martinezii* (11.4).

3.4. Similarity in species composition

Pruning the dendrogram at a cutoff value of 0.25 yielded three groups, defined by their species composition, to be distinguished (Fig. 3). The first group is composed of the three localities with *Fagus* forest and cloud forest in the municipality of Zacualtipán de Ángeles in the state of Hidalgo; the second group includes the municipality of Landa de Matamoros located in the state of Querétaro, and the third group includes the locality of La Banderilla and the fragments of beech forest in the state of Veracruz.

3.5. Taxonomical biodiversity index

The values obtained with this index, estimated for 12 regions or municipalities both in the state of Hidalgo and for external localities in the states of Querétaro and Veracruz, indicate that the highest richness of lycophyte and fern species per unit area was found in the *Fagus* forest of Hidalgo (Table 4).

4. Discussion

The results of the present study constitute the first reference on the species composition of lycophytes and ferns in the *Fagus* forest in Mexico (gamma diversity). At least 82 species grow in this forest; 10 from Lycopodiopsida and the rest from Polypodiopsida. If we take into account that the total area of the forest in the state of Hidalgo is only 108.79 ha, it could be categorized as a plant association with a high taxonomic richness per unit area relative to other temperate humid forests in Mexico and the world.

The values of the non-parametric estimators indicate that a larger sampling effort is required to obtain a more complete inventory of the lycophytes and ferns of the beech forests in the state of Hidalgo. However, it is widely acknowledged that in studies of biological diversity it is often impossible to record the totality of the species of any given area (Álvarez-Zúñiga et al., 2012; Jiménez-Valverde and Hortal, 2003). The percentage of completeness (between 79 and 90%) obtained in this study is therefore more than adequate to give certainty and robustness to the results.

The families with the largest taxonomic diversity in the *Fagus* forest in Hidalgo (Polypodiaceae, Dryopteridaceae, Hymenophyllaceae, Lycopodiaceae, Blechnaceae and Pteridaceae) are also the

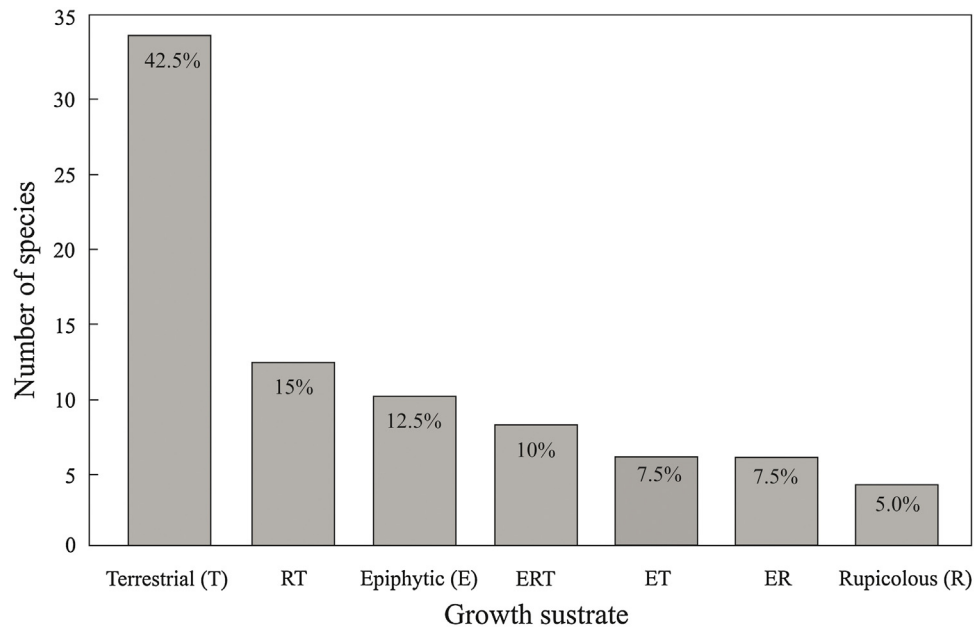


Fig. 2. Growth substrates of lycophyte and fern species of *Fagus* forest in the state of Hidalgo, Mexico.

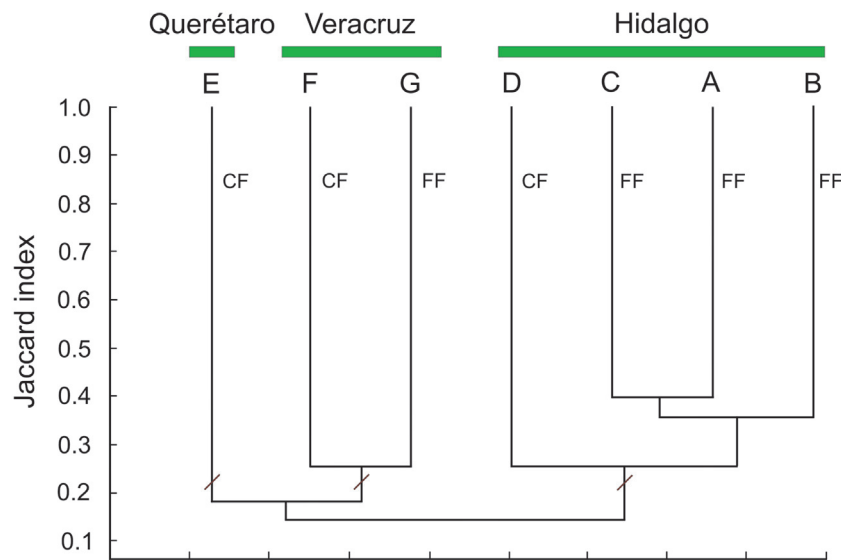


Fig. 3. Dendrogram of cluster analysis showing similarity in composition of lycophyte and fern species among studied localities and external locations. A: El Gosco, Tenango de Doria, B: La Mojonera, Zacualtipán de Ángeles, C: Medio Monte, San Bartolo Tutotepec, D: CF de Zacualtipán de Ángeles, E: CF de la Banderilla, Veracruz, F: CF de Landa de Matamoros, Querétaro, G: Localities with *Fagus* forest in Veracruz.

Table 4

Taxonomical biodiversity index (BI) in regions or municipalities of the state of Hidalgo and Mexico, for which Pteridophyte-exclusive inventories have been generated. Elevation range data is included. RBBM = Reserva de la Biosfera Barranca de Metztitlán; PNM = Parque Nacional Los Mármoles; PNC = Parque Nacional El Chico; AF = *Abies* forest; CF = cloud forest; PQF = *Pinus-Quercus* forest; XC = Xerophytic scrub.

Region or municipality	Elevation (m)	Area (ha)	Species	BI	Reference
Valle del Mezquital, Hidalgo (XC)	1590–2770	683,169	80	5.95	Pérez-Atilano et al. (2015)
RBBM, Hidalgo (XC)	1000–2000	96,000	79	6.89	Cuevas et al. (2013)
PNM, Hidalgo (PQF)	1300–2950	23,150	71	7.06	Ramírez-Cruz et al. (2009)
PNC, Hidalgo (AF)	2282–2982	2739	62	7.83	Serrano (2010)
Tenango de Doria, Hidalgo (CF)	630–2250	21,070	112	11.24	Zúñiga (2009)
Calnali, Hidalgo (CF)	318–2370	19,020	115	11.67	Pérez (2009)
Landa de Matamoros, Querétaro (CF)	800–2200	2700	96	12.15	Cartujano et al. (2002)
Tlanchinol, Hidalgo (CF)	1107–1900	38,000	130	12.32	Álvarez-Zúñiga et al. (2012)
Zacualtipán, Hidalgo (CF)	1004–2050	24,160	125	12.38	Pérez-Paredes et al. (2012)
Banderilla, Veracruz (CF)	1520	2221	128	16.61	Vázquez et al. (2006)
<i>Fagus</i> forests, Mexico (Hidalgo and Veracruz, CF)	1560–1987	115.54	93	19.51	Williams-Linera et al. (2004); Present study
<i>Fagus</i> forests, Hidalgo (CF)	1560–1987	108.79	82	17.48	Present study

most representative at the state, national and global levels, over all prevailing environmental conditions and vegetation types (Acebey et al., 2015; Álvarez-Zúñiga et al., 2012; Carvajal-Hernández and Krömer, 2015; Cuevas et al., 2013; Pérez-Atilano et al., 2015; Pérez-Paredes et al., 2012; Ramírez-Cruz et al., 2009), but their hierarchical distribution can be considered as a reflection of their predilection for humid tropical mountain environments.

The Polypodiaceae species have evolved as epiphytes in humid angiosperm forests, and two of the more iconic genera (*Pleopeltis* and *Polypodium*) reach their peak representation in the Mexican cloud forest (Otto et al., 2009; Schneider et al., 2004; Smith and Tejero-Díez, 2014; Tejero-Díez et al., 2014). The most representative genera of Dryopteridaceae (*Elaphoglossum*) and *Pleopeltis* reach their peak richness in the humid tropical mountain zone, both on terrestrial substrate and on rupicolous-corticulous substrate (Mickel and Smith, 2004; Rouhana et al., 2004). Members of the family Hymenophyllaceae are widely known for their sensitivity to humid atmospheric environments and depend on high moisture availability (Mehlreter, 2008). In contrast, genera of the families with affinity to more seasonal sites, such as Pteridaceae and Thelypteridaceae, are absent or rare in the Mexican beech forest (Tejero-Díez et al., 2014).

The lycophytes and ferns are considered to be environmental indicators in humid mountain forests (Pérez-Paredes et al., 2014; Tejero-Díez et al., 2014), since most of them tend to disappear following land use changes (although several species of Gleicheniaceae and Lycopodiaceae do grow well in disturbed sites). The high number of species present in the municipalities or regions with cloud forest, and in particular in the *Fagus* forest, is probably explained by the consistent moderate temperature, water availability and actual evapotranspiration throughout the year, and the high canopy cover, favoring the growth of both groups of plants (Pérez-Paredes et al., 2014; Tejero-Díez et al., 2014).

In addition, the presence of clearings in the canopy, due mainly to small-scale natural disturbances (tree fall and large fallen branches due to senescence, storms or hurricanes) generates a mosaic of patches in the beech forest in different stages of regeneration (Rodríguez-Ramírez et al., 2016) that promotes the presence of a larger number of plant species, as has been shown in various studies in temperate forests in different parts of the world, including *Fagus* spp. forests (Hukusima et al., 2013; Jardel et al., 2014; Peña et al., 2011; Peters, 1995).

When comparing the richness of lycophyte and fern species per unit area of the beech forest in Mexico, and in particular of the forest in the state of Hidalgo, with species richness in other parts of the world, it is found that the Mexican forest has the highest richness: Floristic studies carried out in European *Fagus sylvatica* forests gave less than fifteen species of lycophytes ferns: v. gr. Gazol (2009) – eight species; Peña et al. (2011) – 11 species; Rodríguez-Gutián et al. (2009), 15 species. In the Asian beech forest, encompassing vast areas (hundreds to thousands of ha) in countries such as China, Korea, Japan and Taiwan, only 145 species are listed (Hukusima et al., 2013).

Peters (1995) notes that the beech forests in each continent differ in plant species richness and composition, which can be related to their respective biogeographical history and the wide latitudinal and climatic range in which they are distributed (20°19'–52°15'). The *Fagus* forests of the subtropical mountains in Eastern China are deciduous or mixed (with elements of both deciduous and perennial forests) as a result of the monsoon climate characterized by marked seasonality, with humid, warm summers and dry, cold winters (Shen et al., 2015). Furthermore, these forests contain a high density of bamboo species, absent from the beech forests of Europe and North America (Hukusima et al., 2013), which suggests greater interspecific competition in the undergrowth layer

and, consequently, a smaller richness of lycophyte and fern species in the ground layer.

Some of the species identified herein are found in two risk categories within the NOM-059-SEMARNAT-2010 (SEMARNAT, 2010). *Alsophila firma*, *Cyathea fulva*, *Dicksonia sellowiana* and *Marattia weinmannifolia* are cataloged as subject to special protection (Pr), and *Psilotum complanatum* is threatened (A). However, it is probable that in the short term, some populations of fern and lycophyte species and other plant groups growing in the beech forests will decrease or disappear, due to the limited area they cover; the unchecked use of the natural resources sheltered by this plant association, such as harvesting of wood, seeds, and plants; and to changing land use (Ortiz-Quijano et al., 2015; Rodríguez-Ramírez et al., 2013; Williams-Linera et al., 2003).

According to Pérez-García et al. (1995), the most common growth types for lycophytes and ferns in diverse types of vegetation in Mexico and the world are the terrestrial and the epiphytic types; the latter is especially favored by high humidity conditions throughout the year and a moderate altitude-dependent mean temperature (15–20 °C), which prevails in ecosystems such as the cloud forest (Tejero-Díez et al., 2014).

The most common growth substrate for lycophytes and ferns in the beech forest in the study was terrestrial (43%). In other studies at the local scale, such as those carried out by Ramírez-Cruz et al. (2009), Álvarez-Zúñiga et al. (2012) and Pérez-Paredes et al. (2012), the same pattern was observed: the majority of species showed a terrestrial habit and, exceptionally, the most common substrate was the epiphytic (Lira and Riba, 1993). The prevailing climate conditions in the humid and sub-humid temperate forests in Mexico (*sensu* Rzedowski, 2006) favor the maintenance of a suitable water balance for lycophytes and ferns in both types of growth substrate (Tejero-Díez et al., 2014).

The species with the highest structural importance in the beech forests of Hidalgo was *Lophosoria quadripinnata*, which is characterized as typical of the cloud forest and by its capacity to grow in disturbed environments (Álvarez-Zúñiga et al., 2012). The results in the present study corroborate this claim, as the dominance (RIV) of this species was high in the El Gosco locality, where a patch of forest of less than 4.5 ha is growing, with a high degree of fragmentation, low connectivity and obvious disturbance (Rodríguez-Ramírez et al., 2013; Ortiz-Quijano et al., 2015). In contrast, in the La Mojonera and Medio Monte sites, the two localities with the largest area of beech forest in Mexico, and limited evidence of disturbance (Villavicencio-Nieto and Pérez-Escandón, 2008; Ortiz-Quijano et al., 2015, 2016; Rodríguez-Ramírez et al., 2013), the structural values of *L. quadripinnata* were smaller.

The use of qualitative species data (absence/presence) for the localities of the Hidalgo study and two other Mexican states demonstrated that the lycophyte and fern species have a certain degree of fidelity (arbitrarily defined in the present study by the degree of floristic similarity between sites) to the environmental conditions prevailing in the *Fagus* forest, as stated by Williams-Linera et al. (2004) for the *Fagus* forests of Veracruz. In contrast, at the external localities with montane cloud forest, where the canopy is dominated or co-dominated by other genera of trees, such as *Liquidambar*, *Magnolia*, *Pinus*, *Podocarpus* and *Quercus* (Jardel et al., 2014), the lycophyte and fern species composition was more diverse than in the beech forests.

However, the higher similarity in species composition in the localities with *Fagus* forest in the state of Hidalgo than at the external localities might be related to the phenomenon known as “distance decay,” in which neighboring localities are more similar to each other than to localities located farther away (Marcantonio et al., 2012). Several authors mention that the Mexican beech forest grows in sites with specific climatic and topographic conditions, with a narrow range of variation (Fang and Lechowicz, 2006; Téllez-

Valdés et al., 2006; Williams-Linera et al., 2003). The results of this study only partially support this claim, since the floristic similarity values between localities with beech forests are low (0.34–0.4) and each site has at least seven different species of lycophytes and ferns, which could be interpreted as an indication that the environmental conditions are not so homogeneous among these forests, although vicarious evolution is still a possibility, in which some shared taxa could be survivors of the original ensemble (Tuomisto et al., 2003).

The results of the present study indicate that the localities with *Fagus grandifolia* subsp. *mexicana* forests in the state of Hidalgo contain a high number of lycophyte and fern species, even though these associations grow in a very small area compared with other regions in Mexico or elsewhere in the world. It is important to note that in addition to its spatial distribution being highly restricted, this forest is subject to strong anthropic stress, so it is necessary to establish management and conservation programs, including permanent monitoring (Williams-Linera et al., 2003) and restoration and recovery of the most affected localities, engaging the local habitants, who directly use the natural resources within or in the periphery of this plant association (Ortiz-Quijano et al., 2015).

5. Conclusions

The floristic composition of the beech forest localities analyzed in the study was relatively similar to that of other sites with cloud forest located in the humid temperate zone of Mexico. In contrast, the structural values of the species showed greater variation between localities, probably because of differences in local environmental conditions, such as the degree of disturbance. The beech forest in the state of Hidalgo stands out for being one of the plant associations with the highest richness of lycophyte and fern species per unit area in the cloud forest in Mexico, and also among temperate forests around the world in which the canopy is dominated by any species of *Fagus*. The general atmospheric conditions in the latitudes where this forest is distributed worldwide along the SMO, and the local environmental conditions in which it grows (e.g., intermediate elevation, steep topography, high humidity and moderate temperature), make it a small refuge for the survival of at least 82 species of lycophytes and ferns (Appendix A).

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Appendix A. List of fern and lycophyte species of the *Fagus* forest in the state of Hidalgo, Mexico (according to phylogeny proposed by Christenhusz et al., 2011 and the Pteridophyte Phylogeny Group: PPG, 2016).

* = species in the NOM-059-SEMARNAT-2010; 1 = new records of species for the state of Hidalgo; E = epiphyte, R = rupicolous, T = terrestrial; Collectors = AHA: Adriana Hernández Álvarez, ASG: Arturo Sánchez González, GPP: Guadalupe Pérez Paredes, MGL: Marisol Gutiérrez Lozano. GS = growth substrate.

Taxonomical category	GS
Lycopodiopsida	
Lycopodiales	
Lycopodiaceae	
1. <i>Diphasiastrum thyoides</i> (Humb. & Bonpl. Ex Willd.) Holub (GPP 60)	T
2. <i>Huperzia serrata</i> (Thunb. Ex Murray) Trevis. (MGL 90; ASG 4475; ASG 4476)	T
3. <i>Lycopodium clavatum</i> L. (ASG 4485)	T
4. <i>Palhinhaea cernua</i> (L.) Vasc. & Franco (MGL 36; MGL 116; ASG 4483)	T
5. <i>Phlegmariurus pringlei</i> (Underw. & F.E. Lloyd) B. Øllg. (GPP 302)	T
6. <i>Phlegmariurus reflexus</i> (Lam.) B. Øllg. (MGL 34; MGL 40)	R, T
Selaginellales	
Selaginellaceae	
7. <i>Selaginella delicatissima</i> Linden ex A. Braun (ASG 4525)	T
8. <i>Selaginella flexuosa</i> Spring. (MGL 49; MGL 83; ASG 4506)	T
9. <i>Selaginella pallescens</i> (C. Presl) Spring (MGL 32; ASG 4514; ASG 4524)	R, T
10. <i>Selaginella silvestris</i> Asplund. (MGL 16; MGL 28; MGL 66; MGL 69; ASG 4441; ASG 4495; ASG 4503)	R, T
Polypodiopsida	
Psilotales	
Psilotaceae	
11. <i>Psilotum complanatum</i> Sw. * (MGL 38; MGL 65; ASG 4444)	E
Ophioglossales	
Ophioglossaceae	
12. <i>Botrychium decompositum</i> M. Martens & Galeotti (MGL 258; MGL 277)	T
Marattiales	
Marattiaceae	
13. <i>Marattia weinmannifolia</i> Liebm. * (MGL 106; ASG 4480; ASG 4507)	T
Hymenophyllales	
Hymenophyllaceae	
14. <i>Didymoglossum reptans</i> (Sw.) C. Presl (MGL 92)	E, R
15. <i>Hymenophyllum crispum</i> Kunth. (ASG 4520)	E, R
16. <i>Hymenophyllum ectocarpon</i> Fée (MGL 93)	E
17. <i>Hymenophyllum polyanthos</i> Sw. (MGL 23; MGL 29; MGL 48; MGL 58; ASG 4456; ASG 4461; ASG 4468; ASG 4470)	E
18. <i>Hymenophyllum tegularis</i> (Desv.) Proctor & Lourteig (MGL 50)	R
19. <i>Hymenophyllum tunbrigense</i> (L.) Sm. (MGL 59; ASG 4462)	R
20. <i>Polyphelebium capillaceum</i> (L.) Ebihara & Dubuisson (MGL 31; ASG 4436)	E, R
21. <i>Polyphelebium hymenophylloides</i> (Bosch) Ebihara & Dubuisson (MGL 278)	R, T
22. <i>Vandenboschia radicans</i> (Sw.) Copel. (MGL 21; MGL 107; ASG 4504)	E, R
Gleicheniales	
Gleichenaceae	
23. <i>Diplopterygium bancroftii</i> (Hook.) A. R. Sm. (MGL 39; ASG 4446; ASG 4486)	R, T
24. <i>Sticherus underwoodianus</i> (Maxon) Nakai. (ASG 4455)	T
Schizaeales	
Anemiaceae	
25. <i>Anemia mexicana</i> Klotzsch var. <i>mexicana</i> (MGL 35)	R
Cyatheales	
Plagiogyriaceae	
26. <i>Plagiogyria pectinata</i> (Liemb.) Lellinger (MGL 53; MGL 86; ASG 4432; ASG 4463)	T
Cyatheaceae	
27. <i>Alsophila firma</i> (Baker) D. S. Conant * (ASG 4517)	T
28. <i>Cyathea fulva</i> (M. Martens & Galeotti) Fée * (ASG 4526)	T
Dicksoniaceae	
29. <i>Dicksonia sellowiana</i> Hook. * (ASG 4516)	T
30. <i>Lophosoria quadripinnata</i> (J. F. Gmel.) C. Chr. (MGL 98; MGL 105; ASG 4484)	T
Polypodiales	
Dennstaedtiaceae	
31. <i>Dennstaedtia globulifera</i> (Poir.) Hieron. (ASG 4496)	T
Pteridaceae	
32. <i>Adiantum andicola</i> Liebm. (MGL 27; MGL 42; MGL 44; ASG 4491)	E, R, T
33. <i>Gaga marginata</i> (Kunth) Fay-Wei Li & Windham (MGL 99; ASG 4513)	T
34. <i>Pteris orizabae</i> M. Martens & Galeotti (MGL 100)	T

35. <i>Scoliosorus ensiformis</i> (Hook.) T. Moore 1 (MGL 95; MGL 115)	E	75. <i>Pleopeltis plebeia</i> (Schltdl. & Cham.) A. R. Sm. & Tejero (MGL 72; MGL 75; MGL 84; MGL 111; ASG 4431; ASG 4479)	E, T
36. <i>Vittaria graminifolia</i> Kaulf. (MGL 19; MGL 51; ASG 4505)	E	78. <i>Polypodium liebmanii</i> C. Chr. (AHA 50)	E
Cystopteridaceae		79. <i>Polypodium plesiosorum</i> Kunze (ASG 4458; ASG 4460)	E, R, T
37. <i>Cystopteris fragilis</i> (L.) Bernh. (MGL 17; MGL 26; ASG 4522)	R, T	80. <i>Polypodium puberulum</i> Schltdl. & Cham. (MGL 75; ASG 4464)	E
Aspleniaceae		81. <i>Polypodium rodhopleuron</i> Kunze (MGL 97; MGL 104; ASG 4472; ASG 4512)	E, R
38. <i>Asplenium auriculatum</i> Sw. (MGL 10; MGL 14; ASG 4432; ASG 4452; ASG 4465)	E, R, T	82. <i>Stenogrammitis prionodes</i> (Mickel & Beitel) Labiak (ASG 60)	E
39. <i>Asplenium blepharophorum</i> Bertol. (MGL 6)	T		
40. <i>Asplenium cuspidatum</i> Lam. (ASG 4527; ASG 4499)	E, R, T		
41. <i>Asplenium monanthes</i> L. (MGL 12; MGL 68; MGL 108; ASG 4437; ASG 4439; ASG 4445)	E, R, T		
42. <i>Asplenium sessilifolium</i> Desv. var. <i>sessilifolium</i> (ASG 4447; ASG 4500; ASG 4502)	R, T		
43. <i>Asplenium serra</i> Langsd. & Fisch (ASG 4466)	T		
Thelypteridaceae			
44. <i>Amauropelta atrovirens</i> (C.Chr.) Salino & T.E. Almeida (MGL 103; ASG 4467; ASG 4477)	T		
45. <i>Amauropelta oligocarpa</i> (Humb. & Bonpl. ex Willd.) Pic. Serm. (ASG 4488)	T		
46. <i>Amauropelta rudis</i> (Kunze) Pic. Serm. (MGL 1)	T		
Blechnaceae			
47. <i>Austroblechnum stoloniferum</i> (Mett. ex E. Fourn.) Gasper & V.A.O. Dittrich (MGL 46; MGL 54; MGL 87)	T		
48. <i>Blechnum appendiculatum</i> Willd. (MGL 4; ASG 4509)	R, T		
49. <i>Woodwardia martinensis</i> Maxon ex Weath. (MGL 63; MGL 70; ASG 4489; ASG 4490)	T		
50. <i>Woodwardia semicordata</i> Mickel & Beitel (ASG 4440; ASG 4515)	T		
51. <i>Woodwardia spinulosa</i> M. Martens & Galeotti (ASG 4493)	T		
Athyriaceae			
52. <i>Diplazium ternatum</i> Liebm. (MGL 11; MGL 89; ASG 4442)	T		
53. <i>Diplazium lonchophyllum</i> Kunze (MGL 41; MGL 109; ASG 4508)	T		
Dryopteridaceae			
54. <i>Arachnoides denticulata</i> (Sw.) Ching (MGL 3; MGL 22; ASG 4487)	T		
55. <i>Ctenitis erinaceae</i> A. R. Sm. (MGL 2; MGL 7; MGL 18; MGL 20; MGL 33; ASG 4482)	T		
56. <i>Dryopteris wallichiana</i> (Spreng.) Hyl. (ASG 4473; ASG 4494; ASG 4501)	T		
57. <i>Elaphoglossum erinaceum</i> (Fée) T. Moore var. <i>erinaceum</i> (MGL 101; ASG 4519)	R, T		
58. <i>Elaphoglossum monicae</i> Mickel (MGL 30; ASG 4418; MGL 4451; MGL 4492)	R, T		
59. <i>Elaphoglossum obscurum</i> (E. Fourn.) C. Chr. (MGL 13; MGL 118; ASG 4511)	R, T		
60. <i>Elaphoglossum peltatum</i> (Sw.) Urb. (MGL 37; MGL 67; MGL 91; MGL 94; MGL 114; ASG 4438; ASG 4450)	E		
61. <i>Elaphoglossum petiolatum</i> (Sw.) Urb. (MGL 102)	E, T		
62. <i>Elaphoglossum seminudum</i> Mickel (MGL 81; MGL 112; MGL 113)	E, T		
63. <i>Phanerophlebia remotispora</i> E. Fourn. (MGL 74)	R, T		
64. <i>Polystichum distans</i> E. Fourn. (MGL 5; MGL 8; MGL 9; MGL 15; MGL 24; MGL 43; MGL 45; MGL 47; MGL 76; ASG 4454)	T		
Lomariopsidaceae			
65. <i>Lomariopsis mexicana</i> Holttum (MGL 71; ASG 4474)	E, T		
Polypodiaceae			
66. <i>Alansmia senilis</i> (Fée) A. R. Sm. Moguel & M. Kessler (ASG 4469; ASG 4523)	R		
67. <i>Campyloneurum amphotensoni</i> Kunze ex Klotzsch (MGL 55; MGL 56; ASG 4448)	E, R, T		
68. <i>Campyloneurum angustifolium</i> (Sw.) Fée (ASG 4510)	E, R, T		
69. <i>Melpomene leptostoma</i> (Fée) A.R. Sm. & R.C. Moran (MGL 25; MGL 52; MGL 57; MGL 88; ASG 4433; ASG 4435; ASG 4453; ASG 4478; ASG 4481; ASG 4521)	E		
70. <i>Melpomene moniliformis</i> (Lag. ex Sw.) A. R. Sm. & R. C. Moran (ASG 4471)	T		
71. <i>Peculuma longepinnulata</i> (E.Fourn.) F.C.Assis & Salino (MGL 110)	E, T		
72. <i>Peculuma sursumcurrens</i> (Coppel.) M. G. Prince (MGL 96; ASG 4498)	E, R, T		
73. <i>Phlebodium pseudoaureum</i> (Cav.) Lellinger (MGL 82; MGL 117)	E, T		
74. <i>Pleopeltis lepidotricha</i> (Fée) A.R.Sm. & Tejero (MGL 62; MGL 64; MGL 80; ASG 4459)	E		
76. <i>Pleopeltis madrensis</i> (J. Sm.) A. R. Sm. & Tejero (MGL 61; MGL 77)	T		
77. <i>Pleopeltis mexicana</i> (Fée) Mickel & Beitel (MGL 78; MGL 85; ASG 4457)	E, R		

References

- Álvarez-Zúñiga, E., Sánchez-González, A., López-Mata, L., Tejero-Díez, J.D., 2012. Composición y abundancia de las Pteridofitas en el Bosque Mesófilo de Montaña del municipio de Tlanchinol, Hidalgo, México. *Bot. Sci.* 90 (2), 163–177.
- Acebey, A.R., Krömer, T., Vázquez-Torres, M., Tejero-Díez, J.D., 2015. Helechos y licófitos de la Reserva de la Biosfera Los Tuxtlas, Veracruz, México. *Bot. Sci.* 93 (2), 313–344.
- Alcántara, A.O., Luna-Vega, I., 2001. Análisis florístico de dos áreas con bosque mesófilo de montaña en el estado de Hidalgo, México: Eloxochitlán y Tlahuelompa. *Acta Bot. Mex.* 54, 51–87.
- Arcand, N.N., Ranker, T.A., 2008. Conservation Biology. In: Ranker, T.A., Haufler, C.H. (Eds.), *Biology and Evolution of Ferns and Lycophytes*. Cambridge University Press, New York, United States of America, pp. 257–283.
- Cartujano, S., Zamudio, S., Alcántara, O., Luna, I., 2002. El bosque mesófilo de montaña en el municipio de Landa de Matamoros, Querétaro, México. *Bol. Soc. Bot. Méx.* 70, 13–43.
- Carvajal-Hernández, C., Krömer, T., 2015. Riqueza y distribución de helechos y licófitos en el gradiente altitudinal del Cofre de Perote, centro de Veracruz, México. *Bot. Sci.* 93 (3), 601–614.
- Chávez, S.M.C., 2014. Diversidad y distribución de angiospermas herbáceas y arbustivas de los bosques de *Fagus grandifolia* subsp. mexicana (Martínez) E. Murray del estado de Hidalgo, México. Undergraduate thesis. Universidad Autónoma del Estado de Hidalgo, Hidalgo, México, pp. 5–72.
- Christenhusz, M.J.M., Zhang, X., Schneider, H., 2011. A linear sequence of extant families and genera of lycophytes and ferns. *Phytotaxa* 19, 7–54.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. (Ser. B)* 345, 101–118.
- Colwell, R.K., 2015. Statistical Estimation of Species Richness and Shared Species from Samples Version 9.1.0. University of Connecticut, Connecticut, <http://viceroy.eeb.uconn.edu/estimate> (Retrieved on 17.11.14).
- Cuevas, H.A.L., Sánchez-González, A., Tejero-Díez, J.D., 2013. Pteridophytes of a semiarid natural protected area in Central Mexico. *Nat. Areas J.* 33, 177–188.
- Fang, J., Lechowicz, M.J., 2006. Climatic limits for the present distribution of beech (*Fagus L.*) species in the world. *J. Biogeogr.* 33, 1804–1819.
- Franco, L.J., Cruz, A.G., Rocha, R.A., Navarrete, S.N., Flores, M.G., Kato, M.E., Sánchez, C.S.A., Abarca, L.G., Bedia, S.C.M., 2001. Segunda edición. In: *Manual de Ecología*. Trillas, México, pp. 93–99.
- García, E., 1988. Modificaciones al Sistema de Clasificación Climática de Köppen, fifth edition. Instituto de Geografía. Universidad Nacional Autónoma de México, Mexico, p. 90.
- Gazol, B.A., 2009. Heterogeneidad espacial de la vegetación en una cuenca forestal del Pirineo Occidental. Doctoral Thesis. Universidad de Navarra, Pamplona, España, 170 pp.
- Godínez-Ibarra, O., Ángeles-Pérez, G., López-Mata, L., García-Moya, E., Valdez-Hernández, J.I., De los Santos-Posadas, H., Trinidad-Santos, A., 2007. Lluvia de semillas y emergencia de plántulas de *Fagus grandifolia* subsp. mexicana en la Mojonera Hidalgo, México. *Rev. Mex. Biodivers.* 78, 117–128.
- Hukusima, T., Matsui, T., Nishio, T., Pignatti, S., Yang, L., You, S.L., Kim, M.H., Yoshikawa, M., Honma, H., Wang, Y., 2013. *Phytosociology of the Beech (Fagus) Forests in East Asia*. Geobotany Studies. Springer, Heidelberg.
- Jardel, P.J.E., Cuevas, G.R., Santiago, P.A.L., 2014. Ecología y manejo de los bosques mesófilos de montaña en México. In: Gual-Díaz, M., Rendón-Correa, A. (Eds.), *Bosques mesófilos de montaña de México: Diversidad, ecología y manejo*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, pp. 141–181.
- Jiménez-Valverde, A., Hortal, J., 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Rev. Ibérica de Aracnol.* 8, 151–161.
- Lira, R., Riba, R., 1993. Las Pteridofitas (helechos y plantas afines) de México. *Rev. Soc. Mex. Hist. Nat.* 44, 99–108.
- Marcantonio, M., Chiarucci, A., Maccherini, S., Guglietta, D., Bacaro, G., 2012. Caratterizzazione della diversità vegetale nei boschi di faggio dell'Italia centro-settentrionale: un approccio metodologico a fini conservazionistici. *Forest* 9, 198–216.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.
- McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4 for Windows. MjM Software Design, Gleneden Beach, Oregon.
- Mehlreiter, K., 2008. Phenology and habitat specificity of tropical ferns. In: Ranker, T.A., Haufler, C.H. (Eds.), *Biology and Evolution of Ferns and Lycophytes*. Cambridge University, Cambridge, pp. 201–221.

- Mehlreiter, K., 2010. Fern conservation. In: Mehlreiter, K., Walker, L.R., Sharpe, J.M. (Eds.), *Fern Ecology*. Cambridge University Press, New York, United States of America, pp. 220–254.
- Mejía, L.C., 2015. *Musgos de los bosques de Fagus grandifolia subsp. mexicana del estado de Hidalgo, México*. Tesis Licenciatura en Biología. Universidad Autónoma del Estado de Hidalgo. Mineral de la Reforma, Hidalgo, México, pp. 5–62.
- Mickel, J.T., Smith, A.R., 2004. *The Pteridophytes of Mexico*. Memoirs of the New York Botanical Garden, New York.
- Mueller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. John Wiley, New York, NY.
- Ortiz-Quijano, A.B., Cuevas-Cardona, C., Sánchez-González, A., 2015. Historia ambiental de tres bosques de haya del estado de Hidalgo, México, periodo 1935–2014. *Historia* 2.0 5 (10), 25–41.
- Ortiz-Quijano, A.B., Sánchez-González, A., López-Mata, A., Villanueva-Díaz, J., 2016. Population structure of *Fagus grandifolia* subsp. *mexicana* in the cloud forest of Hidalgo State, Mexico. *Bot. Sci.* 94 (3), 483–497.
- Otto, E.M., Janßen, T., Kreier, H.P., Schneider, H., 2009. New insights into the phylogeny of *Pleopeltis* and related Neotropical genera (Polypodiaceae, Polypodiopsida). *Mol. Phylogenet. Evol.* 53, 190–201.
- Pérez, C.A., 2009. *Los helechos y lycopodios del municipio de Calnali estado de Hidalgo, Hidalgo, México*. Undergraduate thesis. Universidad Autónoma del Estado de Hidalgo, Hidalgo, México, pp. 5–53.
- Pérez-Atilano, Y., Sánchez-González, A., Tejero-Díez, J.D., 2015. Species richness, distribution and morphological variation of lycophytes and monilophytes in a semi-arid region of Mexico. *Am. Fern J.* 105, 238–256.
- Pérez-García, B., Riba, R., Reyes, J.I., 1995. Helechos mexicanos: formas de crecimiento, hábitat y variantes edáficas. *Contactos* 11, 22–27.
- Pérez-Paredes, M.G., Sánchez-González, A., Tejero-Díez, J.D., 2012. Listado de lycopodios y helechos del municipio de Zacualtipán de Ángeles Hidalgo, México. *Polibotánica* 33, 57–73.
- Pérez-Paredes, M.G., Sánchez-González, A., Tejero-Díez, J.D., 2014. Estructura poblacional y características del hábitat de dos especies de Cyatheaceae del estado de Hidalgo. *Bot. Sci.* 92 (2), 259–271.
- Pteridophyte Phylogeny Group: PPG, 2016. A community-derived classification for extant lycophytes and ferns. *J. Syst. Evol.* 54, 563–603, <http://dx.doi.org/10.1111/jse.12229>.
- Paciencia, M.L.B., Prado, J., 2005. Effects of forest fragmentation on pteridophyte diversity in a tropical rain forest in Brazil. *Plant Ecol.* 180, 87–104.
- Peña, L., Amezcaga, I., Onaindia, M., 2011. At which spatial scale are plant species composition and diversity affected in beech forests? *Ann. For. Sci.* 68, 1351–1362.
- Peters, R., 1995. Architecture and development of Mexican beech forest. In: Box, E.O., Peet, R.K., Masuzawa, T., Yamada, I., Fujiwara, K., Maycock, P.F. (Eds.), *Vegetation Science in Forestry*. Kluwer Academic Publishers, Dordrecht, pp. 325–343.
- Ramírez-Cruz, S., Sánchez-González, A., Tejero-Díez, J.D., 2009. La Pteridoflora del Parque Nacional Los Mármoles, Hidalgo, México. *Bol. Soc. Bot. Méx.* 84, 35–43.
- Rodríguez-Gutián, M.A., Vázquez, J., Real, C., Romero, C., Franco, R., 2009. Revisión de la sintaxonomía de los hayedos del occidente de la Cordillera Cantábrica (Noroeste Ibérico) mediante análisis multivariante. *Lazarroa* 30, 191–218.
- Rodríguez-Ramírez, E., Ch. Sánchez-González, A., Ángeles-Pérez, G., 2013. Current distribution and coverage of the Mexican beech forests (*Fagus grandifolia* subsp. *mexicana*) en Mexico. *End. Species Res.* 20 (3), 205–216.
- Rodríguez-Ramírez, E.Ch., Sánchez-González, A., Ángeles-Pérez, G., 2016. Relationship between vegetation structure and microenvironment in *Fagus grandifolia* subsp. *mexicana* forest relicts in Mexico. *J. Plant Ecol.*, <http://dx.doi.org/10.1093/jpe/rtw138>.
- Rouhana, G., Dubuisson, J.Y., Rakotondrainibe, F., Motley, T.J., Mickel, J.T., Labat, J.N., Moran, R.C., 2004. Molecular phylogeny of the fern genus *Elaphoglossum* (Elaphoglossaceae) based on chloroplast non-coding DNA sequences: contributions of species from the Indian Ocean area. *Mol. Phylogenet. Evol.* 33, 745–763.
- Rowden, A., Robertson, A., Allnutt, T., Heredia, S., Williams-Linera, G., Newton, A., 2004. Conservation genetics of Mexican beech, *Fagus grandifolia* var. *mexicana*. *Conserv. Genet.* 5, 475–484.
- Rzedowski, J., 2006. Vegetación de México. Primera Edición Digital. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, pp. 328–339.
- SEMARNAT (Secretaría del Medio Ambiente y Recursos Naturales), 2010. Norma Oficial Mexicana. NOM-059-SEMARNAT- Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. Diario Oficial de la Federación, México, DF, pp. 2010.
- Schneider, H., Smith, A.R., Cranfill, R., Hildebrand, T.J., Haufler, C.H., Ranker, T.A., 2004. Unraveling the phylogeny of polygrammoid ferns (Polypodiaceae and Grammitidaceae): exploring aspects of the diversification of epiphytic plants. *Mol. Phylogenet. Evol.* 31 (3), 1041–1063.
- Serrano, M.H., 2010. *Helechos y lycopodios del Parque Nacional El Chico, Estado de Hidalgo, Hidalgo, México*. Undergraduate thesis. Universidad Autónoma del Estado de Hidalgo, Hidalgo, México, pp. 5–48.
- Shen, Z.H., Fang, J.Y., Chiu, C.A., Chen, T.Y., 2015. The geographical distribution and differentiation of Chinese beech forests and the association with *Quercus*. *Appl. Veg. Sci.* 18, 23–33.
- Smith, A.R., Tejero-Díez, J.D., 2014. *Pleopeltis* (Polypodiaceae), a redefinition of the genus and nomenclatural novelties. *Bot. Sci.* 92 (1), 1–16.
- Squeo, F., Caviere, L., Arancio, G., Novoa, J., Matthei, O., Marticorena, C., Rodriguez, C., Arroyo, M.T.K., Muñoz, M., 1998. Biodiversidad vegetal de antofagasta. *Rev. Chil. Hist. Nat.* 71, 571–591.
- Téllez-Valdés, O., Dávila-Aranda, P., Lira-Saade, R., 2006. The effects of climate change on the long-term conservation of *Fagus grandifolia* var. *mexicana*: an important species of the Cloud Forest in Eastern Mexico. *Biodivers. Conserv.* 15, 1095–1107.
- Tejero-Díez, J.D., Torres-Díaz, A.N., Gual-Díaz, M., 2014. Lycopodios y helechos en el Bosque Mesófilo de Montaña de México. In: Gual-Díaz, M., Rendón-Correa, A. (Eds.), *Bosques Mesófilos de Montaña de México, diversidad, ecología y manejo*. Comisión nacional para el Conocimiento y Uso de la Biodiversidad CONABIO, México, D.F., pp. 197–220.
- Tuomisto, H., Ruokolainen, K., Yli-Halla, M., 2003. Dispersal, environmental, and floristic variation of western Amazonian forests. *Science* 299, 241–244.
- Vázquez, T.M., Campos, J.J., Cruz, P.A., 2006. Los helechos y plantas afines del bosque mesófilo de montaña de Banderilla Veracruz, México. *Polibotánica* 22, 63–77.
- Valencia, A.S., Flores-Franco, G., 2006. Catálogo de autoridades taxonómicas de las fagáceas (Fagaceae: Magnoliopsida) de México. Facultad de Ciencias, UNAM, Base de datos SNIB-CONABIO, Proyecto CS008, México.
- Vargas-Rodríguez, Y.L., Platt, W., Vázquez-García, J.A., Boquin, G., 2010. Selecting relict montane cloud forest for conservation priorities: the case of western Mexico. *Nat. Areas J.* 30, 156–173.
- Villavicencio-Nieto, M.A., Pérez-Escandón, B.E., 2008. Plantas útiles de Medio Monte, San Bartolo Tutotepec, Hidalgo. Un criterio para establecer un área natural protegida. In: Pulido-Flores, G., López-Escamilla, A.L., Pulido-Silva, M.T. (Eds.), *Estudios biológicos en las áreas naturales del estado de Hidalgo*. Universidad Autónoma del Estado de Hidalgo, México, pp. 19–27.
- Williams-Linera, G., Rowden, A., Newton, A.C., 2003. Distribution and stand characteristics of relict populations of Mexican beech (*Fagus grandifolia* var. *mexicana*). *Biol. Conserv.* 109, 27–36.
- Williams-Linera, G., Palacios-Ríos, M., Hernández-Gómez, R., 2004. Fern richness, tree species surrogacy, and fragment complementarity in a Mexican tropical montane cloud forest. *Biodivers. Conserv.* 14, 119–133.
- Zúñiga, S.J.R., 2009. *Helechos y lycopodios del municipio de Tenango de Doria, estado de Hidalgo, México*. Undergraduate thesis. Universidad Autónoma del Estado de Hidalgo, Hidalgo, México, pp. 5–45.