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Historical relationships of the Mexican cloud forests: a preliminary vicariance model applying Parsimony Analysis of Endemicity to vascular plant taxa

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Abstract

Mexican cloud forests, situated between 600 and 3000 m of elevation, exhibit a remarkable high biotic diversity. They follow a fragmented pattern, similar to that of an archipelago, that makes them suitable to vicariance modelling. A Parsimony Analysis of Endemicity (PAE) was applied to the presence/absence of 1267 species of vascular plants (gymnosperms, angiosperms, and pteridophytes) from twenty-four patches of Mexican cloud forests, in order to postulate a preliminary hypothesis of relationships. The single cladogram obtained grouped the twenty-four cloud forests into five clades. These results indicate that the Sierra Madre Oriental, Sierra Madre del Sur, and Serranías Meridionales floristic provinces do not represent natural units. A preliminary vicariance model is presented to explain the sequence of fragmentation of the Mexican cloud forests.

Keywords
Cloud forests, vascular plants, biogeography, endemicity, Mexico.

Resumen

Los bosques mesófilos de montañas mexicanos, situados entre 600 y 3000 m de elevación, exhiben una alta diversidad biótica. Ellos presentan un patrón fragmentado, similar a un archipiélago, que los hace apropiados para la aplicación de un análisis vicariante. Se aplicó un Análisis de Parsimonia de Endemismos (PAE) a la presencia/ausencia de 1267 especies de plantas vasculares (gimnospermas, angiospermas y pteridofitas) de 24 fragmentos de bosques mesófilos mexicanos, con el fin de postular una hipótesis preliminar de sus relaciones. El único cladograma obtenido agrupó los 24 bosques mesófilos en cinco clados. Estos resultados indican que las provincias florísticas de la Sierra Madre Oriental, Sierra Madre del Sur y Serranías Meridionales no representan unidades naturales. Se presenta un modelo vicariante preliminar para explicar la secuencia de fragmentación de los bosques mesófilos mexicanos.

Palabras clave
Bosques mesófilos de montaña, plantas vasculares, biogeografía, endemismos, México.

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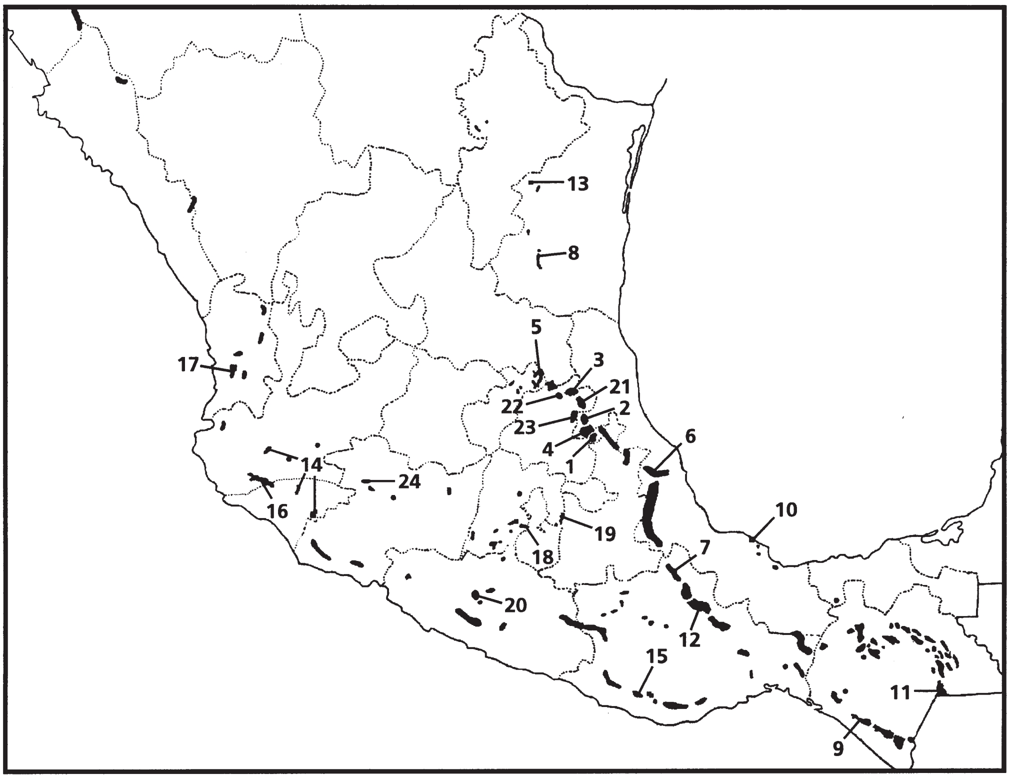

Figure 1 Map of Mexico showing cloud forests localities analysed (modified from Challenger, 1998). (1) Tenango de Doria, Hidalgo; (2) Helechales, Veracruz; (3) Tlanchinol, Hidalgo; (4) Huayacocotla, Veracruz; (5) norte de Querétaro; (6) Teocelo, Veracruz; (7) Huautla de Jiménez, Oaxaca; (8) Gómez Farías, Tamaulipas; (9) El Triunfo, Chiapas; (10) Volcán San Martín, Veracruz; (11) Montebello, Chiapas; (12) La Chinantla, Oaxaca; (13) Sierra de San Carlos, Tamaulipas; (14) Nueva Galicia, Jalisco-Colima-Michoacán; (15) San Jerónimo Coatlán, Oaxaca; (16) Sierra de Manantlán, Jalisco-Colima (17) Serranía San Juan, Nayarit; (18) Ocuilan, Morelos-México; (19) Iztaccíhuatl, Distrito Federal-México; (20) Omiltemi, Guerrero; (21) Molocotlán, Hidalgo; (22) Eloxochitlán, Hidalgo; (23) Tlahuelompa, Hidalgo; (24) Tancítaro, Michoacán. Assignment of these localities to the different floristic provinces detailed in Table 1. Scale = 1:3700 000.

INTRODUCTION

Mexican cloud forests ('bosques mesófilos de montaña' *sensu* Rzedowski, 1978) are difficult to characterize, although they are always found on humid and temperate areas, situated between 600 and 3000 m of elevation (Rzedowski, 1978; Luna *et al.*, 1988). They exhibit a remarkable high diversity of trees, which vary greatly in height, foliar architecture, and phenology (Luna *et al.*, 1994), and a marked predominance of vascular epiphytes and lianas (Webster, 1995), which is probably due to the usual presence of abundant fog. Their distribution follows a fragmented pattern (Fig. 1), similar to that of an archipelago, in which each of the islands has a particular floristic composition.

Several authors (Puig, 1976; Rzedowski, 1978; Luna *et al.*, 1989) have suggested that the Mexican cloud forests are basically composed by floristic elements of three types: (1) temperate, particularly represented by the canopy trees, of Nearctic origin; (2) tropical, mainly represented by herbs, epiphytes, and shrubs, of Neotropical affinities; and (3) endemic, relatively unimportant if considered at the generic level, but very significant at a species level. Relationships of the Mexican cloud forests to floras of the Old World, namely eastern Asia (Sharp, 1953, 1966; Sharp & Iwatsuki, 1965) and tropical Africa (Matuda, 1953), have been also postulated. All these biogeographical considerations, however, have been generally proposed within a dispersalist framework, where Mexico has been treated as the receptor of different floristic elements, being transitional between the Nearctic and Neotropical regions. Vázquez-García (1995) based on a global nonmetric–multidimensional analysis of tree genera from the Mexican cloud forests, obtained a T-shaped arrangement, in which four clusters were apparent: (1) south-west Pacific (2) interior highlands (3) Atlantic, and (4) northern Mesoamerican. Unfortunately, he only included nine islands of this vegetation type in Mexico (Atoyac, Guerrero; Ocuilan, Morelos-México; Cerro Viejo, Jalisco; El Cielo, Tamaulipas; El Triunfo, Chiapas; east of the Sierra de Manantlán, Jalisco; west of the Sierra de Manantlán, Jalisco; Teocelo, Veracruz; and Valle de México, Distrito Federal-México).

The fragmented pattern of these cloud forests makes them suitable to vicariance modelling, and their biotic relationships may be more profitably investigated with cladistic biogeographic methods (Morrone & Crisci, 1995). The lack of cladistic analyses of cloud forest taxa, however, prevent us

Table 1 Units of the analysis, Mexican floristic provinces (*sensu* Rzedowski, 1978) where they are found, and literature consulted. MGC = Mexican Gulf coast; SM = Serranías Meridionales; SMO = Sierra Madre Oriental; ST = Serranías Transístmicas.

Units	Floristic provinces	Literature
1. Tenango de Doria, Hidalgo	SMO	Alcántara & Luna (1997)
2. Helechales, Veracruz	SMO	Ballesteros (1986)
3. Tlanchinol, Hidalgo	SMO	Luna *et al.* (1994)
4. Huayacocotla, Veracruz	SMO	Vargas (1982)
5. North of Querétaro	SMO	Díaz & Palacios-Ríos (1992); Zamudio *et al.* (1992)
6. Teocelo, Veracruz	SMO	Luna *et al.*, (1988)
7. Huautla de Jiménez, Oaxaca	SM	Ruiz (1995)
8. Gómez Farías, Tamaulipas	SMO	Puig (1989)
9. El Triunfo, Chiapas	ST	Long & Heath (1991)
10. Volcán San Martín, Veracruz	MGC	Álvarez del Castillo (1977)
11. Montebello, Chiapas	ST	Carlson (1954)
12. La Chinantla, Oaxaca	SM	Rzedowski & Palacios-Chávez (1977)
13. Sierra de San Carlos, Tamaulipas	SMO	Briones (1991)
14. Nueva Galicia, Jalisco, Colima, and Michoacán	SM	Rzedowski & McVaugh (1966)
15. San Jerónimo Coatlán, Oaxaca	SM	Campos & Villaseñor (1995)
16. Sierra de Manantlán, Jalisco and Colima	SM	Santana (1993); Santiago & Jardel (1993)
17. Sierra de San Juan, Nayarit	SM	Téllez (1995)
18. Ocuilan, Morelos and México	SM	Luna *et al.* (1989)
19. Iztaccíhuatl, Distrito Federal and México	SM	Rzedowski (1969)
20. Omiltemi, Guerrero	SM	Flores (1992–94); Meave *et al.* (1992)
21. Molocotlán, Hidalgo	SMO	Mayorga *et al.* (1998)
22. Eloxochitlán, Hidalgo	SMO	Luna & Alcántara (in prep.)
23. Tlahuelompa, Hidalgo	SMO	Luna & Alcántara (in prep.)
24. Tancítaro, Michoacán	SM	García (1996)

from carrying out a formal cladistic biogeographic analysis that should involve the comparison of taxon-area cladograms. The Parsimony Analysis of Endemicity or PAE (Rosen, 1988; Morrone, 1994, 1998) is a technique that can be applied to postulate a preliminary hypothesis of relationships, which can be then tested under a formal cladistic biogeographic protocol.

Our purpose is to postulate a general hypothesis on the relationships of the Mexican cloud forests, based on the distributional patterns of their vascular plant taxa.

MATERIALS AND METHODS

Data from 1267 species of vascular plants (gymnosperms, angiosperms, and pteridophytes) were obtained from published floristic surveys (Carlson, 1954; Rzedowski & McVaugh, 1966; Rzedowski, 1970; Rzedowski & Palacios-Chávez, 1977; Vargas, 1982; Ballesteros, 1986; Luna *et al.*, 1988, 1989, 1994; Puig, 1989; Briones, 1991; Long & Heath, 1991; Díaz & Palacios-Ríos, 1992; Meave *et al.*, 1992; Zamudio *et al.*, 1992; Santiago & Jardel, 1993; Campos & Villaseñor, 1995; Ruiz, 1995; Téllez, 1995; Alcántara & Luna, 1997; Álvarez del Castillo, 1977), unpublished sources (Mayorga *et al.*, 1998; Luna & Alcántara, in prep.), and data bases from research projects funded by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio) (Flores, 1992–94; Santana, 1993; García, 1996). It is worth noting that these lists were examined in order to detect synonyms and avoid mistakes, updating them with the relevant literature or comunication with specialists.

The units of the analysis were twenty-four Mexican cloud forest localities (Fig. 1, Table 1). The majority of these localities have been assigned to the Mesoamerican Mountain region (Sierra Madre Occidental, Sierra Madre Oriental, Serranías Meridionales, and Serranías Transístmicas floristic provinces) by Rzedowski (1978). The Volcán San Martín, although not included by Rzedowski in this region, contains undoubtely a cloud forest (Challenger, 1998), closely related to the cloud forests of the Serranías Transístmicas province. Localities within the Sierra Madre Occidental were excluded from the analysis, because no complete floristic data were available for them.

The Parsimony Analysis of Endemicity or PAE (Rosen, 1988; Cracraft, 1991; Myers, 1991; Morrone, 1994, 1998; Posadas, 1996) groups areas (analogous to taxa) by their shared taxa (analogous to characters) according to the most parsimonious cladogram. PAE data consist of area × taxa matrices and the resulting cladograms represent nested sets of areas (Morrone & Crisci, 1995).

Taxa were coded for their absence (0) or presence (1) in each area in the data matrix (available upon request to the senior author). Taxa found in a single area -equivalent to autapomorphies-are not useful for assessing relationships, and thus were not included in the matrix. The cladistic analysis was carried with the heuristic search option in PAUP 3.1 (Swofford, 1993). The cladogram was rooted with a hypothetical area coded all zeros.

RESULTS

PAE yielded a single most parsimonious cladogram, with 3581 steps, consistency index of 0.354, and retention index of 0.291

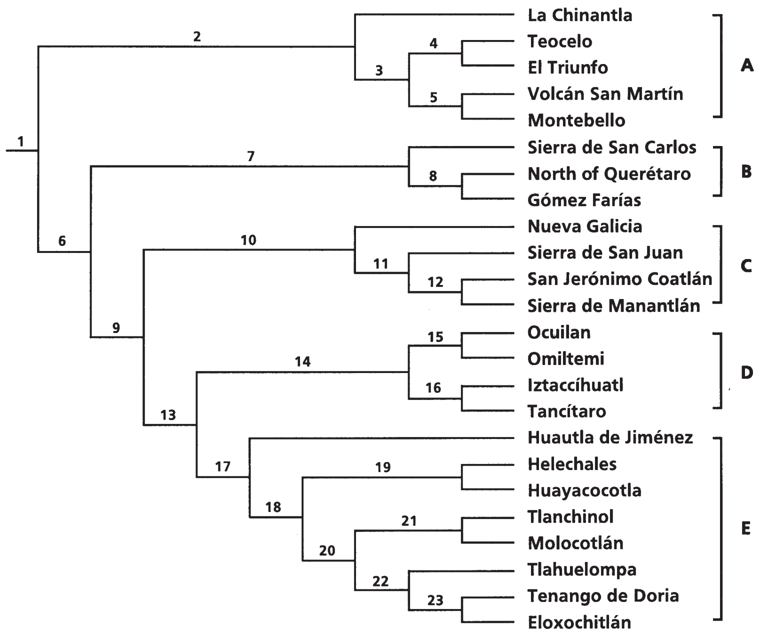

Figure 2 Cladogram obtained by PAE, depicting the relationships of the cloud forests localities examined. A–E correspond to the major clades.

(Fig. 2; species diagnosing the nodes in the cladogram are detailed in Table 2). According to the cladogram, the localities analysed were grouped as follows (Fig. 3).

(1) Serranías Transístmicas province plus portions of the Mexican Gulf coast, Sierra Madre Oriental, and Serranías Meridionales provinces: El Triunfo (Chiapas), Montebello (Chiapas), Volcán San Martín (Veracruz), Teocelo (Veracruz), and Chinantla (Oaxaca).
(2) Northern part of the Sierra Madre Oriental province: Sierra de San Carlos (Tamaulipas), Gómez Farías (Tamaulipas), and north of Querétaro (Querétaro).
(3) Pacific part of the Serranías Meridionales province: Sierra de San Juan (Nayarit), Nueva Galicia (Nayarit, Jalisco, and Colima), Manantlán (Jalisco and Colima), and San Jerónimo Coatlán (Oaxaca).
(4) Central part of the Serranías Meridionales province: Tancítaro (Michoacán), Omiltemi (Guerrero), Ocuilan (Morelos and México), and Iztaccíhuatl (Distrito Federal and México).
(5) Southern part of the Sierra Madre Oriental province plus part of the Serranías Meridionales province: Tlanchinol (Hidalgo), Eloxochitlán (Hidalgo), Molocotlán (Hidalgo), Tlahuelompa (Hidalgo), Huayacocotla (Veracruz), Helechales (Veracruz), Tenango de Doria (Hidalgo), and Huautla de Jiménez (Oaxaca).

DISCUSSION

According to this hypothesis, five major cloud forests diverged sequentially from a formerly continuous forest in Mexico, where major climatic changes provided the isolation events that induced their fragmentation into the present islands. This vicariance model makes predictions about the sequence of fragmentations, which can be tested through the comparison of taxon-area cladograms of the taxa inhabiting them.

Several earlier studies that examined the relationships among Mexican cloud forests show partial agreement with our results. Luna *et al.* (1988) found a close relationship between some cloud forests from Teocelo (central Veracruz) and the Serranías Transístmicas. Luna *et al.* (1989) discussed the affinities of the cloud forests situated in the central portion of the Transmexican Volcanic Belt, which in our analysis appeared as part of the same clade. Puig (1989) found close relationships between cloud forests situated in Tamaulipas and neighbouring localities (belonging to the northern Sierra Madre Oriental) using taxa at a generic level, although this was not so when considering species. Alcántara & Luna (1997) found that the cloud forests in the southern Sierra Madre Oriental were closely related to each other, but distantly related to those in the northern Sierra Madre Oriental and Serranías Transístmicas. On the other hand, the relationships obtained herein partially disagree with the results of Vázquez-García (1995), who found a close relationship between cloud forest localities in the northern and southern parts of the Sierra Madre Oriental.

According to our results, some of the Mexican floristic provinces – at least when taxa from their cloud forests are considered – do not seem to represent natural units, e.g. the Sierra Madre Oriental, Sierra Madre del Sur, and Serranías Meridionales. The Sierra Madre Oriental is split into two clades (B and E), being the barrier separating them the canyons of the río Pánuco basin. On the other hand, the Serranías Meridionales province is spread into four different clades (A, C–E), showing that its different components are more closely related to the Sierra Madre Oriental, Sierra Madre Occidental,

Table 2 Detail of the species defining the nodes in the cladogram. Asterisks indicate species which support only partially the groups (retention index above 0.667 and two steps on the cladogram).

Nodes	Species
1	–
2	–
3	*Tillandsia punctulata* Schltdl. et Cham.
4	*Ilex quercetorum* I.M. Johnst., *Verbesina turbacensis* Kunth, *Croton xalapensis* Kunth, *Hyptis urticoides* Kunth, *Spigelia palmeri* Rose, *Phoradendron piperoides* (Kunth) Trel., *Miconia globulifera* Naudin, *Passiflora sexflora* Juss., *Psychotria* sp., *Belotia mexicana* (DC.) Schum., *Renealmia mexicana* Klotzsch ex Peterson
5	*Inga* sp., *Bletia purpurea* (Lam.) DC., *Maxillaria nagelii* L.O. Williams, *Pleurothallis cardiothallis* Rech.f.
6	–
7	*Crotalaria longirostrata* Hook. et Arn., *Smilax bona-nox* L.
8	*Berberis gracilis* Benth., *Clethra pringlei* S. Watson, *Oyedaea ovalifolia* A. Gray, *Gymnanthes longipes* Müll.Arg., *Phymosia umbellata* (Cav.) Kearney, *Chione mexicana* Standl., *Psychotria erythrocarpa* Schltdl., *Decatropis bicolor* (Zucc.) Radlk., *Witheringia mexicana* (B.L. Rob.) Hunz.
9	–
10	*Ilex brandegeana* Loes.
11	*Costus pictus* D.Don, *Cunila pycnantha* Rob. et Greenm., *Crotalaria quercetorum* Brandegee, *Inga hintonii* Sandwith, *Tephrosia langlassei* Micheli, *Maxillaria variabilis* Bateman ex Lindl.
12	*Vallesia mexicana* Müll.Arg., *Asclepias auriculata* Kunth, *Cordia spinescens* L., *Tillandsia juncea* (Ruiz et Pav.) Poir., *Drymaria gracilis* Cham. et Schltdl. spp. *gracilis*, *Commelina tuberosa* L., *Guardiola tulocarpus* A. Gray, *Podachaenium eminens* (Lag.) Sch.Bip., *Cyperus surinamensis* Rottb., *Euphorbia ariensis* Kunth, *Quercus magnoliifolia* Née, *Quercus vicentensis* Trel., *Panicum parviglume* Hack., *Hyptis oblongifolia* Benth, *Cologania biloba* (Lindl.) Nicholson, *Crotolaria bupleurifolia* Schltdl. et Cham., *Crotalaria mollicula* Kunth, *Desmodium jaliscanum* S.Watson, *Psittacanthus ramiflorus* G.Don, *Clidemia matudae* L.O.Williams, *Ficus velutina* Willd., *Encyclia chondylobulbon* (Rech.f. et Galeotti) Dressler et Pollard, *Ponthieva ephippium* Rech.f., *Stanhopea martiana* Bateman ex Lindl., *Peperomia mexicana* Miq., *Rondeletia juergensenii* Hemsl., *Sommera grandis* (Bartl.) Standl., *Valeriana sorbifolia* Kunth var. *sorbifolia*
13	–
14	–
15	*Tillandsia prodigiosa* (Lem.) Baker, *Cranichis subumbellata* A.Rich. et Galeotti, *Solanum demissum* Lindl.
16	*Peperomia hintonii* Yunck., *Citharexylum affine* D.Don
17	*Oreopanax flaccidus* Marchal, *Quercus affinis* Scheidw.*, *Pinus patula* Schltdl. et Cham.
18	*Epidendrum longipetalum* A.Rich. et Galeotti*, *Alchemilla pectinata* Kunth*
19	*Elaphoglossum lindelii* (Bory ex Fée) Moore, *Tillandsia benthamiana* Baker, *Senecio picridis* Schauer, *Cyperus* aff. *laevigatus* L., *Leucothoe mexicana* (Hemsl.) Small, *Juncus effusus* L., *Myrica pringlei* Greenm., *Passiflora caerulea* L., *Cobaea biaurita* Standl.
20	*Ipomoea purga* (L.) Roth*, *Smithiantha zebrina* (Paxton) Kuntze*, *Juglans mollis* Engelm.*, *Ocotea effusa* (Meisn.) Hemsl., *Smilax tomentosa* Kunth, *Phytolacca purpurascens* A.Braun et Bouché, *Cobaea stipularis* Benth., *Thalictrum pubigerum* Benth.*, *Zanthoxylum* aff. *clava-herculis* L.*, *Zanthoxylum xicense* Miranda, *Vitis popenoei* Fennell
21	*Zephyranthes brevipes* (Baker ex Donn.Sm.) Standl., *Xanthosoma robustum* Schott, *Tagetes micrantha* Cav., *Agrimonia macrocarpa* (Focke ex Donn.Sm.) Rydb., *Triumfetta acrantha* Hochr., *Verbena litoralis* Kunth
22	*Stellaria prostrata* Ellis, *Brickellia glandulosa* (La Llave) McVaugh, *Cirsium jorullense* (Kunth) Spreng., *Spigelia longiflora* M.Martens et Galeotti, *Cuphea procumbens* Ortega, *Acaena elongata* L., *Prunus samydoides* Schltr., *Diodia brasiliensis* Spreng. var. *angulta* (Benth.) Standl.
23	*Matelea* sp., *Begonia maculata* Raddi, *Begonia plebeja* Liebm., *Arenaria bourgeaei* Hemsl., *Schistocarpha kellermanii* Rydb., *Dennstaedtia dissecta* (Sw.) Moore, *Rhynchoglossum azeureum* (Schltdl.) B.L.Burtt, *Isochilus unilateralis* Rob., *Ptelea trifoliata* L., *Physalis pubescens* L., *Phenax hirtus* (Sw.) Wedd.

and Sierra Madre del Sur. These results agree with those of previous authors, which have referred to some of these conclusions. Smith (1941), while analysing the distributional patterns of the species of the lizard genus *Sceloporus*, found that the Sierra Madre Oriental should be divided into two distinct portions: one to the south and another to the north. Liebherr (1991) studied the biogeographic history of the Mexican mountanious habitats inhabited by species of *Elliptoleus* and *Calathus* (Coleoptera: Carabidae). He postulated that there was an ancient fragmentation that separated a tropical from an extratropical biota. The latter was posteriorly fragmented in two areas: the Sierra Madre Oriental and the Sierra Madre Occidental plus part of the Altiplano. According to this author, there are large numbers of shared endemic species between the northern portions of the Sierra Madre Oriental and the Sierra Madre Occidental, and also between these southern portions, so they cannot be considered as natural biogeographic units. Luna *et al*. (1994) also supported the separation of the Sierra Madre Oriental into a northern and a southern portions.

Remarkable patterns of allopatrid speciation and high endemism have been detected in several taxa associated to cloud forests. For instance, Vázquez-García (1997) established five regional archipelagos based on the distributional patterns of species of *Magnolia*. In the future, a formal cladistic biogeographic analysis could provide a test of the vicariance

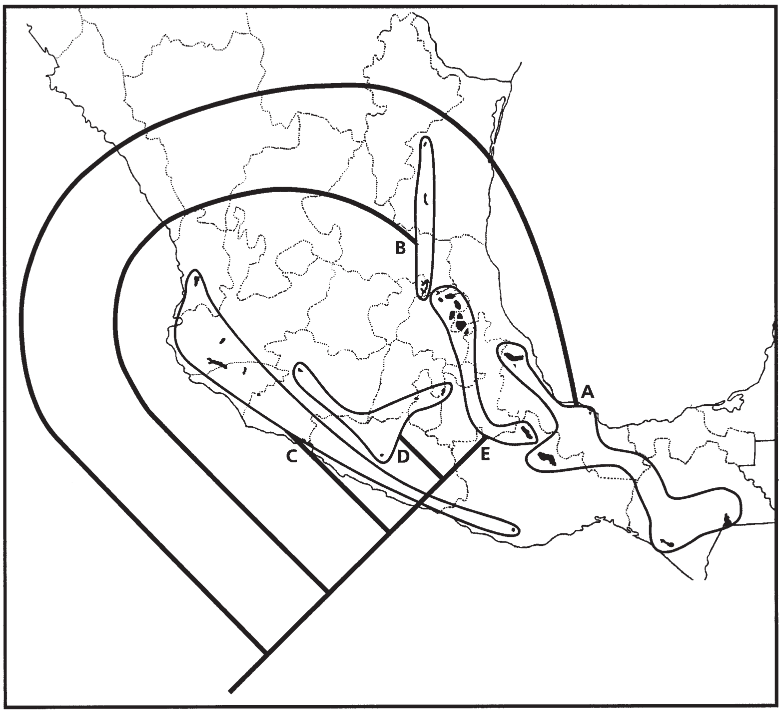

Figure 3 Cloud forests superimposed onto the relationships in the most parsimonious cladogram obtained by PAE. A–E correspond to the major clades.

hypothesis provided herein. This should involve the comparison of area cladograms derived from the cladograms of *Magnolia* and other appropiate taxa, namely *Meliosma* (Sabiaceae), *Ternstroemia* and *Cleyera* (Theaceae), *Cyathea* (Cyatheaceae), *Symplocos* (Symplocaceae), *Clethra* (Clethraceae), *Rhamnus* (Rhamnaceae), and *Styrax* (Styracaceae).

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