

Protection of Mammal Diversity in Central America

CLINTON N. JENKINS* AND CHANDRA GIRI†

*Nicholas School of the Environment and Earth Sciences, Duke University, Box 90328, Durham, NC 27708-0328, U.S.A., email clinton.jenkins@duke.edu

†SAIC/National Center for Earth Resources Observation and Science (EROS), 47914 252nd Street, Sioux Falls, SD 57198-0002, U.S.A.

Abstract: *Central America is exceptionally rich in biodiversity, but varies widely in the attention its countries devote to conservation. Protected areas, widely considered the cornerstone of conservation, were not always created with the intent of conserving that biodiversity. We assessed how well the protected-area system of Central America includes the region's mammal diversity. This first required a refinement of existing range maps to reduce their extensive errors of commission (i.e., predicted presences in places where species do not occur). For this refinement, we used the ecological limits of each species to identify and remove unsuitable areas from the range. We then compared these maps with the locations of protected areas to measure the habitat protected for each of the region's 250 endemic mammals. The species most vulnerable to extinction—those with small ranges—were largely outside protected areas. Nevertheless, the most strictly protected areas tended toward areas with many small-ranged species. To improve the protection coverage of mammal diversity in the region, we identified a set of priority sites that would best complement the existing protected areas. Protecting these new sites would require a relatively small increase in the total area protected, but could greatly enhance mammal conservation.*

Keywords: biodiversity, conservation priorities, hotspot, mammal, protected area, range map, species distribution

Protección de la Diversidad de Mamíferos en América Central

Resumen: *América Central es excepcionalmente rica en biodiversidad, pero varía ampliamente en la atención que sus países dedican a la conservación. Las áreas protegidas, ampliamente consideradas las piedras angulares de la conservación, no siempre fueron creadas con la intención de conservar esa biodiversidad. Evaluamos cuanta biodiversidad de mamíferos de la región está incluida en el sistema de áreas protegidas de América Central. Esto requirió primero del refinamiento de los mapas de distribución para reducir sus extensos errores de comisión (i.e., presencia pronosticada en sitios donde no ocurren las especies). Para este refinamiento, utilizamos los límites ecológicos de cada especie para identificar y remover áreas no adecuadas. Posteriormente comparamos estos mapas con la localización de áreas protegidas para medir el hábitat protegido para cada una de las 250 especies de mamíferos endémicas de la región. Las especies más vulnerables a la extinción—aquellas con áreas de distribución pequeñas—estaban principalmente fuera de las áreas protegidas. Sin embargo, las áreas más estrictamente protegidas tendieron hacia áreas con muchas especies de área de distribución pequeña. Para mejorar la cobertura de protección a la diversidad de mamíferos de la región, identificamos un conjunto de sitios prioritarios que serían el mejor complemento de las áreas protegidas existentes. La protección de estos sitios nuevos requeriría un incremento relativamente pequeño del área protegida total, pero podría incrementar la conservación de mamíferos.*

Palabras Clave: área protegida, biodiversidad, distribución de especies, mamífero, mapa de distribución, prioridades de conservación, sitio de importancia para la conservación

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Introduction

Protected areas are a leading strategy for conserving biodiversity and are the source of much debate. This debate includes whether or not they work (Bruner et al. 2001; Stern et al. 2001; Vanclay 2001; Ferraro & Pattanayak 2006), what they protect, and where we should create new ones (Margules & Pressey 2000). Gaps exist in the protected-area system with regard to vertebrate biodiversity globally (Rodrigues et al. 2004a, 2004b) and specifically for bats in the Americas (Andelman & Willig 2003), at least at coarse scales. Protecting biodiversity though has not been the only, or even the predominant, reason for designating protected areas. Counter examples include places set aside for cultural or scenic values. Given this reality, there is no a priori reason to expect protected areas to be located in areas important for biodiversity. Whatever the reason for their creation, the location of protected areas is critically important. They are the areas likely to retain natural conditions into the future, and so the species within them likely have the best chance to avoid extinction.

To explore the potential of protected areas to conserve biodiversity in Central America, we evaluated how inclusive they are of the region's mammal diversity. We then identified new areas that could improve the coverage of mammal diversity in the region. Other researchers have identified priority areas for mammals in this region and globally (Ceballos et al. 2005; Ceballos & Ehrlich 2006). Nevertheless, the scale of those studies was too coarse (approximately 10,000 km²) to identify specific sites for protection, and they did not include existing protected areas in their assessments. Cantú et al. (2004) explicitly evaluated Mexico's existing and proposed protected areas with respect to how they cover the country's topography, soil, and vegetation types. Nevertheless, they did not recommend alternative sites for protection. Ceballos (2007) continued this line of research at a finer scale in his evaluation of Mexico's protected areas and recommends new areas to protect. We furthered this line of research by analyzing all mammals and protected areas in Central America and recommending priority areas for protection.

Existing maps of biodiversity, unfortunately, are often not precise enough to assess biodiversity protection at a fine scale. The typical range map is an "extent of occurrence" map (Gaston 1994). It shows the maximum extent where a species might occur today or did occur in the recent past. This includes places now lost to deforestation and the like. The consequence is sometimes severe errors of commission in which species are shown as present where they never were or where their populations are now extinct (e.g., Ceballos & Ehrlich 2002). Not correcting these errors can produce a biased view of where biodiversity concentrates (Hurlbert & White 2005; Hurlbert & Jetz 2007). This can then lead to sug-

gesting protection of an area because it holds particular species, when in fact it does not have them. Rodrigues et al. (2004a) found such errors of commission to be the largest source of errors in their gap analysis of the global protected area system. Harris et al. (2005) and Harris and Pimm (2007) explicitly reduced commission errors in their analyses of threatened forest endemic birds, finding it made a critical difference in their conclusions. We pursue a similar approach here.

With other factors held equal, species with habitat inside protected areas are probably less threatened than species with no habitat in protected areas. Protected areas also vary in their level of intended protection. If protected areas efficiently cover biodiversity, then we should expect protection to show a spatial bias toward the places with high biodiversity value and to have stricter protection in those places. To assess protection levels for mammals, we quantified the amount of habitat each species has in current protected areas.

Not all species are of equal concern for conservation. Some Central American species also occur outside the region and may be protected there. We restricted our study to the region's endemic mammals because they can be protected nowhere else. Of the endemic species, those with small ranges likely face a higher risk of extinction than species with larger ranges. Range size is one of the most important factors predisposing a species to extinction (Manne et al. 1999; Purvis et al. 2000; Manne & Pimm 2001). If the goal is to prevent extinctions, then perhaps species with small ranges should be a priority (e.g., Ceballos et al. 1998; Ceballos 2007). We mapped the concentrations of small-ranged species throughout the region and then evaluated their current protection.

To ensure the future survival of all mammals in the region, each species must have enough habitat in which to live. The current protected areas include habitat for about half of the region's endemic mammals. We used systematic planning methods to identify the crucial areas needed for the remaining endemic mammals. If protected, these areas would help establish a completely representative network of areas for mammal conservation.

Methods

The source of original geographic range maps was the NatureServe database (Patterson et al. 2005). On the basis of those maps, we designated 250 species as endemic to the study area (Fig. 1). We defined the study area along political lines rather than excluding northern Mexico as in stricter definitions of Central America. Country borders may not follow biogeographic boundaries, but countries are largely responsible for creating protected areas. For analysis, we converted the range maps to an ArcGIS raster

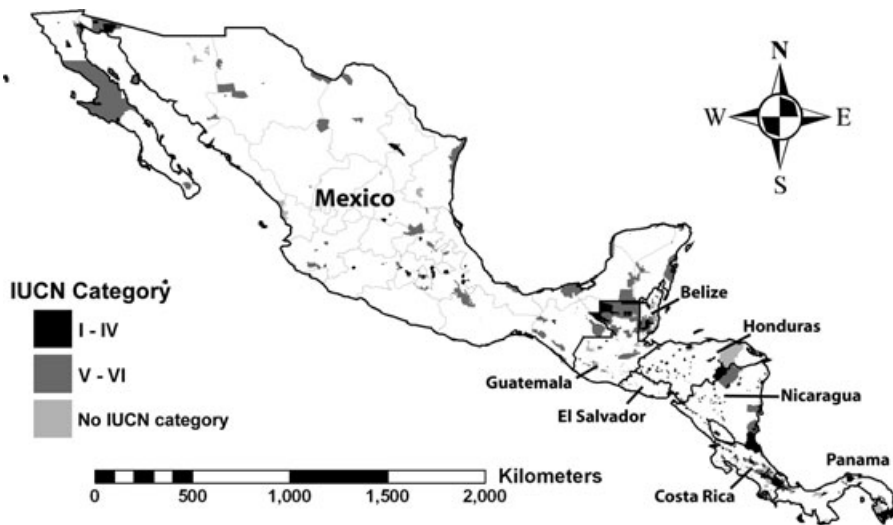


Figure 1. Study region and protected areas in Central America. Countries and Mexican states are outlined in black and gray, respectively. Protected areas are shaded according to World Conservation Union (IUCN) category. Categories I-IV represent strict protection and categories V and VI less strict protection. Some protected areas have not been classified by the IUCN.

geodatabase at a 5-km resolution. Analyses were done in ArcGIS (ESRI, Redlands, California).

For each species we refined the maps by using ecological limits in a deductive model. Variables were elevation range and suitable land cover for a species. These data are from 2 guides to mammals (Emmons 1997; Reid 1997) and species reports from the journal *Mammalian Species*. We found sufficient elevation data for 144 species and land cover data for 153 species. For species with insufficient data, we retained their original range map. To be conservative in considering areas as unsuitable, the elevational range used was the widest range from all sources combined. For example, if one source listed 500–1000 m as the range and another 300–700 m, then the provisional range was 300–1000 m. We then buffered that by 100 m on either side (e.g., 200–1100 m). This reduced the potential for omission errors (eliminating suitable areas) due to poor coverage in the literature or errors in the elevation map.

Land-cover data were from 2 sources, 1 for Mexico only (Mas et al. 2002, 2004) and 1 for the rest of Central America (Giri & Jenkins 2005). The Mas et al. (2002, 2004) data were derived from Landsat satellite imagery (30-m resolution). This provided better spatial and thematic details than Giri and Jenkins (2005), who derived their map from coarser MODIS satellite imagery (500-m resolution). To match the data resolutions, we resampled the Mas et al. (2002, 2004) data to 500 m, which is the general resolution of analysis for our study. We grouped land-cover classes into forest, grassland, pasture, cropland, scrubland/desert, barren, water, and urban classes. For each species we then marked each class as suitable or unsuitable. The models considered water and urban classes as always unsuitable. The category “vegetación hidrofila,” wetland vegetation, in Mas et al. (2002, 2004) was always considered suitable. Species habitat descriptions were rarely specific enough to decide the suitability of this vegetation type.

Elevation data were from the Shuttle Radar Topography Mission (Rabus et al. 2003), downloaded at a 1-km resolution from the Global Land Cover Facility (www.landcover.org). Protected-area data were from the 2006 World Database of Protected Areas (sea.unep-wcmc.org/wdpa). We used only the polygon data from that data set. We used World Conservation Union (IUCN) rankings to define the level of intended protection for protected areas, with categories I–IV for strict protection and V and VI for protection that was not strict (IUCN 1994).

We analyzed the species in 2 sets, all endemic species and only small-ranged species. We considered a small range to be <100,000 km². This cut-off size was arbitrary, but other researchers have found it reasonable (e.g., Manne et al. 1999). Of the 250 endemics, 174 (70%) have ranges of <100,000 km².

We defined the conservation priority of an area in 2 ways. One was by the number of small-ranged species: the more small-ranged species, the higher the priority. In this case, we defined areas with 3 or more and 5 or more small-ranged species as discrete levels of priority. If protected areas are randomly distributed, then the percent coverage of such priority areas should be similar to any other area. If protected areas have a bias toward or away from priority areas, then the percent coverage should differ.

In the second method we used MARXAN software to do a formal, systematic conservation planning analysis (Ball & Possingham 2000; Possingham et al. 2000). This plan identified areas that would best complement the existing reserves and achieve a set of conservation targets. We set a minimum target of protecting 10% of the remaining habitat for each species. For species considered endangered or critically endangered under IUCN rankings, we increased the protection rate to 25% and 100%, respectively. Because the goal of protecting a species' habitat is usually to maintain a viable population and

prevent extinction, we estimated for each species the area of habitat necessary for a population of 10,000 individuals. If this area was greater than previous targets, we used the higher value. Population-density estimates for each species were from Damuth (1987) and Robinson and Redford (1986). For species with no information on population density, we conservatively used the lowest density found among all congeneric species. We obtained density values for 126 species.

Planning units for the analysis were 500-km² hexagons plus the existing protected areas. We used the simulated annealing algorithm plus normal iterative improvement, including a boundary-length modifier. One species in the data set, *Oryzomys nelsoni*, is possibly extinct and was excluded from the analysis. Seven species had no habitat after range refinement; thus, they were excluded (*Neotoma anthonyi*, *N. bunkerii*, *N. martinensis*, *N. varia*, *Peromyscus pseudocrinitus*, *P. sejugis*, *Tylomys fulviventer*). All of these species except *T. fulviventer* are small island endemics. Because of the relatively large range of *Rhogeessa alleni* (254,911 km²), compared to other endangered species, we restricted its target to 10%. Maintaining the 25% target for this one species greatly inflated the area needed for a complete reserve system.

Results

Refinement of Species Ranges

Our refinement models decreased the size of a range an average of 39.1% (Table 1). Elevation and land cover accounted for roughly equal portions of this reduction on average. Patterns differed for large- and small-ranged species, with greater decreases for large-ranged species due to land cover and greater decreases due to elevation for small-ranged species (Table 1). Details for each species are available from the authors.

Table 1. Effects of habitat refinement models on species ranges.^a

	All species	Large-ranged species ^b	Small-ranged species ^c
Median geographic range size (km ²)	23,750	271,000	8338
Avg. decrease in area due to elevation (%)	22.8	11.5	27.7
Avg. decrease in area due to land cover (%)	22.6	31.6	18.6
Avg. decrease in area from geographic range (%)	39.1	38.7	39.3
Median amount of remaining habitat protected (%)	7.8	10.2	7.1

^aThe effect of land cover applies only after the effect of elevation.

^bOriginal geographic range of >100,000 km².

^cOriginal geographic range of <100,000 km².

The total richness of all mammals, before refinement and including nonendemic species, showed 2 obvious patterns (Fig. 2a). Species richness generally increased toward the equator and richness was higher in interior and mountainous areas, especially from southern Mexico south to Panama. Many species on the map in Fig. 2a, however, occur outside Central America and potentially have protection there. From here forward, the term *richness* refers only to richness of endemic species.

For the 250 endemic species, the pattern was very different (Fig. 2b). Northern Mexico and southern Panama showed very low richness because many species in these regions occur farther north and south, respectively. The highest concentrations of endemics were in southwestern to southern Mexico, the mountains of Chiapas and Guatemala, and central Costa Rica.

The richness of small-ranged species differed markedly from overall richness, and several concentrations of small-ranged mammals were evident (Fig. 2c). In some of these areas, species richness overall was also high. Nevertheless, many regions with high overall richness actually had very few small-ranged species (compare Figs. 2b & 2c). For example, the southern part of Mexico (Guerrero and southern Oaxaca) was species rich, but had a low concentration of small-ranged species.

The original geographic ranges, however, were somewhat deceptive in that they overestimated true distributions. When using only the range within a suitable elevation, species richness declined in many areas (Figs. 2d & 2e). For example, the mountainous region between Chiapas, Mexico, and Guatemala had a high total richness on the basis of geographic ranges (Fig. 2b). Factoring in elevation decreased the richness by about one-third overall (Fig. 2d). At the most extreme, richness dropped from 31 species to 5 at the highest elevations (>3000 m) in Huehuetenango Department, Guatemala.

For the small-ranged species, declines in richness were less but still apparent (Figs. 2c & 2e). The Chiapas to Guatemala region was again markedly less rich, as were parts of Costa Rica and Panama. For small-ranged species, one factor reduced the overall effect of elevation in the model compared with larger-ranged species. We simply know less about the small-ranged species. Of the 174 small-ranged species, 87 (50%) had insufficient data on elevation, whereas only 19 (25%) of the 76 larger-ranged species lacked data. This lack of data meant the model could say nothing about what elevations were suitable, so the model assumed all elevations were suitable.

The maps of where species likely retain habitat today (Figs. 2f & 2g) again showed an overall drop in richness from the previous maps. Large declines were in the eastern and southern Mexican states of Veracruz, Tabasco, and Chiapas, which are centers of agriculture (Fig. 2f). Parts of Yucatan State also showed lower richness due to clearing of land for agriculture (Fig. 2f).

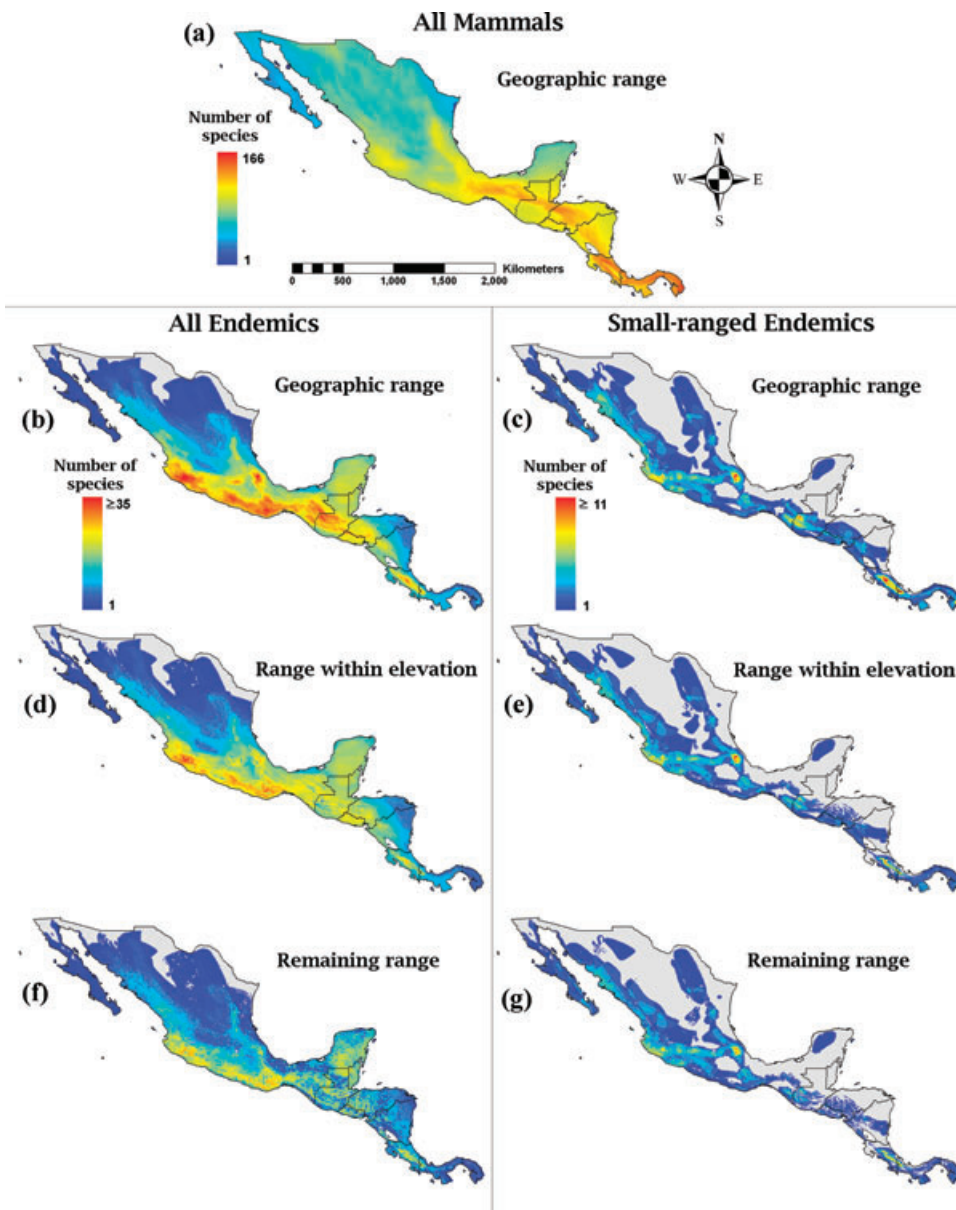


Figure 2. Mammal diversity in Central America: (a) richness of all mammals on the basis of unrefined geographic ranges, (b, d, f) richness of all endemic mammals, and (c, e, g) richness of small-ranged endemics only (<100,000 km²) (geographic range, original unrefined range maps; range within elevation, maps refined with elevation; remaining range, maps refined with both elevation and land cover). In all maps, species richness increases from blue (1 species) to red (166 species for all mammals, ≥35 for endemics, and ≥11 for small-ranged species). Areas with no endemic species are gray.

For small-ranged species including land cover did not greatly change the overall patterns of species richness (Fig. 2g). This is partially because the areas with many small-ranged species did not coincide with major agricultural production. An exception was in the state of Chiapas, Mexico, and across the border into Guatemala. There, areas of relatively high diversity appeared to have been converted to agriculture. Fewer data on land cover needs for small-ranged species was also a factor. Of the 174 small-ranged endemics, 80 (46%) did not have sufficient data, whereas only 17 (22%) of the 76 larger-ranged species lacked data.

Protection Status

Central America has many protected areas, but their distribution is uneven (Fig. 1). About 10.7% of the region has

protection, but the majority of this protection is not strict (Table 2). The protection rates for individual species suggested these areas are not in the most species-rich places. The median rate of habitat protection for all species was 7.8%, lower than the 10.7% regional average (Table 1). For small-ranged species, the rate was an even lower 7.1% (Table 1).

The analysis of small-ranged mammals showed some positive trends. Some relatively large protected areas included many small-ranged species (Fig. 3). Costa Rica in particular protects many small-ranged species. Most of the areas with small-ranged species though were outside of protected areas, and many protected areas had no small-ranged mammals at all (Fig. 3).

Defining priority areas as those with 3 or more small-ranged mammals identified a total area of 287,985 km². That is about the same as the total area currently

Table 2. Percentage of area protected at different levels of protection strictness for the region and for 2 methods of defining priority areas.

	Regional average (%)	≥3 spp. priority area (%)	≥5 spp. priority area (%)*
All protected areas	10.7	8.3	14.0
Strict protection (IUCN I - IV)	3	3.4	7.4
Nonstrict protection (IUCN V - VI)	6.4	3	3.8
No IUCN category	1.3	1.8	2.8

*Statistically different ($p < 0.05$) from regional average with chi-square test.

protected (265,045 km²). Of this priority area, only 8.3% had protection, less than the regional average (Table 2). More positively, the rate of strict protection was slightly higher than the regional rate (Table 2).

Further restricting the priority area to that with 5 or more small-ranged mammals identified a total area of 70,224 km². Protection rates for this area were significantly higher than the regional average, which suggests the focus was on the richest of the rich sites (Table 2). Most of this priority area, however, still lacked protection.

In the complementarity analysis, conservation targets for 113 species were met by existing protected areas. The algorithm consistently chose a subset of areas for new protection in all 500 runs, and we considered these areas irreplaceable for achieving the conservation targets (Fig. 4). Additional areas were chosen in what is termed the “best run” of the model, although these are potentially replaceable with others areas (Fig. 4). Together with the

irreplaceable areas, these composed the most compact set of areas that would achieve all conservation targets (Ball & Possingham 2000).

Discussion

Using readily available data, we produced refined maps of mammal diversity in Central America. Some areas, such as Chiapas, Mexico, and Guatemala, had substantially different predicted richness after accounting for the ecology of individual species. Even with our conservative approach, the apparent ranges of species decreased on average by more than one-third. The approach we used to refine range maps produced a dramatically different picture of biodiversity patterns than if we had not refined the maps. Any approach to systematic conservation planning that uses range maps as an input would be affected.

Our method to reduce errors of commission in the range maps is conceptually simple, but there are risks. Reducing commission errors also tends to increase omission errors. This could lead to overlooking important areas because they appear not to have certain species. The degree to which one minimizes one or the other error is a matter of choice and intent. We chose to reduce the commission errors, but only in areas obviously unsuitable for a given species. Some commission errors likely still existed, but their extent was less.

We had 2 key results for conservation. First, there were large differences between the richness maps of all endemic species and that of small-ranged species. Some areas with many species overall did have many small-ranged species. Other areas clearly did not. Most areas actually had very few or no small-ranged species. Several regions had exceptionally high concentrations

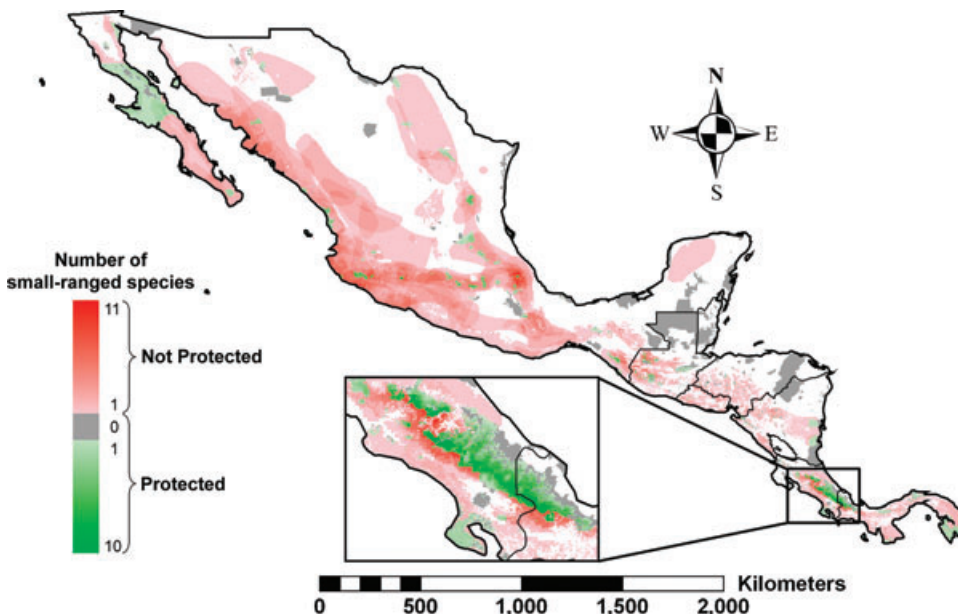


Figure 3. Protected-area coverage of vulnerable mammal diversity. Colored areas have small-ranged mammals, with the intensity of red or green corresponding to the number of species. Red areas have no protection, whereas green areas do. Gray areas have protection but no species of mammals with small ranges.

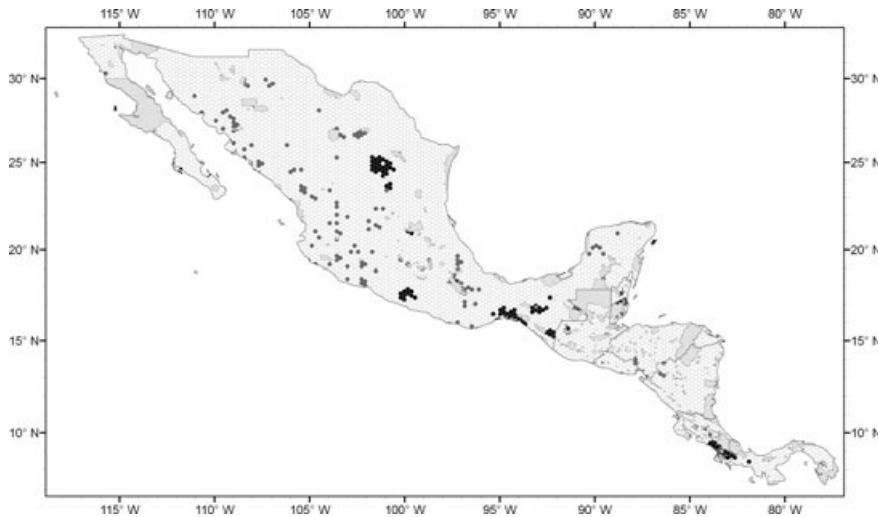


Figure 4. Areas chosen by complementarity analysis as priorities for protection. Gray areas are existing protected areas and are always included in the reserve system. Black filled hexagons were chosen in all runs of the selection algorithm, and we consider them irreplaceable for a complete reserve system. Dark gray, filled hexagons were chosen in the “best run” of the selection algorithm. They are potentially replaceable with other hexagons, but doing so might require more total area for a complete reserve system.

of small-ranged species (Fig. 2). Certainly, these should be conservation priorities, for they contain many vulnerable species, ones that can be protected nowhere else.

Our second key result is the recommendation of specific areas that would complement the existing reserve system. The irreplaceable areas (black in Fig. 4) appear to be critical for any complete reserve system for mammals. Indeed, Ceballos (2007) recommended some of the same areas in Mexico in their independent analysis. Some of the irreplaceable areas would represent expansions of nearby reserves, whereas others are in regions devoid of protected areas. For a completely representative reserve system, there is flexibility in which additional areas to protect and we presented one of many options. Realities on the ground may make some of our chosen areas infeasible to protect, and substitutions would be needed.

We recommend protection of the irreplaceable areas (black in Fig. 4) and areas with exceptional numbers of small-ranged mammals (deep red in Fig. 3) as 2 priority conservation actions. Obviously, the prevention of mammal extinctions is not the only reason to protect areas. Many areas have protection for plants or other animals. In addition, some areas have protection because of scenic beauty, water quality, or other good reasons. Our recommendations are specifically for mammals. It is possible that other taxa concentrate in these places as well, particularly the small-ranged species of those taxa (Pimm & Jenkins 2005). To be sure, analyses of other taxa will be needed.

We recommend quick action to protect these priority sites. A recent study of Mexico found that postponing protection of key sites for conservation led to higher relative costs later to achieve the same goal (Fuller et al. 2007). Presumably, this pattern will continue into the future and possibly be similar for other countries. Acting sooner will be cheaper than acting later.

Acknowledgments

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