

People and mammals in Mexico: conservation conflicts at a national scale

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Received 10 March 2004; accepted in revised form 14 September 2004

Key words: Conservation conflicts, Human population density, Mammals, Mexico, National scale

Abstract. Contrary to much supposition, recent studies, typically at global and continent-wide scales, have documented a positive relationship between spatial variations in human density and species richness of selected groups of vertebrates. How widely this pattern generalises remains unknown, and particularly how well it extends to analyses at the extent of a country and at reasonably fine spatial resolution, and to regions with well-developed mechanised agricultural infrastructure. Here, we demonstrate that there is a positive relationship between human density and mammal species richness across Mexico, and that this appears to follow from similar patterns between spatial environmental variation (particularly net primary productivity, precipitation and temperature) and both human density and mammal species richness. These results have some potentially important implications for conservation planning in the region, particularly given that optimal complementary sets of areas to represent all mammal species in Mexico tend to lie in areas of disproportionately high human density.

Introduction

The on-going regional and global decline in native biodiversity is, ultimately, associated with growth in the human population and the enterprise that sustains it, particularly that which leads to habitat destruction, fragmentation and degradation (Ehrlich 1995; Hannah et al. 1995; Kerr and Currie 1995; Cincotta et al. 2000; Liu et al. 2001; Fairbanks et al. 2002). Whilst the large 'ecological footprint' of components of this population is important, generating pressures in areas often far removed from where the people responsible reside (Rees 2001; Wackernagel et al. 2002), the extent of the conflicts between people and other species also depends in large part on the degree to which spatially they co-occur. If areas of high human density coincide with those containing a high richness of other species, conservation conflicts are likely to be severe. If, however, there is limited overlap between the two then human development activities may compromise the persistence of other species to a lesser extent.

Evidence as to the relationship between the spatial distribution of people and components of biodiversity is mixed. On the one hand, a number of studies

have demonstrated that at local-scales (e.g. areas of the size of a protected area of fine-resolution mapping unit) the abundance and/or occurrence of individual species or groups of species declines with increasing human density (e.g. Hoare and du Toit 1999; Thompson and Jones 1999; Brashares et al. 2001; Harcourt et al. 2001; Parks and Harcourt 2002; Walsh et al. 2003). Unsurprisingly, high human densities and the persistence of many native species, particularly those of large body size, are mutually exclusive. On the other hand, other studies, conducted at more regional scales (e.g. using nations or coarse-resolution mapping units), have documented broad positive relationships between human densities and the native species richness of particular groups of organisms (Hunter and Yonzon 1993; Fjeldså and Rahbek 1998; Balmford et al. 2001; McKinney 2001; Araújo 2003; Luck et al. 2004; Real et al. 2003). Here, species richness and human density tend to be higher in the same areas, arguably because they have historically responded to the same environmental factors, particularly net primary productivity; high productivity provides a larger resource base enabling more species to persist in an area, and may also have proven attractive for the establishment and enabled the subsequent growth of human populations.

Investigations of the broad relationships between human activity and species richness have principally concerned the Old World (but see Dobson et al. 1997), where the history of human occupation is much longer, and have seldom been undertaken at the within-country scale, nor at a data resolution particularly close to that employed even for broad scale conservation planning efforts (but see Chown et al. 2003). This is significant given recent concerns that existing conservation areas, and those which are high priorities for designation as such, may be located in areas of unusually high human population density (Musters et al. 2000; Harcourt et al. 2001; Parks and Harcourt 2002; Chown et al. 2003). In this paper, we address these gaps, in examining relationships between the spatial variation in the distributions of mammal species richness, human population density, landscape transformation, and conservation areas in Mexico.

The mammals of Mexico make an interesting case study for several reasons. First, the high climatic diversity, and complex topography and geological history, have resulted in Mexico having some of the highest levels of extant species richness and endemism of any country in the world (10% of global biodiversity; Mittermeier et al. 1999). Its mammal fauna ranks second in species richness at the global level (Mittermeier et al. 1999), comprising 525 species of which 30% are endemic to the country (Ceballos et al. 2002). Second, a large number of these species have extremely narrow distributions, 131 of all species occur in areas of less than 114,000 km² (Arita et al. 1997). Third, the rest of the mammal fauna shares Mexico with a population of over 98 million people, and includes one of the largest urban settlements (Mexico City) anywhere. Fourth, Mexico has a well-studied history of anthropogenic occupation (Sanders 1979; Bradbury 1982; Butzer and Butzer 1997; Challenger 1998; Grove 2000; Whitmore and Turner 2001).

Methods

Data

Information on mammal distribution was obtained from the National Information System on Mexico's Biodiversity compiled by the Mexican Commission on Biodiversity (CONABIO, <http://www.conabio.gob.mx>). This database used as a starting point the maps of Hall (1981), at a spatial resolution of a half-degree (measures on average 53.25 km on each side), but updating the information with new taxonomic and distributional data published up to the end of 2000 (Arita et al. 1997; Reid 1997; Wilson and Ruff 1999; Ceballos et al. 2002). Although reserves are almost invariably smaller in extent than entire half-degree grid cells, often substantially so, this resolution can usefully be used to seek out areas in need of conservation attention (Chown et al. 2003; Larsen and Rahbek 2003). For the purpose of this study, the analyses were restricted to land mammals, with introduced and insular species excluded. We also omitted coastal cells with less than 25% land area to avoid confounding the influence of area with other effects. A total of 423 mammal species were analysed within a grid of 705 cells.

For each grid cell we distinguished nine categories: (i) the total number of mammal species (out of a possible 423); (ii) the number of threatened species [subsuming all species categorised as vulnerable, endangered, or critical by IUCN (2000); 41 species]; (iii) the 25% most range restricted species (106 species); (iv) the 25% most range widespread species (106 species); (v) the number of endemic species (restricted to Mexican territory; 112 species), and (vi–ix) the numbers of species in each of four separate body mass categories (1st: 0.002–0.016; 2nd: 0.017–0.040; 3rd: 0.041–0.254, 4th: 0.269–587.52 kg, respectively), based on the quartiles of the body mass distribution (body mass information from Silva and Downing 1995; Reid 1997; Wilson and Ruff 1999; ~106 possible species in each category), and for convenience labelled mass 1 (quartile 1) through to mass 4 (quartile 4).

For each grid cell, values of net primary productivity, precipitation, and temperature were calculated, these three variables having been widely recognized as biologically important influences on levels of species richness (see Currie 1991; O'Brien 1998; Kerr and Currie 1999; Gaston 2000; Morin 2000; van Rensburg et al. 2002). The mean annual monthly values of precipitation (mm yr^{-1}) and temperature ($^{\circ}\text{C}$) were derived from data from many meteorological stations ($n = 5181$, Quintas 2000), data on mean annual net primary productivity ($\text{g C m}^{-2} \text{ year}^{-1}$) were derived from the GPPDI global model (Zheng et al. 2001).

Human population density data were obtained from the most recent Mexican population census (INEGI 2001), comprising the numbers of people in all human settlements (cities, towns and villages). A settlement was classified as lying within a given grid cell if the majority of its area fell within that cell, and

the population size of all settlements within that cell were summed. The intersections were carried out using ArcView GIS 3.2a.

The percentage of current land-cover that has been markedly transformed by human activities was determined for each grid cell by summing the areas of five land-cover classes: forest plantations, cultivated lands, urban areas, degraded lands and water bodies. The data were taken from The National Forest Inventory (SEMARNAT 2000), and were based on digital aerial photographs and seasonally standardised Landsat TM (at 1:125,000 scale) satellite imagery captured primarily during 1999–2000.

Data on the size (km^2), geographic limits and shape of 96 protected areas (the vast majority of significant areas) in Mexico, were provided by the National Institute of Ecology (INE, <http://www.ine.gob.mx>). Most of these protected areas correspond to IUCN categories I, II, IV and IX, these being strict nature reserves, national parks, managed nature reserve/wildlife sanctuaries, and biosphere reserves, respectively. These areas were mapped using ArcView 3.2a.

To evaluate the level of human presence bordering existing designated conservation areas, we delineated a buffer 50 km wide around each of the 96 protected areas and then calculated a mean human population density (individuals. km^{-2}) in these 50-km zones. The 50-km buffer was traced using the buffer facility of ArcView 3.2a.

Analyses

Human population density, rare and threatened species richness, and protected area size were all logarithmically (base 10) transformed, and percentage of land transformation was square root transformed, for analysis.

Spatial structure in the data was explored by determining autocorrelograms for each of the major variables in the analyses. Moran's I was calculated for 15 equal-distance classes of about 213 km in width, and spatial correlograms were produced and tested for significant spatial dependence. Since the study covered a relatively large geographic area, grid cell coordinates were not treated as Cartesian coordinates when measuring distances between them. Instead, distances along great circles were calculated to take into account the curvature of the earth's surface. Bonferroni's correction for multiple comparisons was used in assessing overall correlogram significance.

We report the results of two sets of analyses of the relationship amongst mammal species richness, human population density, environmental and landscape variables, both conducted in SAS (version 8.2). Initially, we conducted analyses assuming an independent errors model using the PROC GLM procedure. Spatial autocorrelation may, however, systematically invalidate the assumption of independent errors, distorting classical tests of association and rendering correlation coefficients, regression slopes and associated significance tests very misleading (Clifford et al. 1989; Cressie

1991; Legendre 1993; Lennon 2000; Legendre et al. 2002). To avoid this, a second set of analyses was conducted using the PROC MIXED procedure to implement spatial correlation models (Littell et al. 1996). Our spatial models assumed an exponential covariance structure as this gave a better fit to the null model than five alternative covariance structures: spherical, gaussian, linear, linear log and power.

As a measure of the pattern of complementarity (*sensu* Williams 2001) exhibited by the mammal fauna in Mexico, we identified a set of optimal solutions to the integer linear programming problem of minimising the number of grid cells such that each species is represented in at least one grid cell in the region (Underhill 1994); this is intended as a basis for exploring the issue of complementarity, and not to imply that such representation would be adequate for many purposes. This was done using the CPLEX optimisation software (ILOG 2001). In the present case, numerous equally optimal solutions exist for this problem, and the specific solution found depends on the order in which variables (cells) are introduced. To avoid repeated selection of the same solutions, each time one was sought an additional restriction was added to the problem that excluded the solution previously found (Rodrigues et al. 2000). This procedure obtains a random set of optimal solutions without replacement. Then, we explored the flexibility (Rodrigues et al. 2000) for minimizing the human population within the complementary networks, by determining whether the complementary cells contained greater human population densities than expected by chance. The human population density for all the optimal set solutions representing all species was calculated and then these values were compared with the mean human population density found for 10,000 sets (each consisting of the same number of cells as the complementary sets that represent each mammal species at least once) of randomly selected grid cells.

Results

Spatial variation

Spatial autocorrelograms for mammal species richness, human population density, and the environmental variables exhibited overall statistical significance and statistical significance at most lag distances (Figure 1). Autocorrelation for overall mammal species richness and the environmental variables declined steeply with increasing lag distances. Initially strong positive values rapidly became negative, but with some up-turn towards the longest lag distances. Autocorrelations for human population density and land transformation showed a much shallower pattern of decline towards longer lag distances, becoming positive again at the longest lag distances, likely reflecting similarly low densities of people and their impacts in the most distantly separated areas of Mexico. Figure 2 illustrates the spatial distribution patterns of the main variables across Mexico.

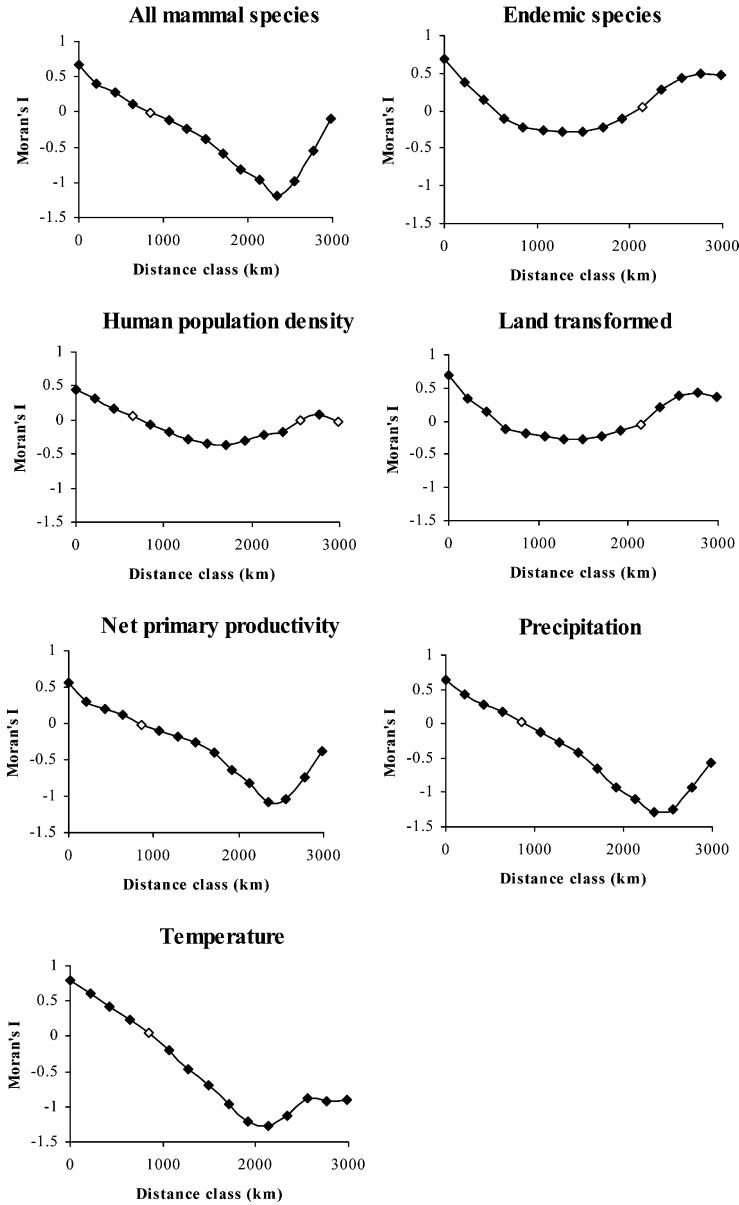


Figure 1. Spatial autocorrelograms of Mammal species and environmental variables across Mexico Distance class values represent maximum distances between pairs of points within each 213 km distance class Sequential Bonferroni correction was applied at $\alpha = 0.001$ to evaluate the statistical significance of each value of Moran's I and the overall significance of each autocorrelogram All autocorrelograms proved statistically significant overall, and filled data points represent statistically significant values.

Mammals are more speciose in the southern part of Mexico, with high richness elsewhere tending to follow the distribution of tropical moist forest. Areas of lowest richness lie in the Baja California Peninsula and the Sonora desert. Endemic and rare species are generally concentrated in areas with intermediate values of overall species richness. The most endemic rich areas lie along the Trans-Mexican Volcanic Belt and the Pacific tropical lowlands of western Mexico, while the most endemic-poor are in the Sonora and

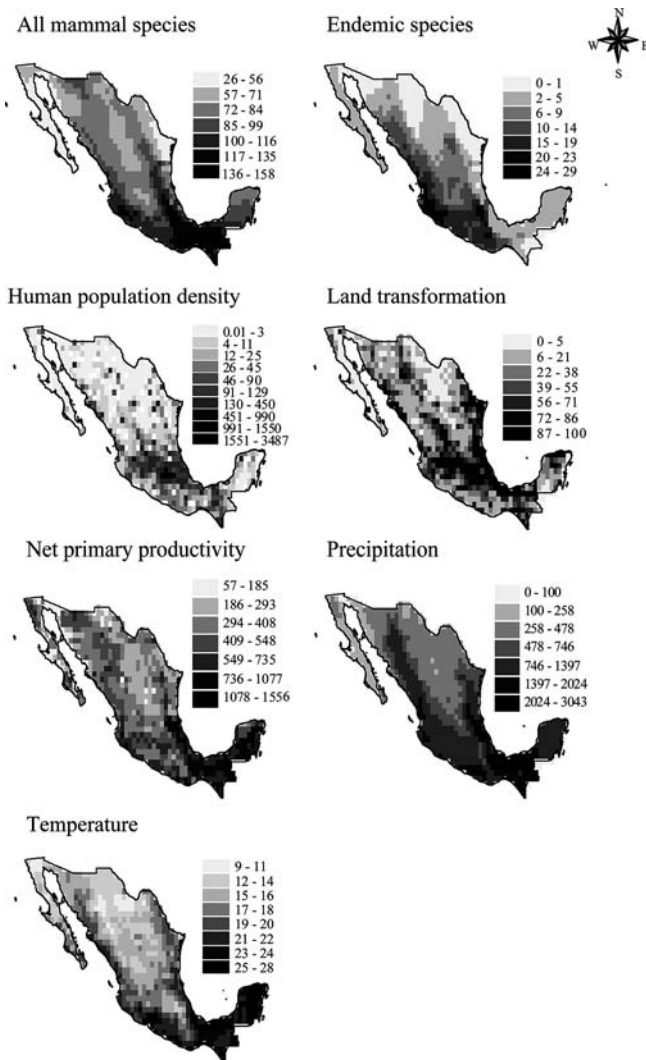


Figure 2. Patterns of distribution of main variables measured in the study. Darker colours correspond to higher values.

Chihuahua deserts and the east slopes of the Sierra Madre Oriental. Rare species are concentrated in the dry deciduous forest on the Pacific coast and montane forest along the Trans-Mexican Volcanic Belt.

The density of the human population across Mexico is highly variable (which is considered to be one of the country's population problems). Whilst the national average density is c 50 persons km^{-2} , there are areas with densities of < 1 persons km^{-2} , and others, particularly in the central Mexican basins, with densities of > 3000 persons km^{-2} . The northern parts of the country, covering big parts of the Sonora and Chihuahua deserts and particularly the Baja California peninsula, have the lowest population densities.

Net primary productivity declines northwards from an average of about $1500 \text{ g C m}^{-2} \text{ year}^{-1}$ on the southern border of Mexico to below $3 \text{ g C m}^{-2} \text{ year}^{-1}$ on the northern border. Precipitation shows similar trends. The driest part of Mexico is the north-west in the interior basins of Chihuahua and Coahuila and, more particularly, in Sonora and Baja California; the Altar and Vizcaino regions (which form part of the Sonora desert) are bone dry and as hot as anywhere on the American continent. Most of the tropical lowlands have mean annual temperatures of over $23 \text{ }^\circ\text{C}$ and are virtually frost-free. The cold land is typically over 2000 m and includes the volcanic highlands of central Mexico, the southern part of the Sierra Madre Oriental, extensive parts of the Sierra Madre Occidental and the higher ranges of Chiapas and Oaxaca. The intermediate zone lying roughly between 1000 and 2000 m is the most densely settled of the altitudinal zones, with daily temperatures ranging through $10 \text{ }^\circ\text{C}$ and rarely suffering frost or very high evaporation rates.

Land transformation has been at its most extensive across the central Mexican basins and the highlands and lowlands of the Gulf of Mexico. The most intensively cultivated areas are within the Bajio region, and the states of Tlaxcala, Puebla and Veracruz in which more than three-fourths of the lands are cropland.

Patterns of covariation

Assuming an independent errors model, total mammal species richness across Mexico is positively related to levels of net primary productivity, precipitation and temperature (Table 1, Figure 3). Inclusion of a quadratic term increases the explained variance in each case, but most markedly for precipitation, and there is no evidence that the relationships exhibit a decline phase. This is almost invariably true also of the subsets of mammal species (Table 1; threatened, endemic, rare, common, and in different mass categories). The weakest relationships are typically exhibited by the endemic, rare and common species, when these are analysed separately, suggesting that the relationships for total mammal species richness are dependent on the mix of species with different spatial distributions.

Table 1. Results of testing for bivariate relationships between measures of mammal species richness and human density, and mean annual net primary productivity (NPP), mean annual precipitation (PPT), and mean annual temperature (TP).

	NSM (LR)	SM (LR)	NSM (QR)	SM (QR)
<i>NPP</i>				
All species	$F_{1,704} = 464.0^{***}, r^2 = 0.41$	$F_{1,704} = 91.5^{**}, AIC = 4612.2$	$F_{1,704} = 124.4^{***}, r^2 = 0.43$	$F_{1,704} = 8.3^{**}, AIC = 4580.5$
Threatened	$F_{1,704} = 412.9^{***}, r^2 = 0.37$	$F_{1,704} = 0.01ns, AIC = -2109.0$	$F_{1,704} = 312.8^{***}, r^2 = 0.40$	$F_{1,704} = 2.9ns, AIC = 2255.3$
Endemic	$F_{1,704} = 23.2^{***}, r^2 = 0.03$	$F_{1,704} = 7.9^{**}, AIC = 3074.9$	$F_{1,704} = 31.8^{***}, r^2 = 0.10$	$F_{1,704} = 8.4^{**}, AIC = 3038.7$
Rare	$F_{1,704} = 123.5^{***}, r^2 = 0.15$	$F_{1,704} = 12.8^{**}, AIC = 2138.0$	$F_{1,704} = 21.1^{**}, r^2 = 0.17$	$F_{1,704} = 22.8^{**}, AIC = 2211.0$
Common	$F_{1,704} = 8.4^{**}, r^2 = 0.18$	$F_{1,704} = 3.4^{*}, AIC = 4018.0$	$F_{1,704} = 19.2^{**}, r^2 = 0.20$	$F_{1,704} = 11.5^{**}, AIC = 4111.0$
Mass1	$F_{1,704} = 283.2^{***}, r^2 = 0.28$	$F_{1,704} = 50.6^{**}, AIC = 3425.5$	$F_{1,704} = 180.7^{***}, r^2 = 0.34$	$F_{1,704} = 2.9^{*}, AIC = 3423.8$
Mass2	$F_{1,704} = 172.9^{***}, r^2 = 0.19$	$F_{1,704} = 0.1ns, AIC = 3293.8$	$F_{1,704} = 118.4^{**}, r^2 = 0.25$	$F_{1,704} = 2.4^{*}, AIC = 3367.9$
Mass3	$F_{1,704} = 504.7^{***}, r^2 = 0.40$	$F_{1,704} = 0.3ns, AIC = 2694.1$	$F_{1,704} = 266.0^{***}, r^2 = 0.43$	$F_{1,704} = 2.8ns, AIC = 2449.0$
Mass4	$F_{1,704} = 365.5^{***}, r^2 = 0.34$	$F_{1,704} = 19.9^{*}, AIC = 2982.1$	$F_{1,704} = 189.2^{***}, r^2 = 0.38$	$F_{1,704} = 12.6^{**}, AIC = 2784.0$
Human population	$F_{1,704} = 129.0^{**}, r^2 = 0.20$	$F_{1,704} = 6.5^{*}, AIC = 1565.7$	$F_{1,704} = 1322.0^{***}, r^2 = 0.28$	$F_{1,704} = 10.5^{**}, AIC = 1537.5$
<i>PPT</i>				
All species	$F_{1,704} = 295.8^{***}, r^2 = 0.29$	$F_{1,704} = 25.8^{*}, AIC = 3618.4$	$F_{1,704} = 579.0^{***}, r^2 = 0.62$	$F_{1,704} = 13.5^{**}, AIC = 4577.0$
Threatened	$F_{1,704} = 593.1^{***}, r^2 = 0.46$	$F_{1,704} = 1.2ns, AIC = -2116.0$	$F_{1,704} = 15.05^{***}, r^2 = 0.47$	$F_{1,704} = 4.87^{**}, AIC = 2256.0$
Endemic	$F_{1,704} = 75.97^{***}, r^2 = 0.11$	$F_{1,704} = 20.4^{*}, AIC = 3025.1$	$F_{1,704} = 147.5^{***}, r^2 = 0.29$	$F_{1,704} = 29.7^{**}, AIC = 3225.2$
Rare	$F_{1,704} = 32.38^{***}, r^2 = 0.04$	$F_{1,704} = 1.3^{*}, AIC = 2140.0$	$F_{1,704} = 21.95^{***}, r^2 = 0.10$	$F_{1,704} = 9.78^{**}, AIC = 2434.3$
Common	$F_{1,704} = 10.1^{**}, r^2 = 0.11$	$F_{1,704} = 5.7^{*}, AIC = 4014.2$	$F_{1,704} = 41.14^{**}, r^2 = 0.17$	$F_{1,704} = 6.06^{**}, AIC = 3928.4$
Mass1	$F_{1,704} = 671.1^{***}, r^2 = 0.49$	$F_{1,704} = 267.0^{**}, AIC = 3442.9$	$F_{1,704} = 453.7^{***}, r^2 = 0.56$	$F_{1,704} = 33.66^{**}, AIC = 3413.4$
Mass2	$F_{1,704} = 347^{***}, r^2 = 0.33$	$F_{1,704} = 0.5ns, AIC = 3294.0$	$F_{1,704} = 239.1^{***}, r^2 = 0.41$	$F_{1,704} = 10.3^{*}, AIC = 3363.2$
Mass3	$F_{1,704} = 907.4^{***}, r^2 = 0.56$	$F_{1,704} = 12.4^{*}, AIC = 2092.6$	$F_{1,704} = 484.1^{***}, r^2 = 0.58$	$F_{1,704} = 25.68^{**}, AIC = 2627.3$
Mass4	$F_{1,704} = 463.4^{***}, r^2 = 0.39$	$F_{1,704} = 4.5^{*}, AIC = 2980.6$	$F_{1,704} = 237.6^{***}, r^2 = 0.41$	$F_{1,704} = 6.9^{*}, AIC = 2784.3$
Human population	$F_{1,704} = 219.2^{***}, r^2 = 0.24$	$F_{1,704} = 12.1^{*}, AIC = 1198.8$	$F_{1,704} = 165.7^{**}, r^2 = 0.32$	$F_{1,704} = 4.6^{*}, AIC = 1552.5$
<i>TP</i>				
All species	$F_{1,704} = 295.8^{***}, r^2 = 0.29$	$F_{1,704} = 10.9^{**}, AIC = 4592.5$	$F_{1,704} = 161.1^{***}, r^2 = 0.31$	$F_{1,704} = 25.2^{**}, AIC = 4536.8$
Threatened	$F_{1,704} = 593.1^{***}, r^2 = 0.46$	$F_{1,704} = 0.4ns, AIC = -2125.0$	$F_{1,704} = 38.5^{***}, r^2 = 0.38$	$F_{1,704} = 3.8^{*}, AIC = 2228.7$
Endemic	$F_{1,704} = 75.97^{***}, r^2 = 0.11$	$F_{1,704} = 7.4^{*}, AIC = 3065.3$	$F_{1,704} = 55.2^{***}, r^2 = 0.13$	$F_{1,704} = 14.9^{*}, AIC = 3006.1$
Rare	$F_{1,704} = 32.38^{***}, r^2 = 0.04$	$F_{1,704} = 0.01ns, AIC = 2132.1$	$F_{1,704} = 4.9^{*}, r^2 = 0.08$	$F_{1,704} = 2.2ns, AIC = 2231.9$
Common	$F_{1,704} = 10.1^{**}, r^2 = 0.11$	$F_{1,704} = 4.9^{*}, AIC = 3411.5$	$F_{1,704} = 35.9^{***}, r^2 = 0.10$	$F_{1,704} = 4.9^{*}, AIC = 3931.7$
Mass1	$F_{1,704} = 671.1^{***}, r^2 = 0.49$	$F_{1,704} = 4.9^{*}, AIC = 3411.5$	$F_{1,704} = 108.3^{***}, r^2 = 0.23$	$F_{1,704} = 6.8^{*}, AIC = 3388.5$
Mass2	$F_{1,704} = 347^{***}, r^2 = 0.33$	$F_{1,704} = 5.1^{*}, AIC = 3279.7$	$F_{1,704} = 72.7^{***}, r^2 = 0.17$	$F_{1,704} = 7.1^{*}, AIC = 3279.7$
Mass3	$F_{1,704} = 907.4^{***}, r^2 = 0.56$	$F_{1,704} = 7.4^{*}, AIC = 2677.3$	$F_{1,704} = 207.9^{***}, r^2 = 0.37$	$F_{1,704} = 4.4^{*}, AIC = 2585.1$
Mass4	$F_{1,704} = 463.4^{***}, r^2 = 0.39$	$F_{1,704} = 4.7^{*}, AIC = 2969.5$	$F_{1,704} = 118.3^{***}, r^2 = 0.25$	$F_{1,704} = 5.3^{*}, AIC = 2985.1$
Human population	$F_{1,704} = 219.2^{***}, r^2 = 0.24$	$F_{1,704} = 3.9^{*}, AIC = 1559.4$	$F_{1,704} = 98.1^{**}, r^2 = 0.22$	$F_{1,704} = 3.3^{*}, AIC = 1512.8$

NSM = Non-spatial model (model fit indicated by r^2), LR = linear regression, QR = quadratic regression, SM = Selected spatial model (model fit indicated by AIC), All relationships were positive. $p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. ns = non significant relationship.

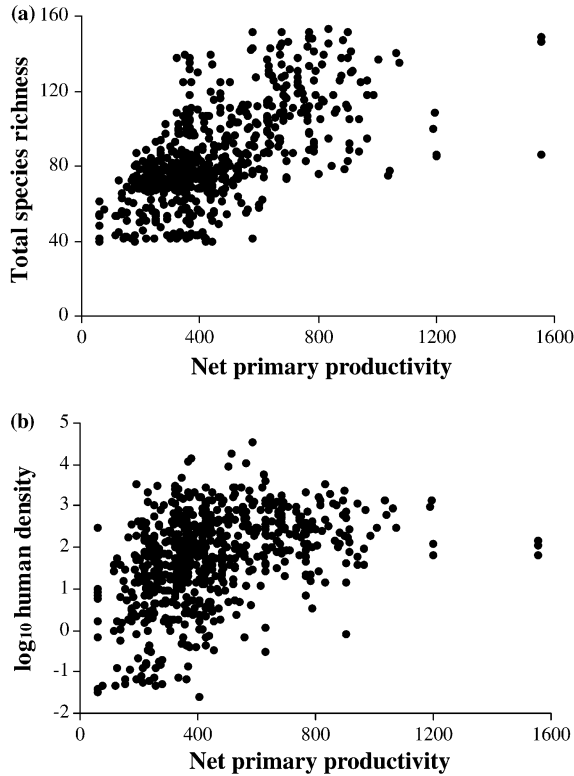


Figure 3. Relationships between net primary productivity and (a) total mammal species richness and (b) \log_{10} human population density.

Controlling for the effects of spatial autocorrelation typically weakens the relationships between mammal species richness and net primary productivity, precipitation or temperature markedly (Table 1). For total species richness these remain statistically significant, but for some combinations of subsets of the mammal assemblage and environmental variables this is not the case. In particular, for threatened species and those of intermediate body mass previously statistically significant relationships are rendered non-significant when controlling for spatial autocorrelation.

As with total mammal species richness, human population density exhibits positive relationships with the environmental variables, whether or not spatial autocorrelation is controlled for (Table 1), although the highest human population densities tend to be associated with somewhat lower levels of net primary productivity than are the highest levels of species richness (Figure 3). In consequence, total mammal species richness and human population density are positively related, using an independent errors model and a model controlling for spatial autocorrelation, with some improvement in model fit with the inclusion of a quadratic term (and no evidence for a decline phase; Table 2,

Table 2. Results of testing for bivariate relationships between measures of mammal species richness and human population density and percentage of land transformed.

	NSM (LR)	SM (LR)	NSM (QR)	SM (QR)
Human population density				
Total richness	F _{1,704} = 134.4 ^{***} , r ² = 0.26	F _{1,704} = 57.5 [*] , AIC = 4602.0	F _{1,704} = 124.9 ^{***} , r ² = 0.27	F _{1,704} = 17.7 [*] , AIC = 4546.0
Threatened	F _{1,704} = 94.1 ^{***} , r ² = 0.12	F _{1,704} = 1.8 ns, AIC = -2127.0	F _{1,704} = 6.5 ^{***} , r ² = 0.20	F _{1,704} = 4.1 ns, AIC = 2222.7
Endemic	F _{1,704} = 229.3 ^{***} , r ² = 0.25	F _{1,704} = 4.9 ^{**} , AIC = 3065.1	F _{1,704} = 97.3 ^{***} , r ² = 0.28	F _{1,704} = 5.3 [*] , AIC = 3008.4
Rare	F _{1,704} = 41.5 ^{**} , r ² = 0.37	F _{1,704} = 8.3 [*] , AIC = 2122.7	F _{1,704} = 12.3 ^{***} , r ² = 0.39	F _{1,704} = 9.2 [*] , AIC = 2183.2
Common	F _{1,704} = 75.1 ^{***} , r ² = 0.41	F _{1,704} = 6.7 [*] , AIC = 4009.0	F _{1,704} = 41.9 ^{***} , r ² = 0.42	F _{1,704} = 3.04 [*] , AIC = 3900.4
Mass1	F _{1,704} = 210.1 ^{***} , r ² = 0.29	F _{1,704} = 2.1 ns, AIC = 2421.2	F _{1,704} = 153.8 ^{***} , r ² = 0.31	F _{1,704} = 4.9 [*] , AIC = 3391.2
Mass2	F _{1,704} = 215.9 ^{***} , r ² = 0.23	F _{1,704} = 16.2 [*] , AIC = 3383.9	F _{1,704} = 127.5 ^{***} , r ² = 0.27	F _{1,704} = 3.6 [*] , AIC = 3334.8
Mass3	F _{1,704} = 175.3 ^{***} , r ² = 0.19	F _{1,704} = 2.0 ns, AIC = 2683.4	F _{1,704} = 76.2 ^{***} , r ² = 0.21	F _{1,704} = 1.78 ns, AIC = 2589.0
Mass4	F _{1,704} = 49.9 ^{**} , r ² = 0.11	F _{1,704} = 0.6 ns, AIC = 2972.2	F _{1,704} = 23.5 ^{**} , r ² = 0.13	F _{1,704} = 2.6 ns, AIC = 2750.6
Land transformed				
Total richness	F _{1,704} = 75.7 ^{***} , r ² = 0.28	F _{1,704} = 21.7 ^{**} , AIC = 4403.7	F _{1,704} = 45.7 ^{***} , r ² = 0.29	F _{1,704} = 16.3 ^{***} , AIC = 4552.1
Threatened	F _{1,704} = 23.8 ^{***} , r ² = 0.03	F _{1,704} = 0.3 ns, AIC = 2124.3	F _{1,704} = 3.3 ^{***} , r ² = 0.10	F _{1,704} = 6.5 ns, AIC = 2228.1
Endemic	F _{1,704} = 81.3 ^{***} , r ² = 0.10	F _{1,704} = 16.8 [*] , AIC = 3066.0	F _{1,704} = 14.4 ^{***} , r ² = 0.11	F _{1,704} = 5.9 [*] , AIC = 3012.3
Rare	F _{1,704} = 237.8 ^{***} , r ² = 0.25	F _{1,704} = 6.9 [*] , AIC = 2132.1	F _{1,704} = 93.4 ^{***} , r ² = 0.30	F _{1,704} = 13.5 [*] , AIC = 1215.1
Common	F _{1,704} = 131.6 ^{***} , r ² = 0.37	F _{1,704} = 14.3 [*] , AIC = 2897.5	F _{1,704} = 22.8 ^{***} , r ² = 0.38	F _{1,704} = 4.2 [*] , AIC = 3930.2
Mass1	F _{1,704} = 17.7 ^{***} , r ² = 0.23	F _{1,704} = 7.8 [*] , AIC = 3423.8	F _{1,704} = 39.4 ^{***} , r ² = 0.25	F _{1,704} = 3.7 [*] , AIC = 3395.3
Mass2	F _{1,704} = 16.28 [*] , r ² = 0.17	F _{1,704} = 0.2 ns, AIC = 3285.5	F _{1,704} = 26.2 ^{***} , r ² = 0.20	F _{1,704} = 2.5 ns, AIC = 3341.0
Mass3	F _{1,704} = 24.4 ^{***} , r ² = 0.13	F _{1,704} = 5.9 [*] , AIC = 2679.6	F _{1,704} = 50.9 ^{***} , r ² = 0.14	F _{1,704} = 8.7 ^{**} , AIC = 2592.9
Mass4	F _{1,704} = 20.3 ^{***} , r ² = 0.02	F _{1,704} = 1.1 ns, AIC = 2974.1	F _{1,704} = 26.3 ^{***} , r ² = 0.10	F _{1,704} = 2.6 ns, AIC = 2757.7

NSM = Nonspatial model (model fit indicated by r²), LR = linear regression, QR = quadratic regression, SM = Selected spatial model (model fit indicated by AIC). All relationships were positive. * p < 0.05, ** p < 0.01, *** p < 0.001. ns = non significant relationship.

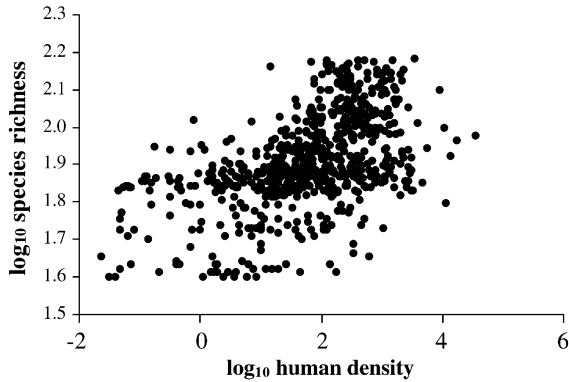


Figure 4. Log-log relationship between total mammal species richness and human population density.

Figure 4). Using an independent errors model, the species richness of subsets of the mammal assemblage is also always significantly positively related to human population density, although in three cases (threatened species and species in two of the mass categories) these relationships lose their statistical significance when controlling for spatial autocorrelation (Table 2).

Patterns of land transformation across Mexico are positively associated with levels of human population density ($r^2 = 0.21$; $AIC = 1517.6$, $F = 13.29$, $p < 0.01$). This is reflected in typically marked positive relationships between the overall numbers of mammal species, the numbers in different subsets of the assemblage, and the level of land transformation (Table 2), with a similar pattern of degradation of these relationships when spatial autocorrelation is controlled for.

Conservation areas

A total of 92 grid cells form part of one or more of each of 100 optimal solutions, each requiring 38 grid cells, to the problem of representing each mammal species in at least one grid cell across Mexico. In the optimal complementarity sets, human population density can vary between 52.9 and 69.4 persons km^{-2} , values significantly higher than expected from a random selection of sites (44.9–46.1 persons km^{-2} , limits of the 95% confidence interval for the 10,000 random draws of 38 cells).

Most existing designated Mexican protected areas are not situated in regions of lower than national average human density (c 50 persons km^{-2}). The size of protected areas is negatively correlated with human population density, such that small-protected areas are more likely than are large protected areas to be located in regions of high human population density ($r^2 = -0.29$, $p < 0.001$; Figure 5).

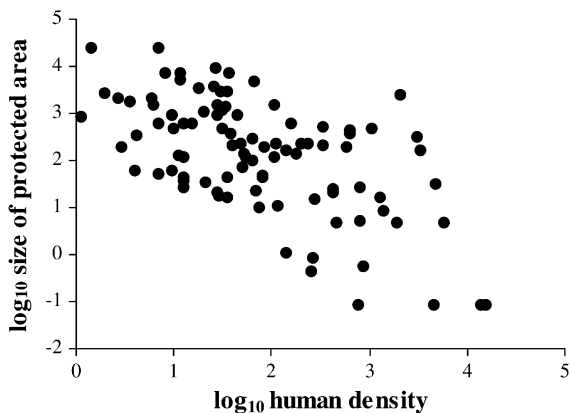


Figure 5. \log_{10} area of 96 Mexican designated protected areas in relation to \log_{10} human population density within a 50 km buffer zone.

Discussion

In keeping with previous analyses at coarser resolutions and/or in other biogeographic regions of the world (see Introduction for references), spatial variation in the species richness of mammals across Mexico is positively correlated with spatial variation in the numbers of people. That is, on average, areas in which there are more mammal species also tend to have more people. The existence of broadly similar relationships of both mammal species richness and human population density with environmental variables supports the argument that the covariation between mammal species richness and human density is a consequence of them responding in similar ways to spatial variation in environmental conditions (Table 1, Figure 3).

It has been argued that positive relationships between numbers of people and patterns of species richness are likely to be more characteristic of regions in which human populations are more dependent on the exploitation of local resources for subsistence agriculture, and therefore more tightly associated with natural patterns of resource provision, than those with a well-developed mechanized agricultural infrastructure (Huston 1993, 2001). However, Mexico has just such a well-developed infrastructure, including extensive areas of intensive agriculture (FAO 2000) and clearly this is not sufficient entirely to disrupt the relationship between human density and mammal species richness at the spatial resolution examined herein. Indeed, the variation about this relationship might be significantly reduced were it possible to improve on the quality of the estimation of the density of humans in different areas.

One explanation for this result is that whilst a well-developed mechanized agricultural infrastructure reduces the immediate dependency of human populations on natural resource provision, and enables production of substantial quantities of foodstuffs from areas where previously this may not have been

possible, in the main such an infrastructure is employed in those same areas that historically tended to provide the greatest natural resource provision. If this is so, then the positive relationship between mammal species richness and human density has persisted in Mexico despite the long history of human occupation of the region, the extensive (and sometimes sophisticated) land transformation that accompanied this, and the ebbs and flows in this transformation associated with the rise and fall of a number of major civilisations. Historical demographic research has estimated that before European conquest, the Mexican population may already have exceeded 20 million people and was larger than that of any other comparable American area (Fox 1971). Central Mexico alone may have had a pre-Columbian population of 11 million people (Fox 1971; Zambardino 1980).

Why has the relationship between mammal species richness and human density persisted in the face of such human population pressures, and the associated land transformation? There are two possible reasons. First, there may be sufficient habitat heterogeneity even at a half-degree resolution to enable such persistence (Redford and Dinerstein 1994), with highly disturbed areas residing alongside much less disturbed ones. The complex topography of Mexico would certainly promote such an effect. This is especially true, for example, of the Mexican Mesa Central where highly fertile agricultural lands, large human settlements, and mountains systems lie in close proximity (Butzer and Butzer 1997). In such a circumstance, one might have imagined that small-bodied, and therefore typically less space demanding, species of mammals would be more likely to exhibit a positive species richness-human density relationship, and large-bodied species requiring large home ranges would be less likely to do so. However, there is no evidence for a simple effect of body size on the likelihood of observing such a relationship for the mammals of Mexico, with all body size classes exhibiting a species richness-human density and a species richness-land transformation relationship when treating data points as independent, and only one of the intermediate body size classes exhibiting a species richness-human density relationship and the smallest and an intermediate body size class exhibiting a species richness-land transformation relationship when controlling for spatial autocorrelation (Table 2).

With this first explanation, the species richness-human density relationship has been an inevitable consequence of patterns of human population establishment and growth, from perhaps before these populations had a major influence on patterns of occurrence of other mammal species (see Woodroffe 2000). The relationship has persisted probably because mammal richness has been depressed across much of the breadth of human densities, and not simply at the highest levels. Some of the largest mammals have suffered massive reductions in their geographic ranges in Mexico in recent history (e.g. black bear, *Ursus americanus* and bison, *Bison bison*) and others have undergone regional extinction (e.g. grey wolf, *Canis lupus*). This depression, perhaps particularly at higher human densities, is likely to be more marked than portrayed in the analyses here, as these take no account of the population viability

of each species in different areas, nor of possible more recent changes in distributions.

The second possible reason that a positive species richness-human density relationship might have persisted is that extant Mexican mammals have a reasonably high resilience to human activities, with those that did not do so having already been lost. Such filtering effects have been argued to have given rise to, for example, the otherwise counter-intuitive observation that Pacific islands with longer histories of human occupation often tend at present to have fewer threatened species (Pimm et al. 1995). In this connection, it is noteworthy that when accounting for spatial autocorrelation, there is no relationship between the species richness of threatened mammals and human density across Mexico.

The positive relationship between mammal species richness and human population density suggests that the conservation of mammals in Mexico may face greater conflicts than might otherwise be the case. Although patterns of complementarity and species richness need not coincide, this inference is confirmed by considering the distribution of those areas that would be required simply to represent each of the mammal species by at least one spatial occurrence. These have significantly higher human densities than would be expected by chance. Turning to protected areas that have already been designated, underlines this message further. These also lie in areas with disproportionately high human population densities. Moreover, the smaller the protected area the higher the human density in the surrounding lands (Figure 5; see Park and Harcourt 2002 and references therein), suggesting that not only do small protected areas suffer from increased external pressures because of their high perimeter to area ratios, but they may suffer disproportionately because the potential external pressures are much more intense (Harcourt et al. 2001).

In conclusion, the results reported here demonstrate that positive relationships between human density and species richness (i) are not restricted to the Old World but are also exhibited in the New World, where the history of human occupation is much shorter, (ii) are exhibited at a within-country scale, (iii) are exhibited at a finer data resolution than that employed in the majority of previous studies, and (iv) may have significant implications for conservation planning in Mexico.

Acknowledgements

We are grateful to A.M. Brewer, K.L. Evans, S.F. Jackson, O. Petchey for assistance and advice. X. López, D. Valenzuela and two anonymous reviewers are thanked for their helpful comments on the manuscript. The Instituto Nacional de Ecología kindly provided access to the National Forest Inventory and protected areas data. L-B.V. is funded by CONACYT (123021) and SEP.

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