



Dispersal limitation and geographical distributions of mammal species

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ABSTRACT

Aim To relate the dispersal limitation of endemic terrestrial mammals in Mexico to species life-history traits and latitude.

Location Mexico.

Methods We modelled species ecological niches projected as potential distributions (*P*) using point occurrence data and 19 environmental variables for 89 endemic mammal species, and compared the areas covered by these ecological niche models with maps of species actual distributions (*R*) based on minimum convex polygons connecting marginal records based on museum specimens. We correlated body mass, food habits (herbivore, omnivore, insectivore, frugivore/granivore), volant and non-volant (fossorial, arboreal, terrestrial) habits and mean latitude to the proportion of occupancy of species potential distributional areas (*R/P*).

Results *R* and *P* were significantly positively correlated, with an overall average *R/P* ratio of 0.49. Less than half of the endemics (41 species) had a high occupancy (*R/P* values ranging from 0.50 to 0.90); a few (four species) showed full occupancy (> 0.90). Body mass and food habits were not correlated with *R/P*, but latitude showed significant correlations with *R/P*; volant mammals tended to show higher *R/P* values than non-volant mammals.

Main conclusions Few species filled most of the spatial extent of their ecological niches. Life-history traits were generally poor predictors of proportional occupancy of species potential distributions. Endemics occurring at higher latitudes showed higher occupancy, suggesting that abiotic factors are likely to limit their distributions. Conversely, species at lower latitudes showed lower occupancy, suggesting that their distributions are limited by biotic factors and/or by geographical or historical barriers that prevent dispersal. The dispersal abilities of volant compared with non-volant endemics can explain the higher occupancy in species potential distributions in the former group. These trends provide a baseline for exploring the importance of life-history traits and abiotic versus biotic factors in limiting species distributions.

Keywords

Abiotic factors, bioclimatic models, dispersion, endemic species, geographical distributions, latitude, life-history traits, mammals, Mexico, potential distribution.

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INTRODUCTION

A fundamental question in biogeography is: 'what factors limit species geographical distributions?' (Dobzhansky, 1950; MacArthur, 1972; Lomolino *et al.*, 2005). A long-standing paradigm balances abiotic and biotic factors in delimiting species distributions: one view emphasizes abiotic factors (e.g. temperature, precipitation, soil nutrients), while the other emphasizes the role of biotic interactions as well (e.g. competition, parasitism, plant–animal interactions, relative species replacement) (MacArthur, 1972; Lomolino *et al.*, 2005). Assessing the relative importance of such factors has long been a major challenge in biogeography (Lomolino *et al.*, 2005).

Recent developments in ecological niche modelling (ENM) provide possible insights into these questions (Svenning & Skov, 2004; Martínez-Meyer, 2005; Soberón & Peterson, 2005; Araújo & Guisan, 2006; Peterson, 2006). By integrating known occurrences with digital maps of relevant environmental parameters, areas suitable for species can be characterized as potential geographical distributions (Soberón & Peterson, 2005; Peterson, 2006). Briefly, three classes of determinants of distributions are involved: (1) abiotic conditions, including physical environmental variables such as temperature, precipitation, soil type, etc. (the focus of ENM); (2) biotic interactions, including mutualism, parasitism and competitive exclusion (the 'biotic niche'); and (3) dispersal limitations and accessibility – although not properly niche characteristics, these factors can constrain the occurrence of species in certain areas (Soberón & Peterson, 2005). The geographical projection of the conditions fitting both biotic and abiotic conditions (irrespective of accessibility) can be termed a species' potential distribution (Holt, 2003; Soberón & Peterson, 2005).

Once a species' ecological niche is modelled, one can compare its potential distribution with its actual distribution (which can be estimated as a minimum convex polygon enclosing known records, e.g. Hall, 1981). If a species' actual distribution matches its entire potential model, then its distribution is likely to be limited mainly by abiotic parameters. However, if the actual distribution fills the potential distribution only partially then other factors, such as limited dispersal abilities, are more likely to limit its distribution (Svenning & Skov, 2004; Soberón & Peterson, 2005; Peterson, 2006).

Few studies have compared species potential and actual distributions. Hoffman (2005) found that potential climatic niche correlated positively with the species' actual distributions among *Arabidopsis* populations. Svenning & Skov (2004) used a bioclimatic model based on three climatic variables to model European tree distributions and found low levels of actual occupancy (<40%), probably owing to limited dispersal capability during post-glacial range expansion. They further noted strong associations between actual occupancy and mean latitude, in which higher-latitude species showed a higher occupancy of potential distributions (Svenning & Skov, 2004).

Here, we estimated the proportional occupancy of species potential distributions for 89 terrestrial endemic mammals of Mexico in relation to their life-history characteristics in order to discern the possible factors that influence species actual distributions. We argue that if species show high occupancy then abiotic factors are probably exclusively responsible for delimiting distributions; conversely, if occupancy is low then other factors, such as interactions among species, barriers to dispersal and biotic factors, may play more significant roles (Pulliam, 2000; Sibly & Brown, 2007; Soberón, 2007).

MATERIALS AND METHODS

We focused on continental terrestrial mammal species endemic to Mexico, considering in particular 89 species that: (1) are taxonomically well known; (2) have available data about collecting localities that are adequately representative of the species' geographical distribution (more than four unique occurrence localities); and (3) show a diversity of locomotion and food habits (see Appendix S1 in Supporting Information). Our study area covers a latitudinal gradient (16–32° N) across a tropical to temperate transitional region resulting in a mosaic of climates (based on the Köppen nomenclatural classification of climate).

Actual distributions (*R*)

We compiled a data set of 4065 unique localities from museum specimen records where data from institutions were obtained from MaNIS (<http://manisnet.org>; mean = 45.67, range 4–512; see Acknowledgements). We checked georeferenced localities carefully using comprehensive mammalian Atlas summaries (Hall, 1981; Ceballos & Giselle, 2005) and created minimum convex polygons enclosing all known records of each species. These distribution maps were refined somewhat by removing climatically unsuitable areas from within the minimum convex polygon; the results were used to represent species actual distributions (*R*). For example, in Fig. 1 we show the example of the volcano rabbit, *Romerolagus diazii*, illustrating the difference between the actual and potential distributional areas: the actual distribution is restricted to the central portion of the Mexican Transvolcanic Belt, whereas the potential distributional area extends farther west and east. These maps assume that species are unable to maintain populations outside climatically suitable areas and avoid potential overestimation, particularly in species with small geographical distributions (Pearson & Dawson, 2005). We also used distributional summaries prepared independently by Arita & Rodríguez-Tapia (2004), (based on Hall, 1981; data base version 2, SNIB-CONABIO, <http://www.conabio.gob.mx>; 5° × 5°), to check our maps. Given that these endemics are abundant species where they occur, and the relatively extensive work that has been conducted on endemics (distributional and taxonomic), we feel confident that for most species our actual distribution maps (*R*) are accurate.

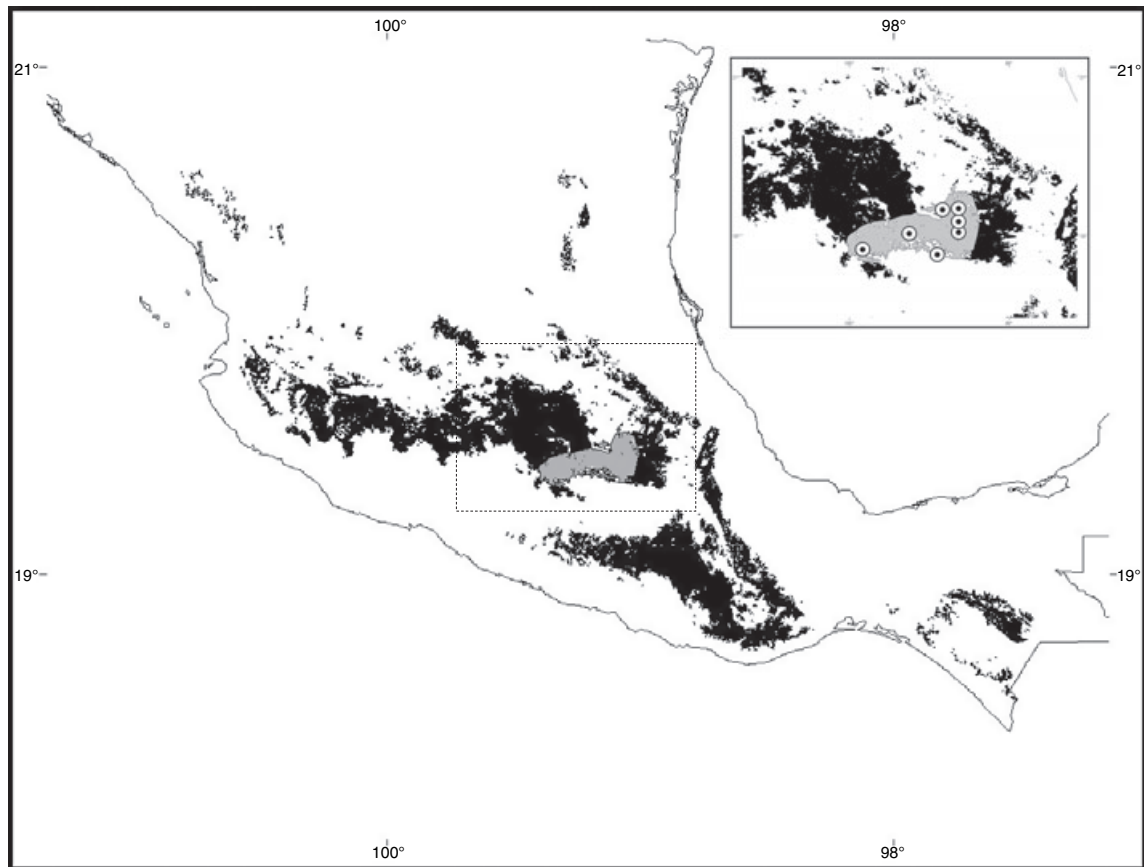


Figure 1 Ecological niche model projected as a potential distribution ($P = 82,318 \text{ km}^2$; black) and actual distribution ($R = 7783 \text{ km}^2$; grey) for the volcano rabbit, *Romerolagus diazi* (Lagomorpha), in central Mexico (mean latitude = 19.06° N). Marginal records (points) were connected to form a minimum convex polygon to estimate the species' actual distribution. Its proportional occupancy rate is 0.09.

Potential distributions (P)

We used the software package Genetic Algorithm for Rule-set Prediction (GARP; Stockwell & Peters, 1999; <http://nhm.ku.edu/desktopgarp/index.html>) for modelling species ecological niches and projecting them as potential distributions. This coarse-grained model of ecological niche is projected into geographical space (Soberón & Peterson, 2005; Peterson, 2007). GARP has seen extensive application to diverse taxonomic groups, including mammals (Peterson *et al.*, 1999; Illoldi-Rangel *et al.*, 2004). Recent studies on ecological niche modelling have observed that GARP generally predicts broader areas than other methods (e.g. Maxent; see Phillips *et al.*, 2006), with more restricted extrapolations of species potential distributions (Elith *et al.*, 2006; Peterson *et al.*, 2007). However, GARP appears to reconstruct species potential distributions better, although with greater uncertainty in commission errors (McNysset & Blackburn, 2006; Peterson *et al.*, 2007). We used GARP because our goal was to capture species potential distributions.

We included 19 bioclimatic variables from Téllez (2004) at 1 km^2 resolution: (1) mean annual temperature; (2) mean diurnal range; (3) isothermality; (4) temperature seasonality; (5) maximum temperature of the warmest month; (6) minimum

temperature of the coldest month, (7) annual temperature range; (8) mean temperature of the wettest month; (9) mean temperature of the driest month; (10) mean temperature of the hottest month; (11) mean temperature of the coldest month; (12) mean annual precipitation; (13) mean precipitation of the wettest month; (14) mean precipitation of the driest month; (15) precipitation seasonality; (16) total precipitation of the wettest quarter; (17) total precipitation of the driest quarter; (18) total precipitation of the hottest quarter; and (19) total precipitation of the coldest quarter of the year. By including so many predictor variables, the risk of overfitting in models probably increases estimates of R/P (see below). We assume that potential errors are relatively constant over the broader suite of species, and hence have developed comparisons using the raw R/P values. Species showing restricted geographical distributions would be likely to suffer the highest overfitting so we excluded species with fewer than four unique occurrence localities.

In GARP analyses, occurrence points are divided evenly into training and testing data sets. GARP works in an iterative process of rule selection, evaluation, testing and incorporation or rejection; a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules) and applied to the training data to develop or evolve a rule. Predictive accuracy

is evaluated based on the testing data. Rules can evolve in ways that mimic DNA evolution (e.g. point mutations, deletions). Change in predictive accuracy between iterations is used to evaluate whether particular rules should be incorporated into the model; the algorithm runs 1000 iterations or until convergence. Spatial predictions of presence and absence can include omission errors (predicted absence in areas of actual presence) and commission errors (predicted presence in areas of actual absence; Fielding & Bell, 1997). Because GARP does not produce unique solutions we developed 100 replicate models of ecological niches for each species. Specifically, we retained the 10 'best subsets' based on optimal error distributions for individual replicate models (with lowest omission error and with intermediate commission error), following (Anderson *et al.*, 2003). This 'best subset' of models was summed to produce predictions of potential distributions as grids with values ranging between 0 (all models agree in predicting absence) to 10 (all models agree in predicting potential presence). Our final potential distribution models included areas where ≥ 8 (of 10) of the replicated models coincided in predictions of presence.

Proportional distribution occupancy (R/P)

To estimate proportional distribution occupancy, we calculated the ratio of the species' actual distributional area (R) to the species' potential distributional area (P). R/P thus ranged from 0 to 1.

Life-history traits

For assigning food habits and the type of locomotion to our set of endemic mammals, we used Eisenberg's (1981) classification as modified by Frisch (1995). We further regrouped type of locomotion into volant and non-volant (terrestrial, arboreal and fossorial). Species were compared according to: (1) food habits, as herbivores ($n = 14$), omnivores ($n = 7$), insectivores ($n = 15$) and frugivores/granivores ($n = 49$); (2) type of locomotion, as volant ($n = 12$) and non-volant ($n = 77$), the latter divided into terrestrial ($n = 33$), arboreal ($n = 13$) and fossorial ($n = 31$); and (3) body mass, estimated as the mean body masses of the two sexes (Arita & Figueroa, 1999).

Latitude

We calculated the mean latitudes of species actual distributions (R) as the mean of northern and southern limits over the 16° latitudinal gradient range of Mexico (16–32° N). As only endemic species were analysed, these latitudinal means do not simply reflect range position with respect to political boundaries.

Statistical analyses

We used a linear regression to relate R and P . We tested the normality of R and P values prior to analysis (SPSS, Q–Q plot

test); best fit was provided by a cube root transformation for each of R and P . To relate species life-history characteristics to their R/P ratios, we used general linear models (SPSS 13.0; SPSS Inc., Chicago, IL, USA). The independent variables with continuous data were latitude and body mass (\log_{10} -transformed). Finally, we compared mean R/P values between families of endemics to estimate possible phylogenetic effects in distributional occupancy using an ANOVA (SPSS 13.0).

RESULTS

In all, 89 continental mammal species endemic to Mexico met the criteria necessary for inclusion in this study. Estimated actual distributional areas (R) ranged from 655 to 815,727 km² (median = 57,861 km², first quartile = 16,311, SD = 185,311 km²), whereas potential distributions (P) ranged 1163–1,120,839 km² (median = 163,644 km², first quartile = 44,619, SD = 291,846 km²). A high proportion of species showed relatively small R (49 species with < 70,000 km²), while only a few had a large R (6 species with > 500,000 km²). Similarly, most endemics showed a relatively small P (27 species with < 70,000 km²), and few had a large P (16 species with > 500,000 km²; Fig. 2a,b). Differences between R and P frequency distributions were significant, where R showed higher skewness ($g_R = 2.01$, $g_P = 1.30$; SE = 0.25) and kurtosis ($g_R = 3.85$, $g_P = 1.14$; SE = 0.5).

R and P

Numbers of point occurrence data and R were positively correlated ($r_s = 0.75$, $P < 0.0001$); more known occurrence points had species with a larger R . R and P were significantly positively correlated ($r^2 = 0.81$; $F_{1,88} = 373.87$, $P < 0.0001$). A significant, although weaker correlation ($r^2 = 0.29$, $F_{1,86} = 36.57$, $P < 0.0001$) was observed between P and the distribution maps of Arita & Rodríguez-Tapia (2004), supporting our use of R as a descriptor of species distributions (Fig. 3a,b). The R/P ratio averaged across all species was 0.49; only 10 species (11% of total) showed values of ≤ 0.2 , 34 species (38%) showed values of 0.2–0.5, and 45 species (51%) showed values > 0.50 (Fig. 3c). We also found a significant positive relationship between latitude and R/P ($F_{1,88} = 10.57$, $P < 0.05$). The latitude response resulted because of particularly low occupancy in species potential distributions south of the latitudinal midpoint of Mexico, such as the Transvolcanic Belt (i.e. < 20°N); conversely, R/P was higher in northern Mexico, such as in the Chihuahuan Desert (> 25°N; Fig. 4).

R/P was not related to body mass ($F_{3,88} = 0.334$, $P > 0.5$), food habits ($F_{3,88} = 0.038$, $P > 0.9$) or mode of locomotion ($F_{3,88} = 1.249$, $P > 0.2$). However, there was a moderate difference in distribution occupancy between volant and non-volant mammals ($F_{1,88} = 3.189$, $P = 0.07$). The relationship of R/P with latitude was similar for volant and non-volant mammals, but the slope was moderately higher for volant species (Fig. 4). We observed no significant difference in R/P between mammal families.

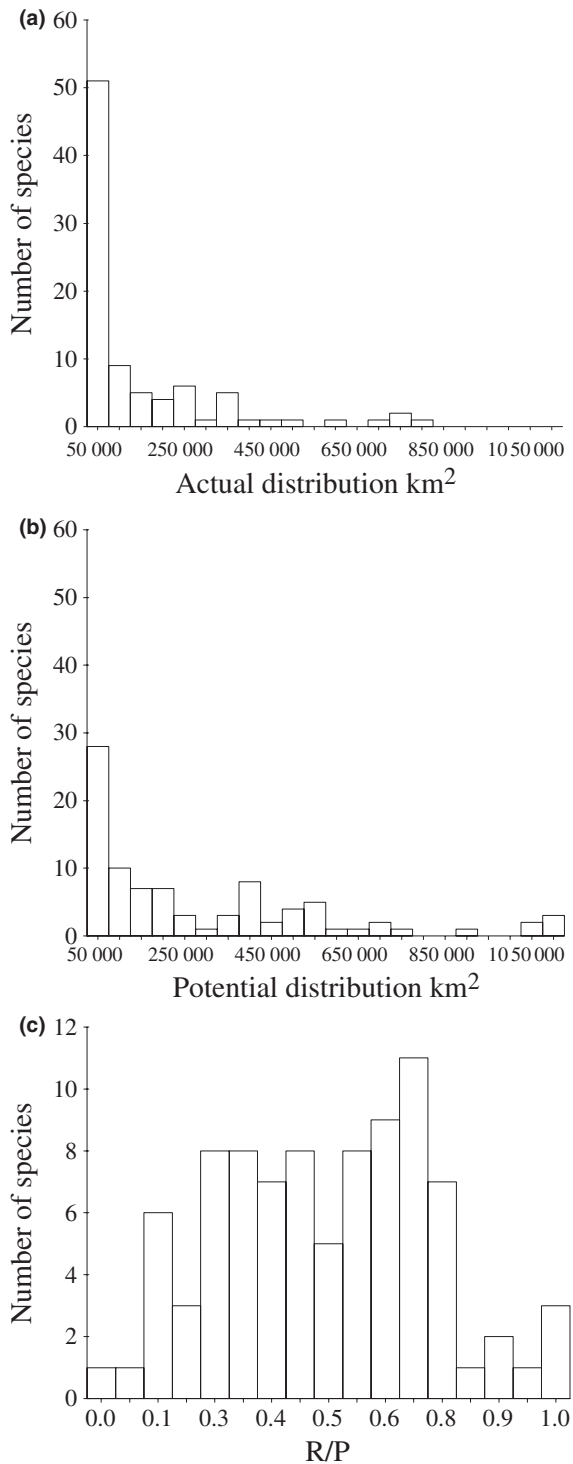


Figure 2 Frequency distributions of actual modelled and proportional distributions for 89 continental endemic mammals in Mexico. (a) Actual distributional areas ranged from 655 to 815,727 km² (median = 57,861 km², first quartile = 16,311, SD = 185,311 km²), (b) modelled ecological niches projected as species' potential distributions ranged from 1163 to 1,120,839 km² (median = 163,644 km², first quartile = 44,619, SD = 291,846 km²) for 89 continental endemic mammal species in Mexico, and (c) the ratio of actual to potential distribution (R/P) (average 0.49).

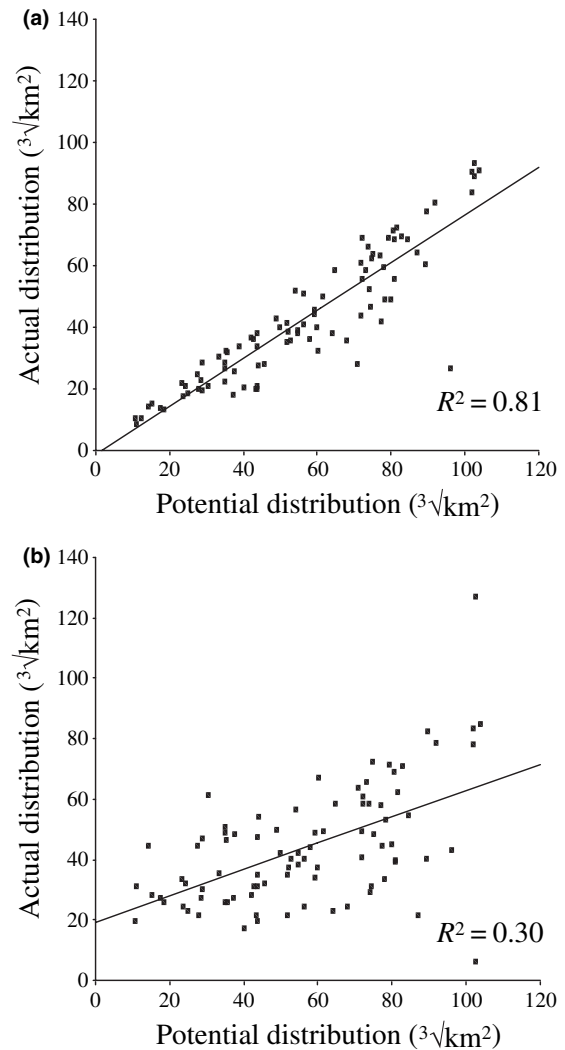


Figure 3 Relationships between modelled ecological niches projected as species' potential distributions for 89 continental endemic mammal species in Mexico and (a) actual distributions built by connecting marginal records and refined by excluding unsuitable environmental conditions ($F_{1,88} = 373.87$, $P < 0.0001$) and (b) species distributions based on Arita & Rodríguez-Tapia (2004) ($F_{1,86} = 36.57$, $P < 0.0001$).

DISCUSSION

We observed significant positive correlations between species actual and potential distributions suggesting that species with a large R also had a large P ; these results are corroborated by similar relationships with the actual distribution maps of Arita & Rodríguez-Tapia (2004) (Fig. 3a,b), and support the idea that R is strongly related to P (Soberón & Peterson, 2005). If environmental climatic factors alone determine species distributions, we would expect a complete occupancy (i.e. $R = P$) or a slope of 1 in the R - P correlation. Observed deviations from this relationship suggest the influence of other factors in shaping actual distributions in this set of endemic species. Overall, our results showed a departure from complete

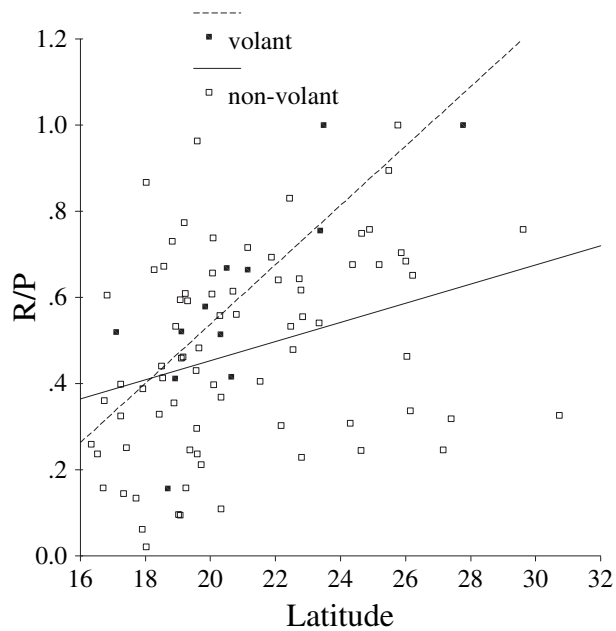


Figure 4 Relationship between ecological niche occupancy (R/P) and latitude for volant and non-volant continental endemic mammals in Mexico: volant $R/P = -0.84 + 0.07 \times \text{latitude}$, $r^2 = 0.65$, $n = 12$; non-volant $R/P = -0.07 + 0.03 \times \text{latitude}$, $r^2 = 0.13$, $n = 77$.

occupancy of potential distribution, in which most species (82%) had an R/P value < 0.70 (Fig. 2c). Other factors, such as biotic interactions, ecological and geographical barriers and limited dispersal capabilities are likely to preclude these species from filling their full potential distribution (see below).

The absence of a relationship between R/P and body mass is unexpected, given that large mammals generally have larger home ranges (Kelt & Van Vuren, 2001), higher dispersal abilities (Gaston, 2000), broader ecological niches (*sensu* Hutchinson, 1959; Ricklefs & Latham, 1992), greater thermoregulatory capacity leading to higher resistance to climate variation (Hone & Benton, 2005) and greater ranges of food items distributed over larger areas (Hone & Benton, 2005). Many studies have explored these questions (Brown, 1981; Brown & Maurer, 1987, 1989; Arita *et al.*, 1990; Pagel *et al.*, 1991; Gaston & Blackburn, 1996). Our results do not reflect this relationship, possibly because our set of endemic species was limited in body mass (< 3500 g), or possibly owing to the nonlinearity of the body mass R/P relationship. Conversely, volant endemics showed higher occupancy of potential distributions than non-volant endemics, probably due to their higher dispersal abilities (Eisenberg, 1981). No relationship was found between food habits and occupancy of species potential distributions, although such a tie might be expected given the differences in dispersal abilities and home ranges between group habits, i.e. herbivores generally show broader dispersal abilities and home ranges than carnivores (Kelt & Van Vuren, 1999, 2001; Servín *et al.*, 2003). Similarly, our expectation of a relationship with mode of locomotion (in the

finer non-volant classification) was not supported, even though the dispersal capabilities of species should be critical (Fleming, 2000; Arita & Rodríguez, 2004).

The ability of species to fill their ecological and geographical potential is closely linked to theories of coexistence (Webb *et al.*, 2002). For example, stable coexistence when resources are limited requires ecological differences between species, in which closely related taxa that are most similar ecologically are likely to be excluded locally (phylogenetically repulsed; Webb *et al.*, 2002). Because closely related species tend to be ecologically similar, it has long been recognized that the phylogenetic relationships between species in communities are likely to influence the structure of the community (Webb *et al.*, 2002). To assess this would require the analysis of ecological niches and their overlap among species within a clade across spatial scales. However, trends in geographical competitive exclusion between species would be likely to prove imperceptible at the scale of the bioclimatic models in this study (Araújo & Guisan, 2006; Soberón, 2007). Historical factors are likely to constrain species from fully occupying their total distributional potential, so continuity or fragmentation of suitable areas through time probably constrains species distributions in many areas. Consequently, the constraining effects of barriers may offer useful explanations for the observed distribution patterns. Allopatric speciation of lineages with conservative ecological niches (Peterson *et al.*, 1999; Kozak & Wiens, 2006) across vicariant distributions could be the case for many small mammals in the Transvolcanic Belt of central Mexico, where high endemism perhaps resulted from significant habitat shifts associated with climate cycles that had profound effects on aridity, seasonality and temperature during the Pleistocene (1.8 Ma–10 ka; MacFadden, 2006).

Yesson & Culham (2006) projected the potential distribution of the plant *Drosera macrantha* in the central regions of Australia using current bioclimatic envelopes. The ancestral bioclimatic envelope for this clade shows that the region of palaeoclimatic suitability was restricted to southern and eastern coastal regions, very similar to the areas currently occupied by this species. Consequently, historical factors as well as the dispersal abilities of species need to be incorporated in explaining why species do not occupy fully their entire current potential distributions. Future work should focus on integrating historical, ecological and life-history traits in explaining the occupancy of species potential distributions.

Interestingly, we observed species with small actual distributions (< 7500 km²) showing both low and high proportions of occupancy, whereas species with larger actual distributions ($> 360,000$ km²) showed consistently high R/P values of > 0.60 . It is likely that species showing small actual distributions with low occupancy may have more difficulties in dispersing to other suitable environmental areas. For example, during the Pleistocene, some endemic mammals had broader distributions in cooler periods; as temperature increased, an upward shift restricted their distributions to the highlands (Escalante *et al.*, 2004, 2007). Several endemics show restricted distributions in isolated highlands in the Sierra Madre

Occidental pine–oak forest (*Neotoma palatina*), Sierra Madre Oriental pine–oak forest (*Neotoma angustapalata*, *Peromyscus bullatus*), Transvolcanic Belt pine–oak forest (*Rhogeessa mira*, *Sorex macrodon*, *Romerolagus diazi*, *Zygoeomys trichopus*, *Liomys spectabilis*), Sierra Madre de Oaxaca pine–oak forest (*Megadontomys cryophilus*, *Habromys lepturus*, *Habromys simulatus*) and in the Sierra Madre del Sur pine–oak forest (*Rheomys mexicanus*, *Habromys chinanteco*).

Conversely, endemics with small actual distributions showing high occupancy could face combinations of environmentally suitable variables that are spatially uncommon. For example, *Myotis peninsularis* occurring in Los Cabos, Baja California Sur tropical dry forest, and *Cratogeomys fumosus* and *Peromyscus simulus* occurring in small patches of dry forest in Jalisco and Nayarit, Mexico, and Sinaloa, Mexico, respectively, are distributed in relict or rare ecoregions (CONABIO, 1999). These species reach high densities and are common year-round (Fa & Sánchez-Cordero, 1993; Fa *et al.*, 1996). However, other endemics with small distributions showing high occupancy live in more extensive ecoregions, such as *Chaetodipus lineatus* in the Mexican Plateau, *Myotis vivesi* in the Sonoran Desert and *Cynomys mexicanus* in the Sierra Madre Oriental pine–oak forest and the northern part of the Mexican Plateau.

The positive relationship between latitude and occupancy of potential distributions documented herein mirrors the results of studies with European tree species that have filled their potential distributions incompletely, supporting the idea of dispersal limitation (Svenning & Skov, 2004). Our results suggest that species at higher latitudes may more often be limited by abiotic factors, consistent with some comments and ideas of previous investigators (see Dobzhansky, 1950; MacArthur, 1972). Svenning & Skov (2004) also found little evidence of a relationship between life-history traits and occupancy of potential distributions, as we observed for our set of endemic mammals. One probable explanation for the observed latitudinal trend in occupancy of species potential distributions is the more homogeneous environment occurring in northern compared with southern Mexico. For example, the ecoregions (typically holding similar vegetation types) occurring in the north of Mexico cover larger proportional areas than in the south of Mexico, and thus present fewer ecological barriers to dispersal (CONABIO, 1999). Conversely, ecoregions in the south are more discontinuous, leading to abrupt changes among vegetation types, resulting in more ecological barriers to dispersal.

Moreover, indirect evidence that biotic factors are important in delimiting distributions in the south comes from higher species turnover rates in the south compared with the north (Arita & Rodríguez, 2004). An additional factor associated with latitude is the reduced land area southwards, given the funnel shape of Mexico. Under the idea of simple geographical constraint, a hypothetical equal-area band across latitudinal ranges would result in similar distributional occupancy by species at higher and lower latitudes, but this idea needs to be tested in more tractable (i.e. less constrained) geographical scenarios.

In summary, occupancy of potential distribution in this set of endemics appears to be influenced by a complex interplay of abiotic and biotic factors as well as by geographical barriers preventing species from dispersing to all areas that present suitable environmental conditions. As a first approximation, a species' range is governed by how well its niche requirements match a spatially varying suite of environmental factors (Brown, 1984), but barriers and constraints to dispersal (dispersal capabilities) can prevent the species from occupying other potentially suitable areas (Holt, 2003). Additional analyses should contrast models of climatically suitable areas that were occupied in the past with species current distributions (Yesson & Culham, 2006). To explore these patterns further we suggest the inclusion of broader sets of species across broader geographical regions so that entire species ranges are included.

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SUPPORTING INFORMATION

The following supporting information is available for this article:

Appendix S1 List of the 89 species of continental endemic mammals of Mexico included in this study.

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