Diversity and Distributions, (Diversity Distrib.) (2004) **10**, 39–54

BIODIVERSITY RESEARCH

Modelling spatial patterns of biodiversity for conservation prioritization in North-eastern Mexico

Miguel A. Ortega-Huerta[1]* and A. T. Peterson[2]

[1]*Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 10, Colima, Colima, México C. P. 28000 and*
[2]*Natural History Museum and Biodiversity Research Center, 1345 Jayhawk Blvd. Lawrence, KS 66045–7561 USA*

*Correspondence: Miguel A. Ortega-Huerta, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 10, Colima, Colima, México C. P. 28000.
Tel.: (312) 316 1000 Ext. 47001.
Fax.: (312) 312 7581.
E-mail: maoh@ibiologia.unam.mx

ABSTRACT

Relationships between spatial patterns of bird and mammal species richness in north-eastern Mexico were analysed in relation to the location of three biosphere reserves (El Abra-Tanchipa, El Cielo, and Sierra Gorda) and 13 priority areas recently identified for conservation. Ecological niches were modelled and potential distributions delimited for 285 bird and 114 mammal species using a genetic algorithm based on locality information from museum specimens and 15 selected environmental attributes. Potential distributions were transformed into hypothesized current distributions based on species–habitat associations as reflected in a recent land-use map. Although species richness was lower when distributions were reduced from potential to current, spatial patterns of potential and current richness were similar. Heuristic, complementarity-based prioritization procedures were used to identify combinations of areas and sites with maximal species representation: the biosphere reserves included 79% of birds and 74% of mammal species; eight priority areas provided an additional 11% of birds and 13% of mammals; the remaining 10% of birds and 13% of mammals were concentrated in new sites across the study area.

Keywords
Biodiversity, biosphere reserves, North-eastern Mexico, prioritization, spatial patterns, species richness.

INTRODUCTION

Mexico is a megadiverse country but has high rates of deforestation and ecological impoverishment (CONABIO, 1999). On one hand, Mexico ranks second worldwide in richness of reptiles, fourth in amphibians, fifth in both mammals and higher plants, and tenth in birds (Conservation International, 1999). On the other hand, during 1990–2000, Mexico had a deforestation rate of 1.1%, which amounts to a nonsustainable 631,000 ha year^{-1} of forest loss (FAO, 2001).

In recent decades, establishment of protected natural areas, biosphere reserves in particular, has been considered an effective strategy for protecting biodiversity, counteracting deforestation, and reconciling productive activities with conservation (MAB-UNESCO, 1984). Protected natural areas are particularly important because current rates of human population growth and habitat loss suggest that most of the world's terrestrial biota will soon be confined to isolated natural reserves and parks (Peters & Darling, 1985; Shafer, 1990; Newmark, 1995). Reserves are nevertheless influenced by extrinsic phenomena at local, regional, and global scales, and will, alone, likely never suffice to protect all biodiversity (Meffe & Carroll, 1997). On size grounds alone, single reserves too often do not even match home-range sizes for large mammals such as carnivores (Grumbine, 1990). Therefore, to evaluate the role of natural protected areas in preserving biodiversity, research should consider reserves in the context of ecological and biogeographical relationships at regional scales (Nilsson & Götmark, 1992; Sarukán *et al.*, 1996).

Given the inadequacy of single reserves, reserve networks become essential for the long-term persistence of biodiversity (Margules *et al.*, 1994; Williams *et al.*, 1996; Flather *et al.*, 1997; Prendergast *et al.*, 1999; Rodrigues & Gaston, 2001). Establishment of reserve systems has become the cornerstone of most conservation strategies (Soulé, 1991), but too often such systems have been based on opportunistic, 'ad-hoc' criteria, such as relative lack of value for commercial land purposes or human habitation, scenic values, recreation and tourism, and historical protection for hunting or water supply (Pressey *et al.*, 1993; Pressey, 1994). Ad-hoc assembly of reserve systems has resulted in biased representation of natural features and increased costs of achieving representative reserve systems (Pressey, 1994).

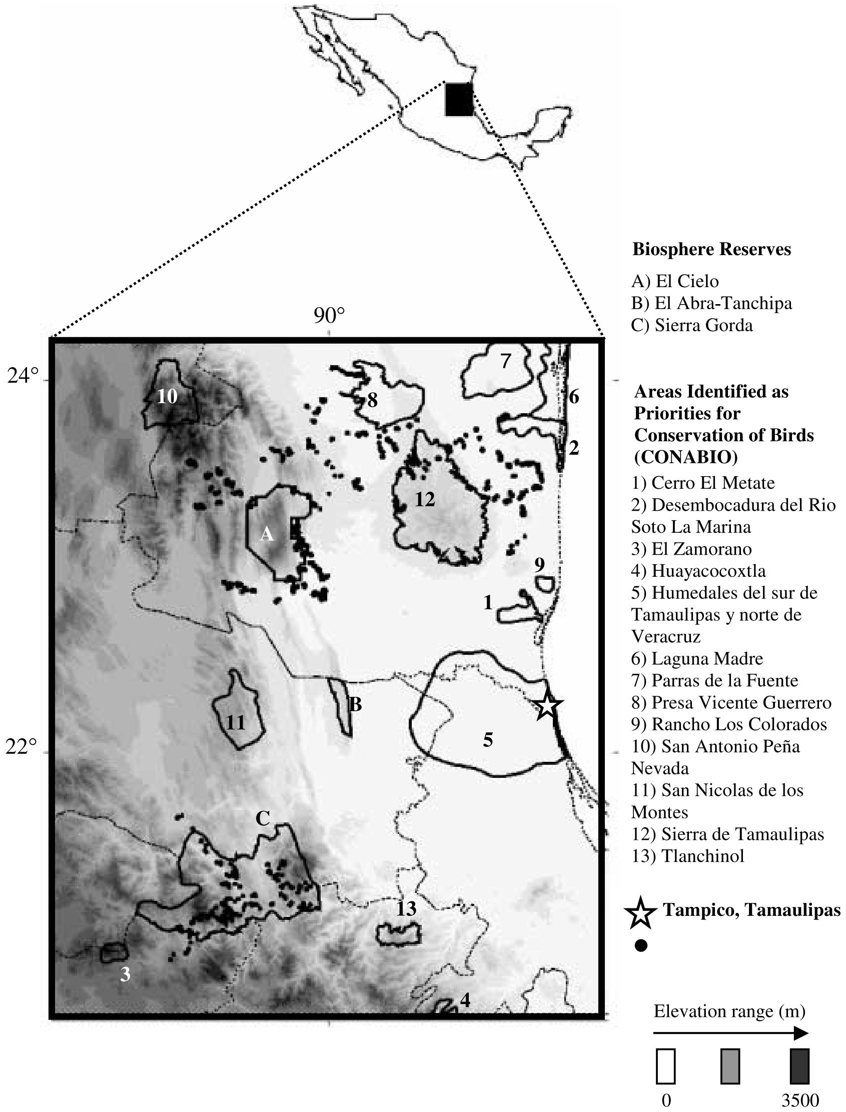

Figure 1 Map of study area in north-eastern Mexico, indicating existing biosphere reserves, 13 areas identified as priorities for bird conservation (CONABIO), and location of training sites, for assessment of habitat types.

To provide a scientific basis for reserve networks, efficient new computational methods (site-selection algorithms) have been developed to identify sets of areas that maximize representation of species (Pressey *et al.*, 1997; Stokland, 1997; Prendergast *et al.*, 1999; Cabeza & Moilanen, 2001). These algorithms have focused on identifying (1) hotspots of richness (areas that individually have highest species richness) (2) hotspots of rarity (areas that individually are richest in rare species), and (3) complementary areas (multiple areas that in combination have the highest species richness) (Hopkinson *et al.*, 2000; Williams *et al.*, 1996), and provide a means of designing reserve networks with explicit criteria and goals.

The objective of this study is to analyse spatial patterns of biodiversity in north-eastern Mexico in relation to established biosphere reserves and areas identified as priorities for conservation (Fig. 1), using birds and mammals as indicator groups. We focus in particular on the location and extent of hotspots of overall species richness and of species considered threatened, endangered or with restricted distributions. We integrate ecological niche modelling as a tool for outlining species' geographical distributions, and use both richness- and complementarity-based approaches to analyse the spatial configurations of species' distributions throughout the region.

STUDY AREA AND METHODS

In general, our approach consists of summarizing species' geographical distributions using ecological niche modelling, based on collection localities associated with natural history museum specimens and on GIS coverages summarizing key environmental attributes. Then, land use/land cover information and species–habitat associations were used to hypothesize the current geographical distributions of species. Finally, these distributions are used to develop systems of protected natural areas under explicit criteria — in particular, species' distributions are considered relative to three biosphere reserves spaced 60–70 km apart in the Sierra Madre Oriental in north-eastern Mexico (El Cielo, Sierra del Abra-Tanchipa, and Sierra Gorda; Fig. 1) and 13 areas recently identified as priority areas for improving the existing system (Benítez *et al.*, 1999).

Occurrence data for species

Data on species' occurrences were gathered for bird and mammal species across the study area. The *Atlas of Mexican Bird Distributions* (Peterson *et al*., 1998) and a parallel data set for the mammals of Mexico (V. Sánchez-Cordero, pers. comm.) were used as the basis for analyses. Species' occurrences had previously been captured from natural history museum specimen tag data, georeferenced to geographical coordinates, and organized in databases by the developers of the respective data sets. Natural history museums contributing to these data resources are listed in the Acknowledgements.

Environmental attributes

Environmental attribute data sets were made available by CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, 2001). In all, 15 environmental variables (elevation, aspect, slope, climate type, ecoregions, physiography, structural physiography, humidity regimes, mean annual temperature, mean annual precipitation, maximum daily temperature, minimum daily temperature, maximum temperature, minimum temperature, and potential vegetation) were chosen for use based on prior analyses of bird and mammal species distributions across Mexico (Peterson *et al*., 1999, 2002). All environmental attributes data sets were transformed to raster (grid) format, with pixels of 0.005 × 0.005° (about 500 × 500 m). The digital elevation model data, with its derivatives slope and aspect, was resampled from a grid of 270 × 270 m resolution.

Ecological niche modelling

Models of potential distributions were developed for each species using the software package Desktop GARP (Genetic Algorithm for Rule set Prediction) (Stockwell & Noble, 1991). GARP was selected because of ample testing of its predictive ability (Peterson & Cohoon, 1999; Peterson, 2001), particularly in Mexico (Peterson *et al*., 2002), and its demonstrated robustness in modelling species' distributions even at relatively low sample sizes (Peterson & Cohoon, 1999; Stockwell & Peterson, 2002a, 2002b).

GARP is a machine-learning approach to modelling ecological niches of species. The software consists of eight subprograms for data preparation, model development, model application, and model communication (Stockwell & Noble, 1991; Stockwell & Peters, 1999). It is capable of simultaneously generating and testing diverse ranges of possible solutions, including categorical, range-rule, and logistic regression models. A set of rules is developed through an evolutionary refinement procedure, testing and refining rules based on random subsets of input data. The goal is to maximize significance and predictive accuracy of the rules (Stockwell & Peters, 1999).

All analyses were developed on an implementation of GARP developed by R. Scachetti-Pereira that is now available for public download (*http://www.lifemapper.org/desktopgarp/*). This implementation, aside from providing a convenient user interface and allowing efficient batch processing of large quantities of models, also allows user-defined percentages of input points to be set aside for independent significance tests of model performance. Hence, given diverse numbers of occurrence records available for particular species, we divided point data set in two groups: (1) species with 2–19 records, and (2) species with ≥ 20 records. For each species in the first group, 20 models were developed based on all available points (i.e. no independent test of model quality), whereas for the second group, 50 models were developed based on half of available points.

Following procedures for selecting 'best subsets' of models developed by Anderson *et al*. (2003), based on a balance of model error components, we reduced the 20–50 models available per species to a best six, as follows: For species with 2–19 records, the six models closest to the mean value of an index of commission error (proportion of study area predicted present) were selected. For species with 20 records, we first selected the 10 models with the lowest omission error (based on independent test data), and then eliminated models with most extreme commission index values (two high, two low). Once six 'best' models were selected for each species, they were summed to generate grids with values ranging 0–6, representing a gradient of coincidence among models (six representing complete agreement in prediction of presence). These graded predictions were converted to binary predictions by identifying areas in which more than half of the models agreed in predicting presence. These individual species maps were summed to produce maps of species richness.

Current distributions and vegetation map accuracy assessment

To obtain an adequate land cover map, we first found it necessary to evaluate the accuracy of existing maps to decide whether new mapping efforts would be necessary. An accuracy assessment of two existing LULC maps for north-eastern Mexico was conducted parallel to this study (Ortega-Huerta, 2002). To model current distributions of species, it was necessary to reduce raw GARP predictions to particular land cover types used by each species. (Note that land use/land cover (LULC) datasets could not be included directly in the modelling process because occurrence data available were relatively old in comparison with LULC information, creating mismatches between the two data sources.) We intersected the binary representations of species' potential distributions with LULC types known to be suitable for each species based on personal experience of A. Townsend Peterson (birds) and on the scientific literature for mammals (Chapman & Feldhamer, 1982; Whitaker, 1995; Emmons, 1997; Fiona, 1997; Wilson & Ruff, 2001).

Biodiversity patterns and conservation prioritization

The principal focus of this project was on spatial patterns of bird and mammal diversity in relation to three biosphere reserves (BRs), and 13 priority areas (NAPCs) also identified as important for protection (Fig. 1). Boundary maps for these areas were obtained from CONABIO, except for the Sierra Gorda BR, for which boundaries were re-digitized from the reserve's management plan given inconsistencies with the CONABIO map.

Table 1 Summary of six prioritizations conducted for both birds and mammals, differing in all species vs. ETRD species, and inclusion of existing and proposed reserves. Non-inclusion of existing or proposed areas means that these areas were not considered specially when conducting the prioritization procedure. ETRD = endangered, threatened or restricted distribution species

Prioritization	Mammal or Bird species group	BRs	NAPCs	New sites
P1	All	T	T	T
P2	All	T	—	T
P3	ETRD	T	T	T
P4	ETRD	T	—	T
P5	All	—	—	T
P6	ETRD	—	—	T

'Presence' of a species in a BR or NAPC was determined based on the proportion of the area covered by the current distribution of a species in relation to the total area. A threshold of presence in ≥ 1% of an area was established as a minimum proportion for presence. Presences of species in areas were summarized by (1) creating a multilayer image (i.e. stacking layers representing each species into a single Erdas-Imagine image file) (2) overlaying the multilayer image with BR and NAPC boundaries; and (3) exporting image statistics in spreadsheet form.

Species' presences were used to develop a series of six area prioritizations for birds and mammals, and including BRs, NAPCs, and as-yet unidentified sites (groups of pixels) in various combinations (Table 1). Prioritizations focused on all species, or just endangered, threatened, or restricted range species (ETRD species, Table 2), and differed in whether existing BRs or NAPCs were included in the species accumulation procedure. The approach is a heuristic method designed to maximize species' representation in the resulting reserve network, based on the principle of complementarity of species composition (e.g. Peterson *et al.*, 2000; Williams *et al.*, 1996; Hopkinson *et al.*, 2000). The area with highest representation of species was selected as a first element in the system; eliminating those species from consideration, subsequent areas were selected based on those areas that were richest in representation of the remaining species.

In general, we counted species as 'protected' in a reserve system if it occurred in one of the areas under consideration — in those prioritizations that included BRs and/or NAPCs, we considered the established areas first, the proposed areas second, and the as-yet unidentified sites last.

RESULTS

Accuracy assessment

In all, 1565 training points were accumulated across the study region (Fig. 1). These points are concentrated in the Sierra Gorda BR and a significant swath of the state of Tamaulipas, with intervening areas unsampled. The rationale was to accord priority to areas near or within the BRs, as they were the focus of much of the analysis.

Considering its overall accuracy (77%), we used a generalization of the Inventario Nacional Forestal 2000 map (SEMARNAT 2000) from 55 land use/land cover classes to 21 classes as the base map for developing current distributions of mammal and bird species. Details of our accuracy assessment analyses and generalization of land use/land cover information are provided elsewhere (Ortega-Huerta, 2002).

Potential vs. current distributions

This study considers GARP predictions as species' potential distributions based on the nature of the ecological niche modelling process, and given that only broad-scale climatic factors and landscape characteristics were included in model development. Example predictions for the 285 species of birds and 114 species of mammals are shown in Fig. 2. Raw GARP predictions were often modified when reduced to current distributions, with large unsuitable areas being masked out (e.g. *Amazona viridigenalis*, Fig. 2a vs. 2b; and *Leopardus pardalis*, Fig. 2e vs. 2f). In other cases, modification was not as severe (e.g. *Puma concolor*, Fig. 2g vs. 2h). The differences between potential and current distributions of species clearly reflect a combination of actual loss of distributional area owing to modification of natural habitats by human presence, and initial overprediction of species' distributional areas by the somewhat general GARP ecological niche models (Peterson & Kluza, 2003).

Modelled species richness patterns for birds and mammals differed from one another and between potential and current versions (Fig. 3). Potential bird richness patterns contained higher concentrations of species than current bird with three relatively small areas (each 50–100 pixels of tropical deciduous forest) of 200 species potentially co-occurring (two south-east of the El Cielo BR, one about 8 km south-west of El Abra-Tanchipa BR). Modelled current species richness of birds was uniformly lower; however, areas with highest concentrations of species (107–120 species) coincide with the potential richness peaks.

Areas with highest potential species richness of mammals (61–68 species) corresponded to the same areas close to El Cielo BR as were identified for birds. Current mammal species richness was notably lower overall: highest concentrations (38–45 species) (Fig. 3) consisted of minute areas (a few pixels) in the same sites as the foci of current bird species richness. A new richness peak was (38–35 species) in northern Veracruz. ETRD richness maps (not shown) coincide fairly well with geographical concentrations for overall species richness.

Prioritization of areas

The six prioritization approaches applied represent variations of procedures for identifying natural areas that maximize species richness. The general goal focuses on (1) identifying geographical concentrations of species (2) assessing the role of three existing BRs (3) assessing the potential role of 13 NAPCs, and (4) evaluating possible new areas not otherwise included. The results of the prioritizations are summarized in Fig. 4 and Tables 3 and 4.

Table 2 Bird and mammal species considered endangered, threatened, or with restricted distribution (ETRD)

Birds		**Mammals**	
Endangered	Source	Endangered	Source
Amazona oratrix	1	*Ateles geoffroyi*	1
Amazona viridigenalis	1	*Eira barbara*	1
Ara militaris	1	*Leopardus pardalis*	1
Crax rubra	1	*Leopardus wiedii*	1
Falco femoralis	1	*Panthera onca*	1
Spizaetus ornatus	1	*Ursus americanus*	1
Threatened		Threatened	
Accipiter striatus	1	*Bassariscus astutus*	1
Aratinga holochlora	1	*Choeronycteris mexicana*	1
Bubo virginianus	1	*Dipodomys merriami*	1
Buteogallus urubitinga	1	*Dipodomys phillipsii*	1
Ciccaba virgata	1	*Glaucomys volans*	1
Dactylortyx thoracicus	1	*Leptonycteris nivalis*	1
Geothlypis flavovelata	1	*Lontra longicaudis*	1
Icterus cucullatus	1	*Neotoma albigula*	1
Icterus graduacauda	1	*Notiosorex crawfordi*	1
Icterus wagleri	1	*Oryzomys palustris*	1
Parabuteo unicinctus	1	*Peromyscus eremiscus*	1
Pionus senilis	1	*Peromyscus leucopus*	1
Ramphastos sulphuratus	1	*Peromyscus maniculatus*	1
Restricted Distribution			
Aphelocoma potosina	2		
Campylopterus curvipennis	2		
Campylorhynchus gularis	2		
Caprimulgus salvini	2		
Colinus graysoni	2		
Corvus imparatus	2		
Dendrortyx barbatus	2		
Icterus fuertesi	2		
Melanerpes grateloupensis	2		
Momotus coeruliceps	2		
Parula nigricola	2		
Piculus senilis	2		
Rhodothraupis celaeno	2		
Sporophila sharpei	2		
Tyrannus couchii	2		
Uropsila leucogastra	2		

1 = SEMARNAP 2000, 2 = A. Townsend Peterson, pers. comm.

Numbers of species occurring in each BR and NAPC vary considerably, reaching maxima in two BRs: El Cielo (211 birds and 74 mammals) and Sierra Gorda (212 birds and 68 mammals). Numbers of bird and mammal species are tightly correlated across BRs and NAPCs ($r = 0.96$), although species richness and area were poorly associated across BRs and NAPCs; 0.56 (birds), 0.55 (mammals), 0.53 (ETRD birds) and 0.17 (ETRD mammals), suggesting that simple area effects were unlikely to be responsible for the order in which areas were added to particular prioritizations.

Overall, the three BRs accounted for 79% of birds and 74% of mammals (prioritizations 1 and 2). El Abra-Tanchipa and El Cielo accounted for 58–74% of ETRD bird and mammal species, respectively, while Sierra Gorda did not add any ETRD bird or mammal species (Fig. 4b,d). Hence, the BRs alone did not include comprehensive representation of bird and mammal species known to occur in the region.

Regarding NAPCs, prioritization 1 resulted in inclusion of five NAPCs for each species group. Because only Humedales and Tlanchinol were included in both prioritizations, the eight NAPCs selected included 11% of birds and 13% of mammals (Fig. 4a,c). Prioritization 3 returned two NAPCs for ETRD birds (total five species) and three NAPCs for ETRD mammals (four species), beyond those species present in El Abra-Tanchipa and El Cielo biosphere reserves (Fig. 4b,d).

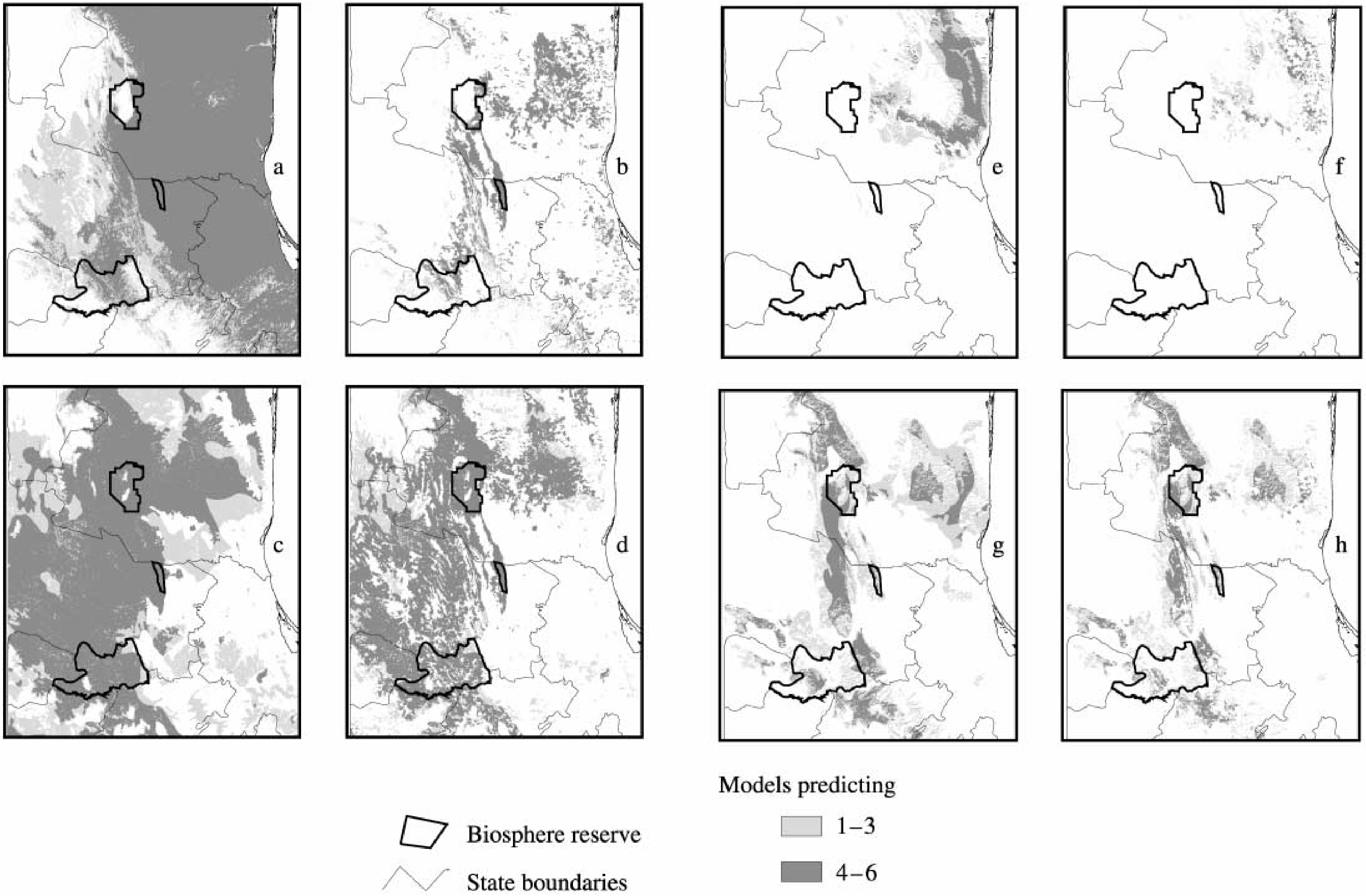

Figure 2 Examples of distributional predictions for birds and mammals: potential (a) and current (b) distributions of the parrot *Amazona viridigenalis*; potential (c) and current (d) distributions of the wren *Catherpes mexicanus*; potential (e) and current (f) predictions of the ocelot *Leopardus pardalis*, and potential (g) and current (h) predictions of the mountain lion *Puma concolor*.

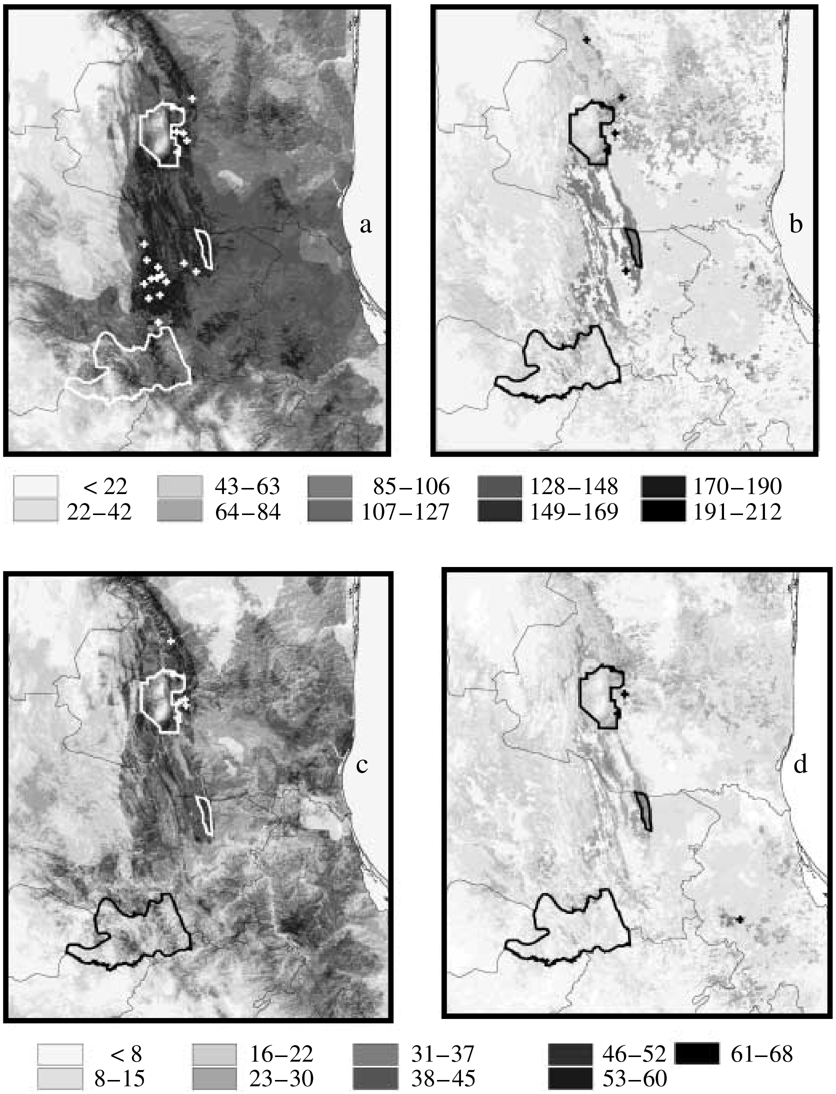

Figure 3 Bird species richness: (a) potential and (b) current. Mammal species richness: (c) potential and (d) current. Cross symbols represent sites with maximum richness.

New sites (sites not presently protected or proposed as potential reserves) resulted from creating composite coverages of species when (1) species were not included by any BR or NAPC (prioritizations 1–4) or (2) existing areas were ignored in the procedure (prioritizations 5–6). Figure 5 summarizes the location of these new sites. Prioritization 1 identified three new sites including 21 birds and one new set of sites with five mammals (Fig. 5a). Prioritization 2, which considered only BRs at the outset, identified five new sets of sites for birds and two for mammals, accounting for 18% and 5% of the total number of species, respectively (Fig. 5b).

Prioritization 5, which did not, a priori, include BRs and NAPCs, resulted in identification of nine new sets of sites for birds. The site identified in the first step (R1 in Fig. 4a) had a slightly higher number of species than El Abra-Tanchipa BR in prioritizations 1 and 2 (118 vs. 113 species, respectively). In the second step, however, El Cielo BR had higher number of species than the corresponding identified set of sites (214 vs. 190 species, respectively). Steps R3, R4, and R5 of Prioritizations 1 and 5, show almost equal numbers of accumulated species. Then, at steps R6, R7, and R8, Prioritization 5 maintained a gap of about 15 species higher than Prioritization 1. The sites identified, though scattered across the region, fall within or near BRs and NAPCs, such as El Cielo, Sierra Gorda, Humedales, Sierra de Tamaulipas, Peña Nevada, San Nicolas, Soto la Marina, and Presa V. Guerrero (Fig. 5e).

On the other hand, in Prioritization 5 for mammals, sites identified had lower numbers of species (9 and 17) than those areas selected in Prioritization 1 (Fig. 4c). The species accumulation process levels out among these prioritizations when the numbers of species accumulated approaches 100 (Fig. 4c). These new sites parallel those of El Cielo, Sierra Gorda, Soto La Marina, San Antonio Peña Nevada, and San Nicolas de los Montes (Fig. 5e).

Finally, Prioritization 6 identified sites better at the outset (higher number of ETRD mammal and bird species) than El Abra-Tanchipa (Fig. 4d,b). With the exception of step 2 for mammals, Prioritization 6 keeps higher numbers than Prioritizations 3 and 4 for both species groups (Figs 4b,d). Four sets of sites identified for ETRD bird species coincided with El Cielo and Sierra Gorda BRs, Humedales, Sierra de Tamaulipas

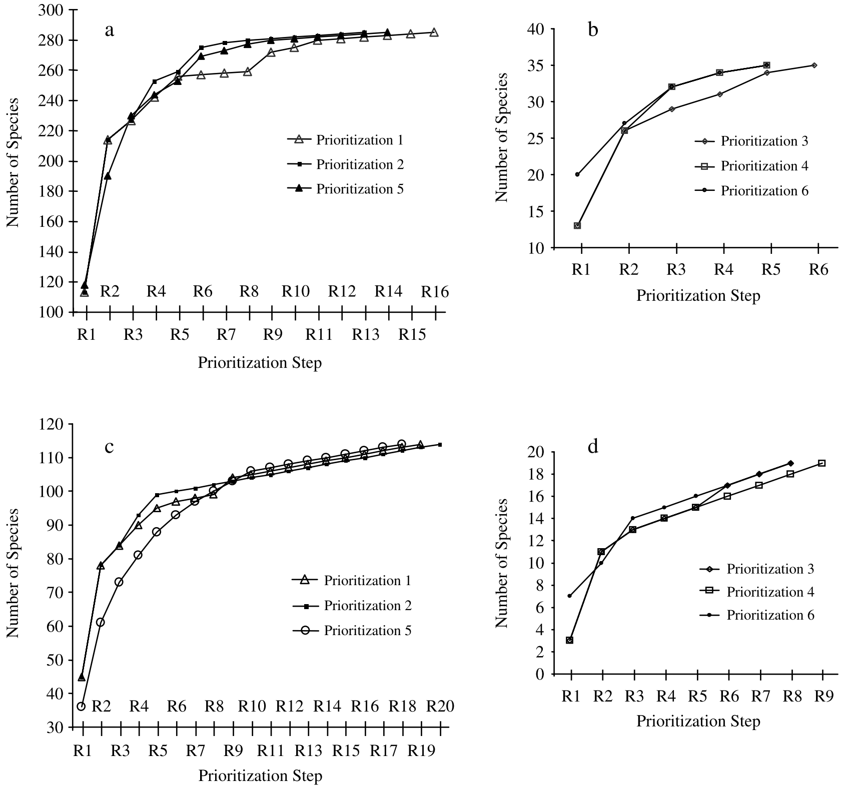

Figure 4 Prioritization of biosphere reserves, potential areas for conservation, and new sites, based on prioritizations (a) 1, 2, and 5, and (b) and 3, 4, and 6 for birds; and (c) 1, 2, and 5, and (d) 3, 4, and 6 for mammals.

and Presa Vicente Guerrero (Fig. 5f). The three sets of sites for ETRD mammals coincided with El Cielo BR and San Nicolas de los Montes (Fig. 5f).

DISCUSSION

Our modelling represents an approximation to the spatial configuration of species assemblages in north-eastern Mexico. Although its basis was the ecological niche modelling approach, we wanted to go beyond the potential distributions of species by reducing the latter into areas still containing habitat suitable for the species. However, the lack of temporal coincidence between land use/land cover data sets and most of our species occurrence information places a degree of uncertainty on our current distributional predictions.

Even though GARP accounts for possible location errors and data shortage, intrinsic in collection site databases, we were limited to some degree by scarcity of data for species, especially for those with restricted distribution. The scale of our study (north-eastern Mexico) and the high resolution of some data (e.g. topography and land use/land cover) called for development of our analyses resolution at 500 m resolution, which we consider the finest resolution possible for using historical collection sites databases.

Current distributions

The IFN map was key in reducing raw GARP predictions to more practical models reflecting current species' distributions. Habitat associations were necessarily incorporated in the modelling process as an a posteriori step owing to temporal discords between available occurrence data and the available land use/land cover information (Peterson & Kluza, 2003). Even though the overall accuracy of the IFN map was ~77%, which may seem low, individual classes had markedly higher accuracies: pine forest (100%), tropical deciduous forest (91%), tropical evergreen forest (100%), tropical semideciduous forest (99%), and scrubland (87%). On the other hand, classes with lower accuracy, such as agriculture (64%) and pine-oak forest (47.4%), were confused with classes with similar management or physiognomy (grassland and oak forest, respectively)

Although the main focus of this project was on modelling current patterns of biodiversity in north-eastern Mexico, comparison with potential distributional patterns may inform regarding their significance. In general, current patterns of richness follow those of potential species richness. Closer examination of the richest potential areas (> 170 species) reveals that they fall in the 100–1000 m elevation zone, in areas originally covered with tropical deciduous and semideciduous forests, cloud forest, and pine-oak forest (Rzedowski, 1978), mostly tropical forest types. Hence lowlands and middle elevations represent hotspots of bird diversity, as has been noted previously in Mexico (e.g. Peterson *et al*., 1993). Although tropical evergreen forest might have been expected to have more significant representation of high potential species richness, perhaps the peripheral nature of this habitat in the study region (Escalante *et al*., 1998) makes for relatively low species diversity.

In previous studies, correspondence in spatial patterns of species richness among taxa has been variable, with some studies

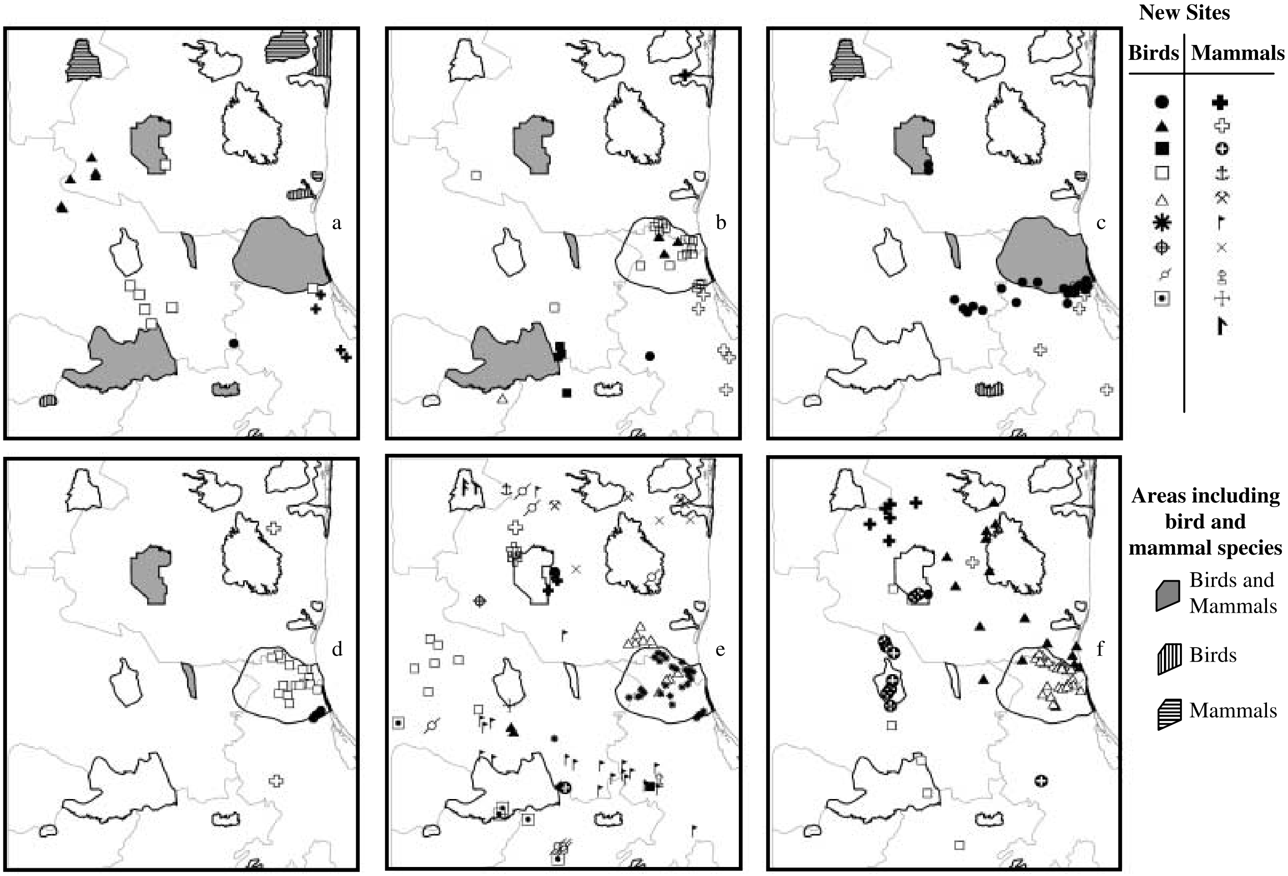

Figure 5 Prioritizations' spatial representation for bird and mammal species. (a) (b), and (e) are prioritizations that include the total number of species (285 birds and 114 mammals) while (c) (d) and (f) are prioritizations that include only those species considered endangered, threatened or with restricted distribution (ERTD) (35 birds and 19 mammals). Different symbols represent identified sites for groups of species as indicated. Empty areas are shown for reference.

finding low correspondence (e.g. Prendergast *et al.*, 1993; Lombard, 1995; Oliver & Beauie, 1996; Kerr, 1997), and others finding close correspondence (e.g. Peterson *et al.*, 1993). We found close correspondence between bird and mammal richness patterns, suggesting that either taxon reveals similar patterns of biodiversity distribution.

Species Richness and Current and Potential Natural Areas. Although the three BRs are located on the major mountain system in the study area, only El Abra-Tanchipa BR includes significant richness peaks. Among the NAPCs, only San Nicolas de los Montes contains a bird richness peak. Other areas of high species richness do not fall in any NAPC or BR; only small patches of high bird richness are found in NAPCs elsewhere.

The three BRs play an important role in protecting a large proportion of the region's current predicted richness of birds (227 species or 79%) and mammals (84 species or 74%). El Cielo and El Abra-Tanchipa protect 74% of ETRD birds and 58% of ETRD mammals. Species not predicted to occur in the BRs included nine ETRD bird species (*Amazona oratrix*, *Aratinga holochlora*, *Geothlypis flavovelata*, *Icterus fuertesi*, *I. graduacauda*, *Parabuteo unicinctus*, *Parula nigrilora*, *Ramphastos sulphuratus*, and *Uropsila leucogastra*), and seven ETRD mammals (*Dipodomys merriami*, *D. phillipsii*, *Leopardus pardalis*, *L. wiedii*, *Lontra longicaudis*, *Oryzomys palustris*, and *Ursus americanus*).

NAPCs that complemented species representation in BRs included: Tlanchinol (adding 14 birds and five mammals), Humedales (15 birds and one mammal), Parras de la Fuente (six mammals), Peña Nevada (two mammals), El Metate (one bird), El Zamorano (one bird), Laguna Madre (one bird), and Los Colorados (one mammal). Four additional sites were also identified (Fig. 5), including 21 birds and four mammals, and five birds and 10 mammals that had disjunct nonoverlapping distributions. Twice as many mammal species as birds had nonoverlapping distributions, suggesting that bird species may co-occur more commonly. Similarly, the maximum potential number of mammal species co-occurring was 68 (60%), compared with a maximum potential number of birds 212 (74%).

The complementarity sites identified in this paper should be interpreted as exploratory places, rather than selected areas. This distinction is particularly important if we consider the key role of selection unit area in determining the minimum percentage of area needed to represent all species within a region (Rodrigues & Gaston, 2001), which is not within the scope of our analysis. Furthermore, this analysis' pixel size as a selection unit furthers

Table 3 Prioritizations 1, 2 and 3, showing the number of species accumulated (No. of Spp. Acc.) at each prioritization step (Prior. Step) by existing biosphere reserves (BR), NAPC (priority areas), and new sites

	Prioritization 1				Prioritization 2				Prioritization 3			
	Bird species		**Mammal species**		**Bird species**		**Mammal species**		**Bird species**		**Mammal species**	
Prior Step	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**
R1	El Abra BR	113	El Abra BR	45	El Abra BR	113	El Abra BR	45	El Abra BR	13	El Abra BR	
R2	El Cielo BR	214	El Cielo BR	78	El Cielo BR	214	El Cielo BR	78	El Cielo BR	26	El Cielo BR	
R3	Sierra Gorda BR	227	Sierra Gorda BR	84	Sierra Gorda BR	227	Sierra Gorda BR	84	Sierra Gorda BR	26	Sierra Gorda BR	
R4	Humedales	242	Parras de la F.	90	New Sites 2a	253	New Sites 2a	93	Humedales	29	Los Colorados	
R5	Tlanchinol	256	Tlanchinol	95	New Sites 2b	259	New Sites 2b	99	Tlanchinol	31	Humedales	
R6	El Metate	257	Peña Nevada	97	New Sites 2c	275	A species Site (*Carollia brevicauda*)	100	New Sites 3a	34	Peña Nevada	
R7	El Zamorano	258	Humedales	98	New Sites 2d	278	A species Site (*Chaetodipus hispidus*)	101	A species site (*Ramphastos sulphuratus*)	35	New Sites 3a	
R8	Laguna Madre	259	Los Colorados	99	New Sites 2e	280	A species Site (*Cratogeomys merriami*)	102			A species Site (*Dipodomys merriami*)	
R9	New Sites 1a	272	New Sites 1a	104	A species Site (*Amazilia violiceps*)	281	A species Site (*Dipodomys phillipsii*)	103			A species Site (*Dipodomys phillipsii*)	
R10	New Sites 1b	275	A species Site (*Carollia perspicillata*)	105	A species Site (*Eremophila alpestris*)	282	A species Site (*Leopardus wiedii*)	104				

	Prioritization 1				Prioritization 2				Prioritization 3			
	Bird species		**Mammal species**		**Bird species**		**Mammal species**		**Bird species**		**Mammal species**	
Prior Step	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**
R11	New Sites 1c	280	A species Site (*Cratogeomys merriami*)	106	A species Site (*Otus guatemalae*)	283	A species Site (*Lontra longicaudis*)	105				
R12	A species Site (*Amazilia violiceps*)	281	A species Site (*Dipodomys phillipsii*)	107	A species Site (*Pheucticus chrysopeplus*)	284	A species Site (*Microtus mexicanus*)	106				
R13	A species Site (*Atlapetes albinucha*)	282	A species Site (*Microtus mexicanus*)	108	A species Site (*Psarocolius montezuma*)	285	A species Site (*Molossus aztecus*)	107				
R14	A species Site (*Eremophila alpestris*)	283	A species Site (*Molossus aztecus*)	109			A species Site (*Oryzomys palustris*)	108				
R15	Aspecies Site (*Pipilo ocai*)	284	A species Site (*Peromyscus melanotis*)	110			A species Site (*Peromyscus melanotis*)	109				
R16	A species Site (*Psarocolius montezuma*)	285	A species Site (*Pipistrellus subflavus*)	111			A species Site (*Pipistrellus subflavus*)	110				
R17			A species Site (*Sciurus oculatus*)	112			A species Site (*Sciurus oculatus*)	111				
R18			A species Site (*Dipodomys merriami*)	113			A species Site (*Ursus americanus*)	112				
R19			A species Site (*Onychomys arenicola*)	114			A species Site (*Dipodomys merriami*)	113				
R20							A species Site (*Onychomys arenicola*)	114				

Table 4 Prioritizations 4, 5, and 6, showing the number of species accumulated (No. of Spp. Acc.) at each prioritization step (Prior. Step) by existing biosphere reserves (BR), NAPC (priority areas), and new sites

	Prioritization 4				Prioritization 5				Prioritization 6			
	Bird species		**Mammal species**		**Bird species**		**Mammal species**		**Bird species**		**Mammal species**	
Prior Step	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**
R1	El Abra BR	13	El Abra BR	3	New Sites 5a	118	New Sites 5a	36	New Sites 6a	20	New Sits 6a	7
R2	El Cielo BR	26	El Cielo BR	11	New Sites 5b	190	New Sites 5b	61	New Sites 6b	27	New Sites 6b	10
R3	Sierra Gorda BR	26	Sierra Gorda BR	11	New Sites 5c	230	New Sites 5c	73	New Sites 6c	32	New Sites 6c	14
R4	New Sites 4a	32	New Sites 4a	13	New Site 5d	244	New Sites 5d	81	New Sites 6d	34	A species Site (*Dipodomys merriami*)	15
R5	New Sites 4b	34	A species Site (*Dipodomys merriami*)	14	New Sites 5e	253	New Sites 5e	88	A species site (*Ramphastos sulphuratus*)	35	A species Site (*Dipodomys phillipsii*)	16
R6	A species site (*Ramphastos sulphuratus*)	35	A species Site (*Dipodomys phillipsii*)	15	New Sites 5f	269	New Sites 5f	93			A species Site (*Ursus americanus*)	17
R7			A species Site (*Leopardus wiedii*)	16	New Sites 5g	273	New Sites 5g	97			A species Site (*Leopardus wiedii*)	18
R8			A species Site (*Lontra longicaudis*)	17	New Sites 5h	277	New Sites 5h	100			A species Site (*Oryzomys palustris*)	19
R9			A species Site (*Oryzomys palustris*)	18	New Sites 5i	280	New Sites 5i	103				

	Prioritization 4				Prioritization 5				Prioritization 6			
	Bird species		**Mammal species**		**Bird species**		**Mammal species**		**Bird species**		**Mammal species**	
Prior Step	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**	**Natural Area/Sites**	**No. of Spp. Acc.**
R10			A species Site (*Ursus americanus*)	19	A species Site (*Otus guatemalae*)	281	New Sites 5j	106				
R11					A species Site (*Petrochelidon pyrrhonota*)	282	A species Site (*Carollia perspicillata*)	107				
R12					A species Site (*Pheucticus chrysopeplus*)	283	A species Site (*Dipodomys merriami*)	108				
R13					A species Site (*Pipilo ocai*)	284	A species Site (*Dipodomys phillipsii*)	109				
R14					A species Site (*Psarocolius montezuma*)	285	A species Site (*Microtus quasiater*)	110				
R15							A species Site (*Molossus aztecus*)	111				
R16							A species Site (*Oryzomys palustris*)	112				
R17							A species Site (*Pipistrellus subflavus*)	113				
R18							A species Site (*Sciurus oculatus*)	114				

the mismatch between actual units of conservation and grid cells from which data on geographical occurrences of species have been mapped. Data resolution influenced the way in which hotspots of species richness were identified. Typically, multiple areas (5–100 pixels each) exhibited highest species richness levels. Then, at each prioritization step, a set of sites was defined as points, located in the centre of every identified area.

Prioritizations 5 and 6, which ignored existing areas, identified an array of sites across the region (Fig. 5). The richest sites for both birds and mammals are located on the eastern boundary of El Cielo biosphere reserve, in the tropical deciduous and semideciduous forests. These areas represent the northernmost limits of the distribution of these vegetation formations. The second richest set of sites for birds is located between San Nicolas de los Montes and Sierra Gorda biosphere reserve in areas with pine-oak forest, while the second richest sites for mammals are on the north-western boundary of El Cielo, in desert scrub.

These results show on one hand, the importance of several vegetation formations in the configuration of the region's biodiversity, as indicated by the predicted current distributions of bird and mammal species. On the other hand, the location of identified new sites reveals the existence of richness hotspots beyond the boundaries of both existing nature reserves and areas already identified as priority for conservation.

CONCLUSION

The basis of the analyses in this study is modelled approximations to potential and current spatial patterns of geographical distributions of bird and mammal species in north-eastern Mexico. Species' current distributions show marked reductions in extent relative to potential distributions, although the spatial patterns of 'hotspots' of modelled diversity are generally coincident. This study's main findings include: (1) distributions of highest potential and current richness coincide closely; (2) recurrent highest richness sites included the surroundings of El Cielo and El Abra-Tanchipa BRs, and San Nicolas de los Montes NAPC; (3) about 3/4 of bird and mammal species are currently protected by the three BRs; and (4) eight potential priority areas added ~12% more of species, with the remaining 13% concentrated in new sites spread across the region.

Further research is needed to relate estimates of species abundance and/or species distributional extent with the size of natural protected areas (current and proposed). This study's results (e.g. new sites with high species richness) can be used to propose modifications to present area system, as well as for analysis of conservation issues such as shape and size of proposed natural reserves.

ACKNOWLEDGEMENTS

We thank the Consejo Nacional de Ciencia y Tecnología (CONACyT) for providing a doctoral scholarship and the Comisión Nacional para el conocimiento y uso de la biodiversidad (CONABIO) for providing the environmental data used in this study. We also thank the Department of Geography, the Kansas Applied Remote Sensing Program, and the Natural History Museum & Biodiversity Research Center at the University of Kansas. Distributional information and access to specimens was provided by Academy of Natural Sciences of Philadelphia, American Museum of Natural History, Bell Museum of Natural History, California Academy of Sciences, Carnegie Museum of Natural History, Cornell University, Delaware Museum of Natural History, Field Museum of Natural History, Los Angeles County Museum of Natural History, Louisiana State University Museum of Natural Science, Moore Laboratory of Zoology, Museo de Zoología Facultad de Ciencias (UNAM), Muséum Nationale d'Histoire Naturelle of Paris, Museum of Comparative Zoology of Harvard University, Museum of Vertebrate Zoology, Museum of Zoology of the University of California at Los Angeles, Natural History Museum (Tring) (BMNH), Natuurhistorische Museum of Leiden, Royal Ontario Museum, Southwestern College, Texas Cooperative Wildlife Collections, U.S. National Museum of Natural History, Universidad Autónoma del Estado de Morelos, Universidad Michoacana San Nicolás de Hidalgo, University of Kansas Natural History Museum, University of Michigan Museum of Zoology, Naturhistorisches Museum of Vienna, Western Foundation of Vertebrate Zoology, and Yale Peabody Museum.

REFERENCES

Anderson, R.P., Lew, D. & Peterson, A.T. (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling*, **162**, 211–232.

Benítez, H., Arizmendi, C. & Márquez, L. (1999) Base de datos de las AICAS. CIPAMEX, CONABIO, FMCN, and CCA. México. Electronically published on the internet, URL: *http://www.conabio.gob.mx*

Cabeza, M. & Moilanen, A. (2001) Design of reserve networks and the persistence of biodiversity. *Trends in Ecology and Evolution*, **16**, 242–248.

Chapman, J.A. & Feldhamer, G.A., eds. (1982) Wild mammals of North America, biology, management, and economics. The John Hopkins University Press.

CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad). (1999). Electronically published on the internet, URL: *http://www.conabio.gob.mx/*

CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad). (2001). Electronically published on the internet, URL: *http://www.conabio.gob.mx/*

Conservation International. (1999). Electronically published on the internet, URL: *http://www.conservation.org/web/fieldact/megadiv/megadiv.htm.*

Escalante-Pilego, P., Navarro-Singuenza, A. & Peterson, T.A. (1998) Un análisis geográfico, ecológico e histórico de la diversidad de aves terrestres de México. *Diversidad biológica de México* (eds T.P. Ramamoorthy, R. Bye, A. Lot and J. Fa), pp. 279–304. Instituto de Biología, Universidad Nacional Autónoma de México. Ciudad Universitaria, México, D. F.

Emmons, L.H. & Feer F. (1997) Neotropical rainforest mammals. The University of Chicago Press, Chicago.

FAO (Organization for Food and Agriculture of the United Nations). (2001) Global forest resources assessment. ISSN 0258–6150, FAO Forestry Paper 140. Electronically published on the internet, URL: *http://www.fao.org/forestry/fo/fra/index.jsp.*

Fiona, A. (1997) *A field guide to the mammals of central America and southeast Mexico*. Oxford University Press.

Flather, C.H., Wilson, K.R., Dean, D.J. & McComb, W.C. (1997) Identifying gaps in conservation networks; of indicators and uncertainty on geographic-based analyses. *Ecological Applications*, **7**, 531–542.

Grumbine, R.E. (1990) Viable populations, reserve size, and federal lands management: a critique. *Conservation Biology*, **4**, 127–134.

Hopkinson, P., Travis, J., Prendergast, J., Evans, J., Gregory, R., Telfer, M. & Williams, P. (2000) A preliminary assessment of the contribution of nature reserves to biodiversity conservation in Great Britain. *Animal Conservation*, **3**, 11–320.

Kerr, T.J. (1997) Species, endemism, and choice of areas for conservation. *Conservation Biology*, **11**, 1094–1100.

Lombard, A.T. (1995) The problems with multi-species conservation: do hotspots, ideal reserves, and existing reserves coincide?. *South African Journal of Zoology*, **30**, 145–163.

Man and Biosphere Programme-UNESCO (MAB). (1984) Action plan for biosphere reserves. First International Biosphere Reserves Congress. Minsk, Belarus. Food and Agriculture Organization (FAO). World Conservation Union (IUCN). UNESCO-UNEP, 1983.

Margules, C.R., Cresswell, I.D. & Nichols, A.O. (1994) A scientific basis for establishing networks of protected areas. *Systematics and Conservation Evaluation* (eds P.L. Forey, C.J. Humpries & R.I. Vane-Wright), pp. 327–350. Clarendon Press, Oxford.

Meffe, G.K. & Carroll, R.C. (1997) Principles of conservation biology. Sinauer Associates. Inc. Publishers, Sunderland, Massachusetts.

Newmark, W.D. (1995) Extinction of mammal populations in western North American national parks. *Conservation Biology*, **9**, 512–526.

Nilsson, C. & Götmark, F. (1992) Protected areas in Sweden: Is natural variety adequately represented?. *Conservation Biology*, **6**, 232–241.

Oliver, L. & Beauie, A.J. (1996) Designing a cost-effective invertebrate survey; a test of methods for rapid assessment of biodiversity. *Ecological Applications*, **6**, 594–607.

Ortega-Huerta, Miguel, A. (2002) Accuracy assessment of the Inventario Forestal Nacional 2000 in northeastern Mexico. Unpublished study.

Peters, L.R. & Darling, S.J. (1985) The greenhouse effect and natural reserves. *Bioscience*, **35**, 707–715.

Peterson, A.T. (2001) Predicting species geographic distributions based on ecological niche modeling. *Condor*, **103**, 599–605.

Peterson, A.T., Ball, L.G. & Cohoon, K.C. (2002) Predicting distributions of tropical birds. *Ibis*, **144**, e27–e32.

Peterson, A.T. & Cohoon, K.P. (1999) Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecological Modelling*, **117**, 159–164.

Peterson, A.T., Egbert, S.L. & Sánchez-Cordero, V. (2000) Geographic analysis of conservation priority: endemic birds and mammals in Veracruz, Mexico. *Biological Conservation*, **93**, 85–94.

Peterson, A.T., Flores-Villela, A.O., Leon-Paniagua, S.L., Llorente-Busquests, A.M., Navarro-Singuenza, G.A., Torres-Chavez, G.M. & Vargas-Fernández, I. (1993) Conservation priorities in Mexico: moving up in the world. *Biodiversity Letters*, **1**, 33–38.

Peterson, A.T. & Kluza, D.A. (2003) New distributional modeling approaches for Gap Analysis. *Animal Conservation*, **6**, 47–54.

Peterson, A.T., Navarro-Siguenza, A.G. & Benitez-Diaz, H. (1998) The need for continued scientific collecting: a geographic analysis of Mexican bird specimens. *Ibis*, **140**, 288–294.

Peterson, A.T., Soberon, J. & Sanchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.

Prendergast, R.J., Quinn, M.R. & Lawton, H.J. (1999) The gaps between theory and practice in selecting nature reserves. *Conservation Biology*, **13**, 484–492.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Evershaun, B.C. & Gibbson, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335–337.

Pressey, R.L. (1994) *Ad hoc* reservations: forward or backward steps in developing representative reserve systems?. *Conservation Biology*, **8**, 662–668.

Pressey, R.L., Humpries, C.J., Margules, C.R., Vane-Wright, R.I. & Williams, P.H. (1993) Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution*, **8**, 124–128.

Pressey, R.L., Possingham, H.P. & Day, J.R. (1997) Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biological Conservation*, **80**, 207–219.

Rodrigues, L.A. & Gaston, J.K. (2001) How large do reserve networks need to be?. *Ecology Letters*, **4**, 602–609.

Rzedowski, J. (1978) Vegetación de México. Editorial Limusa, México D.F.

Sarukán, J., Soberón, J. & Larson-Guerra, J. (1996) Biological conservation in a high beta-diversity country. *Biodiversity* (eds F. Di Castri & T. Younes). Science and Development, CAB International, Wallingford, UK.

SEMARNAP (Secretaria de Medio Ambiente Recursos Naturales y Pesca). (2000) Proyecto de norma oficial Mexicana PROY-NOM-059-ECOL-2000, protección ambiental-especies de flora y fauna silvestres de México-categorias de riesgo y especificaciones para su inclusión, exclusión o cambio-lista de especies en riesgo. Diario Oficial de la Federación. *Lunes* 16 de octubre de 2000.

SEMARNAT (Secretaría del Medio Ambiente y Recursos Naturales). (2000) Vegetación y Usodel Suelo-2000-Inventario Forestal. Mexico, D.F.

Shafer, C.L. (1990) *Nature reserves: island theory and conservation practice*. Smithsonian Institution Press, Washington.

Soulé, M.E. (1991) Conservation: tactics for a constant crisis. *Science*, **253**, 744–750.

Stockwell, D.R. & Noble, I.R. (1991) Induction of sets of rules from animal distribution data: a robust and informative method of data analysis. *Math Computer Simul*, **32**, 249–254.

Stockwell, D.R. & Peters, D. (1999) The GARP modeling system: problems and solutions to automated spatial prediction. *International Journal of Geographyraphical Information Science*, **32**, 143–158.

Stockwell, D.R.B. & Peterson, A.T. (2002a) Controlling bias in biodiversity data. *Predicting species occurrences: issues of scale and accuracy* (eds J.M. Scott, P.J. Heglund & M.L. Morrison), pp. 537–546. Island Press, Washington, D.C.

Stockwell, D.R.B. & Peterson, A.T. (2002b) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1–13.

Stokland, N.J. (1997) Representativeness and efficiency of bird and insect conservation in Norwegian forest reserves. *Conservation Biology*, **11**, 101–111.

Whitaker, J.O. (1995) National Audubon Society field guide to North American mammals. Alfred A. Knopf, New York.

Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C. & Pressey, R. (1996) A comparison of richness hotspots, rarity hotspots, and complementarity areas for conserving diversity of British birds. *Conservation Biology*, **10**, 155–174.

Wilson, D.E. & Ruff, S., eds. (2001) *The Smithsonian book of North American mammals*. Smithsonian Institution Press in association with the American Society of Mammalogists, Washington D. C.