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Source: American Fern Journal, 101(2):81-104. 2011.

Published By: The American Fern Society
DOI: 10.1640/0002-8444-101.2.81
URL: http://www.bioone.org/doi/full/10.1640/0002-8444-101.2.81

American Fern Journal 101(2):81–104 (2011)

Distributional Patterns and Biogeographic Analysis of Ferns in the Sierra Madre Oriental, Mexico

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ABSTRACT.—We analyzed the distributional patterns of 66 species of leptosporangiate ferns inhabiting in the Sierra Madre Oriental (SMO), Mexico, using grid-cells and endemism index values, parsimony analysis of endemicity (PAE) and track analysis. The strict consensus area cladogram obtained with PAE showed a polytomy and four main groups or clades, two of them including only two or three grid-cells. The largest group included grid-cells located along the SMO, mainly in the central-southern portions of the SMO; a second group was located at the southern portion of the SMO in the leeward zone of this mountain chain. The track analysis of the fern taxa allowed us to recognize five generalized tracks in the SMO and their convergence showed five nodes. With endemism index values, 11 grid-cells were identified as important areas for ferns, seven of them corresponding to the group 1 of PAE (from montane environments), and four grid-cells to the group 2 of PAE (from leeward areas of the Sierra Madre Oriental). The results obtained herein slightly agree with other published works using other kinds of organisms. The analyses used herein serve to generate useful information about the biogeographic history of this complex area, and led us to support, detect, test and propose areas, important from biogeographic viewpoint, for ferns.

KEY WORDS.—biogeography, track analysis, parsimony analysis of endemicity, richness, Mexico, leptosporangiate ferns, Sierra Madre Oriental

Ferns are seedless vascular plants distributed worldwide with great species diversity, especially in tropical regions. Mexico represents one of the countries with a very diverse fern flora (Tryon, 1972; Tryon and Tryon, 1984; Mickel and Smith, 2004). According to Hassler and Swale (2001), there is a higher diversity of ferns in South America, with 3,281 species (2,271 endemic to the region), especially in Colombia, Ecuador, Brazil, Venezuela, and Peru. Central America is the second most diverse region, with 2,620 species (616 endemic to the region), mainly in Costa Rica, Panama, and Mexico. Mexico is one of the countries with a high proportion of endemic fern species (including 196 taxa). Mickel and Smith (2004) noted that 113 genera and 877 species of leptosporangiate ferns inhabit Mexico, of which nearly 2% of the genera and 17% of the species are endemic. In Mexico, these plants inhabit a broad range of habitats (Mickel and Smith, 2004) and are distributed mainly in tropical

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montane and temperate vegetation types, but also live in dry habitats (Siqueiros and González, 2006).

Ferns and lycopods are important throughout the forest strata, mainly in the humid mountain zone, because they play an important role in the hydric balance of the forest (Ambrose, 2004); they also play a crucial role in vegetation structure (Hill and Silander Jr., 2001; Paciencia and Prado, 2005). Additionally, ferns, especially in the gametophytic phase, are considered good indicators of environmental changes in the forest due to their sensitivity to the microclimatic and edaphic parameters (Page, 1979a, b).

From a biogeographical viewpoint, ferns have been considered interesting plants (Barrington, 1993; Kato, 1993; Wolf *et al.*, 2001) due to processes involved in their distributional patterns and because different explanations have been used to interpret their geographical distribution, mainly dispersal and vicariance. Early studies explained their distribution based on ecophysiological and reproductive traits; all attributed fern distribution mechanisms to dispersal (i.e., Lyell, 1870; Christ, 1910; Winkler, 1938; Tryon, 1970, 1972, 1985; Smith, 1972; Puentha, 1991; Barrington, 1993). Recently, Karst *et al.*, (2005) demonstrated the role of environmental variables in determining fern distribution at mesoscales, such as soil moisture and humid climatic conditions. According to Wolf *et al.* (2001), despite the fact that many ferns produce bisexual spores capable of travelling long distances, chances of establishing new populations are low; in this way, evidence of historical processes such as allopatric differentiation may sometimes be hidden by dispersal.

The Sierra Madre Oriental (SMO) physiographic and biogeographic province is a mountain chain located in the northeastern part of Mexico (Fig. 1), and from a biological viewpoint is one of the most important mountain systems in Mexico (González-Zamora *et al.*, 2007). The SMO province comprises parts of the following states: Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas, San Luis Potosí, Veracruz, Guanajuato, Querétaro, Hidalgo, and Puebla (Cervantes-Zamora *et al.*, 1990). This province extends to the east to the Gulf of Mexico, in the south to the Trans-Mexican Volcanic Belt, in the west it extends to the Mexican Plateau, and in the north to the northern part of the state of Coahuila, western part of the state of Nuevo León and to the southern part of the United States. The wetter slopes of this mountain chain are considered to be one of the places in the country where fern species diversity and abundance are concentrated (Mickel and Smith, 2004), and ferns constitute a frequent floristic component in temperate forests of the SMO. For many years, the SMO has been recognized as a biogeographic natural region by several authors based on different criteria, but its high biological richness has complicated its natural delimitation (Luna-Vega *et al.*, 2004). Many authors consider it as a natural unique area and other authors as an archipelago of areas (Luna-Vega *et al.*, 2004).

The Mesozoic rocks and the basement complex that constitute the SMO were uplifted, shortened and transported northeastward forming a fold and thrust belt during the Laramide orogeny (Eguiluz de Antuñano *et al.*, 2000). Also, this

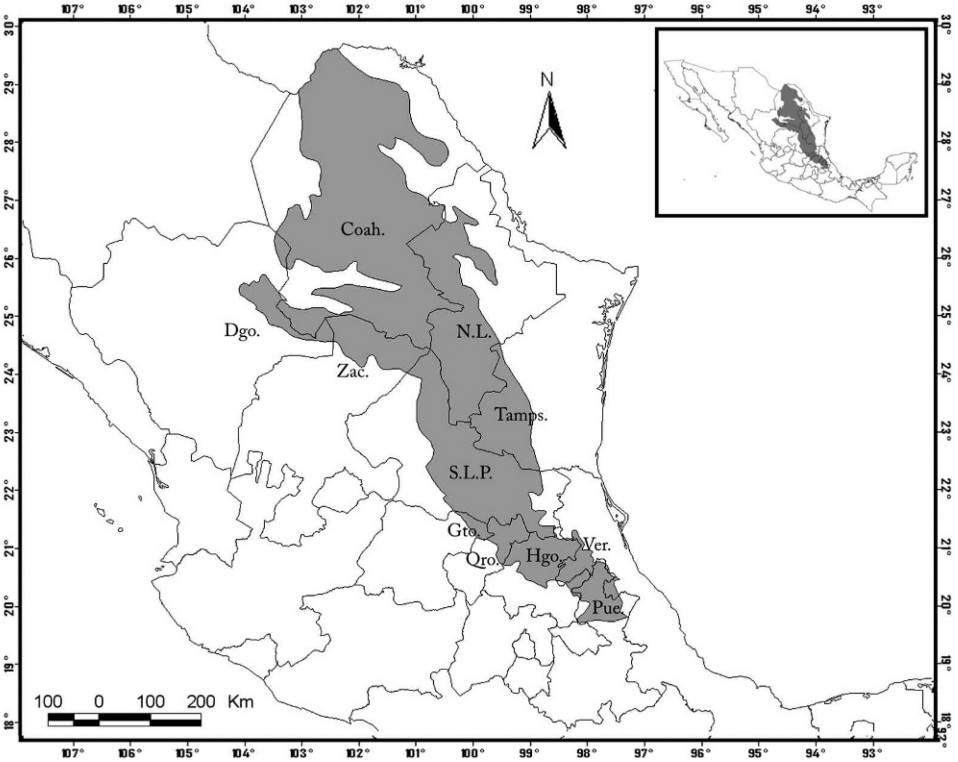

FIG. 1. Study area. The gray area shows the location and limits of the Sierra Madre Oriental (SMO) in Mexico. Abbreviations are: Coah. = Coahuila, Dgo. = Durango, Gto. = Guanajuato, Hgo. = Hidalgo, N.L. = Nuevo León, Pue. = Puebla, Qro. = Querétaro, S.L.P. = San Luis Potosí, Tamps. = Tamaulipas, Ver. = Veracruz, Zac. = Zacatecas.

mountain chain may represent a generally non-extended backarc to the continental arc of the Sierra Madre Occidental (Ortega-Gutiérrez *et al.*, 1994). The climate in this province varies and most of the main climatic types of the country can be found in the region. Climatic diversity is largely due to its complex physiographic heterogeneity and meteorological phenomena, among others factors (Hernández-Cerda and Carrasco-Anaya, 2004).

Different vegetation types occur in the SMO province, but oak and cloud forests are characteristic, with suitable abiotic conditions for the development of ferns. Although the SMO is a montane area with a prevalence of temperate forests, dry habitats are represented in several places, mainly in the inland lowlands near the Mexican Plateau. In the Gulf of Mexico area and southeastern portions of the SMO, precipitation is greater than 1,200 mm, reaching 4,000 mm in the state of Puebla, with only two dry months in the year. Maximum annual temperature in the region ranges from 26° to 30°C, with the exception of the highest areas, and minimum annual temperature is less than 12°C (Hernández-Cerda and Carrasco-Anaya, 2004).

Several studies have been carried out in this region, including some biogeographic analyses with different taxa, including vascular plants (González-Zamora *et al.*, 2007; Luna-Vega *et al.*, 1999, 2000; Santa Anna del Conde *et al.*, 2009), macromycetes (Cifuentes *et al.*, 2004), birds (Navarro *et al.*, 2004), mammals (León-Paniagua *et al.*, 2004), herpetofauna (Canseco-Márquez *et al.*, 2004), and beetles (Márquez and Morrone, 2004). In these studies, the SMO province was divided into two or three subregions, and congruent distributional patterns among organisms with different dispersal capabilities were noted. If the SMO is divided into three sections, it is separated by two geographical features: the Pánuco basin, which is a natural barrier that divides the southern part from the central section, and a second feature, which is comprised of the Saltillo-Monterrey mountain system, consisting of faults and deformations located between the states of Nuevo León and Coahuila, which divide the central part from the northern section (González-Zamora *et al.*, 2007; Santa Anna del Conde *et al.*, 2009). If the SMO is divided into two sections, the Pánuco basin is a barrier that divides this province into two parts (Luna-Vega *et al.*, 1999; Márquez and Morrone, 2004).

In comparison with angiosperms, fern species have been used in few biogeographic works that analyze the distributional patterns of the Mexican biota; these studies took place in the Mexican states of México (Tejero-Díez, 1990) and Veracruz (Palacios-Ríos and Gómez-Pompa, 1997), but the whole Sierra Madre Oriental province was not included in either of these works. Despite showing wider distributional patterns than seed plants, some ferns also exhibit the restricted patterns of distribution shown by seed plants, and it seems that the same factors appear to have shaped these shared patterns. Considering that ferns generally have high dispersal capabilities and wide distribution ranges, in this study we compare the distributions of some species restricted or semi-restricted to the Sierra Madre Oriental to test if their patterns of distribution are congruent with other groups of organisms. This work represents the first biogeographical study in the SMO province based on fern distribution, applying three different historical biogeographic methods.

Our aim was to analyze the distributional patterns and to detect areas of richness and endemism in the Sierra Madre Oriental province based on semi-restricted species of leptosporangiate ferns, applying endemism indices to grid-cells, and biogeographic analyses applying a parsimony analysis of endemicity and the panbiogeographic method. These analyses should generate useful information on the distributional patterns of ferns in this region, and assist in detecting and proposing areas that are important from a biogeographic viewpoint for these vascular plants in northeastern Mexico.

MATERIALS AND METHODS

Distributional Data.—We used 66 species of leptosporangiate ferns belonging to the Polypodiales (Smith *et al.*, 2006), which is one of the major groups of Monilophytes (sensu Pryer *et al.*, 2004). These 66 fern species belong to nine different families and are included in 24 genera. Species selected for this study have distributional areas mainly within the SMO or with areas that extended slightly beyond those boundaries into adjacent areas, such as the Mexican Plateau, Trans-Mexican Volcanic Belt, southern Mexico, and some southern areas of the United States of America and northern Central America. In this study we used the delimitation proposal of the SMO produced by González-Zamora *et al.* (2007) as a framework. The selected species were taxonomically validated based on Mickel and Smith (2004) and do not have synonymy problems.

Distributional data were obtained from the review of more than 900 herbarium specimens deposited in the following collections: National Herbarium of the Instituto de Biología, UNAM (MEXU); Herbarium of the Escuela Nacional de Ciencias Biológicas, IPN (ENCB); Herbaria of the Instituto de Ecología A.C. in Pátzcuaro (IEB) and Xalapa (XAL); and Herbarium of the Facultad de Ciencias, UNAM (FCME). We also obtained some records from the Red Mundial de Información Biótica (REMIB) hosted on the web page of the Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (CONABIO) (http//www.conabio.com.mx). With this information, we constructed a database that includes 1,244 georeferenciated records.

At least 400 fern species inhabit the SMO, most of them widely distributed in Mexico/or reaching adjacent countries in Central America. Fern species were selected based on the combination of the following criteria: (1) species endemic to the SMO, recorded in one or several grid-cells; (2) species endemic to Mexico, and well-represented in the SMO (e.g., *Astrolepis crassifolia*, *A. laevis*); those species well-distributed in continental Mexico, including the SMO, and also represented in one or both peninsulas (Baja California and Yucatán) were excluded, because they have a different biogeographic history from the rest of the country (Contreras-Medina *et al.*, 2007); (3) species represented in Mexico, well-distributed in the SMO, but also present in adjacent countries, considering those species distributed in only one or two states of the United States and one or two countries of Central America, based on the proposal of Megamexico (Rzedowski, 1991), because Mexico by itself is not a natural unit. Species with a wider distribution elsewhere but only with one record within the SMO were not considered (e.g. *Trichomanes bucinatum*), because they can indicate a false endemism to one grid-cell.

Biogeographic Analyses.—From distributional data, geographic distribution maps of each species were obtained using ArcView GIS (ESRI, 1999) and then these distribution maps were projected on a map of the Sierra Madre Oriental proposed by González-Zamora *et al.* (2007). We divided the Sierra Madre Oriental province in 34 grid-cells of 1° latitude × 1° longitude, which were used as area units in the different analyses. These 34 grid-cells contain almost one recorded species. We chose grid-cells of one geographical degree per side, partially to facilitate the data manipulation and to reduce the effect of sampling artefacts, such as mapping errors and unsampled grids in sparsely inhabited areas (Crisp *et al.*, 2001). This scale size was also chosen because it was tested in previous studies on areography and diversity of different groups of Mexican flora (Kohlmann and Sánchez, 1984; García-Mendoza, 1995;

Contreras-Medina and Luna-Vega, 2007; Santa Anna del Conde *et al.*, 2009) and fauna (Escalante *et al.*, 2004; Ochoa and Flores-Villela, 2006).

In the grid-cell analysis we counted the number of species recorded in each grid-cell (richness), and obtained the mean and median values; also we noted those species recorded in more grid-cells.

Parsimony analysis of endemicity (PAE) was developed by Rosen (1988) and Rosen and Smith (1988) to address the shortcomings of phenetic approaches used to assess area relationships of fossil or recent assemblages from different areas (Porzecanski and Cracraft, 2005). This method begins with presence/absence data for a set of sample localities and a particular taxon (Rosen and Smith, 1988). With this information, a data matrix of areas versus taxa is constructed and analysed (Luna-Vega *et al.*, 1999). Shared presences group areas according to the most parsimonious cladogram, which represents nested sets of areas (Morrone and Crisci, 1995). Compared to cladistic biogeography, PAE can be applied to taxa whose phylogenetic relationships are unknown.

In Mexico, PAE has been applied to different biological groups and using different geographic units, such as hydrological basins (Aguilar-Aguilar *et al.*, 2003), grid-cells (Morrone and Escalante, 2002; Rojas-Soto *et al.*, 2003; Méndez-Larios *et al.*, 2005; Contreras-Medina *et al.*, 2007; Santa Anna del Conde *et al.*, 2009), biogeographic provinces (Morrone *et al.*, 1999; Morrone and Escalante, 2002; Dávila-Aranda *et al.*, 2002; Contreras-Medina *et al.*, 2007), and transects (García-Trejo and Navarro, 2004; León-Paniagua *et al.*, 2004).

We used 59 taxa (columns) and 34 grid-cells (rows) to construct the data matrix of the PAE method. In this method, those species found in a single grid-cell are not useful for assessing relationships, and thus were not included in the matrix, because these taxa are equivalent to autapomorphies (Luna-Vega *et al.*, 1999). The matrix included one row coded with all zeros to root the area cladogram. The data matrix analysis was carried out using Nona (Goloboff, 1999) through Winclada (Nixon, 2002), applying multiple TBR, searching on 100,000 initial trees (mult*100), and holding 30 trees per replication (h/10). When more than one parsimonious cladogram resulted from the analysis, a strict consensus cladogram was constructed.

The panbiogeographic approach was originally proposed by Croizat (1958, 1964). The method consists of plotting the localities of organisms on maps and connecting their disjunct distribution areas or localities together with lines called individual tracks. Individual tracks of organisms are then superimposed and if they coincide, the resulting summary lines are considered generalized tracks. Generalized tracks indicate the pre-existence of ancestral biota, which subsequently become fragmented by tectonic and/or climatic changes (Morrone and Crisci, 1995). A baseline is a geological feature such as a river basin crossed by the track. Convergence or intersection of two or more generalized tracks produces a node, which represents a complex and composite geological area (Morrone and Crisci, 1995).

For track analysis (Craw *et al.*, 1999), we used the collection localities of each species, represented by points on the maps of each taxon, and then we drew individual tracks (not shown). For each taxon, the localities within a track were joined by the line of minimum distance between each point (a minimum spanning tree). All the individual track maps were compared and superimposed to define several generalized tracks, using the software 'Trazos' (Rojas, 2004); this is an extension of ArcView GIS (ESRI, 1999) that works under the concept of minimum spanning tree, under Prim algorithm. To run the program, it is necessary to capture the longitude and latitude coordinates of all the collection localities, in order to draw the individual tracks.

Baselines were then identified, which are any geographic, climatic or geological features that spatially match a generalized track. In this work, these baselines were identified on a regional intra-continental scale from geographic, climatic and physiographic data of the SMO. On a regional scale, baselines are more difficult to identify (Contreras-Medina, 2006), because disjunct distributions of organisms are less evident than transoceanic disjunctions (González-Zamora *et al.*, 2007). In the areas of convergence or intersection among two or more generalized tracks, we recognized nodes, and these were compared with previous panbiogeographic studies that include the SMO (Escalante, 2003; Álvarez and Morrone, 2004; Márquez and Morrone, 2004; Morrone and Gutiérrez, 2005; González-Zamora *et al.*, 2007).

In order to evaluate endemism, we used the corrected weighted endemism index proposed and applied by Crisp *et al.* (2001) and Linder (2001) to Australian and African floras respectively. In Mexico, this index has been applied to the geographic distribution of seed plants such as Ternstroemiaceae (Luna-Vega *et al.*, 2004), gymnosperms (Contreras-Medina and Luna-Vega, 2007), and Cactaceae (Santa Anna del Conde *et al.*, 2009). We applied this index to grid-cells, in order to detect endemism centers of ferns. Species richness also known as 'unweighted species richness' was measured as the total count of species within each grid-cell (Linder, 2001). A first index termed 'weighted endemism' was calculated and comprised several steps (Crisp *et al.*, 2001). The first step consisted of dividing each grid-occurrence by the total number of grids in which one species occurs. Thus, a fern species restricted to a single grid scored '1' for that grid, and '0' for all other grids, whereas a fern species found in 10 grids was scored as '0.1' for each of the ten grids, and '0' for all remaining grids; then the sum of all score species values for each grid was obtained. A second index named 'corrected weighted endemism' (Crisp *et al.*, 2001), consisted in dividing the values of weighted endemism index (WE) by the total number of species in each grid cell. Those grid-cells with the highest scores are considered important biogeographic areas for the biological group under study. Grid-cells with only one species recorded were not considered for the analysis of corrected weighted endemism (CWE), because these cells do not include overlapping distributions. Those areas composed by sets of neighboring grid-cells or isolated grid-cells with high values in CWE index represent centers of endemism. Each species was scored as present in a grid-cell independently of whether it was recorded once or numerous times in that grid-cell (Linder, 2001). Because the WE index has been considered as a measure sensitive to diversity (Linder, 2001; Santa Anna del Conde *et al.*, 2009), we decided to work only with the CWE index, which is not significantly correlated with grid diversity. Our study is interested in endemism values more than total richness, so values obtained on richness are based only in those species almost restricted to the SMO province.

Unfortunately Crisp *et al.* (2001) and Linder (2001) do not present a reference parameter to recognize those important areas in the application of CWE index; for this reason, some proposals have been developed such as the use of mean value (Contreras-Medina and Luna-Vega, 2007; Santa Anna del Conde *et al.*, 2009) or an Olmstead-Tukey test (Aguilar-Aguilar *et al.*, 2008). In this study, we evaluated the relationship between richness and endemism with an Olmstead-Tukey corner test of association (Steel and Torrie, 1980); this test was previously successful applied for this index in Mexico (Aguilar-Aguilar *et al.*, 2008). This test produces a graph in which each grid-cell is placed in one of four quadrants, where richness and CWE values are plotted. Extreme values are the best indicators of an association between variables and this test gives them special weight (Steel and Torrie, 1980). Grid-cells located in the upper-right quadrant were identified as the most important biogeographic areas for ferns in northeastern Mexico.

Results

The Sierra Madre Oriental province was divided in 34 grid-cells (Fig. 2), all of them including at least one record. For this study, we included 1244 occurrence records of 66 fern species, included in nine families and 24 genera (Table 1). The three fern species represented in most grid-cells were *Notholaena aschenborniana* in 19 grid-cells, and *Astrolepis crassifolia* and *Cheilanthes aemula* both recorded in 16 grid-cells. Other well-represented taxa were *Anemia mexicana*, *Argyrochosma microphylla* and *Llavea cordifolia*, recorded all of them in more than 10 grid-cells. Richness in the 34 grid-cells was in the range of 1 to 34 species per grid-cell (Table 2), with a mean value = 9.37 species.

Parsimony Analysis of Endemicity.—The analysis of the grid-cell matrix (available upon request) produced 38 most parsimonious cladograms of 179 steps, consistency index of 0.32 and retention index of 0.53. The strict consensus cladogram (Fig. 3) with 212 steps, consistency index of 0.27, and retention index of 0.40, showed a polytomy composed of 17 grid-cells, and four main groups or clades.

Panbiogeographic Analysis.—Distribution analysis of 66 fern species showed that seven species (*Asplenium dianae, A. semipinnatum, Cheilanthes apiacea, C. chipinquensis, Notholaena brachycaulis, N. leonina,* and *Pellaea ribae*) have a very restricted distribution within the Sierra Madre Oriental (endemic to one grid-cell), and thus were not included in the track analysis.

The congruence of the individual tracks of the fern taxa allow for the recognition of five generalized tracks in the SMO (Fig. 4). The individual tracks of *Cheilanthes mexicana, Elaphoglossum viridae, Pellaea notabilis, Polystichum ordinatum, Polypodium subpetiolatum* and *Woodsia mexicana* were not considered because they do not belong to any of the generalized

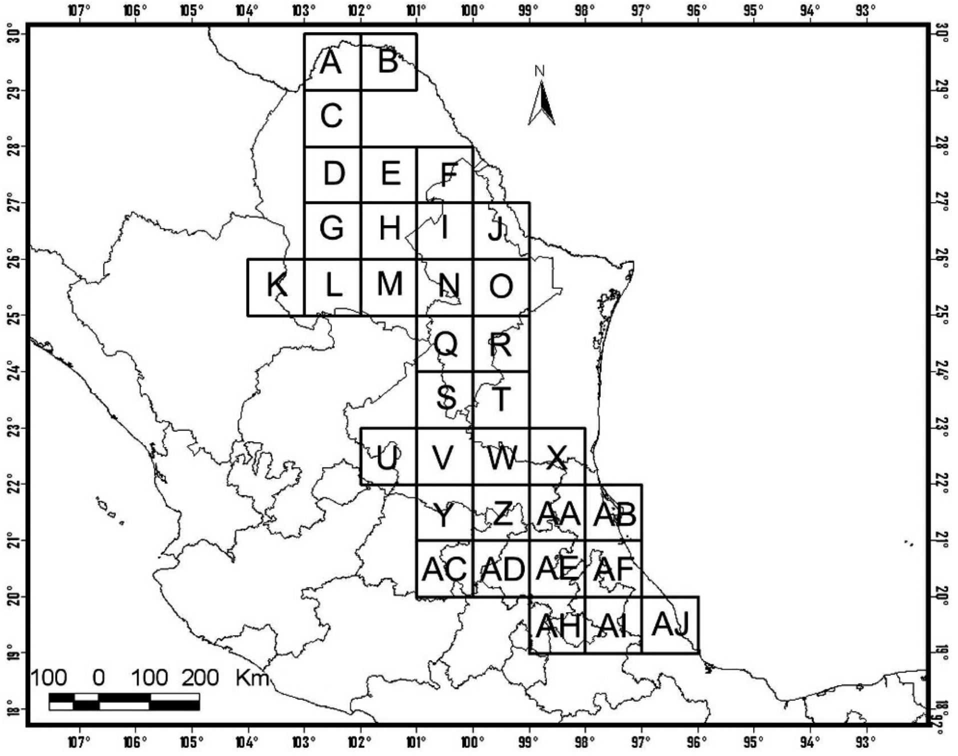

FIG. 2. Grid-cells employed in this study overlaid on a map of the Sierra Madre Oriental.

tracks found. Two generalized tracks are located in the northern part of the Sierra, including the states of Coahuila and Nuevo León, but one of them crosses the Pánuco river basin towards the Sierra Gorda area in the state of Querétaro. A third generalized track is located in the southern portion of the SMO and crosses the Pánuco river basin, and the last two are located in the southern part of this basin. All of these generalized tracks are connected among themselves.

The generalized tracks detected, the number of taxa that support them, and the areas involved are as follows:

(1) Southeastern generalized track (Fig. 4a). This track runs from the limit of the SMO along the Trans-Mexican Volcanic Belt through the central portion of the SMO and crosses the Pánuco river basin, and ends in the boundary between the states of Nuevo León and Tamaulipas. It includes the individual tracks of 20 species (Table 1). This is the largest track and is congruent with tracks obtained in the studies of Álvarez and Morrone (2004) with birds and González-Zamora *et al.* (2007) with Asteraceae.

(2) Northeastern generalized track (Fig. 4b). This track begins in the northern portion of the state of Coahuila and runs throughout the south and ends in the Sierra Gorda area in the state of Querétaro. It consists of the individual tracks of 15 species (Table 1). This track is supported by the tracks obtained by the work of Morrone and Gutiérrez (2005) with fleas.

(3) Southern generalized track (Fig. 4c). This track runs from the Pánuco river basin through the western limit of the SMO and connects with the Trans-Mexican Volcanic Belt. Includes the

Table 1. Selected fern species following the classification of Smith *et al.* (2006), species that support each generalized track, and species that belong to each group of the PAE.

Species	Generalized tracks	Groups
Aspleniaceae		
Asplenium dianae A.R. Sm.		
Asplenium semipinnatum (Hieron.) A.R.Sm.		
Asplenium soleirolioides A.R. Sm.	a	
Holodictyum ghiesbreghtii (E. Fourn.) Maxon	a	
Blechnaceae		
Woodwardia martinezii Maxon ex Weath.	a	2
Dryopteridaceae		
Ctenitis mexicana A.R. Sm.	e	
Dryopteris cinnamomea (Cav.) C.Chr.	a	
Dryopteris pseudofilix-mas (Fée) Rothm.	e	
Elaphoglossum obscurum (E. Fourn.) C. Chr.	a	2
Elaphoglossum vestitum (Schltdl. et Cham.) Schott ex T. Moore	a	2
Elaphoglossum viride (E. Fourn.) C. Chr.		
Elaphoglossum potosianum Christ	b	1
Phanerophlebia gastonyi Yatsk.	a	
Phanerophlebia nobilis (Schltdl. et Cham.) C. Presl	e	
Phanerophlebia remotispora E. Fourn.	b	2
Phanerophlebia umbonata Underw.	b	
Polystichum ordinatum (Kunze) Liebm.		2
Grammitidaceae		
Melpomene leptostoma (Fée) A.R. Sm. et R.C. Moran	a	
Polypodiaceae		
Polypodium arcanum Maxon	a	
Polypodium conterminans Liebm.	e	
Polypodium eatonii Baker	a	2
Polypodium liebmannii C. Chr.	c	
Polypodium longepinnulatum E. Fourn.	a	2
Polypodium madrense J. Sm.	c	
Polypodium martensii Mett.	a	
Polypodium rhodopleuron Kunze	e	2
Polypodium subpetiolatum Hook.		1
Polypodium villagranii Copel.	a	
Pteridaceae		
Argyrochosma delicatula (Maxon et Weath.) Windham	b	
Argyrochosma formosa (Liebm.) Windham	a	1
Argyrochosma microphylla (Mett. ex Kuhn) Windham	b	
Argyrochosma pallens (Weath. ex R.M. Tryon) Windham	c	
Aspidotis meifolia D.C. Eaton	b	1
Astrolepis crassifolia (T. Moore et Houlston) D.M. Benham et Windham	c	
Astrolepis laevis (M. Martens ET Galeotti) Mickel	b	
Bommeria ehrenbergiana (Klotzsch) Underw.	b	
Cheilanthes aemula Maxon	a	
Cheilanthes apiacea Mickel		
Cheilanthes chipinquensis Knobloch et Lellinger		
Cheilanthes cucullans Fée	a	

TABLE 1. Continued.

Species	Generalized tracks	Groups
Cheilanthes hintoniorum Mendenh. et Nesom	b	1
Cheilanthes horridula Maxon	d	
Cheilanthes leucopoda Link	b	
Cheilanthes mexicana Davenp.		
Cheilanthes purpusii T. Reeves	c	1
Cheiloplecton rigidum (Sw.) Fée	b	
Llavea cordifolia Lag.	a	
Mildella fallax (M. Martens et Galeotti) Nesom	a	
Notholaena affinis (Mett.) Hook. ex T. Moore	c	1
Notholaena aschenborniana Klotzsch	e	
Notholaena brachycaulis Mickel		
Notholaena bryopoda Maxon	d	
Notholaena copelandii C.C. Hall	b	
Notholaena galeottii Fée	e	
Notholaena jacalensis Pray	e	
Notholaena leonina Maxon		
Notholaena neglecta Maxon	b	
Notholaena rigida Davenp.	b	
Pecluma sursumcurrens (Copel.) M. G. Price	a	
Pellaea cordifolia (Sessé et Moç.) A.R. Sm.	c	
Pellaea notabilis Maxon		1
Pellaea ribae Mendoza et Windham		
Pellaea villosa (Windham) Windham et Yatsk.	e	
Schizaeaceae		
Anemia mexicana Klotzsch	b	
Thelypteridaceae		
Thelypteris schaffneri (Fée) C. F. Reed	a	
Woodsiaceae		
Woodsia mexicana Fée		

individual tracks of seven species (Table 1). This track is supported by the work of González-Zamora *et al.* (2007) with Asteraceae.

(4) Northern generalized track (Fig. 4d). This track is located at the northern part of the SMO and runs throughout the central part of Coahuila and Nuevo León. Only two species are included in this track (Table 1). This track is congruent with tracks obtained by González-Zamora *et al.* (2007) with Asteraceae.

(5) Sierra Gorda generalized track (Fig. 4e). Located in the southern portion of the SMO, this track is the shortest one and includes only the states of Hidalgo and Querétaro. There are nine species included in this track (Table 1). This track is also supported by the work of Morrone and Gutiérrez (2005) with fleas.

Intersection or convergence in generalized tracks allowed for the recognition of five nodes (Fig. 5), two of them located in northeastern portion of the SMO, two in the southern portion and the last one also located in the south, on the boundary with the Trans-Mexican Volcanic Belt. These nodes are: Nuevo León, Tamaulipas, Landa, Sierra Gorda and Orizaba.

Endemism Analysis.—The endemism analysis was performed with 32 grid-cells that contain at least two fern species (mean value of 10 and median value

TABLE 2. Species richness, endemism and number of records for ferns in each grid-cell. Values of corrected and weighted endemism of each grid-cell in the SMO.

Grid-cells	Number of species	Endemic species	Number of records	Corrected endemism	Weighted endemism
A	4	0	23	0.13	0.52
B	1	0	3	0.06	0.06
C	3	0	14	0.06	0.2
D	2	0	10	0.06	0.13
E	4	0	10	0.08	0.32
F	4	0	5	0.08	0.35
G	4	0	8	0.14	0.58
H	8	0	15	0.15	1.25
I	7	1	13	0.22	1.58
J	3	0	5	0.11	0.34
K	5	0	2	0.15	0.76
L	4	0	3	0.17	0.71
M	4	0	5	0.15	0.6
N	26	2	111	0.24	6.24
O	3	0	6	0.11	0.33
Q	9	0	36	0.12	1.06
R	19	0	72	0.17	3.39
S	4	0	7	0.09	0.39
T	21	2	71	0.24	5.05
U	1	0	3	0.05	0.05
V	14	1	19	0.25	3.49
W	5	0	7	0.12	0.64
X	2	0	1	0.19	0.39
Y	4	0	1	0.2	0.81
Z	34	1	374	0.23	8.06
AA	12	0	11	0.15	1.85
AB	3	0	6	0.15	0.46
AC	6	0	11	0.14	0.88
AD	24	0	81	0.21	5.17
AE	28	0	120	0.21	5.91
AF	11	0	14	0.22	2.43
AH	4	0	22	0.09	0.39
AI	26	0	105	0.21	5.65
AJ	18	0	50	0.26	4.75

of 5), because the concept of area of endemism implies the overlap in distribution areas of two or more endemic taxa. U and B grid-cells were not considered because in them are represented only one species. The resulting CWE values were in the range 0.06–0.26 (mean and median values of 0.15) (Table 2).

From Olmstead-Tukey test application (Steel and Torrie, 1980) with p-value of 0.001, and considering values above the medians (representing richness and CWE index), 11 grid-cells as important areas for ferns were identified, forming a continuum (Fig. 6), from the I grid-cell in the north to the AI-AJ grid-cells in the south.

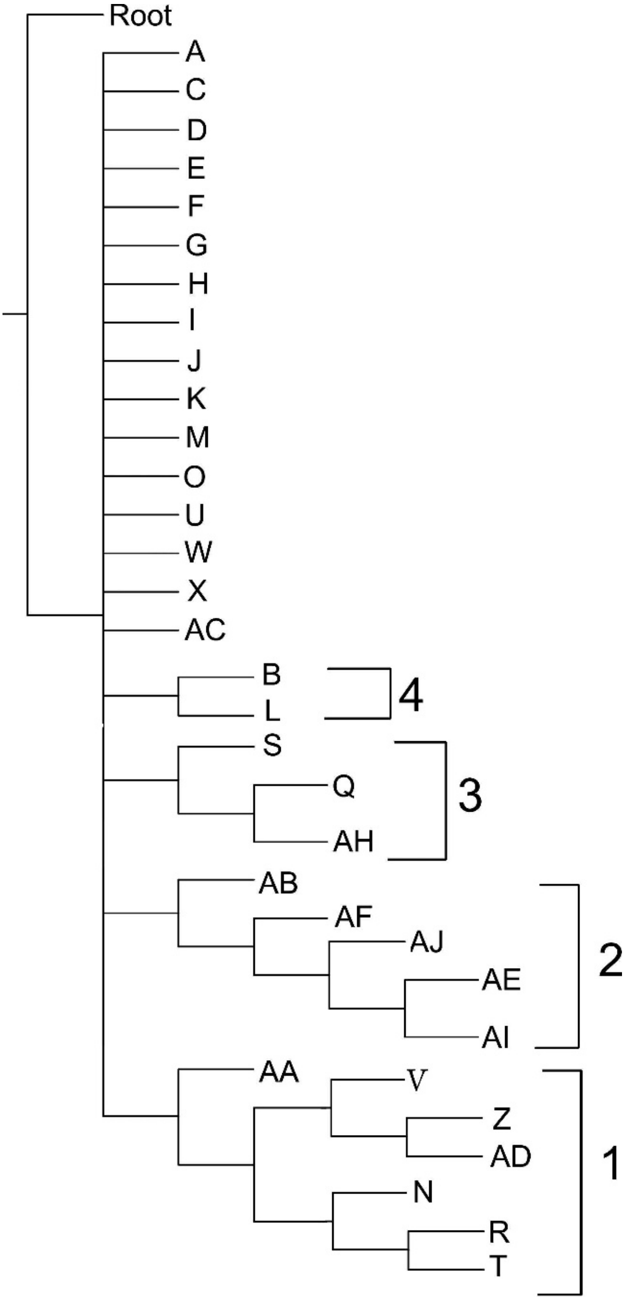

FIG. 3. Strict consensus cladogram obtained with grid-cell analysis. Numbers represent the main groups. The letters corresponds to grid-cells of Fig. 2.

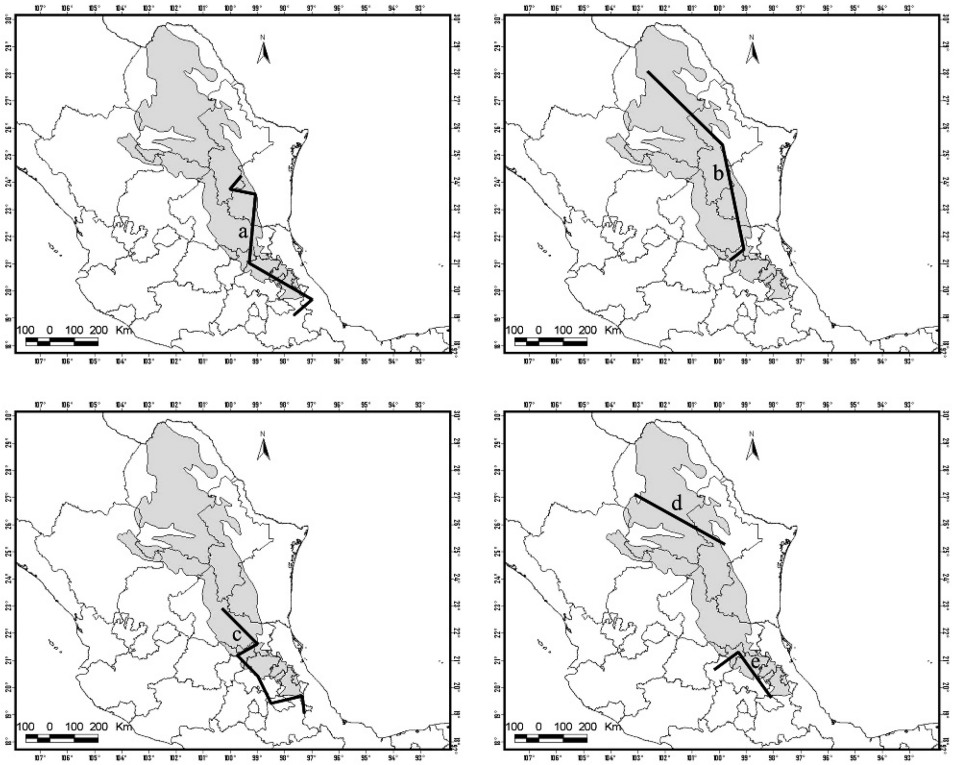

FIG. 4. Generalized tracks found. a) southeastern generalized track; b) northeastern generalized track; c) southern generalized track; d) Sierra Gorda generalized track; e) northern generalized track.

DISCUSSION

Fern species in the SMO are mainly distributed in cloud, oak, pine and mixed forests that develop under temperate climatic conditions, with high rainfalls and humidity. However, some species inhabit other types of vegetation that receive low rainfall, such as arid scrub or tropical thorn forest. Notwithstanding, distributional patterns obtained herein are mainly defined by mountainous landscapes.

The six richest grid-cells with more than 20 fern taxa are located in the southern and central portions of the SMO (grid-cells Z = 34, AE = 28, AI = 26, AD = 24 located in the south mainly in the states of Hidalgo, Querétaro, Puebla, and Veracruz, and grid-cells N = 26 and T = 21 located in the central part in the states of Coahuila, Nuevo León and Tamaulipas). The southern grid-cells coincide with two important areas recognized as terrestrial priority regions for conservation (Fig. 5) or TPR's proposed by CONABIO (Arriaga *et al.*, 2000). Two grid-cells are located at the priority region named as 'Bosques Mesófilos de la Sierra Madre Oriental' (grid-cells AE and AI of Fig. 2), and two more within the 'Reserva de la Biosfera de la Sierra Gorda' (grid-cells Z and AD

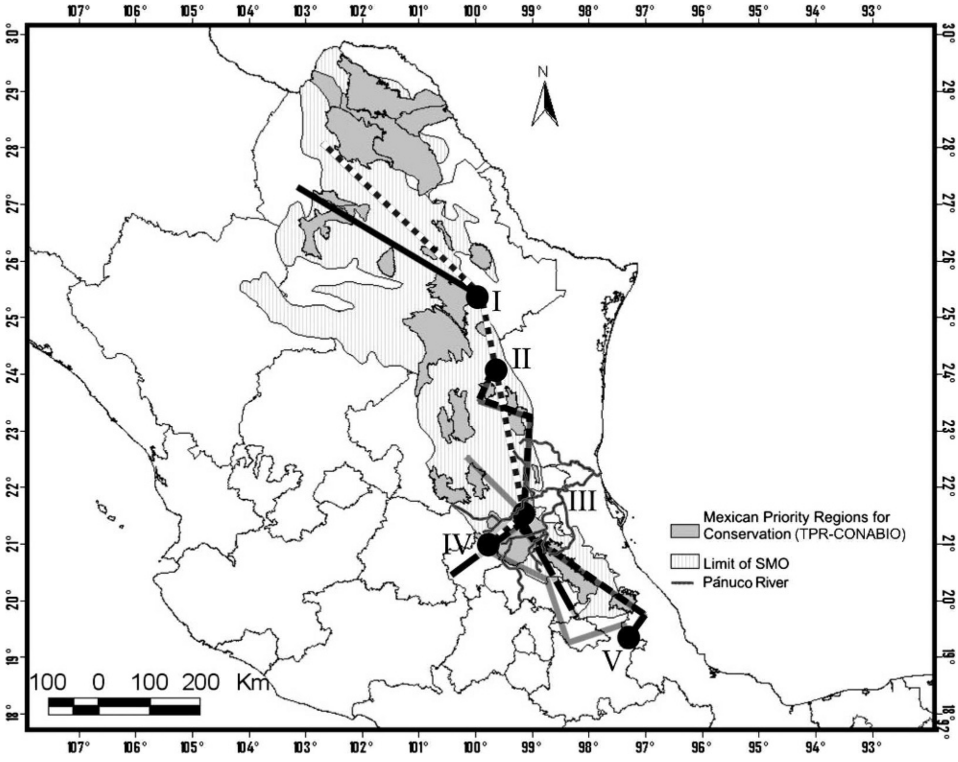

FIG. 5. Generalized tracks, nodes, and congruence with Mexican priority regions of conservation. Nuevo León (I), Tamaulipas (II), Landa (III), Sierra Gorda (IV) and Orizaba (V). Location of the Pánuco River is noted.

of Fig. 2). Two central grid-cells coincide with four TPR's: grid-cell N with El Potosí-Cumbres de Monterrey, and grid-cell T, with three TPR's named Valle de Jaumave, El Cielo and San Antonio-Peña Nevada. Overlap between these grid-cells with TPR's confirm that these areas are important for conservation, because TPR's represent areas with high values of ecosystem and species richness in relation to other areas of Mexico, as well as a functional ecologic integrity where real opportunities for conservation exist (Arriaga *et al.*, 2000). Terrestrial Priority Regions (TPRs) were formulated by an expertise set of Mexican researchers in different fields of biology coordinated by the CONABIO and represent areas with high biodiversity.

Conservation *in situ* could be carried out in protected areas that coincide with those grid-cells containing high fern diversity within the SMO, as in the case of the 'Reserva de la Biosfera Sierra Gorda', which hold native and natural vegetation; a real program of conservation exists in this Mexican Protected Natural Area. Some species studied herein are restricted endemics, and are therefore poorly represented in herbaria; we suggest that conservation strategies are needed for these fern species that inhabit the SMO, because

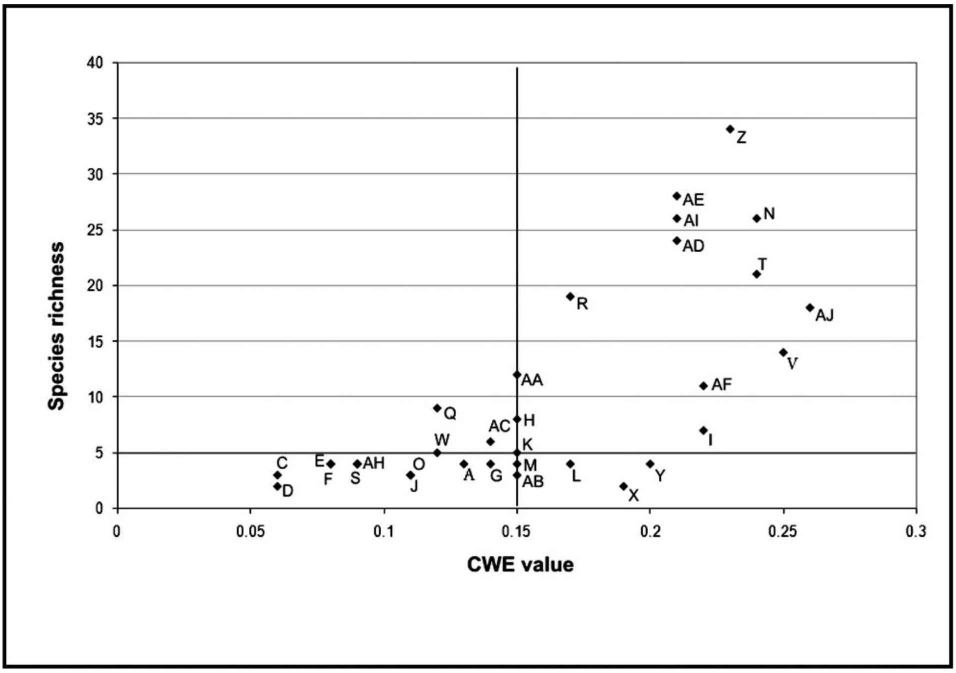

FIG. 6. Olmstead-Tukey corner test of association between richness and corrected weighted endemism (CWE) index. The letters corresponds to grid-cells of Fig. 2. The upper right part of the figure contains the important fern areas of the applied test.

only tree fern species are included in the Norma Oficial Mexicana NOM-059-ECOL-2001 (SEMARNAT, 2002), which is the official document published by the Mexican government that includes native threatened taxa. The following fern species are candidates to be included: *Asplenium dianae, A. semipinnatum, Cheilanthes apiacea, C. chipinquensis, Notholaena brachycaulis, N. leonina,* and *Pellaea ribae*. Demography and population genetics studies with conservation implications are needed for these species; these approaches have been done previously with endangered fern species in other places of the world (Ranker, 1994; Rumsey *et al.*, 1999; Kingston *et al.*, 2004). Genetic diversity is essential for fern species and populations in order to respond to long and short environmental change (Kingston *et al.*, 2004).

In the PAE cladogram, the largest component formed by seven grid-cells (group 1 in Fig. 3) includes areas located at the southern and central portions of the SMO. This component is formed mainly by montane temperate areas, characterizing the mountainous massif of the Sierra Madre Oriental, which might function as a biological corridor for this kind of organisms. This is an important aspect in conservation biology, because natural corridors are considered as useful and as essential components of management of landscapes. They provide connections among patches of habitat and mitigate pernicious effects of landscape fragmentation, also assisting in the maintenance of population and biotic diversity in a region (Inglis and Underwood, 1992; Falcy and Estades, 2007; Williams *et al.*, 2007). Such is the case of the SMO province, because habitat fragmentation is a critical problem mainly in temperate forests due to land use change, especially for coffee, bean and corn plantations and for animal husbandry (Luna-Vega and Alcántara, 2004; Luna-Vega *et al.*, 2006). Interchange of individuals among populations that inhabit in different patches of temperate vegetation may increase local and regional population persistence in order to reduce extinction rates and increasing colonization rates, mainly for small and isolated populations (Rosenberg *et al.*, 1997). This is of particular interest in the case of ferns, especially endemics, but other species with wider distributions can be favored by connections between patches of temperate forests, because neighboring environments are likely to be similar in fern communities, and thus suitable for propagules dispersing short distances, as suggested by Karst *et al.* (2005).

A second and interesting component is located at the southern portion of the SMO (group 2 in Fig. 3), located in the leeward zone of this mountain chain, showing the main role of humidity in the distribution of ferns. Gametophytes need moisture to complete fertilization and most ferns have simple tracheary elements, so is not surprising that fern distribution is strongly linked to water availability (Karst *et al.*, 2005). The abiotic environment at a large scale (as in the present study) may play an important role in determining fern distributions (Karst *et al.*, 2005). The SMO is one of the main physiographic uplifted mountain ranges in Mexico, and wet montane forests cover its lower eastern slopes facing the Gulf of Mexico and give rise to wet pine-oak and cloud forests in a cloud zone above 2,200 m (Mickel and Smith, 2004). This mountain chain extends from the north to the central part of Mexico with peaks 2,000–3,400 m high, with rain and fog nearly every day on the eastern slope, influenced mainly by trade winds (Hernández-Cerda and Carrasco-Anaya, 2004; Mickel and Smith, 2004). These climatic conditions cause an extremely rich fern flora, with tree ferns, filmy ferns, and other groups requiring constant high humidity (Mickel and Smith, 2004), conditions that are reflected in our second component of the PAE cladogram.

The last two groups are smaller and include only two or three grid-cells, respectively (groups 3 and 4). These minor clades possibly represent groups of grid-cells that are supported by widely distributed species (*Astrolepis crassifolia* and *Notholaena aschenborniana*), which share similar habitats and need similar climatic conditions for their growth, and do not necessarily reflect historical relationships.

The largest group in the PAE cladogram (group 1 in Fig. 3) shows that several fern taxa are distributed all along the SMO, mainly in the southern and central portions. This group 1 exemplifies the wide distribution of some species in this region. Long distance dispersal and vicariance have been used as explanations for fern present-day disjunct distributions (Barrington, 1993), but some recent studies have shown that environmental variables can have a dominant role in determining fern distributions, i.e., high humidity, soil moisture and temperate climate, among others (Karst *et al.*, 2005; Ramírez-

Barahona *et al.*, 2011). Unfortunately, vicariance is not detectable in most cases (Wolf *et al.*, 2001), so effective research programs need to be undertaken, especially in the rich fern species areas of Mexico.

The resulting PAE area cladogram contains a polytomy of 17 grid-cells. Polytomies are frequent in this type of analyses, indicating an association with the spatial resolution of grid-cells used (Morrone and Escalante, 2002). Another problem inherent to this method is that the target of parsimony analyses is to find the most parsimonious solution, but biogeographical areas can have more than one history (Morrone and Crisci, 1995; García-Barros *et al.*, 2002).

The generalized tracks and nodes recognized in this work from panbiogeographic analysis reflect a complex biogeographic history of fern taxa involved and the geological and climatic complexity of this mountain region of Mexico. Additionally, they reinforce the idea that the SMO is a component of the Mexican Transition Zone, where Nearctic and Neotropical elements converge (Halffter, 1987). The rise and development of this mountain area has been considered to promote some vicariant events associated with the biotic evolution of the transitional component in northern Mexico (Morrone, 2005), contributing to the complex biogeographic history of this country (Luna-Vega, 2008). From a panbiogeographic perspective, the Pánuco River basin is considered as the main baseline. This river is located in the central part of the SMO (Fig. 5) and divides this mountain chain in two parts: north and south (Smith, 1941; Luna-Vega *et al.*, 1999).

All nodes obtained in this work coincide with those previously obtained with different organisms. From the five nodes obtained, three of them are remarkable. The case of the Nuevo León node (Fig. 5, I) shows the complexity of the area associated to their geological history. The Sierra Gorda and Landa nodes (Fig. 5, III, IV) are interesting in relation to its location as important areas for conservation. They are considered by the Mexican government as natural protected areas under the category of 'Reserva de la Biosfera'; this result supports their category with biogeographic criteria. A third interesting node is located in the southern portion of the SMO bordering with the Trans-Mexican Volcanic Belt (Fig. 5,V), because it represents a complex area where different biogeographic provinces converge, as previously suggested Márquez and Morrone (2004) in their study based on beetles.

The southern portion of the SMO contains high fern diversity in relation to the central and northern portion. The northern portion of the SMO is clearly poor in species and endemism (i.e., grid-cells A, B, C, D, E, F, G, H, J). PAE cladogram shows that the southern-central portion of the SMO includes two different fern components, one related with the leeward region (group 2 in Fig. 3, grid-cells AB, AE, AF, AI and AJ) and another mainly montane (group 1). An idea of a continuous SMO based in the distribution of fern species is based on PAE and CWE index. This represents an important difference with the Luna-Vega *et al.* (1999) study. In the present study, the forests located in the northeastern portion of the state of Querétaro are closely related to those in the central and southern portion of the SMO, and in Luna-Vega *et al.* (1999)

study, they are closely related to the forests of the state of Tamaulipas, located in northern Mexico. Differing from the PAE, the CWE index supports the existence of only one group in the southern-central portion (grid-cells V, Z, AD, AE, AF, AI, AJ). In the panbiogeographic analysis, the Pánuco River basin represents an important physiographic feature dividing the distribution of ferns in the SMO. The slight differences between PAE and CWE index (in relation with grid-cells AA and AB included in PAE and not in CWE) are expected because the areas detected after applying CWE index represent sets of neighbor grid-cells with high values, and are not associated by shared species as those found in the PAE cladogram (Santa Anna del Conde *et al.*, 2009). Our resulting PAE area cladogram represents a hypothesis of area relationship that was contrasted with previous studies for different biological groups and can also be refuted or supported with future studies that include all ferns that inhabit the SMO.

In the northern portion of the SMO, the region of Saltillo-Monterrey (grid-cell N in Fig. 2) appears as an interesting area from a biogeographic point of view, because it shows a convergence of biotas with different origins and relations, based on different analyses with different biological groups (González-Zamora *et al.*, 2007 with Asteraceae; Santa Anna del Conde *et al.*, 2009 with Cactaceae). This grid-cell resulted in panbiogeographic and CWE analyses as an important biogeographic area for ferns in northeastern Mexico; also this area presents a complex geological history (Fischer and Jackson, 1999), reinforcing its inclusion as a node.

The results of the present study suggest that the distributional patterns of endemism of ferns in the SMO are slightly different from those described for other biological groups so we cannot reinforce established generalizations. Ferns have high vagility and can represent an independent valuable test for identification of important biogeographic areas, mainly if they disagree with generalizations about regionalization and biogeographic proposals of Mexican biota. Because dispersal of spores is generally greater than seeds, fern species tend to be more widely distributed and show less endemism than seed plants (Smith, 1993). Another probable explanation to the distributional pattern observed could be the result of climatic differences that does not allow many species to establish, for example, in both sides of the Pánuco River. In this case, we can point to those more tropical southern species that cannot survive in the driest and coldest northern areas, although their spores are still dispersed into these areas. Despite this, ferns sometimes present similar distributional patterns as seed plants, with some narrowly distributed species, which might be considered, with some caution, as a signal of vicariance.

This study analyzes the regional distributional patterns of ferns and establishes an objective way to study the relationship between richness and endemism in non-flowering plants with high vagility. The validity and repeatability of the methods applied in the present study will depend on its application in other parts of the world, mainly in those regions where major geographic centers of fern species are located, such as Central and South America, eastern Africa, Australia, and eastern Asia (Tryon and Tryon, 1984), and also in other mountainous areas of Mexico. In the SMO, a similar study with widely distributed, nonvascular, seedless plants (such as mosses) is needed. Knowledge of the distributional patterns of the species of ferns, as well as the examination of historical and ecological factors that have determined such patterns, provide additional evidence about the biota that currently occur in the SMO (Luna-Vega *et al.*, 1999; González-Zamora *et al.*, 2007). Clearly, this study has improved our knowledge of the complexity and biogeographic history of this eastern montane part of Mexico. These kinds of study can improve the knowledge of the SMO and of the Mexican biota in general.

As suggested by Luna-Vega (2008), we are in an important moment in the understanding of the biogeography of Mexican plants, where ferns still have much to offer (Wolf *et al.*, 2001), and it is important that their distributional data and biogeographic patterns be incorporated into general statements about Mexican biota and biogeographic history of this highly diverse country.

ACKNOWLEDGMENTS

We thank Daniel Tejero-Díez, Juan J. Morrone, Susana Valencia, Jennifer Geiger and three anonymous referees for useful comments and many critical observations, which lead to substantial improvements in the final manuscript. We are also indebted to the staff of the herbaria cited in the text for their courtesy during our review of specimens. Assistance provided by Diana Castañeda and Julio Ramírez is gratefully appreciated. Support from projects PAPIIT IN-209108 and FOSEMARNAT-2004-C01-311 are gratefully acknowledged.

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