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ORIGINAL PAPER

Species richness, endemism and conservation of Mexican gymnosperms

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Abstract An analysis of the distribution patterns of 124 Mexican gymnosperm species was undertaken, in order to detect the Mexican areas with high species richness and endemism, and with this information to propose areas for conservation. Our study includes an analysis of species richness, endemism and distributional patterns of Mexican species of gymnosperms based on three different area units (states, biogeographic provinces and grid-cells of $1° \times 1°$ latitude/longitude). The richest areas in species and endemism do not coincide; in this way, the Sierra Madre Oriental province, the state of Veracruz and a grid-cell located in the state of Oaxaca were the areas with the highest number of species, whereas the Golfo de México province, the state of Chiapas and a grid-cell located in this state were the richest areas in endemic species. A weighted endemism and corrected weighted endemism indices were calculated, and those grid-cells with high values in both indices and with high species richness were considered as hotspots; these grid-cells are mainly located in Southern and Central Mexico.

Keywords Areography · Conservation · Endemism · Gymnosperms · Mexico · Species richness

Introduction

Since the first proposals of biogeographical regionalizations of the world (Sclater 1858; Wallace 1876), Mexico has been considered a transitional zone between the Nearctic and Neotropical biogeographic regions (Halffter 1987). Recently, based on panbiogeographic studies, Contreras-Medina and Eliosa-León (2001) and Morrone and Márquez (2001) proposed that the Mexican biota shows different biogeographic relationships as suggested by two North American tracks, one at the east and other

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at the west, and a Gondwanic track, that relate Mexico to the rest of the Neotropical region. The geographic distribution of the elements that constitute the Mexican biota has been the result of vicariance, dispersal events and local extinction, as well as climatic changes and speciation processes in situ (Salinas-Moreno et al. 2004), in a complex plate tectonic scenario (Ferrusquía-Villafranca 1993; Ortega et al. 2000).

At the end of the Cretaceous period, the Laramidian orogeny started and determined the main physiographic features of the mountains in Mexico and northern Central America (Halffter 1987; Salinas-Moreno et al. 2004), with the exception of the Transmexican Volcanic Belt that started in the Mid-Tertiary (Ferrusquía-Villafranca 1993; Ortega et al. 2000). Climatic changes during the Pleistocene (Toledo 1982) and orogenic processes contributed to the diversification of the genus *Pinus* in Mexico (Eguiluz 1985; Farjon and Styles 1997). In this scenario, barriers and corridors, as Pleistocenic refugia, played an important role in the spatial evolution of the Mexican gymnosperms (e.g. Perry et al. 1998; Contreras-Medina et al. 2001b; González and Vovides 2002).

Gymnosperms are seed plants that mainly inhabit temperate zones of both hemispheres and have been important elements in fossil and extant plant communities; their appearance in the late Paleozoic represents one of the most important evolutionary phases among the patterns of vascular plant diversification (Niklas et al. 1983). Due to their antiquity, they represent an interesting group for distributional analysis from an historical biogeography approach. In several Mexican floristic studies, gymnosperms represent approximately 2% of species diversity, in contrast with angiosperms and pteridophytes (Contreras-Medina 2004). Notwithstanding, Mexico represents the country with more species of some genera, such as *Ceratozamia*, *Dioon* and *Pinus* (Contreras-Medina 2004) and plays an important role in gymnosperm diversity at a world-wide level (see Takhtajan 1986; Osborne 1995).

Mexican gymnosperms are distributed mainly in temperate forests and arid scrubs. Studies about the geographic distribution of gymnosperms in Mexico are imperative not only theoretically but practically, especially for those groups with great economic value such as *Abies* and *Pinus*, and those threatened taxa included in some risk categories, like cycads. Floristic richness of Mexican gymnosperms is represented by nearly 130 species, included in 14 genera and six families, such diversity represents 15% in a world-wide level; species endemism is frequent, even at state level, mainly in Zamiaceae.

Areography (also named chorology) is defined as the study of distributional areas of taxa (Rapoport 1975; Rapoport and Monjeau 2001). This type of studies can offer information about areas of richness and endemicity of faunistic and floristic groups in a country or continent, and may also contribute to the delimitation of biogeographic regions. Some previous works that have applied this approach to Mexican plant taxa were carried out by Kohlmann and Sánchez (1984) with *Bursera*, Valdés and Cabral (1993) with grasses, and García-Mendoza (1995) with Agavaceae.

Our aim is to detect Mexican areas of richness and endemism of gymnosperms based on their presence on states, biogeographic provinces, and grid-cells and to compare the results obtained. With this task we will be able to generate useful information to carry out several aspects on the geographical distribution of these seed plants in the country, and to detect some important areas for conservation based on this group of plants.

Materials and methods

Distributional data of gymnosperm species were obtained from the revision of 1465 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); Herbarium of the Missouri Botanical Garden (MO); Herbaria of the Instituto de Ecología A.C. in Xalapa City (XCAL) and Pátzcuaro City (IEB); Herbarium of the Facultad de Ciencias, UNAM (FCME); Herbarium of the Universidad de Guadalajara (IBUG); Herbarium of the Departamento de Bosques, Universidad Autónoma Chapingo (CHAP); Herbario Nacional Forestal (INIF); Herbarium of the Universidad Veracruzana (XALU); and Herbarium of the Universidad de Sonora (USON). In addition, some floristic and revisionary studies were reviewed (Zanoni and Adams 1979; Wiggins 1980; Zanoni 1982; Vovides et al. 1983; Stevenson et al. 1986; Patterson 1988; Espinosa 1991; McVaugh 1992; Zamudio 1992, 2002; Moretti et al. 1993; Zamudio and Carranza 1994; Fonseca 1994; Farjon and Styles 1997; Medina and Dávila 1997; Narave and Taylor 1997; Vovides 1999; Aguirre-Planter et al. 2000; Felger 2000; Contreras-Medina et al. 2001a, 2003). Finally, in order to obtain field data and to make field observations of natural populations of some gymnosperm species, field exploration was carried out in the Mexican states of Hidalgo, Querétaro, Estado de México, Puebla, and Oaxaca.

In order to perform the biogeographic analysis, Mexican states, biogeographic provinces and $1° \times 1°$ latitude/longitude squares were used as units of study. We included a state level in the analysis because in Mexico, as well as in other countries, conservation decisions are generally undertaken considering political boundaries, rather than natural criteria (Dávila-Aranda et al. 2004), and because in megadiverse countries distributional data tend to be organized on the basis of geopolitical units (Gaston and Williams 1996). In order to recognise some patterns at the state level (Fig. 1a), we followed the criteria suggested by Dávila-Aranda et al. (2004), grouping the species in four sets based on their patterns of distribution: (1) scarcely distributed (species recorded only in one state); (2) narrowly distributed (2–4 states); (3) normally distributed (5–9 states); and (4) widely distributed (10 or more states). We also used the Mexican biogeographic provinces proposed by the Comisión Nacional Para el Uso y Conocimiento de la Biodiversidad (CONABIO) (Arriaga et al. 1997), which represent a regionalization of the country based on four different sources (vascular plants, herpetofauna, mammals and morphotectonics, Fig. 1b). In each province, the contribution of endemic gymnosperm species was evaluated and those biogeographic provinces with more species were remarked. Despite more recent regionalizations of Mexico have been proposed (e.g. Morrone 2001), the scheme of CONABIO has the advantage of having been generated in digital format, so the distributional data of gymnosperms can be analysed with a Geographic Information System (GIS).

In many cases the size of the Mexican states studied herein (i.e. Chihuahua versus Tlaxcala) and the biogeographic provinces (i.e. Altiplano Norte versus Soconusco) are extremely different. Thus, it was necessary to carry out an alternative biogeographic analysis with standard units of the same size. For this reason, we chose squares of one geographical degree per side, partially to facilitate the data manipulation and to reduce the effect of sampling artifacts, such as mapping errors and


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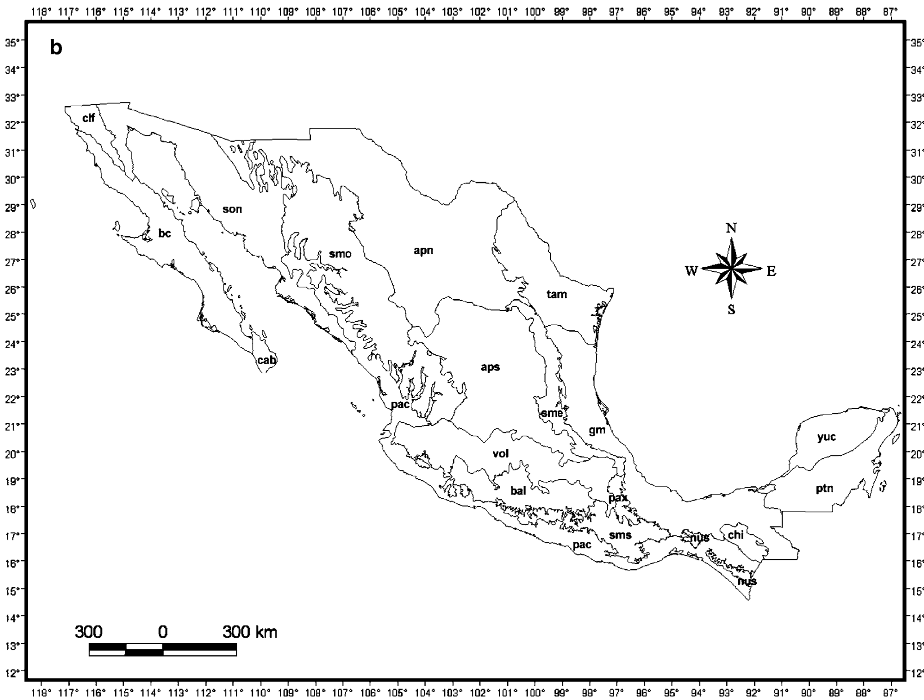
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◀**Fig. 1** (**a**) The 32 Mexican states. Abbreviations are: AGS = Aguascalientes, BC = Baja California, BCS = Baja California Sur, CAMP = Campeche, CHIS = Chiapas, CHIH = Chihuahua, COA = Coahuila, COL = Colima, DF = Distrito Federal, DUR = Durango, GTO = Guanajuato, GRO = Guerrero, HGO = Hidalgo, JAL = Jalisco, MEX = México, MICH = Michoacán, MOR = Morelos, NAY = Nayarit, NL = Nuevo. León, OAX = Oaxaca, PUE = Puebla, QR = Quintana Roo, QRO = Querétaro, SLP = San Luis Potosí, SIN = Sinaloa, SON = Sonora, TAB = Tabasco, TAMP = Tamaulipas, TLA = Tlaxcala, VER = Veracruz, YUC = Yucatán, ZAC = Zacatecas; (**b**) the 19 biogeographic provinces of Mexico according to Arriaga et al. (1997). Abbreviations are: apn = Altiplano Norte, aps = Altiplano Sur, bal = Depresión del Balsas, bc = Baja California, clf = California, cab = Del Cabo, chi = Los Altos de Chiapas, gm = Golfo de México, nus = Soconusco, oax = Oaxaca, pac = Costa del Pacífico, ptn = Petén, sme = Sierra Madre Oriental, smo = Sierra Madre Occidental, sms = Sierra Madre del Sur, son = Sonorense, tam = Tamaulipeca, vol = Eje Volcánico, yuc = Yucatán

unsampled grids in sparsely inhabited areas (Crisp et al. 2001). This scale size was chosen because it was tested in previous works on areography and diversity of different groups of Mexican flora (e.g. Kohlmann and Sánchez 1984; García-Mendoza 1995; Dávila-Aranda et al. 2004). We applied richness and endemism indices proposed by Crisp et al. (2001) and Linder (2001) to these grid-cells, which were previously applied to Australian and African floras, respectively, dividing the study areas in squares of one or two geographical degrees per side, in order to detect centres of species richness and endemism of vascular plants. The use of equal-area grids has also been considered as an important tool for studying biogeographic patterns in biological diversity (McAllister et al. 1994).

Species richness was measured simply as the total count of species within each grid-cell and is also known as unweighted species richness (Linder 2001). A first index termed 'weighted endemism' was related to species richness (Crisp et al. 2001). The first step consisted in dividing each grid-occurrence by the total number of grids in which one species occurs. Thus, a species restricted to a single grid was scored as '1' for that grid, and '0' for all other grids, and a species found in four grids, was scored as '0.25' for each of the four 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 weighted endemism index by the total count of species in each grid cell. Those grid-cells with the highest scores in the first index were considered as centres of richness and for the second index as centres of endemism (see Crisp et al. 2001 and Linder 2001 for further details). Grid-cells with none or one species recorded were deleted from the analysis of corrected weighted endemism and are not shown in the resultant map. Grid-cells values obtained for weighted endemism and corrected weighted endemism indices were ranged from 1 to 10. Each species was scored as present in a grid-cell independently of the number of times recorded in it (Linder 2001).

In our work, we do not deal with patterns of similarity among states, biogeographic provinces or grid-cells. We considered as endemic species those with ranges limited to a state or biogeographic province. Species restricted to a single cell were considered endemics with a small distribution range (narrow endemics).

Geographic distribution maps of each gymnosperm species were obtained using ArcView GIS (ESRI 1999). The map of known distribution of each species was first projected on a map of Mexico with state divisions, second on a map of biogeographic provinces produced by CONABIO (Arriaga et al. 1997), and third on a grid map of Mexico divided in cells of 1° per side, in order to detect those richest areas in endemism and species of gymnosperms in Mexico.

Finally, we selected those grid-cells with more endemic species to Mexico and/or more species richness and compared them with the Mexican priority regions for conservation of CONABIO (Arriaga et al. 2000), which represent areas with high biodiversity, formulated by an expertise set of national researchers coordinated by CONABIO; also we compare our results with others based in other groups of plants.

Results and discussion

State analysis

Sixty-eight species of gymnosperms are endemic to Mexico, representing 56% of the total number of taxa recorded in the country. Notwithstanding that these endemic species are found at different states, many of them are concentrated in southern Mexico, in the states of Chiapas, Oaxaca and Veracruz, especially those of Zamiaceae (Table 1). Many states do not include any endemic species, mainly those

Table 1 Families, genera, species richness, and endemism of wild gymnosperms in the 32 Mexican states

States	Number of species	Number of genera	Number of families	Number of endemic species
Veracruz	**39**	**12**	**6**	**5**
Oaxaca	**38**	**12**	**6**	**6**
Nuevo León	**33**	**11**	**5**	1
Chihuahua	**33**	7	3	0
Coahuila	**32**	8	3	0
Chiapas	**31**	**10**	**5**	**7**
Hidalgo	**31**	**12**	**6**	0
Jalisco	31	8	4	1
Durango	30	9	4	0
San Luis Potosí	29	**11**	**6**	1
Puebla	28	**12**	**6**	1
Michoacán	25	8	4	1
Querétaro	25	**12**	**6**	0
Tamaulipas	25	**11**	**6**	1
Guerrero	24	8	4	0
Zacatecas	24	5	3	1
Sonora	22	8	4	0
México	20	5	2	0
Distrito Federal	16	5	2	0
Nayarit	16	6	3	0
Baja California	15	5	3	0
Morelos	15	4	2	0
Tlaxcala	14	4	2	0
Sinaloa	13	4	2	0
Guanajuato	12	5	3	0
Aguascalientes	9	4	3	0
Colima	5	4	3	0
Tabasco	4	3	2	1
Quintana Roo	2	2	2	0
Baja California Sur	1	1	1	0
Campeche	1	1	1	0
Yucatán	1	1	1	0

Numbers in bold represent the higher in each category located in northeastern Mexico and central and northern portions of the Pacific coast. States richest in species are: Veracruz, Oaxaca, Nuevo León, Chihuahua, Chiapas, Coahuila, Hidalgo, Jalisco, Durango, San Luis Potosí and Puebla (Fig. 2a). These states are located in southern, central, and northern Mexico, which suggests that they do not obey a latitudinal gradient, following the distribution of the main Mexican mountain chains (i.e. Sierra Madre Oriental, Sierra Madre Occidental, Transmexican Volcanic Belt, and Serranías Transístmicas). States poor in species are Baja California Sur, Campeche, and Yucatán, located in the Baja California and Yucatán peninsulae.

Results obtained show that nine out of the 14 genera represented in Mexico have at least one endemic species, which is more evident in the cases of *Ceratozamia* (13 species) and *Dioon* (10 species); most of the species of these genera are restricted to the Mexican territory.

Several species are shared with adjacent parts of Central America (i.e. *Abies guatemalensis* Rehder, *Pinus teocote* Schltdl. et Cham., *Zamia herrerae* Calderón et Standl.) and with the United States of America (e.g. *Abies concolor* (Gordon et Glendinning) Hildebrand, *Calocedrus decurrens* (Torr.) Florin, *Ephedra nevadensis* S. Watson, and *Pinus coulteri* D. Don). Thus, the percentage of endemism may increase if a broader geographical approach is undertaken. The inclusion of some parts of Central America and southern United States of America generate a more natural geographic regionalization, as suggested by several authors (Rzedowski 1991; Morrone 2001).

There are 47 species that are scarcely distributed in Mexico and 26 of them are represented in only one state (Table 1); also 28 of them are endemic to Mexico. Many of these species are only known from one or few localities, such as *Ceratozamia kuesteriana* Regel, *Dioon califanoi* De Luca et Sabato, and *Pinus maximartinezii* Rzedowski, and the remaining species are distributed also in adjacent countries. Twenty-seven species are narrowly distributed (2–4 states), 12 of them are only found in two states and 15 species of Pinaceae and Zamiaceae are endemic to Mexico. A third group (distributed in 5–9 states) includes 25 species; nine of them are endemic to the Mexican territory. Twenty-one species are distributed in 10 or more states, and eight are endemic to Mexico. *Pinus teocote* Schltdl. et Cham. and *Taxodium mucronatum* Ten. (the National Mexican tree) seem to be the species of gymnosperms most widely distributed (23 states), and represent the dominant trees in some Mexican temperate and riparian forests, respectively.

Biogeographic provinces analysis

Mexican gymnosperms are distributed mainly in the Mesoamerican Mountain region sensu Rzedowski (1978), in which are concentrated more than a half (near 70 species); this region includes the following biogeographic provinces: Sierra Madre Occidental, Sierra Madre Oriental, Eje Volcánico, Sierra Madre del Sur and Altos de Chiapas (Fig. 2b).

The Sierra Madre Oriental province harbours the high number of species (50); this province has been previously considered as an important richness area of Mexican gymnosperms (Contreras-Medina 2004); other rich provinces are Eje Volcánico and Sierra Madre Occidental (35 species each), Sierra Madre del Sur (27), Altiplano Norte (25), Golfo de México (23), Soconusco (22) and Altos de Chiapas (21) (Table 2). Provinces with fewer numbers of species are Depresión del Balsas,

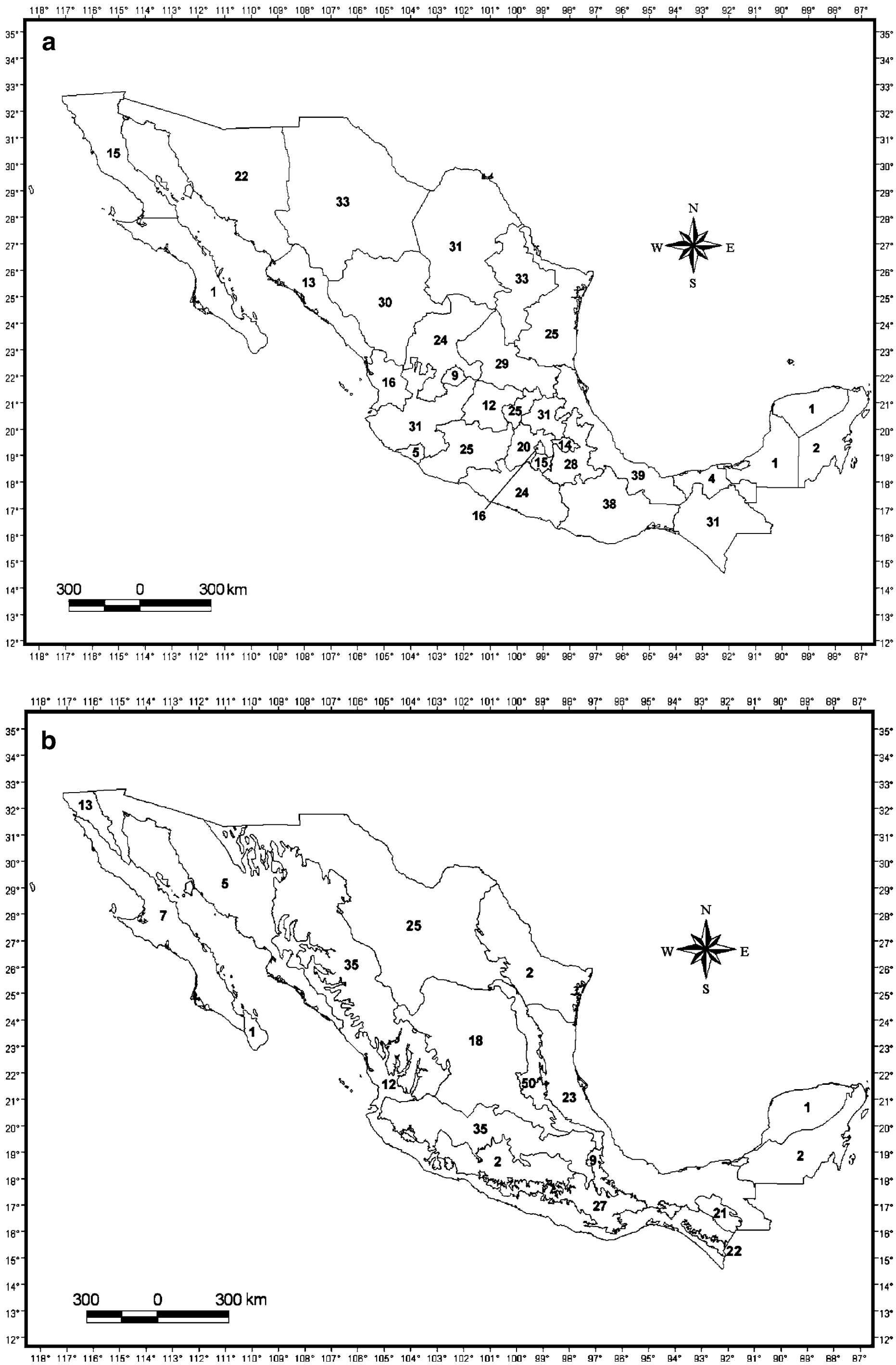

Fig. 2 (**a**) Species richness recorded in each Mexican states; (**b**) species richness recorded in each Mexican biogeographic provinces (sensu Arriaga et al. 1997). See Fig. 1b for province names

Table 2 Families, genera, species richness, and endemic species of wild gymnosperms in the 19 Mexican biogeographic provinces

Biogeographic provinces	Number of species	Number of genera	Number of families	Number of endemic species
Sierra Madre Oriental	**50**	**13**	**6**	**10**
Eje Volcánico	**35**	**8**	4	2
Sierra Madre Occidental	**35**	7	2	2
Sierra Madre del Sur	**27**	**9**	**5**	1
Altiplano Norte	**25**	5	3	0
Golfo de México	23	7	4	**12**
Soconusco	22	**9**	4	**5**
Altos de Chiapas	21	**9**	5	0
Altiplano Sur	18	6	3	0
California	13	5	3	0
Costa del pacífico	12	6	4	**3**
Oaxaca	9	5	3	**4**
Baja California	7	3	3	0
Sonorense	5	4	4	0
Depresión del Balsas	2	2	2	0
Petén	2	2	2	0
Tamaulipeca	2	2	2	0
Del Cabo	1	1	1	0
Yucatán	1	1	1	0

Numbers in bold represent the higher in each category

Petén and Tamaulipeca with two species each, and finally Yucatán and Del Cabo provinces with one species each.

Nearly one third of the Mexican species of gymnosperms are restricted to one province, mainly in the case of the following provinces: Golfo de México (12), Sierra Madre Oriental (10), Soconusco (5), Oaxaca (4), and Costa del Pacífico (3) (Table 2). The geographic distribution of some species agree and has been useful to define the province in which they inhabit, i.e. *Pinus coulteri* D. Don is diagnostic to the Californian province (Espinosa et al. 2000) and *Pinus greggii* Parl. and *Ceratozamia kuesteriana* Regel are both endemic to the Sierra Madre Oriental province (Contreras-Medina 2004). Species that have been recorded in a large number of provinces are *Taxodium mucronatum* (12 provinces) and *Pinus teocote* (8 provinces), followed by *Cupressus lusitanica* Mill., *Juniperus flaccida* Schltdl., and *Pinus oocarpa* Schltdl. (7 provinces).

Grid-cells analysis

Mexico was divided in 240 grid-cells and from these, 164 cells include at least one record; for purposes of this work, we included 1155 occurrence records of 124 species of gymnosperms from six families: Cupressaceae, Ephedraceae, Pinaceae, Podocarpaceae, Taxaceae, and Zamiaceae. Statistics revealed that the mean range is 9 grid-cells, the median is 5 cells, and the mode is a single cell (24 species); this last result indicates that nearly one fifth of gymnosperms are distributed in small ranges of Mexico. Similar statistical parameters with this methodology were obtained by Crisp et al. (2001) for the Australian flora. Taxa represented in more grid-cells were *Pinus cembroides* Zucc. and *P. teocote* Schltdl. et Cham., recorded in 44 grid-cells each.

Grid-cells richest in species were concentrated in different areas (Fig. 3a), mainly located in the following biogeographic provinces, all of them represented by

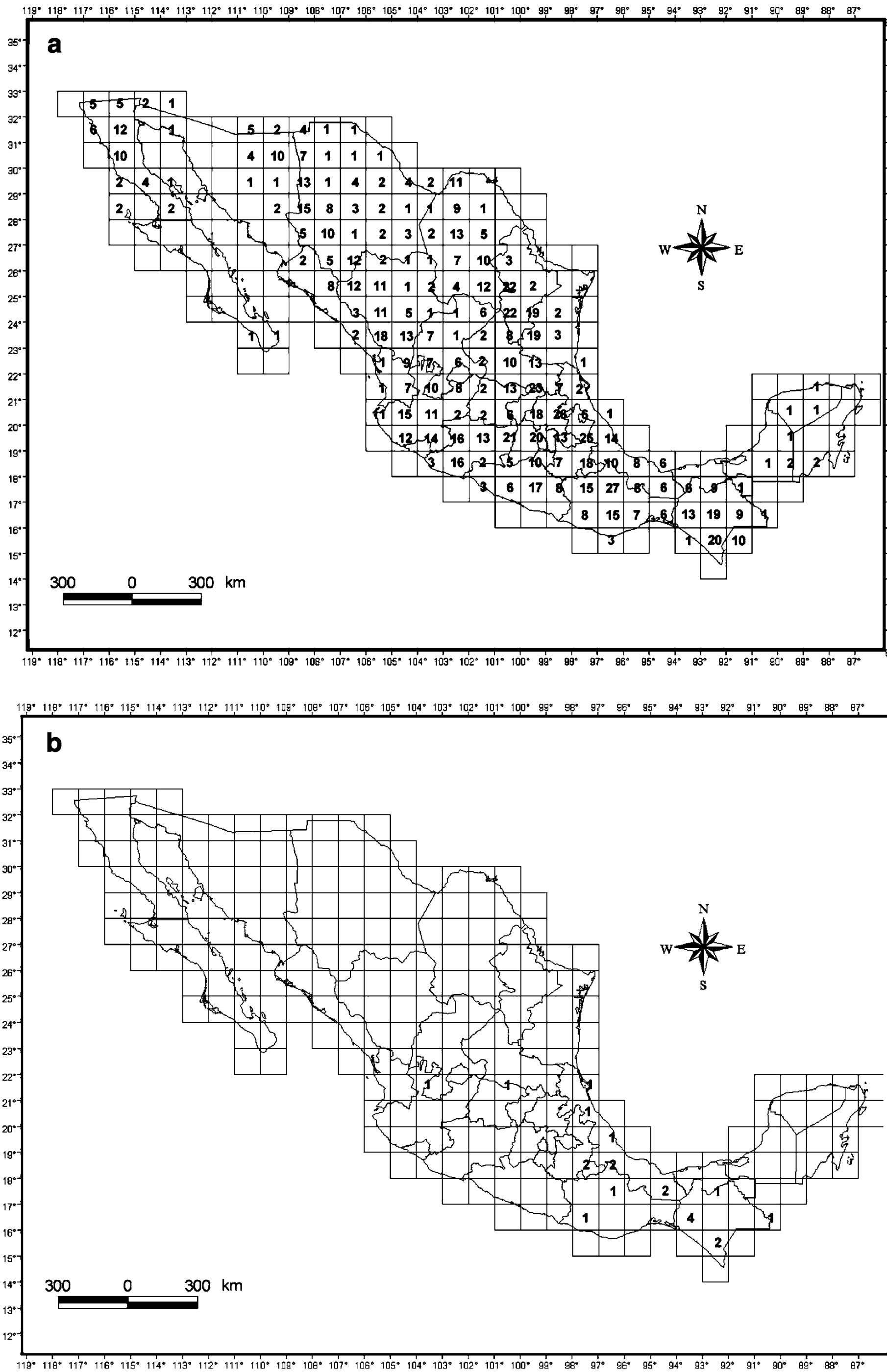

Fig. 3 (**a**) Species richness mapped in 1° × 1° grid-cells; (**b**) species of Mexican gymnosperms restricted to one grid-cell mapped in 1° × 1° grid-cells

mountain chains: Sierra Madre Oriental, Eje Volcánico, Sierra Madre del Sur, Los Altos de Chiapas, and Sierra Madre Occidental. The Sierra Madre Oriental, located in eastern Mexico, comprises most of the richest grid-cells; six of the 12 grid-cells scoring highest for species diversity are located in this province. This result confirms that this area is the richest in species of gymnosperms in Mexico, as suggested earlier by Contreras-Medina (2004). The Transmexican Volcanic Belt (Eje Volcánico province) is other mountain chain that contains several grid-cells with more than 19 species, three of them high-scored. The state of Chiapas comprises four provinces, two of them almost restricted to this state (Soconusco and Los Altos de Chiapas); in these two provinces are located two of the most richest cells (20 and 19 species, respectively) of the country. The richest cell (containing 27 species) is located at the Sierra Madre del Sur province, in the state of Oaxaca (Fig. 3a).

Results obtained in the grid-cells analysis support the state and province analyses done above. They coincide that the Yucatán Peninsula and the southern part of Baja California are the poorest regions in gymnosperm species.

Gymnosperm species occurring in a single grid-cell are shown in Fig. 3b. These species are distributed mainly in southeastern and central Mexico and in the northern portion of the Baja California Peninsula. All the species in the continental plate are endemic to the country, whereas those located in Baja California are shared with the United States of America.

Ranges values of grid-cells obtained for weighted endemism and corrected weighted endemism indices of Mexican gymnosperms are shown in Table 3. With the values of weighted endemism (which counts all the species in an inverse proportion to their range), we produced a map that resembles the pattern of species richness (Fig. 4a). This is an expected result, because Crisp et al. (2001) suggested that there is a high correlation between weighted endemism and species richness.

The map representing the values of corrected weighted endemism (Fig. 4b) showed a remarkable correspondence with several biogeographic provinces. This index emphasizes such areas that are not necessarily high in species richness, but have a high proportion of species with restricted distributions. This is the case of the grid-cells located near the Gulf of Mexico, all of them not considered as richest areas in species (compare Figs. 3a and 4b).

The northern portion of the Baja California Peninsula includes many grid-cells with high values of corrected weighted endemism (Fig. 4b). This is because several species shared with the United States inhabit in this area, with a distribution restricted to the western portion of North America, especially to the Californian Province proposed by Takhtajan (1986) in a floristic regionalization of the world.

Table 3 Range values of grid-cells obtained for weighted endemism and corrected weighted endemism indices of Mexican gymnosperms, ranged from 1 to 10

Ranges	Weighted endemism	Corrected endemism
1	0–0.504	0–0.053
2	0.505–1.009	0.054–0.107
3	1.010–1.514	0.108–0.161
4	1.515–2.019	0.162–0.215
5	2.020–2.524	0.216–0.269
6	2.525–3.029	0.270–0.323
7	3.030–3.534	0.324–0.377
8	3.535–4.039	0.378–0.431
9	4.040–4.544	0.432–0.485
10	4.545–5.049	0.486–0.539

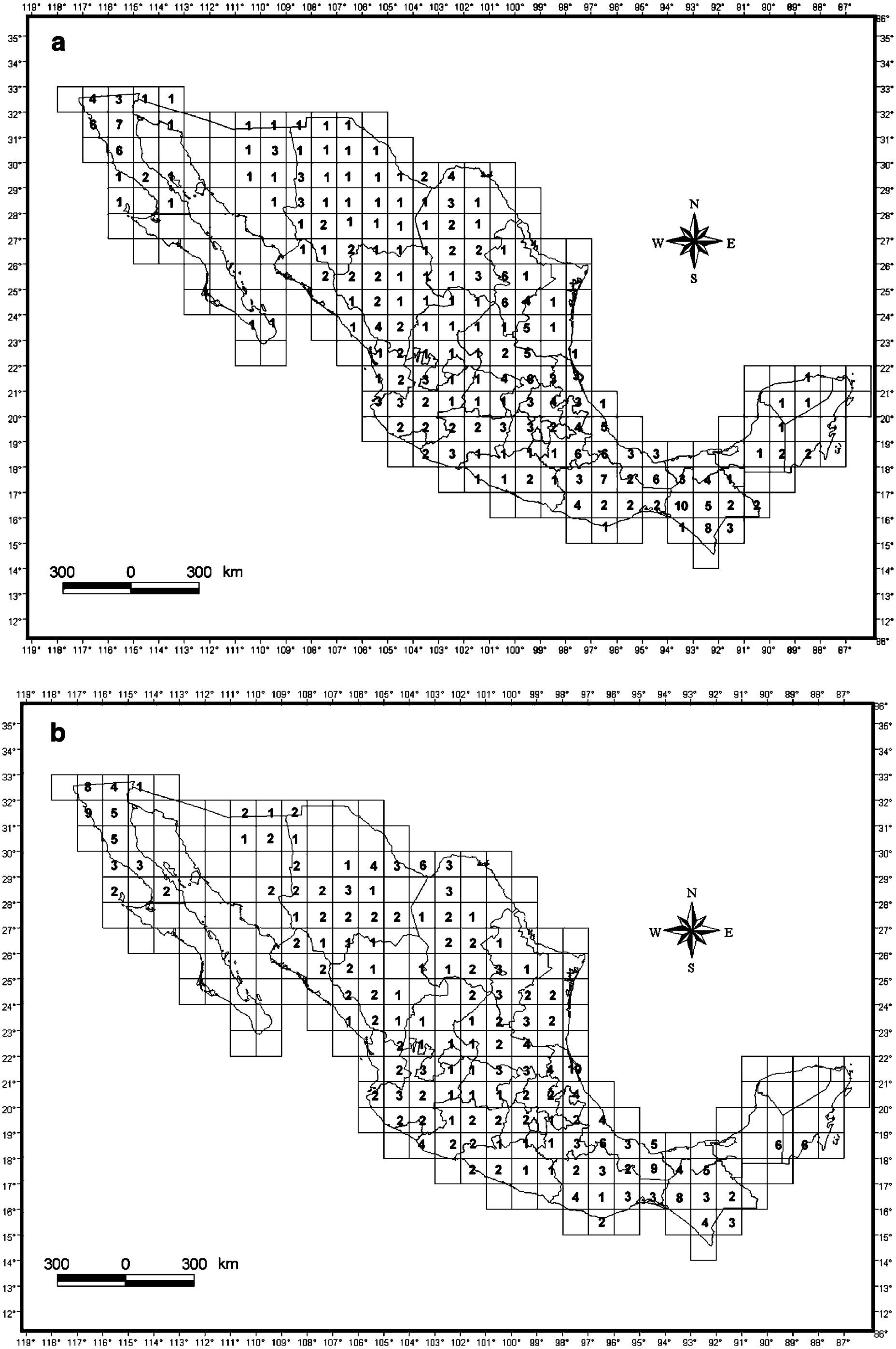

Fig. 4 (**a**) Weighted endemism of Mexican gymnosperms. The value in each grid-cell represents the sum of weights for all species occurring in each grid-cell, and ranged from 1 to 10; (**b**) corrected weighted endemism of Mexican gymnosperms. The value in each grid-cell is the weighted endemism for that grid-cell, divided by the grid-diversity of the grid-cell, and ranged from 1 to 10

We noted that several of the endemic species restricted to a single grid-cell are located in the Golfo de México province, comprising grid-cells located mainly at the states of Veracruz and Oaxaca; in fact, the state of Veracruz (located almost completely in this province) is one of the states including more endemic species (Table 1). This province appears as an area of endemism (Fig. 4b) but not as an area of high species richness (Fig. 3a). In fact, this province contains the highest number of gymnosperm endemic species (Table 2).

Another apparently important area is located in the southern portion of the Yucatán Peninsula (Fig. 4b), where *Pinus caribaea* Morelet and *Zamia polymorpha* D. W. Stevenson inhabit. This fact may be the result of the delimitation of the study area, because *P. caribaea* is also distributed in other countries of Central America and the Caribbean, but in Mexico occurs only in two grid-cells.

The term 'hotspot' has been used to refer to areas where high levels of richness, threat and endemism coincide (Myers 1988). It has been proposed that biogeographic methods can contribute to the recognition of gymnosperm 'hotspots' based on the coincidence of panbiogeographic nodes, pleistocenic refugia and areas of endemism (Contreras-Medina et al. 2001b). In this study, some grid-cells coincide in their high values in both indices and thus were considered as hotspots (Fig. 4). Since human impact in these grid-cells is not evaluated herein, our hotspots are based only in the data produced by the two indices. We also considered another meaning of hotspot that has been used to refer to those areas with extreme taxonomic richness (Gaston and Williams 1996). Those areas detected by two indices are located in southeastern Mexico (three) and one in the northern portion of the Baja California Peninsula, and contain almost two gymnosperm species each restricted to one grid-cell; only the grid-cell located in the state of Chiapas contains four restricted species; the grid-cells with more species are located in Sierra Madre del Sur, Eje Volcánico and Sierra Madre Oriental (Fig. 3a).

With the previous analyses, we detected seven grid-cells richest in species and/or endemic species for these seed plants (Fig. 3). Some grid-cells found in southern Mexico are congruent in location with the Mesoamerican hotspot of Myers et al. (2000), with three richest in species and/or endemic grid-cells detected for Mexican Ternstroemiaceae (Fig. 5 in Luna et al. 2004) and with some rich in characteristic species grid-cells to Mexican cloud forest conditions (Fig. 5 in Luna et al. 2006).

Finally, when we compared those grid-cells richest in species and /or endemics with the Mexican priority regions for conservation (RTP's) of CONABIO (Arriaga et al. 2000), we detected that they coincide with eight RTP's: Punta Banda, Sierra de Juárez and San Telmo (Baja California state), and Bosques Mesófilos de Montaña de la Sierra Madre Oriental, Cuetzalan, Pico de Orizaba, Sierras del Norte de Oaxaca and Selva Zoque-La Sepultura (southeastern Mexico). The grid-cell located in Baja California coincide with portions of three RTP's.

Conclusions

Veracruz and Oaxaca are the states with the most species of gymnosperms in Mexico; this richness pattern is congruent with other groups of plants as Asteraceae, Cucurbitaceae, Fabaceae, and Poaceae (Dávila-Aranda et al. 2004). Both Mexican states have been earlier ranked in the first places of diversity for these angiosperm families (Dávila-Aranda et al. 2004). Our results coincides with the work of Mittermeier and

Mittermeier (1992),which suggested that these two states, as well as Chiapas, Guerrero, and Michoacán are the Mexican states with the most biodiversity.

Mexican gymnosperm diversity as well as species endemicity are concentrated in some states; many species that inhabit the northern states are also represented in the United States of America, and in general belong to genera with Nearctic affinities, as *Abies* and *Picea*. In the case of the southern states, some species share their distributions with the adjacent countries of Central America, as *Ceratozamia* and *Zamia*.

Pattern of species diversity did not followed a latitudinal gradient; most of the richest states are located in southeastern and eastern Mexico, but also in the north are located some of the richest states (Chihuahua, Coahuila, Durango, and Nuevo León). This fact can be explained if we consider that most of the Nearctic gymnosperm genera, such as *Abies*, *Cupressus*, *Juniperus*, *Pinus*, and *Picea* are more diverse in the Holarctic kingdom, and that those states located in northern Mexico are not the exception and therefore influenced by this distributional pattern.

The so-called 'peninsula effect', which implies the reduction in diversity towards the end of a peninsula (Gaston and Williams 1996) is evident in the geographic distribution of Mexican gymnosperms. In the distal portions of the Yucatán and Baja California peninsula only one species inhabits, *Zamia polymorpha* and *Pinus cembroides*, respectively. However, it has proven that this effect is occasional, rather than a quite general phenomenon (Gaston and Williams 1996).

If we compare the three levels of analysis done herein, we can observe that the state and grid-cell analyses include more artificial geographic units than the province analysis. However, a determined set of grid-cells may produce a larger unit and may show a partial correspondence with a particular biogeographic subprovince. In this work we support the idea suggested previously by Luna et al. (2004), that it is more informative and operative to use small geographic units instead of using the Mexican states, only in the case when we want to detect areas with high values of richness and endemicity. We need to have in mind that it is important to do this in order to detect areas with conservation priorities, but it is also important to protect the non-living environment (Bonn and Gaston 2005), that is to protect biodiversity in all its manifestations, where priority areas for nature conservation are needed to be recognised and networks of protected areas established and maintained (Bonn and Gaston 2005). Analyses of these types are fundamental to undertake other biogeographic studies applying other methods such as track analysis and cladistic biogeography.

Coincidence between richest in species and/or endemism grid-cells with some Mexican priority regions for conservation (RTP's) of CONABIO (Arriaga et al. 2000), suggest that these grid-cells are important for conservation, because these areas harbour high biodiversity. Comparatively, these areas have 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).

Some problems that have been detected with the grid-cell methodology (Crisp et al. 2001) and which we were not completely able to avoid are: (1) the existence of cells without distributional information, (2) the topographic variation found in each grid-cell (each grid-cell comprises an area of approximately 12,100 km^2) that may include different types of abiotic factors (climate, soil, vegetation, etc.) as well as altitudinal parameters, and (3) absence of updated distribution data, at least for rare, threatened, and new species.

Results obtained in this work support the identity of several biogeographic provinces based on high-scored values of several grid-cells obtained from the corrected weighted endemism for the Mexican gymnosperms. It appears that range restricted species are not distributed randomly over the landscape (Crisp et al. 2001), and in the case of Mexican gymnosperms they are aggregated in some areas of endemism that correspond and are useful to define and corroborate the naturalness of the Mexican biogeographic provinces. Grid-cells with high values in both indices and high richness (considered as hotspots herein) are important for conservation, especially those recognised by the corrected weighted endemism, because they have a high proportion of unique species; these grid-cells deserve special attention in Mexican future conservation plans. Those endemic taxa occurring in a single grid-cell are at high risk of human impact and could lead to extinction (McAllister et al. 1994). Gaston (1994) mentioned that most of the species that have small range sizes have more probability of extinction than others with wide range sizes. This is especially true for some gymnosperm species such as *Ceratozamia euryphyllidia* Vázquez-Torres et al., *C. hildae* G. Landry et M. Wilson, *C. norstogii* D. W. Stevenson, *C. zaragozae* Medellín-Leal, *Dioon califanoi* De Luca et Sabato, *D. caputoi* De Luca, Sabato et Vázquez-Torres, *D. holmgrenii* De Luca, Sabato et Vázquez-Torres, *D. rzedowskii* De Luca, Sabato et Vázquez-Torres, *Pinus maximartinezii* Rzedowski, *P. rzedowskii* Madrigal et Caballero, *Zamia inermis* Vovides, Rees et Vazquez-Torres, *Z. purpurea* Vovides, Rees et Vázquez-Torres, and *Z. soconuscensis* Schutzman et al. All of these taxa are examples of species with small ranges that are mostly represented by relatively few individuals within those ranges. In relation to cycads has been estimated that these species include less than 2,500 adult individuals in wild conditions (Osborne 1995). Some species of pines included in this study were considered by Farjon and Styles (1997) of urgent concern for conservation, namely *Pinus culminicola*, *P. rzedowskii*, *P. maximartinezii*, *P. pinceana*, *P. jaliscana*, *P. nelsonii*, and *P. strobus*. Approximately 71 species (57%) of Mexican gymnosperms have been included in some risk category in the latest version of the Mexican official publication named 'Norma Oficial Mexicana 059' (NOM-059-ECOL, Secretaria del Medio Ambiente y Recursos Naturales 2002), which includes native and introduced threatened taxa. In this document are included all the restricted-distribution species cited above in the categories of threatened, endangered or with special protection. For some Mexican gymnosperms several conservation strategies have been proposed (i.e. Styles 1993; Vovides and Iglesias 1994; Farjon and Styles 1997; Sosa et al. 1998; Luna et al. 2006), but it is important to continue with this task.

In general, areas of high species richness coincide with those areas of endemism generated by the corrected weighted endemism. Two exceptions are the Golfo de México province and California province which are not areas of high species richness, although they are confirmed as areas of endemism; in fact, two out of the five grid-cells scoring highest for this index are found in the Golfo de México province, whereas in the California province are found some of the high-scored grid-cells for this same index.

Several areas of high species richness agree with those proposed by Eguiluz (1985) and Styles (1993) for Mexican pines, especially those related to mountain chains, as Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Sierra Madre del Sur, Sierra de San Cristóbal, and Sierra Madre de Chiapas. This resemblance may be due to the influence of the number of species of pines (41), which represents one third of the total of gymnosperm species used in the present study. In relation to an altitudinal range, Mexican species of pines are mainly classified in the categories of montane (1,000–2,600 m) and high montane (2,500–4,000 m), showing a close relationship to montane habitats (Farjon and Styles 1997). Many other gymnosperm species belonging to different genera, such as *Abies*, *Ceratozamia*, *Cupressus*, *Ephedra*, *Juniperus*, *Picea*, and *Taxus*, are also mainly classified as montane species (Contreras-Medina 2004).

Repeatability of the grid-cell method applying the two indices explained above must be tested using other data sources from other well-documented groups, such as non-vascular plants, angiosperms, birds, butterflies and mammals, especially for those distributed in the Mexican montane chains, in order to compare the distributional patterns suggested herein for gymnosperms.

This study represents an example of the value of specimen-based data, such as are held in museums and herbaria of the world. Most of the distributional data of the species of gymnosperms used in this work were obtained from an exhaustive analysis of hundred of specimens of Mexican and North American herbaria. The information from herbaria is of special value because permanently preserved specimens can be physically examined, reexamined on subsequent occasions, and any reservations about identification noted (Hall 1994).

The present study contrasts with those mainly based only on literature, which did not corroborate distributional data and may contain identification and distribution mistakes; i.e. the biogeographic regionalization of Mexico by Espinosa et al. (2000) includes distributional incongruences in the case of the species of pines. Also, we have to consider that the distribution map of any plant species or taxon based strictly on herbarium specimens is in practical terms unrealistic, and assumptions that such maps may be error-free are unjustified, because locating and examining all herbarium specimens of a widely distributed taxon is a process that is not feasible (Hall 1994); this fact is especially evident in the case of the genus *Pinus*, because several species are widely distributed in the country. Revision of herbarium specimens and scientific literature citing voucher specimens and geographical localities should be considered as a major source of data for mapping (Hall 1994), and not those publications, which contain only distributional maps.

Distributional data from scientific collections are only useful if they are available (Crisp et al. 2001); this availability depends on the coordination of Mexican herbaria, and in this kind of studies serious problems are present, shortly commented above; despite this, the present analysis should be considered as a first biogeographic approximation of the areography of Mexican gymnosperms. However, resultant numbers of species richness and endemics per state, biogeographic province or grid-cell as presented above, are relevant to make conservation plans (McAllister et al. 1994). The identification of areas of high taxonomic diversity at more moderate scales than geopolitical and biogeographic regions, such as grid-cells used herein, has been a topic of some concern to conservationists (Gaston and Williams 1996).

The 'Red Mexicana Sobre la Biodiversidad' (REMIB) of the Comisión Nacional Para el Uso y Conocimiento de la Biodiversidad (CONABIO), located in Mexico City, has achieved accession to scientific collections. It represents a web-based flora and fauna information system developed by the cooperation of several American and Mexican scientific institutions. Unfortunately, it only provides direct access to some of the main specimen-based data. This information net has poor distributional information of threatened and rare species, as well as several errors in the determination of the specimens. Other problems are that data on the web do not correspond with specimen labels, and it is not continuously updated; however, it represents a first attempt to make accessible information of Mexican scientific collections.

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