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Application of parsimony analysis of endemicity to Mexican gymnosperm distributions: grid-cells, biogeographical provinces and track analysis

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Parsimony analysis of endemicity (PAE) was used to analyse the distributional patterns of 124 species of Mexican gymnosperms, using two different sample units: grid-cells and biogeographical provinces. PAE analyses were based on distributional data from herbarium specimens and specialized literature. Two data matrices were constructed for 60 grid-cells of 2° and 14 biogeographical provinces. The analysis of the 2° grid-cell matrix led to 7084 cladograms. The strict consensus cladogram showed several clades equivalent to the results obtained with the biogeographical provinces. Three clades agree with some principal regions of distribution of Mexican pines, previously identified by several authors, located at the northern portion of the Baja California peninsula, the Sierra Madre Occidental, and the Sierra Madre Oriental. These areas represent important centres of species diversity and endemism for Mexican gymnosperms. The analysis of the province matrix led to two most parsimonious cladograms, which only differed in the position of the Sierra Madre Occidental province. The iterative procedure PAE with progressive character elimination was applied to identify generalized tracks, where clades of provinces were considered equivalent to generalized tracks, and each time a cladogram was obtained, species defining its clades were deleted and a new run was undertaken. We found five generalized tracks, mainly located in montane provinces. The distribution patterns of gymnosperms agree with the existence of several Mexican biogeographical provinces, and a different historical biogeography of the Mexican peninsulas from the rest of the country is evident. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 405–417.

ADDITIONAL KEYWORDS: area cladograms – biogeography – biodiversity – generalized tracks – Mexican mountains – Nearctic – Neotropical – panbiogeography.

INTRODUCTION

Gymnosperms are woody plants mainly distributed in temperate forests and arid scrubs, which inhabit temperate zones of both hemispheres and have been important elements in fossil and extant plant communities (Contreras-Medina & Luna, 2002). Presence of gymnosperms in the fossil record of Mexico that can be related to extant genera are traced back to the Eocene (Martínez-Hernández & Ramírez, 1996). These plants deserve special attention from the historical biogeographical viewpoint due to their antiquity, and because tectonic events and climatic change have been important to shape their distributional patterns. Studies on the geographical distribution of these plants in Mexico are imperative not only theoretically, but also practically, especially for some groups with great economic value and some threatened taxa included in some risk category.

Gymnosperms represent approximately 2% of the Mexican plant species diversity, in contrast to angiosperms and pteridophytes (Contreras-Medina, 2004). Mexico is the richest country in species of *Ceratozamia*, *Dioon*, and *Pinus* (Contreras-Medina,

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2004) and represents an important centre of diversity and endemism at worldwide level (Osborne, 1995; Farjon & Styles, 1997).

Parsimony analysis of endemicity (PAE) was developed by Rosen (1984, 1988) and Rosen & Smith (1988) to address the shortcomings of phenetic approaches used to assess area relationships of fossil or recent assemblages from different areas (Porzecanski & Cracraft, 2005). It takes as starting point the presence/absence of data for a set of sample localities and a particular taxon (Rosen & Smith, 1988). With this information, a data matrix of areas × taxa is constructed and analysed (Luna *et al*., 2001). Shared presences are analogous to synapomorphies in phylogenetic systematics, and areas are grouped according to the most parsimonious cladogram, which represent nested sets of areas. The cladogram is rooted with a hypothetical area or locality coded with all zeros, and represents a sample area or locality without any of the taxa from the remaining localities or areas. Compared to cladistic biogeography, PAE can be applied to taxa whose phylogenetic relationships are unknown. Notwithstanding that phylogenies comprising Mexican species of *Ceratozamia* (González & Vovides, 2002), *Dioon* (Moretti *et al*., 1993), *Ephedra* (Huang, Giannasi & Price, 2005), and *Pinus* (Gernandt *et al*., 2005) are available, other taxa, namely *Taxus*, *Taxodium*, *Cupressus*, *Juniperus*, and *Podocarpus*, among others, do not have these analyses. Thus, we run a PAE to include all the Mexican species of gymnosperms, which led us generate hypotheses about the biogeography of these seed plants.

PAE was originally applied using localities as units (Rosen & Smith, 1988; Rosen, 1988). Other authors have used this method to assess relationships among predetermined areas of endemism (Craw, 1988; Cracraft, 1991; Morrone, 1994b; Morrone *et al*., 1999; Espinosa *et al*., 2000; Ron, 2000; Aguilar-Aguilar *et al*., 2003), grid-cells (Morrone, 1994a; Cavieres *et al*., 2002; Morrone & Escalante, 2002; Rojas-Soto, Alcántara & Navarro, 2003; Méndez-Larios *et al*., 2005), hydrological basins (Aguilar-Aguilar *et al*., 2003), real and virtual islands (Maldonado & Uriz, 1995; Morrone, 1998; Luna *et al*., 1999, 2001; Trejo-Torres & Ackerman, 2001), and transects (Trejo-Torres & Ackerman, 2002; García-Trejo & Navarro, 2004; León-Paniagua *et al*., 2004; Navarro *et al*., 2004). An additional implementation is track analysis (Craw, Grehan & Heads, 1999; Luna *et al*., 2001; Morrone & Márquez, 2001). To determine areas of endemism, grid-cells were used in such a way that nested sets observed in the cladogram represented areas of endemism, if each set was supported by at least two taxa (Morrone, 1994a; Morrone & Escalante, 2002). Craw *et al*. (1999) considered that PAE is a method for recognizing generalized tracks through the discovery of nested sets of biogeographical units, which was previously suggested by Smith (1992) and further applied by Luna *et al*. (2001) and Morrone & Márquez (2001).

In Mexico, PAE has been applied to different geographical units. Grid-cells as unit areas have been applied to Mexican terrestrial mammals (Morrone & Escalante, 2002), birds of the Baja California Peninsula (Rojas-Soto *et al*., 2003), and flowering plants of the Valle de Tehuacán-Cuicatlán (Méndez-Larios *et al*., 2005). Gymnosperms have been never included in this type of analysis.

In the present study, we analyse the distributional patterns of Mexican gymnosperms using PAE with two different sample units (grid-cells and predetermined areas of endemism, represented by biogeographical provinces) and also detect generalized tracks. We intend to test previous hypotheses and to explore the potential of gymnosperms for biogeographical analyses.

MATERIAL AND METHODS

Distributional data of gymnosperm species were obtained from the revision of 1462 herbarium specimens deposited in the following collections: MO, MEXU, ENCB, XAL, IEB, XALU, IBUG, FCME, and INIF (acronym *sensu* Holmgren, Holmgren & Barnett, 1990). In addition, floristic and revisionary published studies were reviewed (Zanoni & Adams, 1979; Wiggins, 1980; Zanoni, 1982; Vovides, 1983, 1999; Stevenson *et al*., 1986; Patterson, 1988; Espinosa, 1991; McVaugh, 1992; Zamudio, 1992, 2002; Moretti *et al*., 1993; Fonseca, 1994; Zamudio & Carranza, 1994; Farjon & Styles, 1997; Medina & Dávila, 1997; Narave & Taylor, 1997; Aguirre-Planter, Furnier & Eguiarte, 2000; Felger, 2000; Contreras-Medina, Luna & Alcántara, 2001, 2003). Botanical field explorations were carried out in the states of Hidalgo, Querétaro, Estado de México, Puebla, and Oaxaca to obtain field data and additional distribution information of some species.

We used two different units of analysis to run PAE: grid-cells of 2° latitude × 2° longitude and Mexican biogeographical provinces (Fig. 1) proposed by Morrone (2005). We used 124 species (columns) to construct two data matrices; the number of areas (rows) varied according to the different units analysed, 60 grid-cells of 2° latitude × 2° longitude (Supplementary Material, Table S1) and 14 biogeographical provinces (Supplementary Material, Table S2). Both matrices included one row coded with all zeros to root the area cladograms. The analyses were carried out with the heuristic search option in Nona (Goloboff, 1999) through Winclada (Nixon, 2002). When more than one cladogram resulted from the analysis, a strict consensus cladogram was constructed.

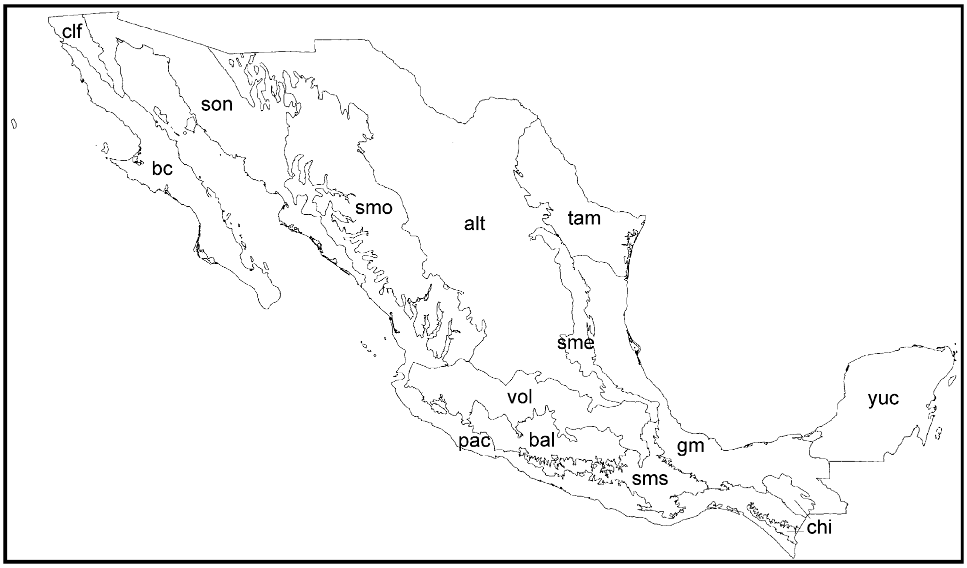

Figure 1. Biogeographical provinces of Mexico according to Morrone (2005). alt, Mexican Plateau; bal, Balsas Basin; bc, Baja California; clf, California; chi, Chiapas; gm, Gulf of Mexico; pac, Pacific Coast; sme, Sierra Madre Oriental; smo, Sierra Madre Occidental; sms, Sierra Madre del Sur; son, Sonora; tam, Tamaulipas; vol, Transmexican Volcanic Belt; yuc, Yucatan Peninsula.

Morrone (1994a) proposed PAE as a tool to detect areas of endemism, using grid-cells as units based on their shared species, where one group of grid-cells defined at least by two taxa represents an area of endemism. We draw the grid-cells on a map of Mexico, including only those where at least one species was recorded. With this information, we constructed a data matrix (Supplementary Material, Table S1) as explained above and a parsimony analysis was performed. The resultant cladogram grouped those grid-cells with shared species, and those groups were superimposed onto the map of grid-cells, delimiting the areas of endemism.

The application of PAE using Mexican biogeographical provinces to construct generalized tracks was implemented by Morrone & Márquez (2001). The nested sets of biogeographical provinces obtained from the resulting cladograms were used to construct generalized tracks. PAE may be considered as a method of nesting panbiogeographical tracks in a hierarchical scheme (Smith, 1992). Details about the panbiogeographical approach are provided by Craw *et al.* (1999). We followed the iterative procedure PAE with progressive character elimination (Luna *et al.*, 2000; García-Barros *et al.*, 2002) where, each time that a set of cladograms was obtained, the species defining the clades (synapomorphies) were deleted and a new run was undertaken. The major clades obtained and supported by the congruent distributions of two or more species in each run were converted into generalized tracks, by joining together the provinces included in the same clade by their minimal geographical distance. Gymnosperm species defining each track are listed in Table 1.

Table 1. Generalized tracks and examples of species defining them

Track	Total of species involved	Examples
a	5	*Ephedra californica*, *Juniperus californica*, and *Pinus lambertiana*
b	24	*Cupressus lusitanica*, *Juniperus flaccida*, *Pinus leiophylla*, *Pinus teocote*, and *Pseudotsuga menziesii*
c	2	*Ceratozamia latifolia* and *Ceratozamia microstrobila*
d	3	*Abies hickelii*, *Pinus lawsonii*, and *Pinus pringlei*
e	2	*Podocarpus oleifolius* and *Zamia splendens*

RESULTS AND DISCUSSION

GRID-CELLS

The analysis of the grid-cell matrix produced 7084 cladograms of 382 steps, consistency index of 0.32 and

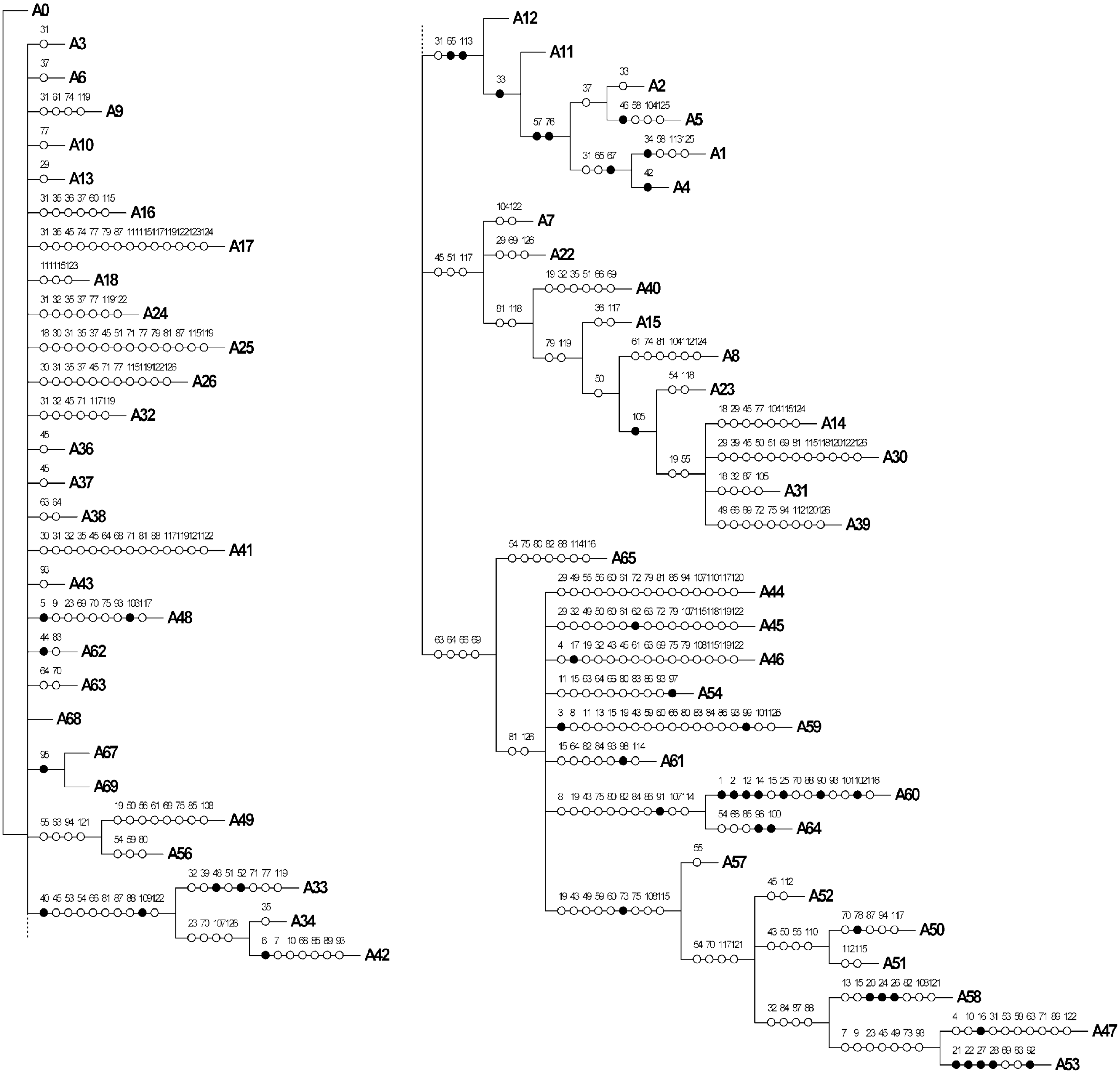

Figure 2. Strict consensus cladogram obtained with the 2° grid-cell analysis. Each number represents one grid-cell. For reference numbers, see Fig. 3. Numbers above branches represent species which correspond with data matrix in the Supplementary Material, Table S1. Black circles in the branches represent synapomorphies, whereas white circles represent homoplasies.

retention index of 0.56. The strict consensus cladogram (Fig. 2), with 462 steps, a consistency index of 0.27, and a retention index of 0.43, showed a polytomy composed of 21 grid-cells, three major components and three small clades (composed of two or three grid-cells each). The largest component (1) comprised grid-cells from central and southern Mexico, the second set represents the Sierra Madre Occidental province (smo) (2), and the third major component includes those grid-cells located in the northern part of the Baja California peninsula (3). Among the small clades, a set of three grid-cells are located in northeastern Mexico (4), in the northern portion of the Sierra Madre Oriental (sme) province; another clade with two grid-cells (5) is located in western Mexico in the Pacific Coast province (pac); and a third one grouped into two grid-cells is located in the Yucatan peninsula (6) (Fig. 3).

The largest component (1) corresponds to the classic Mesoamerican pattern (Vivó, 1943; Rzedowski,

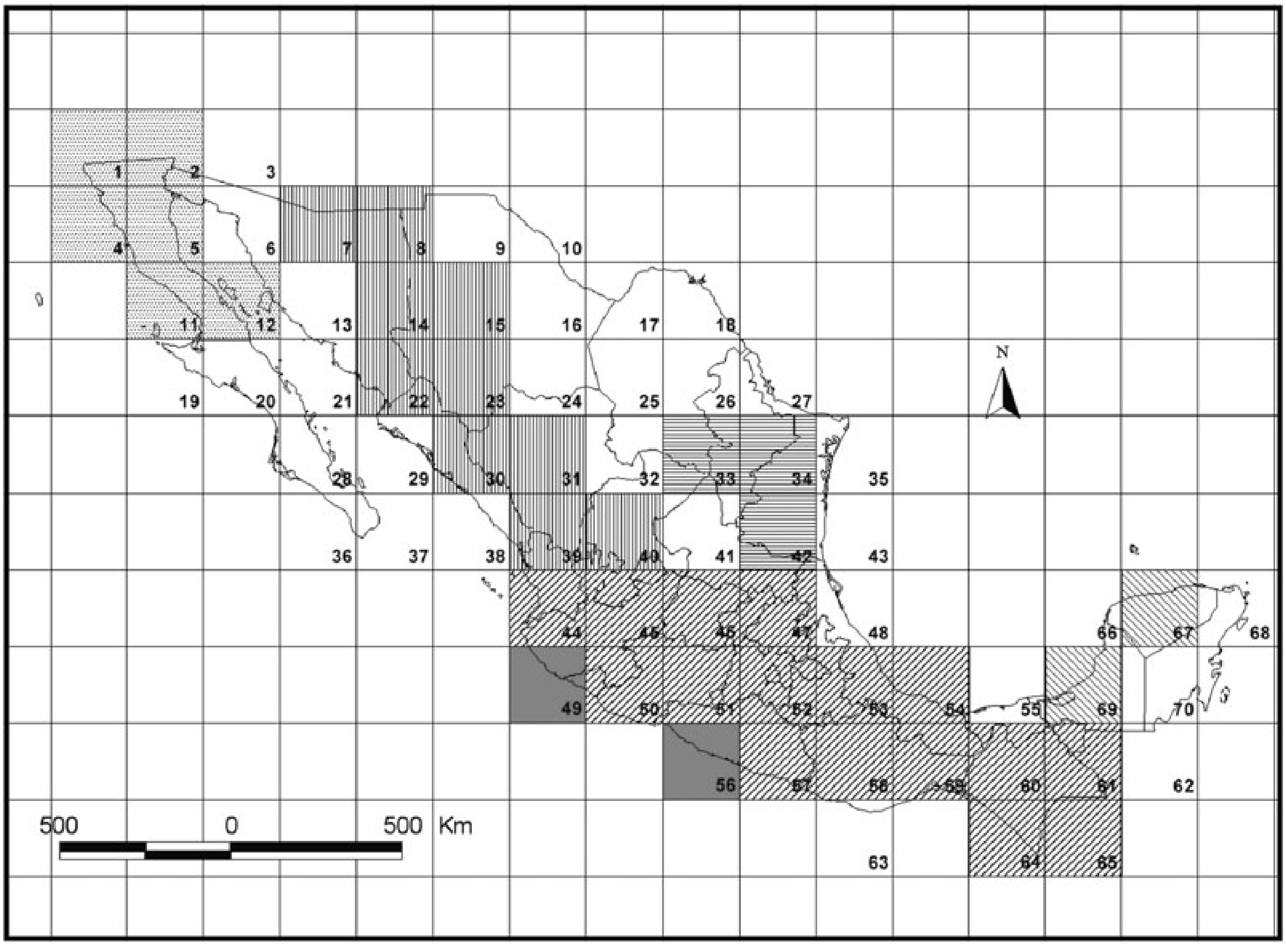

Figure 3. Map obtained for the 2° grid-cell matrix, based on the cladogram of Fig. 2, showing the spatial representation of grid-cell components. Each set of grid-cells shades represent the different groups of grid-cells obtained in the cladogram of Fig. 2.

1978; Halffter, 1987; Morrone & Márquez, 2001), which includes southern and central Mexico and Central America. Two of the smaller components (5 and 6) are equivalent to the biogeographical provinces with the same name, but the inclusion of only two grid-cells in each one of them did not allow any inference to be made about their precise delimitation. Among these components, three sets of grid-cells agree with some principal regions of distribution of Mexican pines, as previously proposed (Eguiluz, 1985; Styles, 1993; Farjon & Styles, 1997), which are located at the northern portion of the Baja California peninsula, the Sierra Madre Occidental, and the Sierra Madre Oriental. Based on the congruence of our results with these proposals, we suggest that these areas represent important centres of diversity and endemism for Mexican gymnosperms.

An exploratory analysis using grid-cells of 1° did not show congruent patterns. This same problem was observed by Morrone & Escalante (2002) with mammals, demonstrating that the results obtained with larger Mexican grid-cells are better than those obtained with smaller ones (in their case, 1° and 0.5°). Based on a phenetic analysis, Ramírez-Pulido & Castro-Campillo (1990) proposed a Mexican regionalization using grid-cells of 2°, obtaining 19 mastofaunistic provinces. We obtained a better resolution with the grid-cells of 2°, results that are congruent with the biogeographical provinces analysis undertaken and explained below, mainly in the case of the Sierra Madre Occidental province (smo). As previously suggested by Linder (2001), we consider that the choice of the grid-cell size is decisive to undertake biogeographical analyses. The selection of small size grid-cells (0.5° or 1°) can result in poor resolution of the resultant area cladograms (Morrone & Escalante, 2002). We can affirm this after an exploratory analysis of Mexican gymnosperm species using grid-cells of 1° (not shown), where we obtained more than 10 000

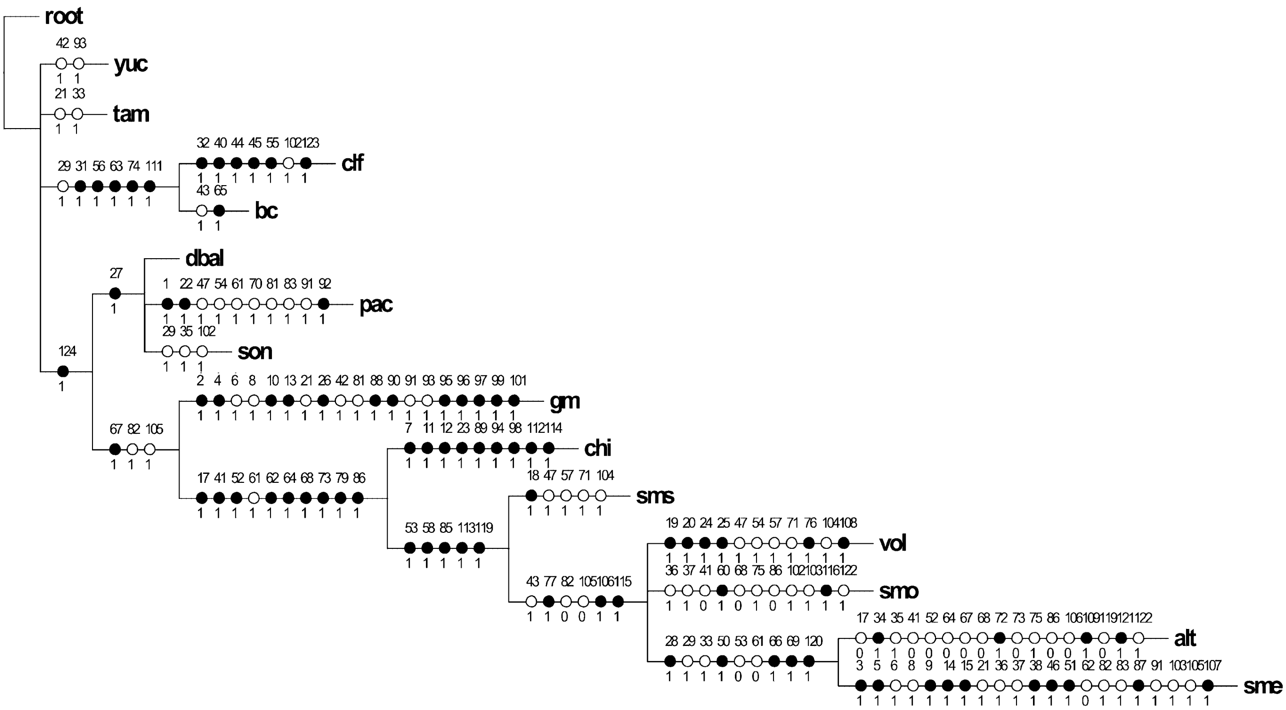

Figure 4. Strict consensus cladogram obtained with the provinces matrix, depicting the relationships of the Mexican biogeographical provinces. Labels are the names of the provinces. Numbers above branches represent species and numbers below represent character state (presence/absence) of each species. Black circles in the branches represent synapomorphies, whereas white circles represent homoplasy. alt, Mexican Plateau; bc, Baja California; clf, California; chi, Chiapas; dbal, Balsas Basin; gm, Gulf of Mexico; pac, Pacific Coast; sme, Sierra Madre Oriental; smo, Sierra Madre Occidental; sms, Sierra Madre del Sur; son, Sonora; tam, Tamaulipas; vol, Transmexican Volcanic Belt; yuc, Yucatan Peninsula.

cladograms, whose consensus cladogram had a big polytomy, with only few grid-cells grouped.

BIOGEOGRAPHICAL PROVINCES

For the biogeographical province matrix, we obtained two cladograms with 186 steps, a consistency index of 0.66 and a retention index of 0.57. The consensus cladogram, of 191 steps, consistency index of 0.64 and retention index of 0.54, is shown in Figure 4. Both cladograms were very similar, and only differed in the position of the Sierra Madre Occidental (smo), which in one cladogram is related to the Transmexican Volcanic Belt province (vol), and in the second cladogram is the sister group to the Sierra Madre Oriental (sme)-Mexican Plateau (alt) provinces. The consensus cladogram was used to draw the generalized tracks, as explained below. In this cladogram, one component included the California (clf) and Baja California (bc) provinces, supported by five gymnosperm species, *Ephedra californica* S. Watson, *Juniperus californica* Carrière, *Pinus lambertiana* Douglas, *P. monophylla* Torrey et Frémont, and *P. quadrifolia* Sudworth. The Yucatan peninsula (yuc) is also separated from the rest of continental Mexico. The Tamaulipas (tam) province has an uncertain position in the cladogram. A large component including the majority of the Mexican continental provinces (excluding both peninsulas) is divided in two clades: the first one comprises three lowland provinces located in western Mexico (pac, dbal, son), and a second one includes all the mountainous provinces (chi, sms, vol, smo, sme) as well as the Mexican Plateau (alt) and Gulf of Mexico (gm) provinces. In the latter, the Gulf of Mexico province (gm) is located at the base, followed by two southern provinces (sms and chi) and, finally, a clade including the Sierra Madre Occidental (smo), Transmexican Volcanic Belt (vol), Sierra Madre Oriental (sme), and Mexican Plateau (alt) provinces.

Previous PAEs that examined the relationships among Mexican biogeographical provinces partially agree with our results. Morrone *et al.* (1999) and Espinosa *et al.* (2000), based on distributional data of birds, insects, and vascular plants, found two major components: one (Nearctic) that includes all the northern Mexican provinces, and another (Neotropical) that includes the remaining central and southern provinces. In both studies, these authors grouped all the provinces of the Baja California peninsula in the same clade, as well as the provinces of the Yucatan peninsula, reflecting the separate histories of both peninsulas from the rest of continental Mexico. Also in both studies, all the montane provinces were located in different clades whereas, in the present study, all the main montane provinces were included in the same clade, as in the study by Morrone & Márquez (2001). Another consistent pattern is the relationship of the Chiapas and Gulf of Mexico provinces, which always appears in the same clade, as was the case in our study, usually as sister areas. This implies a close relationship between eastern and southern Mexico, representing a recurrent pattern frequently found in several works with different methodologies and taxa (Smith, 1941; Aguilar-Aguilar *et al*., 2003).

Morrone & Escalante (2002), when analysing Mexican terrestrial mammals, found a basal divergence of the Baja California peninsula in their cladogram. In addition, some areas from eastern and western Mexico were located at the base of a large component, and the relationships among the Neotropical provinces were very similar to those detected herein. An important difference of the present study versus that of Morrone & Escalante (2002) is the relationship found by them for the Yucatan peninsula with southern provinces; and similar results were also obtained by Aguilar-Aguilar *et al*. (2003) with helminth parasites. The Yucatan peninsula is also well differentiated and separated from the rest of continental Mexico, and our results suggest that it can be considered as a single biogeographical unit, as was previously established by Rzedowski (1978), Morrone (2005), and Morrone & Escalante (2002), among others. In the results from the present study, the Baja California peninsula can be differentiated from the rest of the country, as suggested previously by Morrone *et al*. (1999), Espinosa *et al*. (2000), and Morrone & Escalante (2002).

The uncertain position of the Tamaulipas (tam) province is possibly due to the relatively few gymnosperm species that it harbours. Similar results in the placement of the poorest-in-species areas in uncertain positions have been obtained by Glasby & Álvarez (1999) and Trejo-Torres & Ackerman (2001) with PAE, and Contreras-Medina & Luna (2002) with a cladistic biogeographical analysis. Another explanation about the uncertain position of certain areas may be due, as noted by Glasby & Álvarez (1999), to long-distance dispersal processes, latitudinal gradients, degree of isolation, or other undetected historical patterns. The Tamaulipas province is more closely related to some eastern North American provinces (Katinas *et al*., 2004). In this sense, the restriction of the present study to the Mexican territory may reflect in some way its uncertain position.

The changing position of the Sierra Madre Occidental may be mainly due to the geographical distribution of several pine species and the transitional character of many of the provinces studied. Some gymnosperm species that inhabit the USA are also distributed in some portions of the Sierra Madre Occidental, the Sierra Madre Oriental, and the Mexican Plateau provinces, which reflects the relationships suggested in one cladogram, such as *Cupressus arizonica* Greene, *Pinus arizonica* Engelmann, *Pinus engelmannii* Carrière and *Juniperus erythrocarpa* Cory. In the other cladogram, the relationship between the Transmexican Volcanic Belt and Sierra Madre Occidental provinces is supported by the geographical distribution of some pine species that inhabit the latter and also are found in the western portion of the Transmexican Volcanic Belt province, such as *Pinus durangensis* Martínez, *Pinus lumholtzii* B.L. Robinson et Fernald, and *Pinus praetermissa* Styles et McVaugh, as well as one juniper species (*Juniperus jaliscana* Pérez de la Rosa). The above results may be due to the transition nature of the Mexican mountain provinces (Morrone, 2005).

Rzedowski (1978) included all the mountain provinces (sme, smo, vol, sms, and chi) in a single region named Mesoamerican Mountain region. Morrone & Márquez (2001) and Katinas *et al*. (2004) found similar results with PAE, where most of these provinces are grouped in the same clade, with the exception of the Chiapas (chi) province, which is located in a different clade in the first work, and was not analysed in the second one. Our results support the proposal of Rzedowski because all the mountain provinces are in the same clade, but differ in the position of the Sierra Madre Oriental, which is sister area to the Mexican Plateau in both cladograms, and they are sister group to the Sierra Madre Occidental. According to Liebherr (1991), there are large numbers of shared endemic species of Coleoptera between the northern portions of the Sierra Madre Oriental and the Sierra Madre Occidental. Morrone *et al*. (1999) and Espinosa *et al*. (2000) showed different area relationships (i.e. the Sierra Madre del Sur is related to the Balsas Basin, Pacific Coast and Transmexican Volcanic Belt provinces; Chiapas is included in other clade and is related to the Gulf of Mexico and Soconusco provinces; the Sierra Madre Occidental is related to the Sonora province; and the Sierra Madre Oriental is related to the Mexican Plateau). These results confirm that Mexico (or at least a great part of it) represents a transition zone, where biotic events of 'hybridization' have occurred, allowing the mixture of different biotic components (Morrone, 2005). Transition zones deserve special attention because they

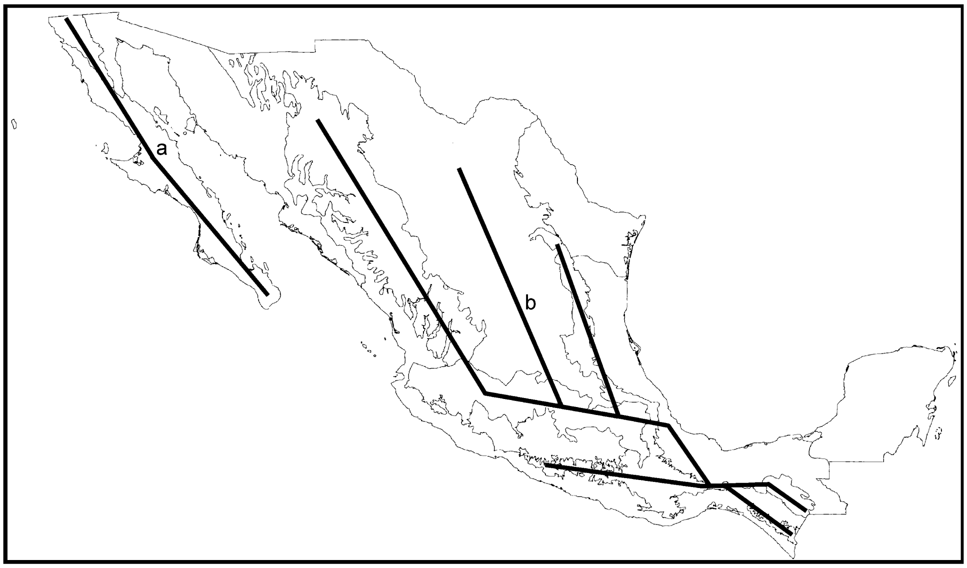

Figure 5. Main clades of the cladogram of Fig. 4 superimposed onto the map as generalized tracks in the Baja California peninsula (a) and in the Mesoamerican Mountain region (b).

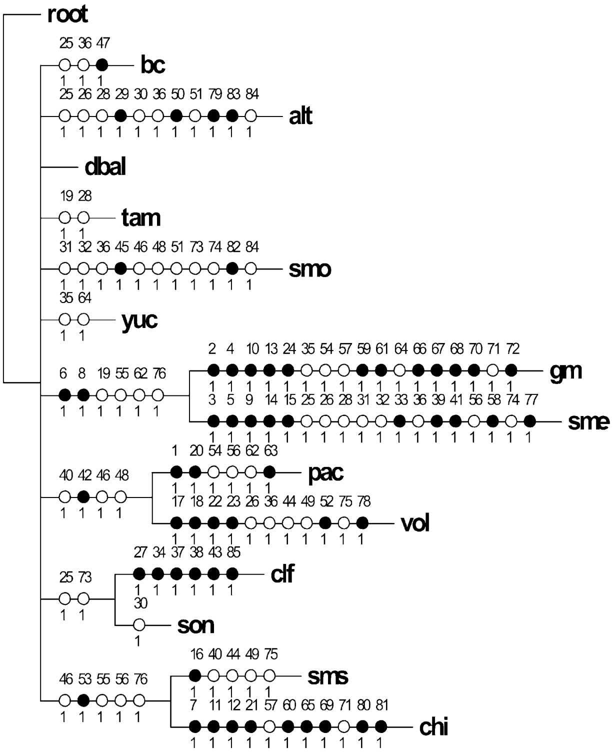

Figure 6. Strict consensus cladogram obtained from nine most parsimonious trees in the second run. Numbers above branches represent species and numbers below represent character state (presence/absence) of each species. Black circles in the branches represent synapomorphies, whereas white circles represent homoplasies.

represent sites of intensive biotic interaction (Ruggiero & Ezcurra, 2003) and may exhibit an unusual high biodiversity.

TRACK ANALYSIS

The main clades in the consensus cladogram obtained in the biogeographical provinces analysis were mapped as generalized tracks (Fig. 5). Subsequently, we performed parsimony analyses deleting the species defining the tracks in the previous run. The second analysis yielded nine cladograms (114 steps, a consistency index of 0.74, and a retention index of 0.45). A strict consensus cladogram (121 steps, a consistency index of 0.70, and a retention index of 0.32) was constructed (Fig. 6); the main clade was mapped as a generalized track (Fig. 7). The third analysis yielded a single cladogram (108 steps, a consistency index of 0.75, and a retention index of 0.44) (Fig. 8); its two main clades were mapped as generalized tracks (Fig. 9). In the fourth run, 20 cladograms were obtained (92 steps, a consistency index of 0.79, and a retention index of 0.47); in their consensus cladogram only two clades were obtained (not shown), but they were supported on homoplasies, so we decided to stop the analysis here.

In the five generalized tracks obtained, we observed that at least one montane province is included except for track a, which suggests that the Mexican montane areas have played an important role in the spatial evolution of gymnosperms. The existence of several generalized tracks is evidence of the complexity of

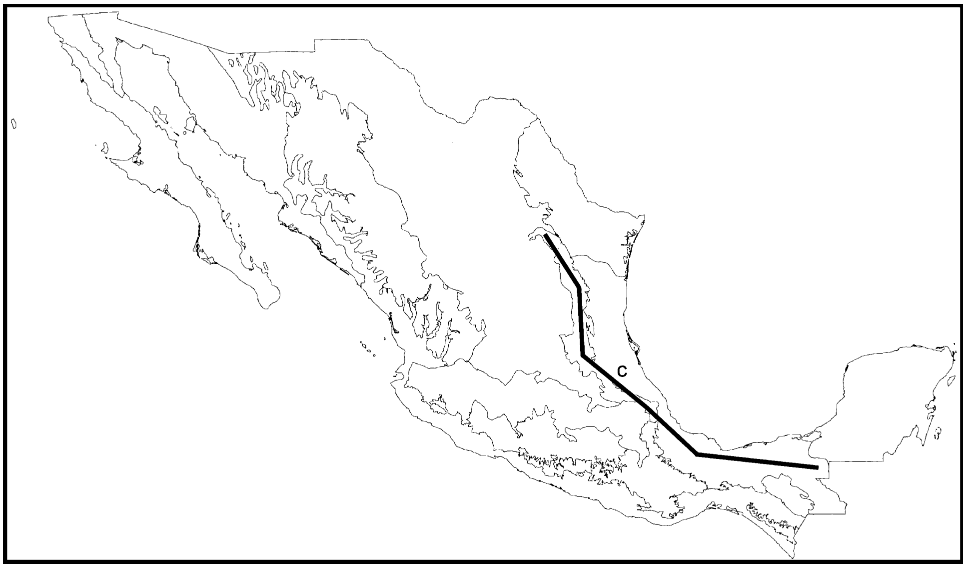

Figure 7. Main clade of the strict consensus cladogram obtained from nine new cladograms in the second run, superimposed onto the map as a generalized track in eastern Mexico (c).

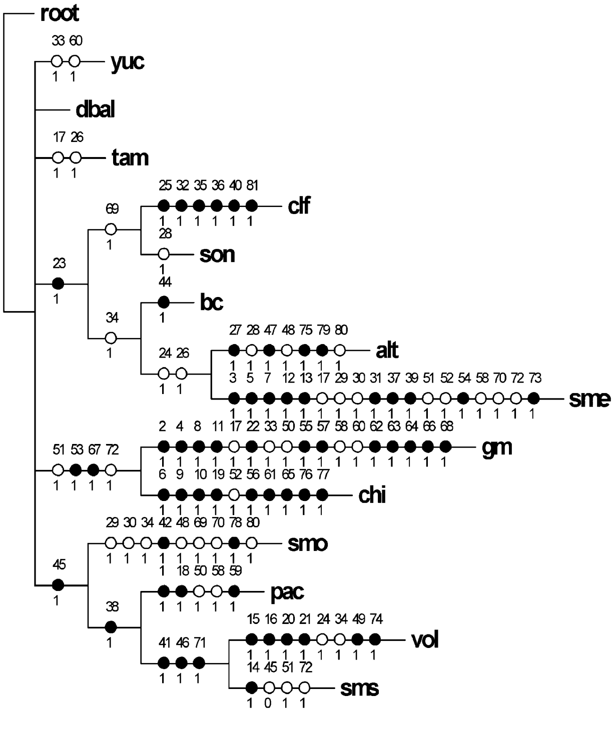

Figure 8. Most parsimonious cladogram obtained in the third run. Numbers above branches represent species and numbers below represent character state (presence/absence) of each species. Black circles in the branches represent synapomorphies, whereas white circles represent homoplasies.

Mexico. Four generalized tracks obtained (b–e) coincide mainly with the Mountain Mesoamerican pattern proposed by Halffter (1976, 1978, 1987) and with the Mountain Mesoamerican biotic element of Morrone (2005). A different historical biogeography of the Mexican peninsulas from the rest of the Mexican territory is evident, mainly in the first run. Some species that inhabit Mexico have most of their distributional area in the USA, especially those distributed in the Baja California peninsula, reflecting a Nearctic distributional pattern. This is represented in the generalized track a. Tracks c and d are based mainly on endemic species, where the Sierra Madre Oriental and Transmexican Volcanic Belt, both mountain chains, contain most of the biodiversity of gymnosperm species in the country and the former include a high number of endemic species. Tracks b and e are based on a combination of endemic species and taxa distributed in Mexico and Central America, reflecting a Neotropical distributional pattern.

CONCLUSIONS

Smaller grid-sizes result in a finer resolution of distributional patterns, but increase artificially the number of empty grid-cells, especially in those cases where species were assigned to an incorrect grid-cell by error (Linder, 2001). Some general patterns are evident in our area cladogram using grid-cells of 2°, so we can conclude that the use of larger size grid-cells minimizes the occurrence of false absences, as Linder (2001) earlier suggested. The 2° grid-cell appears to

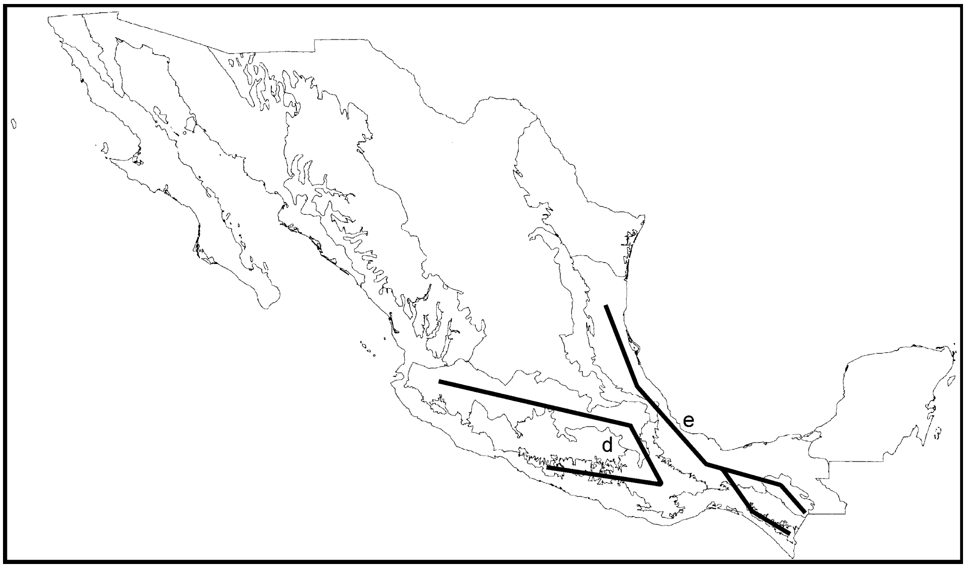

Figure 9. Main clades of the cladogram obtained in the third run, superimposed onto the map as generalized tracks in the Serranías Meridionales region (d) and in eastern and southern Mexico (e).

be an adequate resolution to be explored in future biogeographical analysis using PAE and other parsimony methods of the Mexican biota.

The track analysis shows that the Mexican mountain chains have played an important role in the spatial evolution of gymnosperms because these areas are represented in all generalized tracks and represent areas where the highest biodiversity of these plants in the country are concentrated, which also reflects speciation events in these mountain chains. The track analysis also suggests that the Baja California and Yucatan peninsulas have had independent biogeographical histories from continental Mexico because the generalized track in the California peninsula is isolated from the remaining tracks and the Yucatan peninsula is not included in any track. Our analysis supports the idea that Mexico represents a complex area, as demonstrated by the analyses of Contreras-Medina & Eliosa-León (2001) with several taxa, Álvarez & Morrone (2004) with birds, Escalante, Rodríguez & Morrone (2004) with terrestrial mammals, and Morrone & Gutiérrez (2005) with fleas. Our data indicate that Mexico is an evolutionary 'active' zone, which led to the speciation of several lineages, especially *Pinus*, *Ceratozamia*, and *Dioon*, and the local extinction of other lineages, especially *Picea* and *Tsuga* in southern and central Mexico (Clisby & Sears, 1955; Palacios & Rzedowski, 1993; Lozano-García & Xelhuantzi-López, 1997; Graham, 1999). These facts have been suggested with other sources of evidence, supporting the idea that Mexico represents an important centre of diversity and endemism at the worldwide level for gymnosperms (Farjon & Styles, 1997; Osborne, 1995).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1. Data matrix (grid-cells of 2° versus gymnosperm species) for the parsimony analysis of endemicity.
Table S2. Data matrix (gymnosperm species versus biogeographical provinces) for the parsimony analysis of endemicity.

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