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## Areas of endemism of Mexican mammals: reanalysis applying the optimality criterion

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Received 11 March 2009; accepted for publication 27 April 2009

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In order to test Mexican areas of endemism of mammals identified by previous parsimony analyses of endemism (PAEs), we applied the optimality criterion to three data matrices (based on point records, potential distributional models and the fill option in software NDM). We modelled the ecological niches of 429 terrestrial mammal species using the genetic algorithm for rule-set prediction (GARP) and models were projected as potential distributional areas. We overlapped the point occurrence data and the individual maps of potential distributions to a grid of 1° latitude–longitude. Three matrices of 247 grid cells (areas) and 429 species were built: (1) a binary matrix with ‘0’ for absence and ‘1’ for presence of at least one record of the species inside the grid-cell; (2) a three-state matrix similar to (1) but assigning the state ‘2’ to the assumed presence in the model of potential distribution; and (3) a three-state matrix similar to (2), but applying the fill option of software NDM instead of using a model. The optimality criterion was performed in NDM version 2.7 and results were examined with VNDM version 2.7. The first and second matrices showed 13 areas of endemism and the third identified 16 areas of endemism. NDM provided a better resolution than PAE, allowing us to identify several new areas of endemism, previously undetected. Ecological niche models, projected as potential distributional areas, and the optimality criterion are very useful to identify areas of endemism, although they should be used with caution because they may overpredict potential distributional areas. PAE seems to underestimate the areas of endemism identified. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 98, 468–478.

**ADDITIONAL KEYWORDS:** ecological niche models – endemism – Mexico – NDM software – parsimony analysis of endemism.

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### INTRODUCTION

Areas of endemism are basic units of analysis in evolutionary biogeography (Morrone, 2008). There are many methods to identify areas of endemism based on different approaches (Rosen, 1988; Rosen & Smith, 1988; Harold & Mooi, 1994; Morrone, 1994; Crisp *et al.*, 2001; Linder, 2001; Hausdorf, 2002; Szumik *et al.*, 2002; Hausdorf & Hennig, 2003; Mast & Nyffeler, 2003; Szumik & Goloboff, 2004; Deo & DeSalle, 2006; Giokas & Sfenthourakis, 2007; Dos

Santos *et al.*, 2008). Parsimony analysis of endemism (PAE) (Rosen, 1988; Morrone, 1994) uses a parsimony algorithm to obtain an area cladogram, based on the taxa inhabiting the study areas, where the clades are treated as areas of endemism. It has been widely used to identify areas of endemism for different taxa in several regions (see Morrone & Escalante, 2002; Escalante & Morrone, 2003; Nihei, 2006; Morrone, 2008). In Mexico, areas of endemism have been identified for mammals, birds, helminths, insects and plants (e.g. Aguilar-Aguilar, Contreras-Medina & Salgado-Maldonado, 2003; Espadas-Manrique, Durán & Argáez, 2003; Rojas-Soto, Alcántara-Ayala & Navarro, 2003; García-Trejo & Navarro, 2004;

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Méndez-Larios *et al.*, 2005; Corona, Toledo & Morrone, 2007; Vargas, Guzmán & Breedy, 2008).

Mexico is situated between the Nearctic and Neotropical regions and most of the country has been characterized as a transition zone (Escalante, Rodríguez & Morrone, 2004; Morrone, 2005). It harbours 11% of the mammal species of the world, with more than 160 species restricted to the country (Ceballos & Oliva, 2005). In a recent biogeographic regionalization, Morrone (2005) recognized 14 biogeographic provinces; however, some of them do not coincide with those obtained for mammals (see Escalante, Morrone & Rodríguez, 2007a). Escalante, Espinosa & Morrone (2003) found five areas of endemism, namely the Mexican Plateau, the Baja California Peninsula (with a nested area within it), Chiapas, the Isthmus of Tehuantepec and the Yucatan Peninsula. Escalante *et al.* (2007c) added the Mexican Pacific Coast and the Sierra Madre Occidental and a nested area within Chiapas. The areas of endemism in the former study were supported by 24 species of Rodentia (66%), seven species of Chiroptera (19%), three species of Lagomorpha (8%) and two species of Soricomorpha (6%). In the second analysis, there were 58 species of Rodentia (70%), 14 of Chiroptera (18%), five of Soricomorpha (6%), three of Lagomorpha (4%) and one of Xenarthra, Carnivora and Cetartiodactyla (1% each one). Rodentia and Chiroptera are the most diverse mammal orders in Mexico and their species have relatively small distributional areas. Species of Carnivora and Primates have wider areas of distribution and are not particularly useful for identifying areas of endemism at the level of biogeographic provinces, but they may help identify patterns at other levels in the biogeographic hierarchy (dominions, regions, etc.).

Ecological niche models projected as potential distribution areas have been used to improve identification of areas of endemism (Espadas-Manrique *et al.*, 2003; Rojas-Soto *et al.*, 2003; Escalante *et al.*, 2007c). Many algorithms to model ecological niches have been devised (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005) and some papers comparing their performance have been published (Elith *et al.*, 2005; Hernández *et al.*, 2006; Stockman, Beamer & Bond, 2006; Sergio *et al.*, 2007; Tsoar *et al.*, 2007). Although there is no agreement over the superiority of an algorithm over others when modelling ecological niches, the genetic algorithm for rule-set prediction (GARP) has been predominantly used in parsimony analyses of endemism and has proven to be appropriate for predicting mammal species distributions (Illoldi-Rangel, Sánchez-Cordero & Peterson, 2004; Sánchez-Cordero *et al.*, 2005a, b).

Szumik *et al.* (2002) and Szumik & Goloboff (2004) formalized a method for identifying areas of endemism that takes into account the general concept of

areas of endemism, where species are scored according to how well their distribution matches a given area (sets of grid cells) and the areas with higher scores are retained (Szumik & Goloboff, 2004; Szumik & Roig-Juñent, 2005). This optimality criterion is implemented in the computer program NDM and its viewer VNDM (Goloboff, 2005; available at <http://www.zmuc.dk/public/phylogeny>).

Our objectives are twofold: to undertake a new analysis of the Mexican terrestrial mammals by using the optimality criterion devised, using both crude data points and models of potential distribution; and to compare the areas of endemism obtained herein with those previous ones identified with PAE.

## MATERIAL AND METHODS

Altogether, 19 058 specimen records of 429 terrestrial mammal species occurring in Mexico were used (Escalante *et al.*, 2007c). English vernacular names follow Wilson & Reeder (2005). We modelled the ecological niche for each species using GARP (Stockwell & Peters, 1999) and the models were projected as potential distribution areas (for details, see Escalante *et al.*, 2007c).

We overlapped the point occurrence data and the individual maps of potential distributions to a grid of 1° latitude–longitude nationwide. Three matrices of 247 grid cells (areas) and 429 species were built: (1) a binary matrix with ‘0’ for absence and ‘1’ for presence of at least one record of the species inside the grid cell; (2) a three-state matrix similar to (1) but assigning the state ‘2’ to the assumed presence in the model of potential distribution; and (3) a three-state matrix similar to (2), but applying the fill option of the program NDM instead of using a model. The states ‘1’ and ‘2’ are the results of the fill option of the program VNDM (fill = 20 and assumed = 40); where fill 20 indicates to the program that if a species record is close to the edge of a cell (20% of its ratio) this species is present for the adjacent cell; the option ‘assumed’ indicates to the program that this species is probably present in the neighbouring cell (see program documentation). The optimality criterion was performed in NDM version 2.7 for the three matrices (Goloboff, 2005; <http://www.zmuc.dk/public/phylogeny>), using default parameters: save sets of areas with two or more endemic species, save sets with score above 2.000 and retain suboptimal sets of 0.90 worst fit and using edge proportion option (see program documentation). Optimal sets were chosen when having above 50% of different endemic species to the highest score. Consensus areas were obtained using 30% of similarity in species, against any of the other areas in the consensus.

Results were examined with VNDM version 2.7 (Goloboff, 2005; <http://www.zmuk.dk/public/phylogeny>). Endemic species and areas of endemism were identified and mapped with Arc View 3.2 (ESRI, 1999). Areas of endemism were compared with previous analyses (Escalante *et al.*, 2003, 2007c) and with Morrone's (2005) regionalization.

## RESULTS

The analysis of the binary matrix (only records) led to the identification of 72 areas and 15 consensus areas with 92 endemic species. The consensus areas represent 13 areas of endemism: (1) Baja California Peninsula; (2) Central Mexican Pacific Coast; (3) Chiapas; (4) Chiapas–Yucatan Peninsula; (5) Isthmus of Tehuantepec; (6) Neotropical; (7) North Baja California; (8) Northern Mexican Pacific Coast; (9) North-eastern Mexican Plateau; (10) Southern Mexican Pacific Coast; (11) Transitional–Neotropical; (12) Tropical Mesoamerican; and (13) Yucatan Peninsula (see Supporting Information).

The analysis of the three-state matrix (models) led to the identification of 77 areas, summarized in 22 consensus areas with 101 endemic species. The consensus areas represent 13 areas of endemism: (1) Baja California Peninsula; (2) Central Mexican Pacific Coast; (3) Chiapas; (4) Isthmus of Tehuantepec; (5) Mexican Transition Zone; (6) Mountain Mesoamerican; (7) Neotropical; (8) North Baja California; (9) Northern Mexican Pacific Coast; (10) Southern Mexican Pacific Coast; (11) Trans-Mexican Volcanic Belt, Eastern district; (12) Tropical Mesoamerican; and (13) Yucatan Peninsula (see Supporting Information).

The analysis of the fill matrix (three-state matrix using fill option) led to the identification of 49 possible areas, summarized in 24 consensus areas, with 119 endemic species. Sixteen areas of endemism were identified from the consensus areas: (1) Baja California Peninsula; (2) California; (3) Central Mexican Pacific Coast; (4) Chiapas; (5) Isthmus of Tehuantepec; (6) Neotropical; (7) Northern Baja California; (8) Northern Mexican Pacific Coast; (9) North-eastern Mexican

Plateau; (10) Transitional–Neotropical; (11) Sierra Madre Oriental; (12) Southern Mexican Plateau; (13) Trans-Mexican Volcanic Belt, Eastern district; (14) Trans-Mexican Volcanic Belt, Western district; (15) Tropical Mesoamerican; and (16) Yucatan Peninsula (see Supporting Information; Figs 1–4).

## DISCUSSION

Escalante *et al.* (2007c) found seven areas of endemism defined by two or more geographic synapomorphies and autapomorphies by using potential distribution models with GARP and PAE. The number of areas of endemism and their endemic species are shown in Table 1, where they are compared with the results of the present analysis.

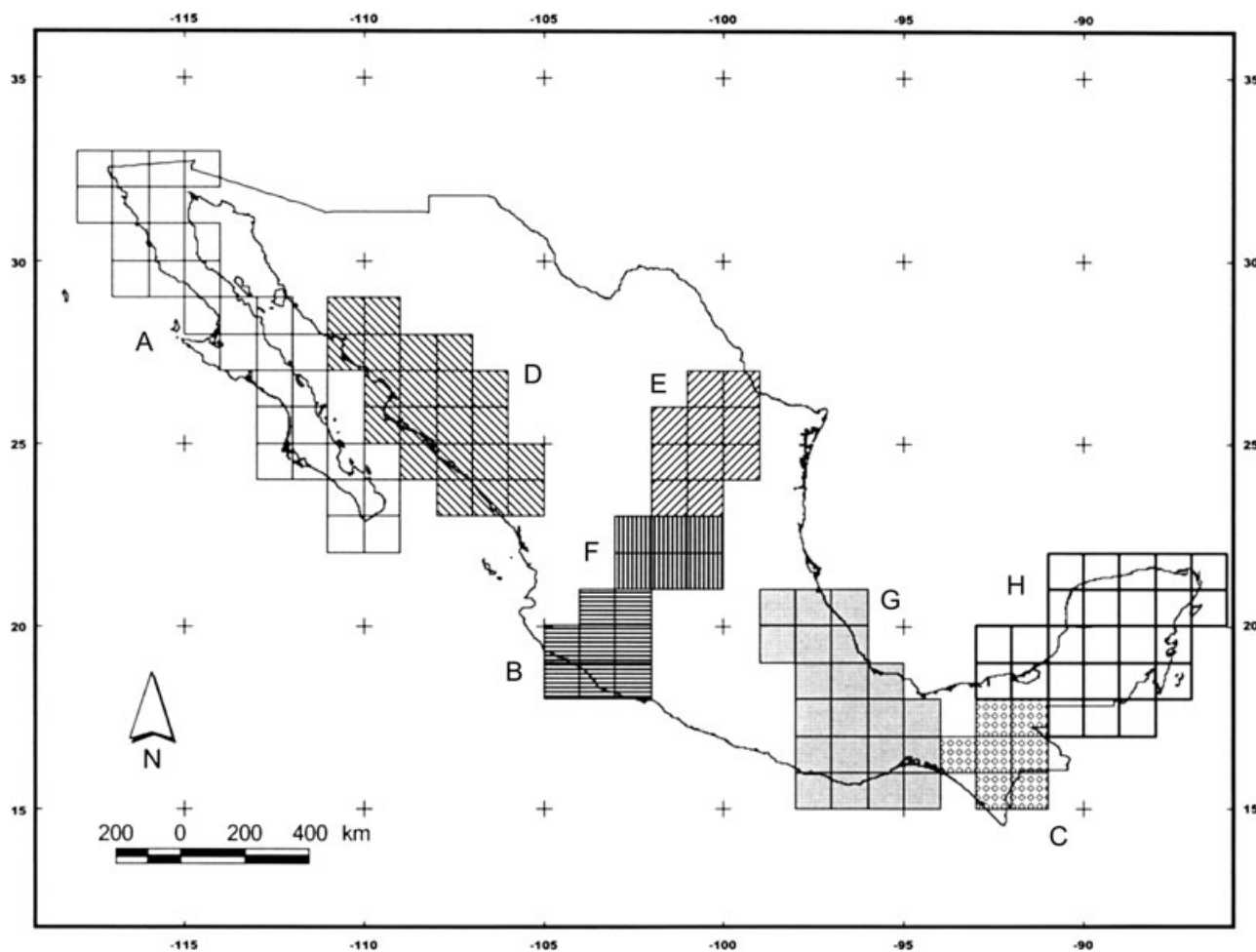
Baja California Peninsula: recovered in our three analyses. In the binary matrix, only three species have a score: two of them are rodents [*Dipodomys simulans* (Dulzura kangaroo rat) and *Neotoma lepida* (desert woodrat)], and they have already been identified for this area (Escalante *et al.*, 2003, 2007c); and *Sylvilagus bachmani* (brush rabbit), which is also endemic to this area. In the three-state and fill matrices, another two species were added: *Ammospermophilus leucurus* (white-tailed antelope squirrel) and *Myotis evotis* (long-eared myotis), identified in previous analyses; whereas *Tamias obscurus* (California chipmunk) and *Spermophilus atripicallus* (Baja California rock squirrel) are new additions to this area.

The Baja California Peninsula showed a nested area of endemism; within it, the Northern Baja California Peninsula (NBCP) and California, similar to BCP2 and BCP3 from Escalante *et al.* (2003). California was recovered only in the third matrix, identified by six species, some of them nested within NBCP. California corresponds only to the northern part of the peninsula above 28° latitude and NBCP includes almost the whole peninsula except El Cabo (around 24° latitude). NBCP was found in all matrices, but in the matrix with the fill option it had few species.

Central Mexican Pacific Coast: corresponds to the Mexican Pacific Coast of Escalante *et al.* (2007c), with

**Table 1.** Comparison of areas of endemism and endemic species from parsimony analysis of endemism (PAE) (\*Escalante *et al.*, 2003, \*\*Escalante *et al.*, 2007c) and NDM (this paper)

Comparison	PAE – data points*	PAE – models of potential distribution (k = 0)**	NDM – binary matrix	NDM – three-states matrix	NDM – binary matrix and fill
Number of areas of endemism	5	7	13	13	16
Number of endemic species	9	35 (+17 possible synapomorphies)	92	101	119



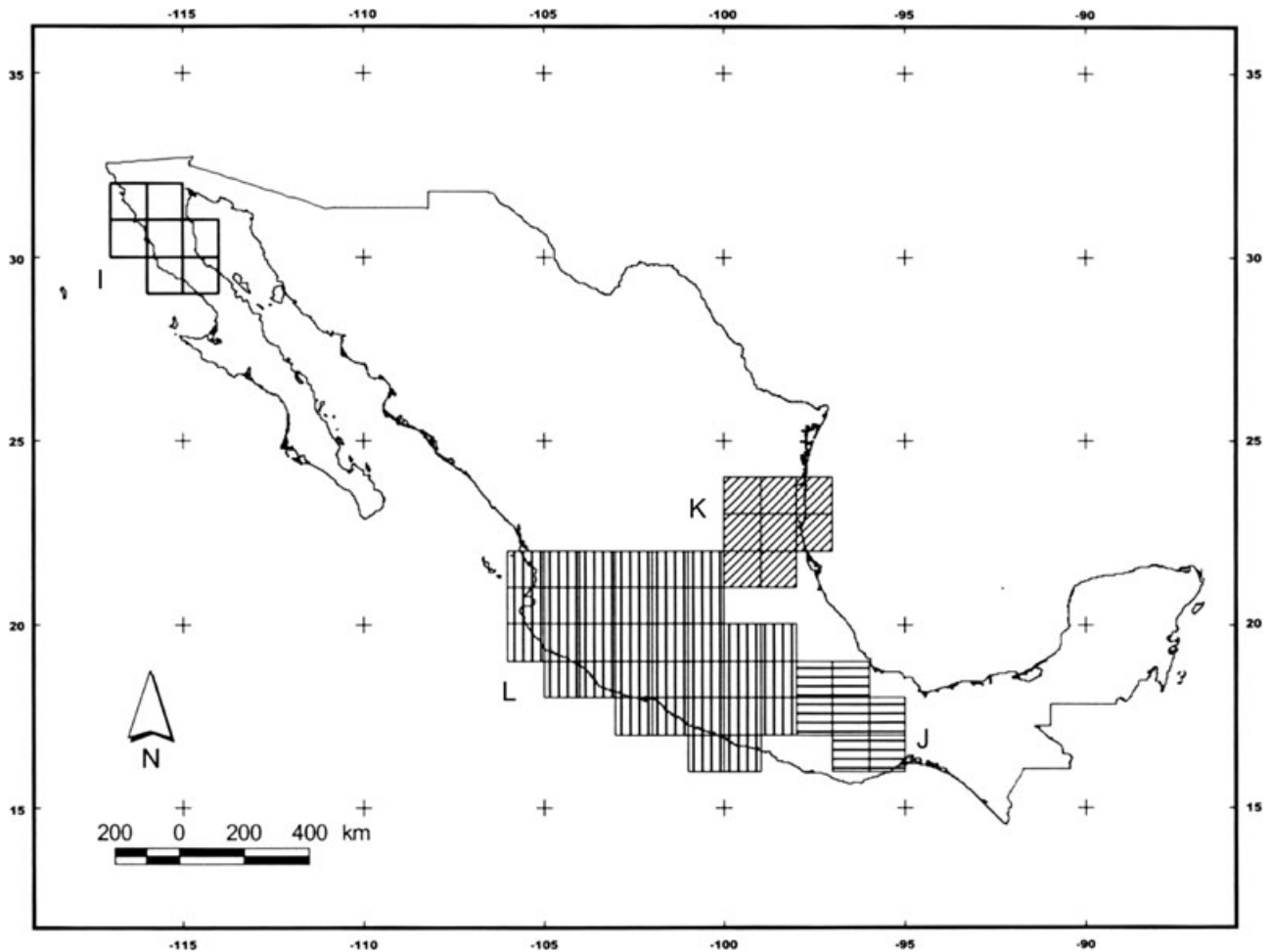
**Figure 1.** Areas of endemism for Mexican mammals obtained from the binary matrix using fill options. A, Baja California Peninsula. B, Central Mexican Pacific Coast. C, Chiapas. D, Northern Mexican Pacific Coast. E, North-eastern Mexican Plateau. F, Southern Mexican Plateau. G, Trans-Mexican Volcanic Belt, Eastern district. H, Yucatán Peninsula.

*Cratogeomys fumosus* (smoky pocket gopher) and *Xenomys nelsoni* (Magdalena woodrat) as endemic species. We recovered this area of endemism in our three analyses; however, the endemic species are not the same, although *C. fumosus* and *X. nelsoni* were identified for the matrix with the fill option. We found another two species, *Pappogeomys alcorni* (Rodentia, Alcorn's pocket gopher) and *Rhoogessa mira* (Chiroptera, least yellow bat), for this area, but some species extend their distributional area north or south of this area (i.e. *Rhoogessa alleni*, the Allen's yellow bat, extends to Guerrero and Oaxaca, with a very low score in the three-state matrix: 0.364). Thus, we only considered the species of the fill matrix as endemic.

Chiapas: Escalante *et al.* (2007c) identified this area of endemism, with a nested area of endemism within it in the south and another one in the north. Here, we found an area of endemism in Chiapas for all the matrices, which have the same species, except

for the third matrix, where *Microtus guatemalensis* (Guatemalan vole), *Scalopus aquaticus* (eastern mole) and *Tylomys bullaris* (Chiapan climbing rat) are added. *Cabassous centralis* (northern naked-tailed armadillo) and *Saccopteryx leptura* (lesser sac-winged bat) were identified for Chiapas by Escalante *et al.* (2007c). *Microtus guatemalensis*, *Peromyscus zarhynchus* (Chiapan deermouse) and *T. bullaris* were defined for the Northern Chiapas area of endemism and *Sciurus variegatoides* (variegated squirrel) for the Southern Chiapas area of Escalante *et al.* (2007c). We did not recover that nested area, but some endemic species are distributed only in the highlands and others occupy only the lowlands (they were overlapped with a digital elevation model (DEM). This finding should be confirmed with other methods.

Chiapas–Yucatan Peninsula: this pattern was recovered only in the first matrix, with point records. Three species were distributed in the Yucatan Penin-

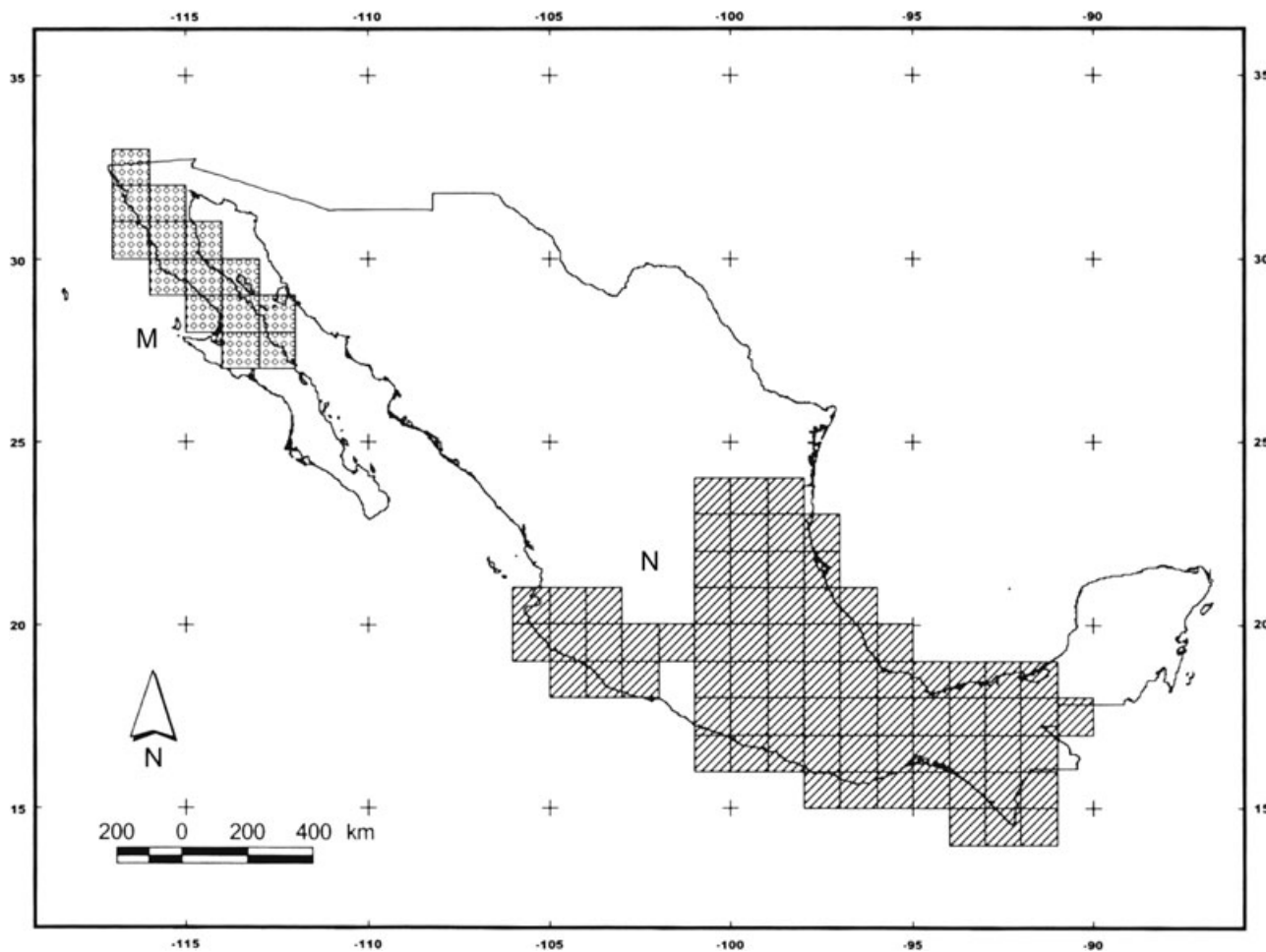


**Figure 2.** Areas of endemism for Mexican mammals obtained from the binary matrix using fill options. I, California. J, Isthmus of Tehuantepec. K, Sierra Madre Oriental. L, Trans-Mexican Volcanic Belt, Western district.

sula and Tabasco, southern Veracruz and the lowlands of Chiapas, but there are possible allopatric areas between Campeche and Veracruz, in the state of Tabasco. This area was not recovered with GARP and the fill option matrices, probably because of the under-representation of the collection data. *Mimon benetti* [(southern golden bat), also named *M. cozumelae*, see Ceballos & Oliva, 2005; Ramírez-Pulido, Arroyo-Cabrales & Castro-Campillo, 2005] is distributed in Tabasco, but *Dasyprocta punctata* (Central American agouti) may not be present therein (Ceballos & Oliva, 2005). It will be necessary to use other strategies to infer areas of distribution because in this case GARP did not help us identify this pattern.

Isthmus of Tehuantepec: this is the most complex area, because it has many endemic species and the highest score. It was discussed by Escalante *et al.* (2003, 2007c) and we recovered it in all matrices, having more than 20 species; however, some endemic species have a low score for this area (i.e. *Crato-*

*geomys merriami*, 0.507). Therefore, the Isthmus of Tehuantepec is an area of endemism characterized by the exclusive presence of *Cryptotis magna* (big Mexican small-eared shrew), *Habromys lepturus* (Zempoaltepec deer mouse), *Lepus flavigularis* (Tehuantepec jackrabbit), *Liomys salvini* (Salvin's spiny pocket mouse), *Megadontomys cryophilus* (Oaxacan big-toothed deer mouse), *Microtus oaxacensis* (Tarabundí vole), *M. umbrosus* (Zempoaltepec vole), *Myotis albescens* (silver-tipped myotis), *Orthogeomys lanius* (big pocket gopher), *O. cuniculus* (Oaxacan pocket gopher) and *Rheomys mexicanus* (Mexican ichthyomyine). In addition, other species give score to this area, mainly in the binary and the three-state matrices. We identified almost all the species reported by Escalante *et al.* (2003, 2007c), except *Molossops greenhalli* (bat), *Saccopteryx leptura* (lesser sac-winged bat) and *Sciurus variegatoides goldmani* (variegated squirrel), although the former (known also as *Cynomops mexicanus*; Ceballos &



**Figure 3.** Areas of endemism for Mexican mammals obtained from the binary matrix using fill options. M, Northern Baja California. N, Transitional–Neotropical.

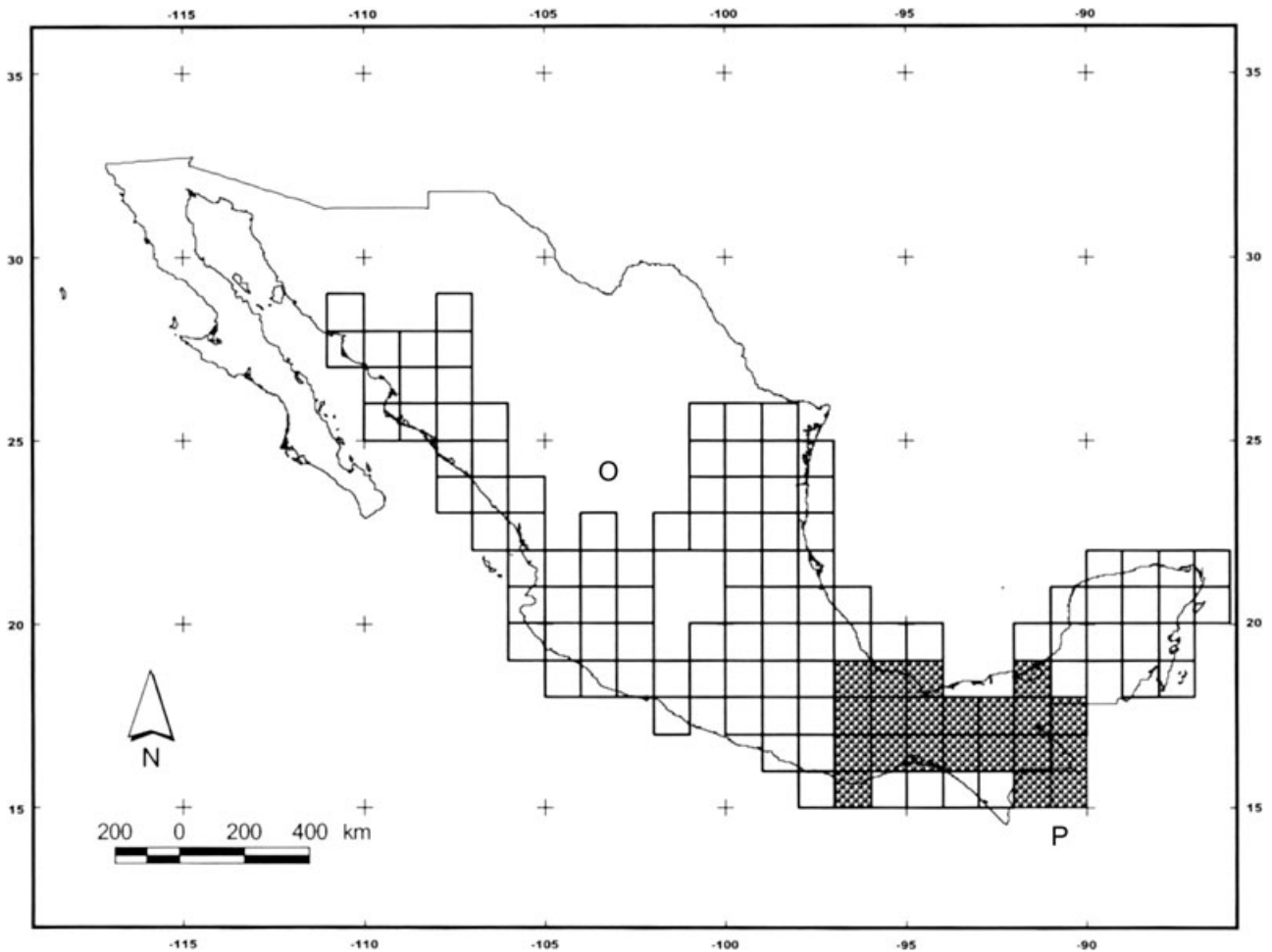
Oliva, 2005) is present along all the southern Pacific coast and the two latter are distributed in Chiapas (Ceballos & Oliva, 2005). The boundaries of this area should be analysed with detailed information about its species and environmental characteristics.

**Mexican Transition Zone:** identified only in the three-state matrix. It is defined by four species; all of them are distributed in the six provinces reported as the Mexican Transition Zone by Escalante *et al.* (2004): Chiapas, the Balsas Basin, the Sierra Madre Oriental, the Sierra Madre Occidental, the Sierra Madre del Sur and the Trans-Mexican Volcanic Belt. Although all of them are distributed in the highlands, they are also present on the coasts. This might be as a result of a mixed pattern with Neotropical and Nearctic elements, with predominance of the former. Three species are bats, which are found mainly between 500 and 2000 m, although they can be found up to 3000 m, and some of them continue their distribution to southern Mexico although they are not distributed in the Yucatan Peninsula.

**Mountain Mesoamerican:** identified only in the three-state matrix. This pattern is very similar to that of the Mexican Transition Zone, but delimited by different species. It includes mainly the Chiapas, Sierra Madre del Sur, Sierra Madre Occidental and eastern Trans-Mexican Volcanic Belt provinces from the Mexican Transition Zone and some lowlands from southern Mexico. There are two species of Soricomorpha in this area [*Sorex ventralis* (chestnut-bellied shrew) and *S. veraepacis* (Verapaz shrew)], both only from high altitudes (Ceballos & Oliva, 2005).

**Neotropical region:** recovered in all the matrices. It includes all the southern coasts of Mexico and the Yucatan Peninsula. Most of the species extend north of 23° latitude, except *Desmodus rotundus* (common vampire bat), *Pteronotus davyi* (Davy's naked-backed bat) and *P. parnellii* (common moustached bat), which extend to 27.5° latitude. It was not identified in the PAE.

**Northern Mexican Pacific Coast:** also found in all matrices, it was not found in previous analyses. All



**Figure 4.** Areas of endemism for Mexican mammals obtained from the binary matrix using fill options. O, Neotropical. P, Tropical Mesoamerican.

endemic species are rodents, except *Lepus alleni* (antelope jackrabbit). This area of endemism is situated on the Pacific lowland coasts between 22° and 31° latitude.

North-eastern Mexican Plateau: identified in the binary and fill matrices. Escalante *et al.* (2003) named it Northern High Plateau and Escalante *et al.* (2007c) as Mexican Plateau. All the species have been recovered previously, except for *Sciurus alleni* (Allen's squirrel), but Escalante *et al.* (2007c) identified with PAE more species than this analysis. This area is controversial because, although it has been recognized for mammals, only three regionalizations have considered it (Ramírez-Pulido & Castro-Campillo, 1990; Arriaga *et al.*, 1997; Escalante *et al.*, 2007a).

Sierra Madre Oriental: not identified in previous studies, it was recovered herein only in the fill matrix. It has three endemic species of Rodentia, although *Geomys tropicalis* (tropical pocket gopher) has a low

score (0.6) and is distributed mainly in the coastal lowlands (Ceballos & Oliva, 2005).

Southern Mexican Pacific Coast: it was recovered in the binary and three-state matrices, but with different species. For the binary matrix, the endemic species are restricted to a small non-coastal area. In contrast, species in the three-state matrix are widely distributed in coastal areas. This pattern was not identified in previous analyses.

Southern Mexican Plateau: identified only in the fill matrix. It has three endemic species, but it is necessary to confirm the presence of *Geomys personatus* (Texas pocket gopher). This area was not recovered in any previous analysis, although Escalante *et al.* (2007a) already suspected the existence of a different province in this area. It corresponds to the Altiplano Sur (Zacatecano-Potosino) province of Arriaga *et al.* (1997) and the Zacatecana province of Ramírez-Pulido & Castro-Campillo (1990).

Trans-Mexican Volcanic Belt, Eastern district: the Trans-Mexican Volcanic Belt has been questioned as a province (Corona *et al.*, 2007; Escalante *et al.*, 2007b), because it does not have sympatric endemic species. In our analysis, we recovered two different areas of endemism for Central Mexico. It was not found in Escalante *et al.* (2003, 2007c) PAE. Escalante *et al.* (2007b) identified an eastern district in this province based on a 0.5° grid and we follow this proposed hierarchical level. This district was identified in the three-state and fill matrices and some species were endemic in both analyses. However, some species of the fill matrix have more widely distributional areas and they have rather low scores (i.e. *Dermanura tolteca* and *D. phaetotis*).

Trans-Mexican Volcanic Belt, Western district: recovered only in the fill matrix. Although it is delimited by six endemic species, they have low scores [score = 2.53, i.e. the score for *Osgoodomys banderanus* (Osgood's deer mouse) is 0.495]. We think that further analyses are necessary to confirm this area of endemism.

Transitional–Neotropical: similar to the Mexican Transition Zone, but is supported by different endemic species. It is mainly on both coasts (Gulf and Pacific) and in the province of Sierra Madre del Sur. No previous analysis has recovered this pattern and we found it in the binary and fill matrices.

Tropical Mesoamerican: recovered in all the matrices and it includes all the lowlands from Chiapas, Tabasco and southern Veracruz. It is similar to the Chiapas–Yucatan Peninsula pattern, but it does not include the Yucatan Peninsula. It has not been identified in previous analyses. For the binary and three-state matrices, we found widely distributed species with low scores, but for the fill matrix we found restricted species for this area. We found one species of Primates (*Alouatta palliata*, the mantled howler) and another of Pilosa (*Cyclopes didactylus*, the silky anteater). This area may extend into Central America.

Yucatan Peninsula: recovered in all the matrices and it has also been found in previous analyses. Escalante *et al.* (2003) identified two endemic species, whereas Escalante *et al.* (2007c) obtained eight endemic species and we found herein seven species, in addition to *Reithrodontomys gracilis* (slender harvest mouse) and *Otonyctomys hatti* (Yucatan vesper rat). We did not find the endemic species of Escalante *et al.* (2003), *Miconycteris schmidtorum* (Schmidt's big-eared bat) and *Mimon crenolatum* (striped hairy-nosed bat) and we could not identify *Molossus bondae* of Escalante *et al.* (2007c). This species might not be present in Mexico (Ramírez-Pulido *et al.*, 2005).

The analysis combining niche models and the optimality criterion led to finding areas of endemism

previously unidentified. Additionally, it provided new species diagnosing the areas of endemism. Parsimony analysis of endemicity seems to underestimate the areas of endemism identified, so it should not be used as the single approach. Identification of areas of endemism is a complex biogeographical issue and no one method has proved to be more effective than another. We hope this analysis encourages others to explore the conceptual and methodological implications of the approaches proposed to identify areas of endemism.

PAE has been criticized, but few analyses have been undertaken to compare its performance with other methods used to identify areas of endemism (Morrone, 2008). Moline & Linder (2006) found that a phenetic clustering approach performed better than PAE and NDM in its ability to identify areas of endemism. In this case, however, it is understandable that PAE performed poorly, because there were more grid cells than taxa in the matrix. Casagrande & Taher (2007) compared PAE, the optimality criterion and biotic elements, finding that NDM performed better than PAE in noisy conditions. Carine *et al.* (2009) carried out an analysis comparing unweighted pair group method with arithmetic mean (UPGMA), PAE and NDM for 609 taxa of spermatophytes. They found that NDM performed better than UPGMA and PAE and proposed it as the most appropriate method to identify areas of endemism.

However, PAE was able to identify patterns when distributional areas showed no significant overlap. In our analyses, NDM found more areas of endemism than PAE, even using only data points, with a single exception (the Sierra Madre Occidental). Moreover, areas of endemism identified by NDM were supported by a higher number of species. Additionally, PAE was not able to recognize overlapped areas of endemism, but only strictly allopatric ones. But PAE can be used to build a hierarchical system (see Escalante *et al.*, 2007d) and, although NDM finds areas of endemism of different sizes (e.g. Neotropical region, Chiapas province) and has a tool to find included/including sets, it does not show an explicit hierarchy.

NDM, in contrast to the other methods available, identifies areas of endemism by considering the position of the taxa occurring in a given area. The optimality criterion evaluates explicitly the congruence between distributions based on the concept of area of endemism, whereas PAE derives areas of endemism indirectly from a presence/absence matrix analysed with an algorithm used in phylogenetic systematics.

PAE with models of distributional areas performed better than PAE with point records (Rojas-Soto *et al.*, 2003; Escalante *et al.*, 2007c), because point data underestimate the real distributional areas. Predictive models provided an improved inference of distri-



butional areas. NDM using the matrix with GARP predictions allowed us to identify more areas of endemism than with the binary matrix, but less than with the matrix with the fill option. This may be as a result of over prediction in GARP models, because ecological niche models predict areas in terms of ecological distance and not because of their shortest geographical distance. In contrast, the fill option of NDM resolved the problem regarding artificial disjunctions by geographic proximity; however, we should be cautious when choosing the percentage to be used in the fill and assumed options.

#### ACKNOWLEDGEMENTS

Malte Ebach, Rob Whittaker and two anonymous reviewers provided useful comments on the manuscript. Tania Escalante thanks DGAPA-UNAM for two postdoctoral scholarships (PROFIP 2004–06, 2006–07) and Claudia Szumik thanks CONICET and FONCYT. Gerardo Rodríguez and Miguel Linaje helped us with SIG and GARP modelling. A preliminary version of this paper was presented at the VII Reunión Argentina de Cladística y Biogeografía, San Isidro, Argentina, 15 November 2007.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Description of areas of endemism of Mexican mammal and their endemic species identified with the optimality criterion.

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