

# Deforestation affects biogeographical regionalization: a case study contrasting potential and extant distributions of Mexican terrestrial mammals

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## Abstract

We used ecological niche modelling projected as species' potential (based on the original vegetation map) and extant (based on the 2000 land use and vegetation map) distributions to analyse changes on patterns of endemism of terrestrial mammals occurring in Mexico. Based on the biogeographic method of Parsimony Analysis of Endemicity, we obtained cladograms under scenarios of species' potential distribution (t1) and extant distributions (t2). We found that the resolution of consensus cladogram in t2 was poorer, while there were more geographic synapomorphies in t1, and more autapomorphies in t2 due to a reduction of species' distributions as a consequence of deforestation. We defined a hierarchical regionalization with two regions with the cladogram of t1; a transitional zone, two subregions, five dominions, and 15 provinces. Conversely, the consensus cladogram of t2 had a basal trichotomy, and the position of the Sierra Madre Occidental changed compared with t1. In t1 and t2, the Yucatán Peninsula+Chiapas+Isthmus of Tehuantepec clade was maintained, although in t2 it was separated from the remaining areas of the country. The impact of deforestation on species distributions strongly affected the biogeographic regionalization of terrestrial mammals in Mexico.

**Keywords:** *Biogeographic provinces, deforestation, ecological niche modelling, land use and vegetation map, Mexican Transition Zone, mammals, species distributions*

## Introduction

Biogeographic regionalization consists of hierarchical systems for categorizing biodiversity into realms, regions, dominions, provinces, and districts (Cabrera & Willink 1973; Brown & Lomolino 1998). Typical biogeographic schemes rely on geographic, palaeontological,

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faunistic or floristic criteria, but few studies attempt to build natural regionalization systems (Espinosa-Organista et al. 2001; Morrone et al. 2002). Recent approaches based on patterns of successively nested endemism propose hierarchical schemes based on a historical perspective, in which the biotic or biogeographic province, the smallest endemism area identified, is the basic unit (Espinosa-Organista et al. 2001). Patterns of successively nested endemism can be identified using Parsimony Analysis of Endemicity (PAE) (Rosen 1988; Rosen & Smith 1988; Morrone 1994). Briefly, in a PAE cladogram, groups of areas sharing unique endemic taxa are identified assuming a common biogeographic history.

Several biogeographic regionalizations, based on global similarity of faunas and habitats (vegetation, climate), have been developed for Mexico, some of them using predominantly terrestrial mammals (e.g. Ramírez-Pulido & Castro-Campillo 1990, 1993; Ramírez-Pulido et al. 1994; Arriaga et al. 1997; see Morrone 2005). Morrone (2005) synthesized the main Mexican biogeographical schemes developed in the 20th century, emphasizing those employing patterns of distributions of vegetation, animals and habitat characteristics. An underlying assumption of these approaches is that biotic similarity does not necessarily imply naturalness; consequently, recent methods for regionalization in Mexico are based on identifying biogeographic homology (Morrone et al. 1999, 2002; Espinosa Organista et al. 2000; Morrone 2001, 2005; Morrone & Márquez 2001, 2003).

A potential shortcoming of previous biogeographic regionalizations efforts based on species' point occurrence data from museum specimens involves their taxonomic and geographic biases (Sánchez-Cordero et al. 2001). To improve the distributional maps of species obtained from museum data, we can use novel approaches of species' ecological niche modelling (Stockwell & Peters 1999). Ecological niche modelling projected as species' potential distributions using point occurrence data, environmental layers and GIS platform provides a robust predictor for species presence and absence in a given region (Peterson et al. 2000, 2006; Illoldi-Rangel et al. 2004). Species potential distribution models seem to improve significantly identification of endemism areas (Escalante et al. 2003, in press; Rojas-Soto et al. 2003), and consequently biogeographical regionalization, which holds promise for further research (Guisan & Thuiller 2005).

The geographical classification of areas is also relevant for conservation planning (Brown et al. 1993; Márquez et al. 2001). The transformation of natural landscapes into agrosystems and urban settlements is a major threat for biodiversity conservation. Several investigations have analysed the implications of climatic change on species distributions and their conservation status (Peterson et al. 2001, 2002b; Walther et al. 2002; Hannah et al. 2005; Thuiller et al. 2005), whereas others have investigated the impact of landscape fragmentation on species distribution, richness, density, and abundance (Bethke & Nudds 1995; Kolozsvary & Swihart 1999; Debinski & Holt 2000; Sánchez-Cordero et al. 2005a, 2005b). High deforestation rates usually result in reduction of species distributions (Sánchez-Cordero et al. 2004, 2005a, 2005b; Fuller et al. 2007). Since deforestation impacts species distributions, we suspect that distributional patterns derived from individual species distributions change accordingly; examples depicting species distributional changes under t1 and t2 scenarios are shown in Figure 1.

Natural patterns of endemism are the bases of hierarchical biogeographic regionalizations, but those can be modified by transformation of natural habitats. To our knowledge, this is the first study addressing the impact of transformation of natural habitats on patterns of endemism and regionalization. Understanding the biological implications of land use

changes is relevant in predicting patterns of biodiversity (Peterson & Navarro-Sigüenza 2006; Peterson et al. 2006). Our aim was to determine the impact of deforestation on patterns of endemism by contrasting potential and extant distributions using terrestrial mammals in Mexico as a case study. Specifically, we show changes in distributional patterns of terrestrial mammals under two scenarios: by modelling species' ecological niche projected as potential distributions (t1), using the original natural vegetation map, and projected as extant distributions (t2), using the 2000 land use and vegetation map (Figure 1).

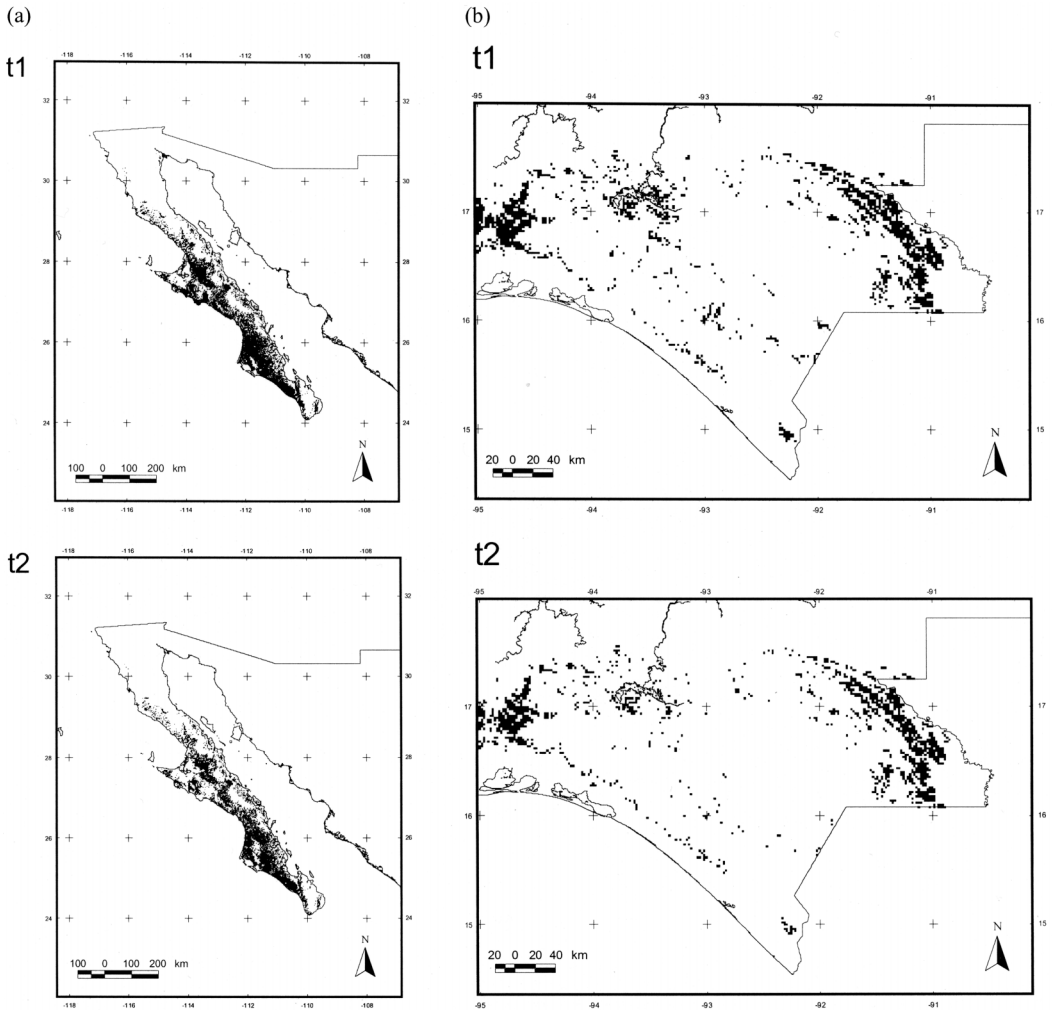


Figure 1. Ecological niche modelling projected as potential (based on the natural vegetation, t1) and extant (based on land use and natural vegetation, t2) distribution of two terrestrial mammals. Black areas depict part of distributions of (a) *Chaetodipus spinatus* in the Baja California Peninsula, and (b) *Cabassous centralis* in Chiapas.

## Materials and methods

### *Point occurrence data*

We used a database of 19,058 museum specimen records in unique localities of 429 terrestrial mammals occurring in Mexico, following taxonomic nomenclature of Villa and Cervantes (2003). Point occurrence data for each species were compiled from national and international scientific collections (see Acknowledgements) and from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio, [www.conabio.gob.mx](http://www.conabio.gob.mx)), and were georeferenced to the nearest  $0.01^\circ$  of longitude and latitude for each locality using 1:250,000 topographic maps (Conabio 1998; [www.conabio.gob.mx](http://www.conabio.gob.mx)). The database had 6574 unique localities for Mexico. The average of unique localities per species was 42.5; most species (>200) had less than 15 unique localities, whereas one species (*Liomys irroratus*) showed 660 unique localities.

### *Ecological niche modelling and species' potential and extant distributions*

To overcome geographic biases on delimiting species distributions, we generated models of ecological niche for each species, using the Genetic Algorithm for Rule set Prediction (GARP; Stockwell & Peters 1999; available for download at [www.lifemapper.org/desktopgarp](http://www.lifemapper.org/desktopgarp)). We characterized ecological niches using environmental data layers ( $0.04 \times 0.04$  pixel resolution), including one dataset with elevation, slope, and aspect (from the US Geological Survey's Hydro-1K data set; [www.usgs.gov](http://www.usgs.gov)); climatic parameters, including mean annual precipitation, mean daily precipitation, maximum daily precipitation, minimum and maximum daily temperature, and mean annual temperature (Conabio, [www.conabio.gob.mx](http://www.conabio.gob.mx)); and a map (t1) with the original natural vegetation (see Rzedowski 1990), producing species' potential distributions. We also used another dataset with a map (t2) including the 2000 land use (transformed areas) and natural vegetation (see SEMARNAT 2001) and other environmental layers. Using the module of GARP for the projection, we produced species' extant distributions (t2).

For each species (both datasets), we ran 100 replicate models, retaining the 20 models with lowest omission error. We retained the 10 models with moderate commission error (i.e. we discarded the 10 models with areas predicted as 'present' showing greatest deviations from the overall median areas predicted as present across all models). This "best subset" of models was summed producing species' distributional maps (Anderson et al. 2003). We further refined these distribution models by delimiting presumed distributional over-predictions with the physiographic provinces (Cervantes-Zamora et al. 1990) where species have been collected. Finally, models of species' potential and extant distributions were overlapped to a grid of  $1^\circ$  latitude  $\times$   $1^\circ$  longitude.

### *Biogeographical regionalization*

Two matrices (matrix t1, using species distributions t1; and matrix t2, using species distributions t2) for PAE were performed for 248 quadrats. If a taxon was present in a quadrat, the entry was assigned '1', and if it was absent, the entry was assigned '0'. A hypothetical area coded with '0' for all columns was added to root the cladogram. Both PAE (t1 and t2) were performed in PAUP 4.0b10 (Swofford 2002), using ACCTRAN optimization (Geraads 1998) and  $k=0$  (Goloboff 1993; Luna-Vega et al. 2000; Escalante et al. 2007). We employed consistency (CI) and retention (RI) indices to choose important

taxa: CI=1.0 denotes geographic synapomorphies (endemic taxa) or geographic autapomorphies (characteristic taxa), whereas CI=0.50 may indicate possibly endemic taxa (only when they are geographic synapomorphies with a posterior reversal, indicating a probable extinction) (Escalante et al. 2003). Occasionally, CI=0.33 may as well indicate possibly endemic taxa. For t1 and t2, characteristic and endemic species were mapped with Arc View 3.2 (ESRI 1999), and these species and cladograms were used for biogeographic regionalizations. Province boundaries were taken from the digital maps of Ramírez-Pulido and Castro-Campillo (1990) and Arriaga et al. (1997).

## Results

The matrix t1 had 39 uninformative (autapomorphic) species and resulted in 1140 cladograms of 4505 steps (CI=0.09 and RI=0.79). The strict consensus cladogram had 4532 steps (CI=0.09 and RI=0.79) and 52 geographic synapomorphies (including all CI>0.33). The matrix t2 had 44 uninformative species and resulted in 3100 cladograms (which is the top number of cladograms able to be retained by our computer) of 4267 steps (CI=0.08 and RI=0.80). The strict consensus cladogram had 4271 steps (CI=0.08 and RI=0.80), with 49 geographic synapomorphies (including all with CI>0.33). Synapomorphic and autapomorphic species and their status, and the simplified consensus cladograms under t1 and t2 scenarios are shown in Table I and Figure 2, respectively. By using the potential distribution maps of synapomorphic and autapomorphic species, we obtained a mammalian biogeographic regionalization of Mexico (Table II). In some cases, we estimated the covered area of the species' potential (t1) and extant (t2) distributions, respectively, and calculated the percentage of transformed area.

We found important differences between cladograms produced using species potential and extant distributions. The cladogram resolution in t2 was poorer than t1, because the consensus cladogram had more polytomies and CI was lower. The number of cladograms for t1 was lower than t2, because we were not able to obtain all possible cladograms for t2; however, all cladograms and the consensus cladogram obtained in t2 were shorter than t1 (this had more steps). From 52 geographic synapomorphies in t1, only 49 were present in t2, whereas 10 species were added as synapomorphies and three species as autapomorphies in t2 (Table I). Eleven synapomorphic species in t1 were not identified in t2. There were three autapomorphies in t2 that appeared in t1 as possible synapomorphies (CI>0.33): *Orthogeomys cuniculus*, *Perognathus longimembris* and *Thyroptera tricolor*; these species were present in two or three quadrats in t1, but were reduced to one quadrat in t2. There were three geographic synapomorphies in t1 (being only in two quadrats) that changed to autapomorphies in t2, due to their reduction of their areas of distribution: *Corynorhinus mexicanus*, *Neotoma bunkerii*, and *Macrophyllum macrophyllum*. Five species changed their CI, from 0.5 in t1 to 1.0 in t2: *Mimon crenulatum*, *Molossus bondae*, *Peromyscus guardia*, *Scapanus latimanus*, and *Sorex sclateri*. Four species changed from synapomorphies in t1 CI=1.0 to CI=0.5 in t2: *Microtus californicus*, *Phyllostomus stenops*, *Sorex ornatus* and *Tylomys bullaris*. In each case (change of CI=0.5 to CI=1.0 and vice versa), the species' distributions were not remarkably reduced, but the changes were due to a different cladogram topology.

The consensus cladogram of t2 had a basal trichotomy, whereas in t1 it was absent (Figure 2a, b). In t1, the northwest (Sonora+Baja California Peninsula+Sierra Madre Occidental) was initially separated from the rest of country, which was not observed in t2. Moreover, the Sierra Madre Occidental was not linked in t2 to Sonora and the Baja

Table I. Geographic autapomorphies (A) and synapomorphies (S) of PAE cladograms for t1 and t2.

Species	t1	t2
<i>Ammospermophilus harrisi</i> (Audubon and Bachman, 1854)	S	S
<i>Ammospermophilus insularis</i> Nelson and Goldman, 1909	A	A
<i>Ammospermophilus interpres</i> (Merriam, 1890)	A	A
<i>Ammospermophilus leucurus</i> (Merriam, 1889)	S	S
<i>Bison bison</i> (Linnaeus, 1758)	S	S
<i>Cabassou centralis</i> (Miller, 1899)	S	–
<i>Centronycteris maximiliani</i> (Fischer, 1829)	A	A
<i>Chaetodipus arenarius</i> (Merriam, 1894)	S	S
<i>Chaetodipus californicus</i> (Merriam, 1889)	–	S
<i>Chaetodipus dalquesti</i> (Mearns, 1898)	S	S
<i>Chaetodipus fallax</i> (Merriam, 1889)	S	S
<i>Chaetodipus spinatus</i> (Merriam, 1889)	S	–
<i>Corynorhinus mexicanus</i> G. M. Allen, 1916	S	A
<i>Cratogeomys castanops</i> (Baird, 1852)	S	S
<i>Cratogeomys fumosus</i> (Merriam, 1892)	S	S
<i>Cratogeomys neglectus</i> (Merriam, 1902)	A	A
<i>Cryptotis goodwini</i> Jackson, 1933	A	A
<i>Dipodomys compactus</i> True, 1889	A	A
<i>Dipodomys gravipes</i> Huey, 1925	S	S
<i>Dipodomys simulans</i> Merriam, 1904	S	S
<i>Enchistenes hartii</i> (Thomas, 1892)	S	S
<i>Euderma maculatum</i> (J. A. Allen, 1891)	A	A
<i>Geomys personatus</i> True, 1889	A	A
<i>Geomys tropicalis</i> Goldman, 1915	S	S
<i>Habromys lepturus</i> (Merriam, 1898)	S	S
<i>Habromys lophurus</i> (Osgood, 1904)	A	A
<i>Heteromys gaumeri</i> J. A. Allen and Chapman, 1897	S	S
<i>Lepus insularis</i> Bryant, 1891	A	A
<i>Lichonycteris obscura</i> Thomas, 1895	A	A
<i>Liomys salvini</i> (Thomas, 1893)	A	A
<i>Macrophyllum macrophyllum</i> (Schinz, 1821)	S	A
<i>Megadontomys cryophilus</i> (Musser, 1964)	S	S
<i>Megadontomys nelsoni</i> (Merriam, 1898)	A	A
<i>Microtus californicus</i> (Peale, 1848)	S	–
<i>Microtus guatemalensis</i> Merriam, 1898	S	S
<i>Microtus oaxacensis</i> Goodwin, 1966	S	S
<i>Microtus pennsylvanicus</i> (Ord, 1815)	S	–
<i>Microtus umbrosus</i> Merriam, 1898	S	S
<i>Micronycteris brachyotis</i> (Dobson, 1879)	S	S
<i>Micronycteris schmidtorum</i> Sanborn, 1935	S	S
<i>Mimon crenolatum</i> (E. Geoffroy, 1810)	–	S
<i>Molossus bondae</i> J. A. Allen, 1904	–	S
<i>Molossus coibensis</i> J. A. Allen, 1904	S	S
<i>Molossops greenhalli</i> (Goodwin, 1958)	A	A
<i>Myotis ciliolabrum</i> (Merriam, 1886)	A	A
<i>Myotis peninsularis</i> Miller, 1898	S	S
<i>Myotis planiceps</i> Baker, 1955	S	S
<i>Nelsonia goldmani</i> Merriam, 1903	A	A
<i>Neotoma anthonyi</i> J. A. Allen, 1898	A	A
<i>Neotoma bryanti</i> Merriam, 1887	A	A
<i>Neotoma bunkeri</i> Burt, 1932	S	A
<i>Neotoma fuscipes</i> Baird, 1858	S	–
<i>Neotoma lepida</i> Thomas, 1893	S	S
<i>Neotoma martinensis</i> Goldman, 1905	A	A

Table I. (Continued)

Species	t1	t2
<i>Neotoma nelsoni</i> Goldman, 1905	A	A
<i>Neotoma palatina</i> Goldman, 1905	S	S
<i>Neotoma varia</i> Burt, 1932	A	A
<i>Onychomys arenicola</i> Mearns, 1896	S	S
<i>Orthogeomys cuniculus</i> Elliot, 1905	–	A
<i>Orthogeomys lanius</i> (Elliot, 1905)	A	A
<i>Otonyctomys hatti</i> Anthony, 1932	S	–
<i>Pappogeomys alcorni</i> Russell, 1957	A	A
<i>Perognathus longimembris</i> (Coues, 1875)	–	A
<i>Peromyscus californicus</i> (Gambel, 1848)	S	S
<i>Peromyscus caniceps</i> Burt, 1932	A	A
<i>Peromyscus crinitus</i> (Merriam, 1891)	A	A
<i>Peromyscus eva</i> Thomas, 1898	S	S
<i>Peromyscus guardia</i> Townsend, 1912	–	S
<i>Peromyscus hooperi</i> Lee and Schmidly, 1977	A	A
<i>Peromyscus interparietalis</i> Burt, 1932	A	A
<i>Peromyscus melanocarpus</i> Osgood, 1904	–	S
<i>Peromyscus melanophrys</i> (Coues, 1874)	–	S
<i>Peromyscus nasutus</i> (J. A. Allen, 1891)	S	S
<i>Peromyscus pembertoni</i> Burt, 1932	A	A
<i>Peromyscus pseudocrinitus</i> Burt, 1932	A	A
<i>Peromyscus yucatanicus</i> J. A. Allen and Chapman, 1897	S	S
<i>Peromyscus zarhynchus</i> Merriam, 1898	S	–
<i>Phyllostomus stenops</i> (Peters, 1865)	S	–
<i>Procyon pygmaeus</i> Merriam, 1901	S	S
<i>Rheomys mexicanus</i> Goodwin, 1959	–	S
<i>Rheomys thomasi</i> Dickey, 1928	A	A
<i>Rhogeessa aeneus</i> Goodwin, 1958	S	S
<i>Rhogeessa genowaysi</i> Baker, 1984	A	A
<i>Rhogeessa mira</i> La Val, 1973	A	A
<i>Saccopteryx leptura</i> (Schreber, 1774)	S	S
<i>Scapanus latimanus</i> (Bachman, 1842)	–	S
<i>Sciurus aberti</i> Woodhouse, 1853	–	S
<i>Sciurus griseus</i> Ord, 1818	S	–
<i>Sciurus variegatoides</i> Ogilby, 1839	S	S
<i>Scotinomys teguina</i> (Alston, 1877)	A	A
<i>Sorex arizonae</i> Diersing and Hoffmeister, 1977	A	A
<i>Sorex emarginatus</i> Jackson, 1925	A	A
<i>Sorex ornatus</i> Merriam, 1895	S	–
<i>Sorex sclateri</i> Merriam, 1897	–	S
<i>Sorex stizodon</i> Merriam, 1895	A	A
<i>Sylvilagus bachmani</i> (Waterhouse, 1839)	S	S
<i>Sylvilagus insomus</i> Nelson, 1904	A	S
<i>Sylvilagus mansuetus</i> Nelson, 1907	S	S
<i>Tamiasciurus mearnsi</i> (Townsend, 1897)	A	A
<i>Thyoptera tricolor</i> Spix, 1823	–	A
<i>Tylomys bullaris</i> Merriam, 1901	S	–
<i>Tylomys tumbalensis</i> Merriam, 1901	A	A
<i>Xenomys nelsoni</i> Merriam, 1892	S	S
<i>Zygozomys trichopus</i> Merriam, 1895	S	S

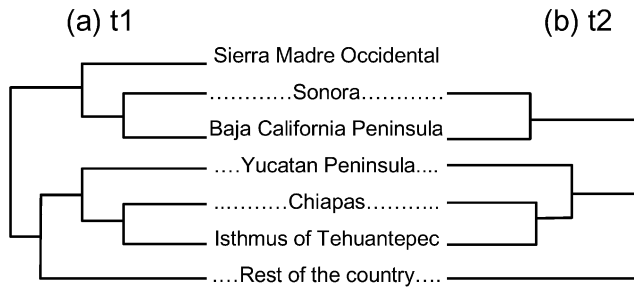


Figure 2. Simplified consensus cladograms of (a) t1 (natural vegetation), and (b) t2 (land use and vegetation map based on the 2000 Inventario Forestal Nacional (SEMARNAT 2001).

California Peninsula. In both t1 and t2, the Yucatán Peninsula+Chiapas+Isthmus of Tehuantepec clade was maintained, although in t2 it was separated from the remaining areas of the country.

## Discussion

### *Mammalian biogeographic regionalization*

Based on the consensus cladogram t1, we built a biogeographical regionalization of the terrestrial mammals in Mexico, contrasting differences with t2 (Figure 3; Table II).

*Regions.* Traditionally, Mexico has been divided into the Nearctic and Neotropical regions (Figure 3; Table II), with a transitional zone referred to as the Mexican Transition Zone (Halffter 1962, 1965, 1972, 1974, 1976, 1978, 1987; Escalante et al. 2004; Morrone 2005). The Nearctic region corresponds to the northern part of Mexico, including the Baja California Peninsula, Northern High Plateau, and the states of Tamaulipas and Nuevo León. The Neotropical region is located in the south of the country, including the lowlands of the Pacific and Gulf coasts, and the Yucatán Peninsula. Morrone and Márquez (2003) identified a Mountain Mexican component equivalent to the Mexican Transition Zone (Escalante et al. 2004, 2005; Morrone & Gutiérrez 2005), including the Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Sierra Madre del Sur, and probably the Balsas Basin and Chiapas Highlands. The Sonora+Baja California Peninsula+Sierra Madre Occidental clade can be considered equivalent to the Nearctic region, whereas the Yucatán Peninsula+Chiapas+Isthmus of Tehuantepec clade can be equated to the Neotropical region. The rest of the country may belong to the Mexican Transition Zone, including the Sierra Madre Oriental, Transmexican Volcanic Belt, Sierra Madre del Sur, Balsas Basin, and Northern High Plateau. The division in regions is more evident in t1 than t2, suggesting a loss of distributional patterns (Figure 2a, b).

The Sonora+Baja California Peninsula+Sierra Madre Occidental clade is separated from the rest of the country in t1. It was justified by *Lasiurus xanthinus*, but this species is distributed mostly in the Nearctic region in Mexico. For the other clade (rest of the country) of t1, the species that justified this grouping were *Philander opossum* and *Sigmodon hispidus*, both occurring throughout the Neotropical region in Mexico. The species restricted to the Neotropical region, located in the Yucatán Peninsula+Chiapas+Isthmus of Tehuantepec clade, were *Alouatta pigra*, *Artibeus jamaicensis*, *Ateles geoffroyi*, *Lontra longicaudis*, *Mazama americana*, *Odocoileus virginianus*, and *Saccopteryx bilineata* (Table II).



Table II. Mexican biogeographic regionalization based on mammalian distributional patterns with their endemic taxa. The location of provinces in the Mexican states is also shown.

Regions and subregions	Dominions	Provinces	Mexican states
Nearctic ( <i>Lasiurus xanthinus</i> *)			
North American Pacific (same as the Nearctic region)	Californian ( <i>Ammospermophilus leucurus</i> , <i>Chaetodipus arenarius</i> , <i>Dipodomys simulans</i> , <i>Neotoma lepida</i> , and <i>Sylvilagus bachmani</i> )	California ( <i>Chaetodipus californicus</i> , <i>C. fallax</i> , <i>Dipodomys grayipes</i> , <i>Microtus californicus</i> , <i>Neotoma anthonyi</i> , <i>N. bryantii</i> , <i>N. fuscipes</i> , <i>N. martinensis</i> , <i>Perognathus longimembris</i> , <i>Peromyscus californicus</i> , <i>P. guardia</i> , <i>P. interparietalis</i> , <i>Scapanus latimanus</i> , <i>Scturus griseus</i> , <i>Sorex ornatus</i> , and <i>Tamiasciurus nearnsi</i> )	Baja California
		Baja California ( <i>Ammospermophilus insularis</i> , <i>Chaetodipus dalquesti</i> , <i>C. spinatus</i> , <i>Lepus insularis</i> , <i>Myotis peninsularis</i> , <i>Neotoma bunkerii</i> , <i>Peromyscus caniceps</i> , <i>P. eva</i> , <i>P. pseudocrinatus</i> , and <i>Sylvilagus mansuetus</i> )	Baja California Sur
	Continental	Sonoran ( <i>Neotoma varia</i> , <i>Peromyscus erinitus</i> , <i>P. pembertoni</i> , and <i>Sorex arizonae</i> )	Sonora
		Mexican Plateau ( <i>Ammospermophilus interpres</i> , <i>Bison bison</i> , <i>Cratogeomys castaneops</i> , <i>Dipodomys compactus</i> , <i>Geomys personatus</i> , <i>Microtus pennsylvanicus</i> , <i>Myotis planiceps</i> , <i>Oryzomys arenicola</i> , <i>Peromyscus hooperi</i> , and <i>P. nasutus</i> )	Coahuila, Chihuahua, Zacatecas, Nuevo León and San Luis Potosí and likely the USA
		Tamaulipas ( <i>Nycticeus humeralis</i> * and <i>Oryzomys leucogaster</i> *)	Northern portion of the states of Nuevo León and Tamaulipas
Neotropical+Mexican Transition Zone			
Mexican Transition Zone			
Mexican Transition Zone	Mountain Mexican ( <i>Megadontomys nelsoni</i> )	Sierra Madre Occidental ( <i>Sciurus aberi</i> , <i>Eudermis maculatum</i> , and <i>Neotoma palatina</i> )	Chihuahua, Durango, and Zacatecas
		Sierra Madre Oriental ( <i>Corynorhinus mexicanus</i> and <i>Cratogeomys neglectus</i> )	Crosses from north to the middle of country in the states of Nuevo León, Tamaulipas, San Luis Potosí, Querétaro, Hidalgo, Puebla and Veracruz
		Transmexican Volcanic Belt ( <i>Nelsonia goldmani</i> , <i>Neotoma nelsoni</i> , <i>Pappogeomys alcorni</i> , <i>Sorex emarginatus</i> , and <i>Zygoeomys trichopus</i> )	Crosses the country transversally, throughout the states of Jalisco, Michoacán, Guanajuato, Querétaro, México, Distrito Federal, Morelos, Puebla, Tlaxcala and Veracruz
		Balsas Basin	Michoacán, Jalisco, Guerrero, Morelos and Puebla
		Sierra Madre del Sur ( <i>Liomys salvini</i> , <i>Myotis ciliolabrum</i> , and <i>Sylvilagus insomus</i> )	Guerrero and Oaxaca

Table II. (Continued)

Regions and subregions	Dominions	Provinces	Mexican states
Neotropical ( <i>Alouatta pigra</i> *, <i>Aribeus jamaicensis</i> *, <i>Ateles geoffroyi</i> *, <i>Lontra longicaudis</i> *, <i>Mazama americana</i> *, <i>Odocoileus virginianus</i> *, and <i>Saccoteryx bilineata</i> *)	Mesoamerican		Sinaloa, Nayarit, Jalisco, Colima, Michoacán, Guerrero and Tehuantepec
Caribbean			Oaxaca, north of the Isthmus of Tehuantepec
		Mexican Gulf ( <i>Geomys tropicalis</i> and <i>Orthogeomys lanius</i> )	Lowlands of the Mexican Gulf coast, from southern Tamaulipas to Tabasco
		Isthmus of Tehuantepec ( <i>Centronycteris maximiliani</i> , <i>Enchisthenes harti</i> , <i>Habromys lepturus</i> , <i>Megadontomys cyphillus</i> , <i>Microtus oaxacensis</i> , <i>M. umbrosus</i> , <i>Molossops greenhalli</i> , <i>Orthogeomys tuniculus</i> , and <i>Rheomys mexicanus</i> )	Oaxaca and a small portion of Puebla and Veracruz
		Chiapas ( <i>Cabassous centralis</i> , <i>Cryptotis goodwini</i> , <i>Habromys lophurus</i> , <i>Lichonycteris obscura</i> , <i>Macrophyllum macrophyllum</i> , <i>Micronycteris brachyotis</i> , <i>Microtus guatemalensis</i> , <i>Molossus coibensis</i> , <i>Peromyscus zarhynchus</i> , <i>Rheomys thomasi</i> , <i>Rhogeessa genowaysi</i> , <i>Saccoteryx leptura</i> , <i>Sciurus variegatoides</i> , <i>Sorex sclateri</i> , <i>S. stizodon</i> , <i>Scotinomys teguina</i> , <i>Thyroptera tricolor</i> , <i>Tylomys bullaris</i> , and <i>T. tumbalensis</i> )	Chiapas, eastern Oaxaca and southern Veracruz and Tabasco
	Antillean	Yucatan Peninsula ( <i>Heteromys gaumeri</i> , <i>Mimon crenolatum</i> , <i>Micronycteris schmidtorum</i> , <i>Molossus bondae</i> , <i>Otonyctomys hatti</i> , <i>Peromyscus yucatanicus</i> , <i>Procyon pygmaeus</i> , and <i>Rhogeessa aeneus</i> )	Campeche, Yucatán and Quintana Roo

The consistency (CI) and retention (RI) indices have been used to identify geographic synapomorphies (similar to cladistic analysis), which should be overlapped to delineate areas of endemism. Only CI and  $RI > 0.5$  (or even 0.33) can be used as possible synapomorphies (Escalante et al. 2003). However, on our cladograms, there are major clades justified by species with poor CI, but better RI. Because RI had advantages over CI (Farris 1989), we still maintained some species with low CI in major clades (marked with \*). All the other species had CI and  $RI > 0.5$ .

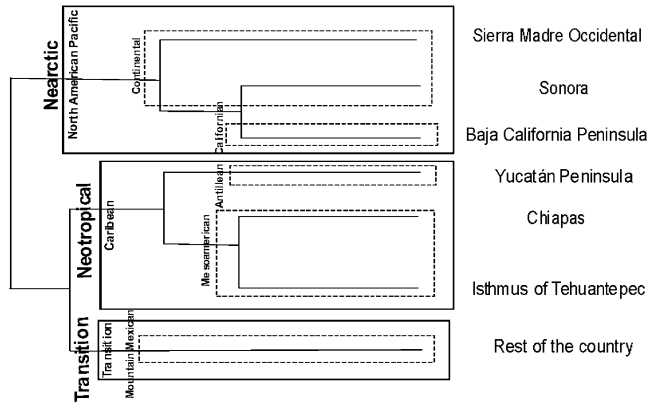


Figure 3. Mexican regionalization based on consensus cladogram of t1.

For t2, the first clade was identified by *Lasiurus xanthinus*, which corresponds to the Nearctic region. The second clade was defined by *Artibeus jamaicensis* and *Odocoileus virginianus*, both with similar distributions to *Philander opossum* and *Sigmodon hispidus* on t1. In t2, the species that supported the Neotropical region of t1 had more steps (*Philander opossum*: L=10; *Sigmodon hispidus*: L=29), and were in a different position on the cladogram than in t1. The third clade was defined by *Baiomys taylori*, *Mephitis mephitis*, *Myotis californica*, and *Sylvilagus floridanus*. *Baiomys taylori* is distributed nationwide, except for the Baja California and Yucatán Peninsulas; *Mephitis mephitis* is restricted to the north; *Myotis californica* is restricted to the north and Baja California Peninsula; and *Sylvilagus floridanus* is distributed nationwide, except Baja California Peninsula.

**Subregions.** We followed the classification of Morrone et al. (1999) and Morrone (2001), who described the North American Pacific and Caribbean subregions, and added a Mexican Transition Zone.

**Dominions.** We propose the following dominions under t1:

1. Californian dominion: corresponds to the entire Baja California Peninsula clade. Escalante et al. (2003) found a similar clade for ecoregions. Its endemic species are *Ammospermophilus leucurus*, *Chaetodipus arenarius*, *Dipodomys simulans*, *Neotoma lepida* and *Sylvilagus bachmani*. This dominion is maintained in both t1 and t2.
2. Continental dominion: we found it as a paraphyletic clade in the cladogram of t1, and we consider the boundaries of this domain controversial. Basically, it includes the northern half of the country, except the Baja California Peninsula.
3. Mexican Transition Zone: is represented by the main mountain provinces, including the Sierra Madre Occidental, Sierra Madre Oriental, Transmexican Volcanic Belt, Balsas Basin and Sierra Madre del Sur. Escalante et al. (2004) suggested that the Chiapas Highlands should be included in the Mexican Transition Zone. This zone was recognized by the presence of panbiogeographic nodes of mammals (Escalante et al. 2004), but we did not find any synapomorphy, except *Corynorhinus mexicanus* (synapomorphy in t1) is distributed in the Sierra Madre Oriental and Transmexican Volcanic Belt, whereas *Megadontomys nelsoni* (autapomorphy) is distributed in the boundary of these provinces.

4. Mesoamerican dominion: Morrone and Márquez (2003) defined this dominion including all the tropical areas of Mexico, mainly the centre-southern coasts, Isthmus of Tehuantepec and Chiapas, except the Yucatán Peninsula. We did not find species distributed in all the dominion, since all Neotropical species identified occurred also in the Yucatán Peninsula. Thus, this domain requires additional analyses with the inclusion of more taxa.
5. Antillean dominion: it includes the Yucatán Peninsula. Its endemic species are the same as the Yucatán Peninsula province (see below).

*Provinces.* The latest regionalization of Mexican mammals considered 20 provinces (Ramírez-Pulido & Castro-Campillo 1990). Morrone (2001, 2005) and Morrone et al. (2002) recognized 14 provinces using other taxa and mammals. We propose 15 provinces based on our cladogram of t1 and the three previous regionalizations (Figure 4):

1. California: Ramírez-Pulido and Castro-Campillo (1990), Morrone (2001), and Morrone et al. (2002) considered this province restricted to the northern part of the Baja California Peninsula, but we found that the pattern extended toward the middle of the Baja California Peninsula. Moreover, Riddle et al. (2000) suggested that the faunas from arid lands in northern and southern regions of the Baja California Peninsula evolved independently. Escalante et al. (2003) found an area of endemism similar to this province, named Baja California Peninsula 3 (BCP3). Its endemic species are *Chaetodipus californicus*, *C. fallax*, *Dipodomys gravipes*, *Microtus californicus*, *Neotoma anthonyi* (insular), *N. bryanti* (insular), *N. fuscipes*, *N. martinensis* (insular), *Perognathus longimembris*, *Peromyscus californicus*, *P. guardia* (insular), *P. interparietalis* (insular), *Scapanus latimanus*, *Sciurus griseus*, *Sorex ornatus* and *Tamiasciurus mearnsi*. Although seven species (*Chaetodipus californicus*, *N. fuscipes*, *Perognathus longimembris*, *P. guardia*, *Scapanus latimanus*, *Sciurus griseus*, and *Sorex ornatus*) changed their status in t2 compared to t1, the general pattern remained.
2. Baja California: *Ammospermophilus insularis* (insular), *Chaetodipus dalquesti*, *C. spinatus* (Figure 1b), *Lepus insularis* (insular), *Myotis peninsularis*, *Neotoma bunkerii* (insular), *Peromyscus caniceps* (insular), *P. eva*, *P. pseudocrinitus* (insular) and *Sylvilagus mansuetus* (insular) are its endemic species. This province occupies the central and southern part of the Baja California Peninsula, corresponding to the nested areas of endemism of Baja California Peninsula 1 and 2 (BCP1 and BCP2) of Escalante et al. (2003). Although Ramírez-Pulido and Castro-Campillo (1990) proposed the Cape zone as a separate province, we included it in the Baja California (see also Rojas-Soto et al. 2003; Morrone 2005).
3. Sonora: in our cladograms, the Sonoran province was related to the Baja California and California provinces, with the Alto Golfo de California connecting them. Although the Baja California Peninsula was isolated from the continent some million years ago (late Miocene; Viniegra 1992), the Baja California Peninsular Desert is a subset of the neighbouring Sonoran desert, on the basis of similarities in plant forms and assemblages (Shreve 1942; MacMahon 1988; Riddle et al. 2000). In t1 and t2 cladograms, this province coincides with the state of Sonora, with the endemics *Neotoma varia* (insular), *Peromyscus crinitus*, *P. pembertonii* (insular) and *Sorex arizonae*.

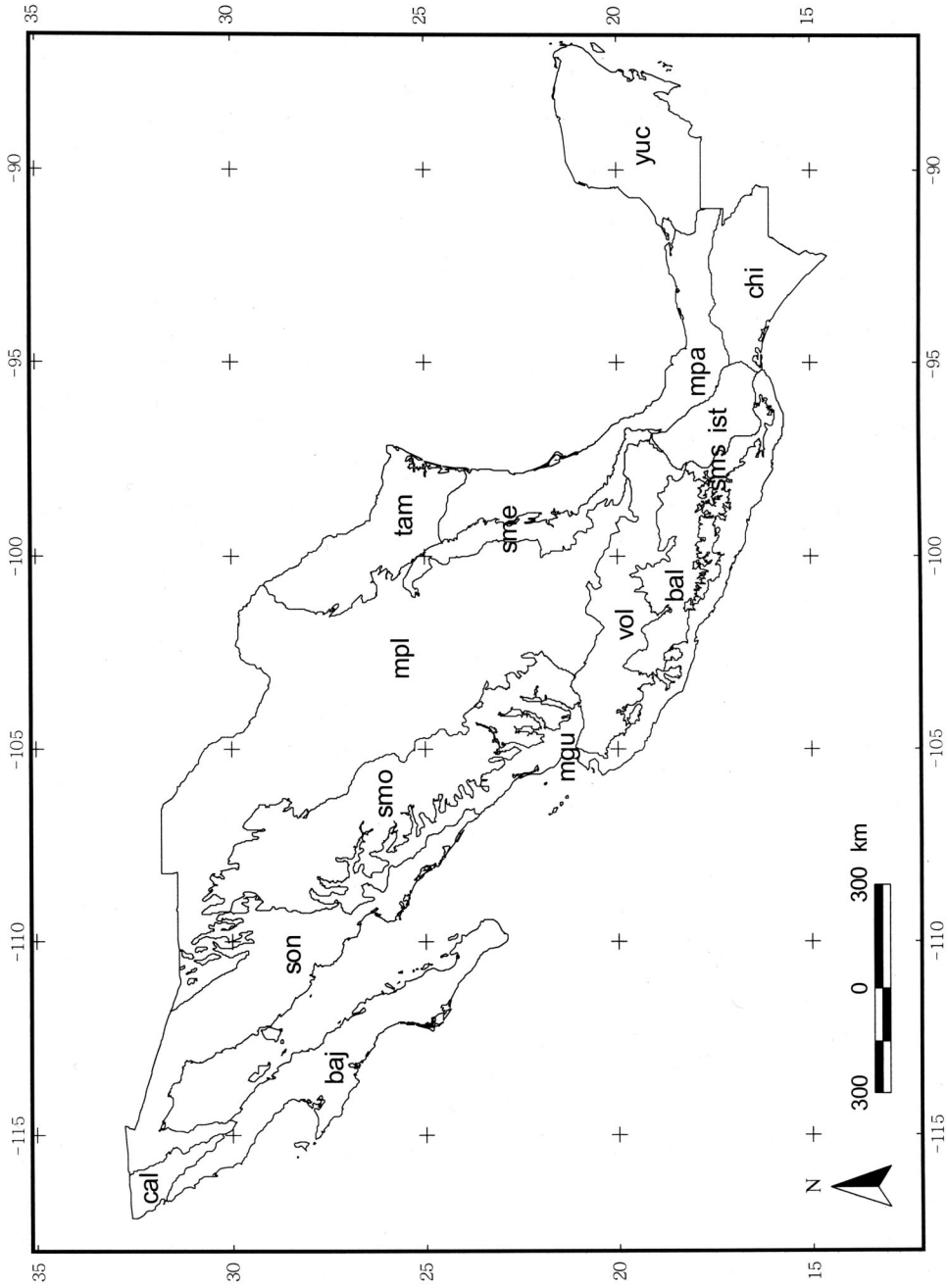


Figure 4. Map of Mexican provinces based on models of species' distributions in tl: baj, Baja California; bal, Balsas Basin; cal, California; chi, Chiapas; ist, Isthmus of Tehuantepec; mgu, Mexican Gulf; mpa, Mexican Pacific Coast; mpl, Mexican Plateau; sme, Sierra Madre Oriental; smo, Sierra Madre Occidental; sms, Sierra Madre del Sur; son, Sonora; tam, Tamaulipas; vol, Transmexican Volcanic Belt; yuc, Yucatán Peninsula.

4. Mexican Plateau: has been divided in two different provinces: Northern and Southern Plateau (Arriaga et al. 1997; Escalante et al. in press), but we failed to find this separation. It was defined by species that may extend their distributions to the rest of North America: *Ammospermophilus interpres*, *Bison bison*, *Cratogeomys castanops*, *Dipodomys compactus*, *Geomys personatus*, *Microtus pennsylvanicus*, *Myotis planiceps*, *Onychomys arenicola*, *Peromyscus hooperi*, and *P. nasutus*. *Microtus pennsylvanicus* was not an endemic under t2 due to 19% reduction of its distribution.
5. Tamaulipas: we failed to identify important species (endemic and autapomorphic), although a detailed analysis of species of clades of the rest of the country allowed identification of two species, mostly distributed in this province: *Nycticeius humeralis* and *Onychomys leucogaster*. They reduced their distributions in t2 by 35% and 18%, respectively.
6. Sierra Madre Occidental: located on the homonymous physiographic province. Escalante et al. (2004) did not find panbiogeographic nodes, and our analysis under t1 showed that the Sierra Madre Occidental province is more closely related to the Nearctic than to the Neotropical provinces. This pattern suggests that this province perhaps does belong to the Nearctic region. Conversely, Marshall and Liebherr (2000) undertook a cladistic biogeographic analysis, where they considered that the northern portion of the Sierra Madre Occidental and the Mexican Plateau are a unique area of endemism, whereas a small area in the south differs from the rest of the province. We found few endemics: *Sciurus aberti* inhabits the entire province, but was only recognized as a synapomorphy under t2, because it also occurs in a small part of the Mexican Plateau. *Euderma maculatum* occurs in a small area in the central part, and *Neotoma palatina* is located only in the south. Surprisingly, under t2, this area was relocated to the clade of the rest of the country, far from the Nearctic provinces of Sonora and Baja California Peninsula, and close to the northern Mexican Plateau (Figure 2b).
7. Sierra Madre Oriental: Espinosa-Organista et al. (2004) identified the Sierra Madre Oriental province with the endemics *Neotoma mexicana navus*, *Peromyscus fuvus*, *Sorex milleri*, and *Sciurus oculatus*. León-Paniagua et al. (2004) undertook a PAE for the terrestrial mammals of the Sierra Madre Oriental, finding five exclusive species: *Cratogeomys neglectus*, *Habromys simulatus*, *Sorex macrodon*, *S. milleri* and *Spermophilus pertotensis*. We found only *Cratogeomys neglectus* as an exclusive species under t1 and t2, whereas *Corynorhinus mexicanus* was autapomorphic in t2 (in t1 was synapomorphic for the Sierra Madre Oriental and the Transmexican Volcanic Belt).
8. Transmexican Volcanic Belt: this province has been recognized as an important zone of endemism for the terrestrial mammals in Mexico (Fa 1989; Fa & Morales 1991; Escalante et al. 2002; Monroy-Vilchis et al. 1999). In our analyses, *Nelsonia goldmani*, *Neotoma nelsoni*, *Pappogeomys alcorni*, *Sorex emarginatus*, and *Zygoeomys trichopus* were autapomorphic for this province under t1 and t2. *Corynorhinus mexicanus* was originally distributed in the Sierra Madre Oriental and the Transmexican Volcanic Belt in t1, but in t2 it was lost from the Transmexican Volcanic Belt. *Megadontomys nelsoni* was on the Transmexican Volcanic Belt in t1, and it was restricted to the Sierra Madre Oriental province in t2.

9. Balsas Basin: the Balsas Basin is located in the lowlands south to the Transmexican Volcanic Belt. We were not able to identify endemic species for this province.
10. Sierra Madre del Sur: *Liomys salvini*, *Myotis ciliolabrum* and *Sylvilagus insonus* are characteristic of this province under t1 and t2.
11. Mexican Pacific: its endemic species are *Cratogeomys fumosus* and *Xenomys nelsoni*, found as possible geographic synapomorphies under t1 and t2, whereas *Rhogeessa mira* was autapomorphic. *Megatomomys thomasi*, *Peromyscus melanocarpus* and *P. melanophrys* occur in this province, but expand their distribution to the Balsas Basin and adjacent provinces. *Peromyscus melanocarpus* and *P. melanophrys* were synapomorphies in t2.
12. Mexican Gulf: *Geomys tropicalis* occurred in the northern portion of this province as a synapomorphy under t1 and t2, but with an evident reduction of its distributions of 50%. *Orthogeomys lanius* was autapomorphic under both t1 and t2.
13. Isthmus of Tehuantepec: the Oaxaca province was synonymized by Morrone (2001) with the Sierra Madre del Sur province. Ramírez-Pulido and Castro-Campillo (1990) defined this province as Oaxaco-Tehuacanense; we followed their limits for this province, although it requires further refinement including other taxa. Escalante et al. (2004) found a generalized track in this zone, suggesting a shared history of its biota. The endemics under t1 were *Centronycteris maximiliani*, *Enchistenes hartii*, *Habromys lepturus*, *Megadontomys cryophilus*, *Microtus oaxacensis*, *M. umbrosus*, *Molossops greenhalli*, *Orthogeomys cuniculus* and *Rheomys mexicanus*. *Orthogeomys cuniculus* changed its status of synapomorphy in t1 to apomorphy in t2. *Rheomys mexicanus* was not identified in t1, but in t2 was present as a synapomorphy.
14. Chiapas: our analyses coincided with the Chiapaneca province of Ramírez-Pulido and Castro-Campillo (1990), which is larger than the province of Morrone (2001), who added the Soconusco province of Arriaga et al. (1997). It is likely that the lowlands of Chiapas do not belong to this province. Escalante et al. (2003) found an important area of endemism for mammals in the highlands of Chiapas, and Escalante et al. (2004) identified two panbiogeographic nodes in this province (nodes 8 and 9). Further, Escalante (2003) prioritized Altos de Chiapas as an important area for mammal conservation. We found the following species (some with their distributions extended to Central America): *Cabassous centralis* (Figure 1a), *Saccopteryx leptura* and *Micronycteris brachyotis*. Chiapas had a nested pattern of endemism, suggesting the presence of two districts: (a) Altos de Chiapas (northern Chiapas): only the northern part of Chiapas and Oaxaca, Veracruz and Tabasco, based on *Cryptotis goodwini*, *Habromys lophurus*, *Lichonycteris obscura*, *Macrophyllum macrophyllum*, *Microtus guatemalensis*, *Peromyscus zarhynchus*, *Scotinomys teguina*, *Sorex sclateri*, *S. stizodon*, *Tylomys bullaris* and *T. tumbalensis*; and (b) Soconusco (southern Chiapas): based on *Molossus coibensis*, *Rheomys thomasi*, *Rhogeessa genowaysi*, *Sciurus variegatoides* and *Thyroptera tricolor*.
15. Yucatán Peninsula: its endemic species are *Heteromys gaumeri*, *Mimon crenolatum* (in the southern part only), *Micronycteris schmidtorum*, *Molossus bondae*, *Otonyctomys hatti*, *Peromyscus yucatanicus*, *Procyon pygmaeus* (insular) and *Rhogeessa aeneus*. This province is equivalent to Ramírez-Pulido and Castro-Campillo's (1990) and Morrone's (2001) provinces, and Escalante et al. (2003) found a similar endemism area. Under t1 and t2, this province was identified, but five species changed their status in the cladograms between both scenarios.

*Changes in biogeographical regionalization*

By combining ecological niche modelling and PAE, we produced two biogeographic regionalizations under an historical scenario of no deforestation (scenario t1), and including deforestation (transformed areas into agrosystems and urban settlements; scenario t2). Presumably, species show ecological niche conservatism, so transformed areas constitute unsuitable niches for population persistence. Consequently, deforestation can have profound effects on species distributions (Sánchez-Cordero et al. 2005b; Fuller et al. 2007), and consequently on biogeographic regionalization.

Relevant changes between t1 and t2 cladograms were observed, resulting in dramatic loss of biogeographical patterns at major scales. In the t2 cladogram, the boundary between Nearctic and Neotropical virtually disappears. In addition, the Sierra Madre Occidental province was not identified. Those changes probably are due to modification of individual distributional areas of species when a change in ecological conditions occurs. Species distributional areas may change by (1) reducing distribution areas including only remnant suitable habitats, (2) modifying their distributional area using transformed habitats, and/or (3) moving to other remnant suitable habitats (Holt 1990). As species can respond differentially to drastic habitat transformation, distributions are consequently modified, and therefore, biogeographic patterns are lost.

The Nearctic–Neotropic regions and the transitional zone are biogeographic patterns that were conformed over evolutionary times. Each region has a distinctive biota, with particular geological and ecological conditions, and a shared history. Nevertheless, these patterns can be lost due to intensive transformation and degradation of natural habitats (see Challenger 1998). Similarly, the Sierra Madre Occidental is a relevant montianous chain in Mexico, harbouring part of the richest pine–oak forest in the world, but only a few large patches of forest remain capable of maintaining its rich biota (Ricketts et al. 1999). This province has been identified by species of different taxa (Morrone 2005); so, it is likely that loss of biogeographic patterns for mammals may reflect equivalent loss of patterns for other taxa.

**Conclusions**

Changes on biogeographic regionalizations should be expected over evolutionary time. Changes in distributional patterns of biota result from unique geologic, geographic, and climatic changes at a global scale. In ecological time scales, climate change (Peterson et al. 2002a, 2002b) and deforestation (Sánchez-Cordero et al. 2005b) can presumably modify biogeographic regionalizations as well. We showed that changes in species' distributions attributable to deforestation (scenario t2) resulted in significant changes in biogeographical regionalization using terrestrial mammals as a case study. If further deforestation continues, it is likely that some natural patterns of species distributions may be lost. Studies incorporating areas of endemism and transition zones can help identify conservation priorities.

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