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Incorporating connectivity into conservation planning: A multi-criteria case study from central Mexico

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ABSTRACT

The interdigitation of the Neararctic and Neotropical biogeographic zones in the Transvolcanic Belt (TVB) of central Mexico provides the region with high faunal richness and endemicity. Biodiversity conservation in the TVB must accommodate the region's human population of more than 40 million. The current study presents conservation plans for the TVB intended to protect 99 non-volant mammal species while minimizing the impact on the human population. A rarity-complementarity algorithm was used to select a conservation area network (CAN) from sites with untransformed vegetation to represent 10% of each species' habitat. In addition, a new method was developed for augmenting the connectivity of CANs using graph theory. External sites were assigned quality scores based on the frequency with which they were selected at different targets of representation for species. Graph algorithms identified the highest-quality sites needed to link all conservation areas in an economical manner. These connectivity areas can facilitate migration or egress of biota in the event of local environmental stress. The network initialized with existing protected areas occupied 9.13% of the TVB, whereas the network built from scratch occupied 6.02%. In both cases, an additional area of only about 1.5% of the region was required to link all conservation areas in the network. Finally, a multiple criterion synchronization technique was used to select those connected networks which minimized both total area and human population impact.

1. Introduction

A central tenet of conservation planning is that fragmented and isolated conservation areas are inadequate for the long term persistence of biodiversity, especially if turnover in the conservation areas is high (Margules et al., 1994; Virolainen et al., 1999). Place prioritization algorithms have attempted to address this by minimizing the perimeter length of the network of conservation areas (McDonnell et al., 2002; Nalle et al., 2002; Onal and Briers, 2002) or the total distance between the areas (Fischer and Church, 2003; Onal and Briers, 2003). However, such a strategy does not ensure that a contiguous stretch of protected sites links the conservation areas. Several methods have been proposed for selecting such stretches, which are intended to serve primarily as dispersal corridors for animals (Williams, 1998; Van Langevelde et al.,

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2000; Cerdeira et al., 2005; Onal and Briers, 2005). A shortcoming of these methods is that they are intractable for the large biodiversity data sets being made available through species' ecological niche modeling (Soberón and Peterson, 2004). In addition to incorporating connectivity, conservation plans for populous regions must address the needs of the human population using multi-criteria analysis (reviewed in Moffett and Sarkar, 2006).

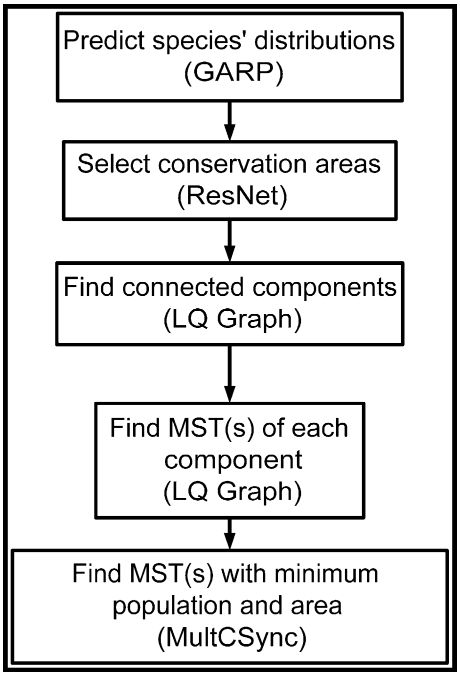

Fig. 1 – Flowchart of the conservation planning framework for the Transvolcanic Belt.

The objective of this study is to develop a framework for conservation planning that integrates ecological niche modeling, the selection of conservation areas, connectivity establishment, and multi-criteria analysis. What is novel about the approach presented here is the combination of these four techniques (Fig. 1) and the connectivity establishment procedure, which is able to handle much larger data sets than previous algorithms (Fuller and Sarkar, 2006). The framework is illustrated by developing a conservation plan for the Transvolcanic Belt (TVB) of central Mexico.

The TVB is particularly suited for a multi-criteria analysis because it has a high population but also high faunal endemism. In particular, the TVB contains all of the known endemic non-volant mammalian genera in Mexico and half of known endemic non-volant mammal species, most of which are small mammals (Fa and Morales, 1993; Escalante et al., 2004). Significant threats to biodiversity in the TVB include high deforestation and other forms of habitat transformation to satisfy the needs of a human population of nearly 40 million (Instituto Nacional de Geografía, Estadísitica e Informática, 2000; Velázquez et al., 2001). The TVB contains a large number of decreed natural protected areas (NPAs) most of which are small, with areas less than 10 km^2 (Fig. 2). Some of these NPAs were among the first decreed in the country but most were selected on the basis of political or scenic criteria rather than biological content (Alcérreca-Aguirre et al., 1988). For example, even vascular plant inventories are available for less than one-third of the NPAs, suggesting that they were not designated based on known biodiversity content (Villaseñor et al., 2005).

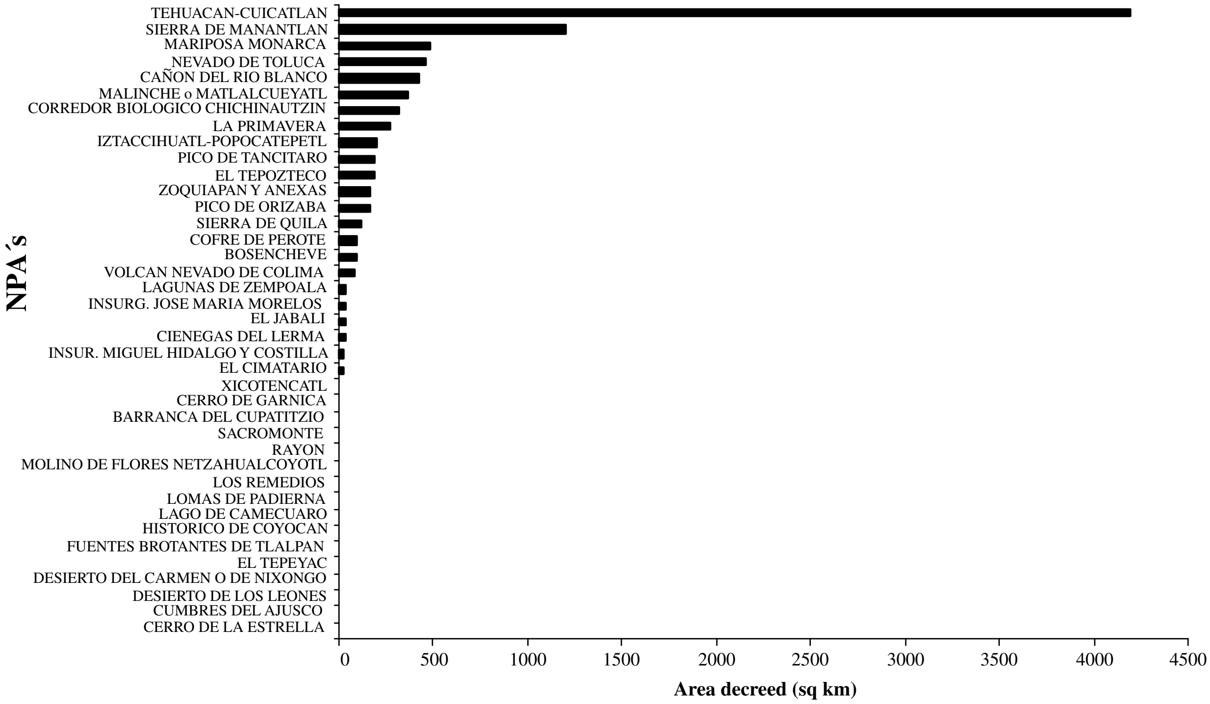

Fig. 2 – Main natural protected areas (NPAs) ranked by decreed area located in the Transvolcanic Belt and included in this study. The smallest NPAs, including Lago de Camécuaro and José María Morelos, are less than 10 km^2.

As a result, these NPAs are known to be collectively inadequate for conserving the TVB's high biodiversity (Sánchez-Cordero et al., 2004). One option to address these problems would be to increase the size of the NPAs. However, due to the high deforestation, development, and consequent habitat fragmentation in the TVB, almost all the NPAs cannot be enlarged to include more relatively intact biological habitat (see Fig. 3; Munguía, 2004; Sánchez-Cordero et al., 2005a,b).

An alternative strategy to avoid the negative effects of the small size of individual protected areas is to use relatively intact or restorable habitat to establish connectivity between units of a conservation area network (CAN). A CAN is defined as a set of areas managed for the persistence of biodiversity into the future (Sarkar, 2003). The term "conservation area" is preferred over the more traditional "reserve" because the latter term has the connotation that almost all human activity is banned in the protected areas (Sarkar, 2003). While conservation areas should consist of habitat already suited for the long-term persistence of biodiversity features, the connectivity areas may consist of less "high quality" areas. The connectivity areas may have some degree of human-induced transformation but may retain secondary vegetation and may be suitable for the migration of mammal species or as a temporary refuge. Connectivity areas may also comprise areas that are degraded but potentially restorable; restoration to reasonably adequate habitat is much more easily achievable (both in terms of scientific knowledge and economic resources) than restoration into the high quality habitat required for a conservation area (Daily et al., 2003; Gove et al., 2005). Existing protected areas in the TVB have small human populations engaged in agriculture, forestry, and mineral extraction (Bocco et al., 2005; Méndez-Larios et al., 2005). The appropriate policy for each conservation or connectivity area must be determined by local context. It can include human exclusion, habitat restoration, sustainable resource extraction, or even some types of agricultural production (Sarkar, 2005).

The aim of this study is to propose a regional landscape-scale plan for the TVB using all 99 non-volant mammals that occur in the region. Potential users of the plan include the Mexican governmental agencies, Comisión Nacional Para el Conocimiento y Uso de la Biodiversidad (CONABIO) and Comisión Nacional de Áreas Naturales Protegidas (CONANP) or non-governmental organizations in Mexico such as PRONATURA. Non-volant mammals are used because of their high regional extinction risk in the TVB (Sánchez-Cordero et al., 2005a,b), high endemicity, high species richness, and their role as important seed-dispersers in the ecosystem (Sánchez-Cordero and Martínez-Gallardo, 1998; Sánchez-Rojas et al., 2004; Briones-Salas et al., 2006). In Mexico, non-volant mammals are also one of the best known biological groups nationwide, and the species' distributions are well documented (Fa and Morales, 1993; Arita et al., 1997; Villa and Cervantes, 2003).

The specific protocol developed here for integrating connectivity into conservation planning appears to be new. However, as this analysis of the TVB shows, this protocol can be used for any region for which minimal information on species' biogeographic distributions is available.

2. Methods

2.1. *Biogeographic region*

The TVB was partitioned into sites with (i) primary vegetation, (ii) secondary vegetation or (iii) neither; sites of type (iii) were considered anthropogenically transformed beyond restoration and excluded from the analysis. The first stage of the plan, that is, place prioritization for biodiversity representation in CANs, used standard techniques of site selection to represent a specified proportion of the habitat of each species in the network in as few sites as possible. During this stage, only type (i) sites were used. Previous work has shown that these areas, as determined using remote-sensed data, formed the most suitable habitat for the mammal species of Mexico (Sánchez-Cordero et al., 2004, 2005a,b).

The TVB was divided into 106,026 sites at a $0.01° \times 0.01°$ resolution of longitude × latitude. Site area varied between 1.153 and 1.179 km^2, with an average of 1.163 km^2 (SD = 0.00496). The total area was 123,355 km^2. Remote-sensed data were used to identify sites with relatively intact primary vegetation [type (i)], sites with secondary vegetation [type (ii)], and sites with neither [type (iii)] (Mas et al., 2004). Sites from the last category (38,274 sites with a total area of 44,511 km^2 or 36.08% of the TVB) were excluded from this analysis because they do not belong to the modeled ecological niches of the non-volant mammals considered here (Sánchez-Cordero et al., 2005a,b). Species appear to show niche conservatism over long time scales, and invasion of newly formed ecological niches may not result in persistent populations without recurrent immigration from adjacent untransformed habitats (Peterson et al., 1999; Peterson and Holt, 2003).

2.2. *Modeling species' distributions*

The geographical distribution of 99 non-volant mammal species (see Villa and Cervantes, 2003, for taxonomic nomenclature), were modeled using point occurrence data and environmental layers. The former were obtained from museum voucher specimens from national and international scientific collections (see Acknowledgments). The latter consisted of 10 environmental coverages at $0.04° \times 0.04°$ pixel resolution, which summarized potential vegetation types, elevation, slope, and aspect, according to the Hydro 1K methodology (United States Geological Survey, 1998), and climatic parameters including mean annual precipitation, mean daily precipitation, maximum daily precipitation, minimum and maximum daily temperature, and mean annual temperature obtained from CONABIO (2002).

Modeled species' distributions were constructed with the Genetic Algorithm for Rule-set Prediction software package (GARP; Stockwell and Peters, 1999). GARP uses ecological-environmental abiotic and biotic variables of known species' occurrence points to produce coarse-grained species' ecological niche models ("Grinnelian" models; Grinnell, 1917) projected as potential distributions. In GARP, occurrence points are divided evenly into training and testing data sets. An iterative algorithm consisting of rule selection, evaluation, testing, and subsequent incorporation or rejection is used to "evolve" a most predictively accurate set of rules from an

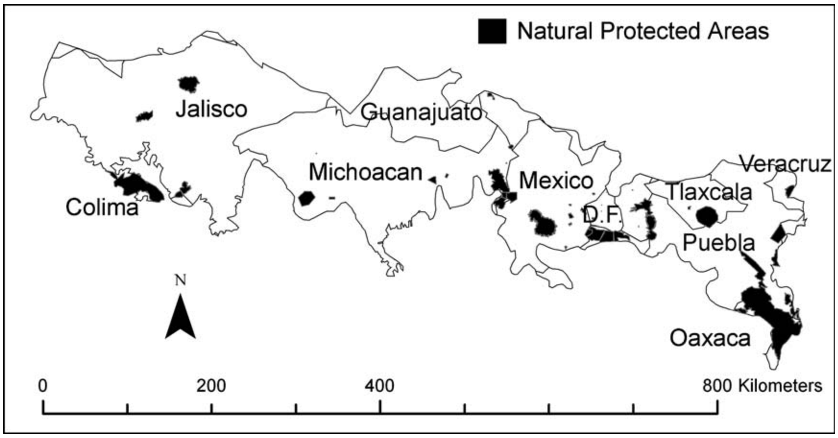

Fig. 3 – Natural protected areas of the Transvolcanic Belt (black) with state names. "D.F.: Distrito Federal".

original set of possibilities (e.g., logistic regression, bioclimatic rules). The algorithm runs for 1000 iterations or until convergence (see Stockwell and Peterson, 2002). The final rules are then used to predict the total distribution for each species.

GARP has proven a robust tool for predicting species' geographic distributions for mammals (Illoldi-Rangel et al., 2004) and other taxa in Mexico (Garcia, 2006). Because GARP does not produce a unique solution, its use here followed published recommendations for the construction of optimal subsets of replicate models (Anderson et al., 2003). For each analysis, 100 replicate models at a 0.01° × 0.01° resolution were produced, the 20 models with lowest omission error were initially retained, and the 10 models with commission errors close to the median finally adopted for subsequent use. Further modeling refinement consisted of rejecting obvious over-predictions for microendemics (for example, disjunction distributions) based on Hall (1981). Species' extant distributions were then calculated by overlaying the Inventario Nacional Forestal 2000 map (Mas et al., 2004) and excluding only areas holding highly transformed habitat (type (iii) sites). The extant distribution models were used for the connectivity analyses (see below).

2.3. *Place prioritization protocols*

Two CANs were selected using the rarity-complementarity algorithm in the ResNet software package to represent 10% of the modeled distribution of each species restricted to type (i) sites (Garson et al., 2002). The algorithm included an adjacency criterion that breaks ties by selecting new sites physically adjacent to previously selected sites. This results in a spatially-aggregated CAN. In the first CAN, the algorithm was initialized with the 39 existing natural protected areas (the "NPA" solution) (Fig. 3). The second CAN was designed while ignoring the existing protected areas and initializing the algorithm with the site containing the rarest species (the "rarity" solution). It has been suggested that heuristics such as those implemented in ResNet provide significantly sub-optimal solutions (Rodrigues and Gaston, 2002). To test this, the conservation area selection problem was represented as an integer program in the GAMS modeling language (Brooke et al., 1998) and the optimal solution was obtained using a branch-and-bound algorithm in the CPLEX 9.1 integer programming solver (ILOG, 2003).

2.4. *Landscape quality score*

Suppose planners wish to protect an at-risk species subject to the following constraints: at most 1% of the habitat of each species can be protected or at most 99% of the habitat can be protected. A site first selected when the first constraint is in effect is more critical for the species' persistence than one first selected under the latter constraint. This assumption was used to score sites in the TVB such that sites first selected at low targets of representation earned higher quality scores than those first selected at higher targets. ResNet was used to prioritize sites to represent species' habitat in the TVB at 20 target levels (5–100% at increments of 5%). One hundred replicates of each of the 20 place prioritizations were generated. Each replicate used a different random reshuffling of the rows of input file. Since ResNet uses a heuristic algorithm in which ties are broken by selecting a site at random, this could result in different solutions in each replicate. The final site quality scores were weighted by the frequency of selection at a given target level so that sites selected frequently at low targets had the highest scores.

2.5. *Graph-theoretical connectivity protocols*

The second stage, that is, the establishment of connectivity in the networks by linking conservation areas, required the development of some new techniques. The connectivity areas were selected with graph algorithms, which select paths that directly link conservation areas via high-quality sites that are not currently part of the conservation areas. This permits organisms, particularly mobile animals, in one conservation area to disperse to another using a path of contiguously protected sites. Graphs have previously been used for conservation planning but only for one or two species at a time (Bunn et al., 2000; Urban and Keitt, 2001). This analysis extends these techniques to an arbitrary number of species and other biodiversity surrogates. Both type (i) and type (ii) sites were used for selecting the connectivity areas. Type (ii) sites are less intact than those of type (i) but still potentially restorable to adequate habitat for the relevant species. Thus, type (ii) sites were considered suitable for connecting conservation areas, but not adequate as sites for conservation areas themselves.

The LQGraph software package (Fuller and Sarkar, 2005) was used to find all least-cost paths between the conservation areas in both the NPA and rarity solutions. Costs were assigned so that a path consisting of many sites with high landscape quality scores had a low cost (Fuller and Sarkar, 2006). In addition, LQGraph filtered the least cost paths to find a minimum spanning tree (MST), the minimum number of paths required to link all conservation areas via high-quality sites. MSTs should be given priority for conservation because they represent the minimal connectivity-maintaining regions between conservation areas (Urban and Keitt, 2001).

In the TVB, a mammal in one conservation area may be able to disperse to nearby conservation areas but not to more distant conservation areas in the network due to the large percentage of type (iii) sites in the landscape. To quantify this, "connected components" of the NPA and rarity solutions were identified. These connected components are sets of conservation areas such that an individual in one conservation area within the set could reach any other conservation area within it by traversing only paths consisting of selected high-quality sites. A conservation area with a large number of components is highly fragmented from the perspective of an individual attempting to disperse among the conservation areas.

Random graphs ($n = 1000$; Siek et al., 2002) were generated to provide a null model for comparing connectivity properties of the graphs corresponding to the NPA and rarity solutions. In the random graphs, the number of vertices equaled the number of conservation areas in the NPA and rarity solutions but edges were assigned at random between the vertices. Finally, spatial statistics (Syrjala, 1996) were used to assess whether the NPA and rarity solutions had the same configurations and whether their MSTs were spatially similar.

2.6. Multi-criteria analysis

The third stage used multi-criteria analysis to select the conservation plan with the minimal area and human impact (measured as the human population of sites in the plan). LQGraph finds all MSTs of a CAN. Alternative MSTs are interchangeable with respect to their connectivity properties but may differ in other criteria relevant for biodiversity conservation. All the MSTs were ordered by their area and human population. Population data were obtained from CONABIO (2002, www.conabio.gob.mx) and Instituto Nacional de Geografía, Estadísitica e Informática (2000, www.inegi.gob.mx). The GIS model provided data on areas (km^2).

Each MST is a "solution" to the multiple-criterion decision problem of how to minimize the human impact of the conservation plan while representing the non-volant mammals in a connected network of conservation areas. The "best" solutions were the non-dominated ones, which were identified using the methodology of Sarkar and Garson (2004) with the MultCSync 1.0 software package (Moffett et al., 2004). One solution is said to "dominate" another if it is better than the other by at least one criterion (e.g., area or human population), and no worse by any criterion. A solution is called "non-dominated" if it is not dominated by any other solution. In the present study, a "non-dominated solution" is a set of conservation areas and connectivity areas such that the geographical area and human population are as small as possible.

3. Results

3.1. Species

The species used in this study were 99 non-volant mammal species consisting of 14 species endemic to the TVB, 24 species endemic to Mexico, and 61 non-endemic species. Extant species' distributions ranged from 50 to 52,770 km^2 (0.04–42.77% of the total area) for the endemics to the TVB, 1290–69,000 km^2 (1.05–55.93% of the total area) for the endemics to Mexico, and 1070–54,970 km^2 (0.87–44.56% of the total area) for the non-endemics (Table 1).

3.2. Conservation areas and landscape quality analyses

The 39 existing protected areas had a total area of 9179 km^2 or 7.4% of the TVB. More than half of the decreed NPAs have areas less than 100 km^2 and only two are larger than 1000 km^2. The NPA-initialized solution contained 9658 sites with a total area of 11,264.4 km^2 or 9.13% of the TVB, whereas the rarity-initialized solution contained 6382 sites with an area of 7431.32 km^2 or 6.02% of the TVB. Both solutions were at most 0.04% suboptimal. In the conservation planning literature, a solution within 1% of the optimum is generally considered optimal (Onal, 2004). These results confirm previous findings that the rarity-complementarity algoirthm implemented in ResNet is competitive with optimal solution methods (Sarkar et al., 2004). The graph-based representation of the NPA solution had 442 conservation areas, 4823 paths between conservation areas, and 25 components (Table 2). The graph corresponding to the rarity solution had 409 conservation areas, 4030 paths, and 39 components.

3.3. Connectivity analyses

The least cost paths between the conservation areas occupied 20.76% of the TVB in the NPA solution and 22.66% in the rarity solution, which is too large a portion of the landscape to be included in a conservation plan in such a populous region (Table 2). Thus, the least cost paths were filtered to find MSTs. The MSTs established connectivity among conservation areas using only 6.9% and 1.02% of the area of the least cost paths in the respective solutions. Thus, connectivity can be established via MSTs more economically than via least-cost paths.

In the comparison to random graphs, the graph corresponding to the NPA solution had fewer ($p = 0.042$) and the graph corresponding to the rarity solution ($p \gg 0.05$) had more components (randomization test, Manly, 1997). The number of components of the graph can be thought of as a measure of connectivity in the following sense. If the graph has few components, an animal in one conservation area is likely to be able to disperse to almost any other conservation area in the network. Based on this measure, the NPA solution is better connected and better facilitates dispersal than the rarity solution.

Table 1 – List of non-volant mammals in the Transvolcanic Belt (TVB) of central Mexico, consisting of 61 non-endemics to Mexico (NE), 24 endemics to Mexico (E), and 14 microendemics to the TVB (M)

Species	Actual distribution (km^2)	Geographic position
Rodentia		
Glaucomys volans	52,350	NE
Sciurus aureogaster	50,320	NE
Sciurus colliaei	25,940	E
Sciurus deppei	37,560	NE
Sciurus nayaritensis	43,750	NE
Sciurus oculatus	17,310	E
Spermophilus adocetus	19,270	E
Spermophilus mexicanus	41,110	NE
Spermophilus perotensis	11,030	M
Spermophilus variegatus	48,910	NE
Spermophilus spilosoma	12,190	NE
Cratogeomys gymnurus	44,440	M
Cratogeomys merriami	53,050	E
Cratogeomys tylorhynus	52,770	M
Pappogeomys alcorni	130	M
Pappogeomys bulleri	24,140	E
Thomomys umbrinus	52,870	NE
Zygogeomys trichopus	7740	M
Dipodomys phillipsii	53,350	E
Liomys pictus	41,740	NE
Liomys irroratus	53,300	NE
Liomys spectabilis	17,030	M
Perognatus flavus	1070	NE
Baiomys musculus	43,560	NE
Baiomys taylori	44,280	NE
Habromys simulatus	12,410	E
Hodomys alleni	25,000	E
Nelsonia neotomodon	18,590	M
Neotoma albigula	14,070	NE
Neotoma mexicana	47,900	NE
Neotoma nelsoni	50	M
Neotomodon alstoni	47,900	E
Nyctomys sumichrasti	47,180	NE
Oligoryzomys fulvescens	49,260	NE
Oryzomys couesi	43,030	NE
Oryzomys alfaroi	50,170	NE
Oryzomys melanotis	30,090	E
Osgoodomys banderanus	40,620	E
Peromyscus aztecus	49,200	NE
Peromyscus bullatus	280	M
Peromyscus difficilis	69,000	E
Peromyscus furvus	40,910	E
Peromyscus leucopus	23,830	NE
Peromyscus maniculatus	39,310	NE
Peromyscus mekisturus	1290	E
Peromyscus melanophrys	24,390	E
Peromyscus melanotis	52,880	NE
Peromyscus mexicanus	42,940	NE
Peromyscus pectoralis	39,060	NE
Peromyscus spicilegus	38,370	E
Peromyscus truei	50,910	NE
Reithrodontomys chrysopsis	50,670	M
Reithrodontomys fulvescens	35,690	NE
Reithrodontomys hirsutus	14,700	M
Reithrodontomys megalotis	52,400	NE
Reithrodontomys mexicanus	39,540	NE
Reithrodontomys microdon	32,330	NE
Reithrodontomys sumichrasti	50,640	NE
Sigmodon alleni	37,680	E
Sigmodon fulviventer	37,020	NE
Sigmodon hispidus	45,110	NE
Sigmodon leucotis	43,270	E
Sigmodon mascotensis	43,190	E
Microtus mexicanus	51,680	NE
Microtus quasiater	48,750	M
Carnivora		
Urocyon cinereoargenteus	52,870	NE
Canis latrans	30,090	NE
Bassariscus astutus	54,970	NE
Nasua narica	42,410	NE
Procyon lotor	40,400	NE
Conepatus mesoleucus	37,640	NE
Mephitis macroura	47,050	NE
Spilogale putorius	42,040	NE
Spilogale pygmaea	13,870	E
Mustela frenata	53,440	NE
Lontra longicaudis	37,210	NE
Taxidea taxus	9810	NE
Puma concolor	35,780	NE
Leopardus wiedii	23,340	NE
Lynx rufus	42,460	NE
Insectivora		
Cryptotys goldmani	53,140	NE
Cryptotys mexicana	53,060	E
Cryptotys parva	50,300	NE
Megasorex gigas	35,580	E
Notiosorex crawfordi	27,490	NE
Sorex emarginatus	5480	E
Sorex macrodon	12,330	M
Sorex saussurei	50,510	NE
	5930	NE
Lagomorpha		
Lepus californicus		
Lepus callotis	42,320	NE
Sylvilagus audubonii	8950	NE
Sylvilagus cunicularis	49,180	E
Sylvilagus floridianus	50,500	NE
Romerolagus diazii	20,350	M
Didelphimorphia		
Didelphis marsupialis	49,730	NE
Didelphis virginianus	43,670	NE
Artiodactyla		
Odocoileus virginianus	42,090	NE
Tayassu tajacu	38,040	NE
Xenathra		
Dasypus novemcinctus	42,260	NE

Actual distribution predictions were produced by including only remnant untransformed habitat based on the Inventario Nacional Forestal 2000 within the species' potential distributions (see Section 2 for details).

In the MSTs based on the NPA solution, on average an additional 1520.97 (SD = 905.49) sites (in addition to the CAN sites) with an average area of 1766.64 km^2 (SD = 1051.54) or 1.43% of the area of the TVB are prioritized (Fig. 4). In the MSTs based on the rarity solution, on average an additional 247 (SD = 485.46) sites (in addition to the CAN sites) with an

Table 2 – Statistics of graph models for establishing conservation area networks (CAN) in the Transvolcanic Belt

	NPA solution	Rarity solution
CAN area (km^2)	11,264.4	7431.32
Percentage of TVB in CAN	9.13	6.02
Number of conservation areas	442	409
Number of connected components	25	39
Number of least-cost paths	4283	4030
Area of least-cost paths (km^2)	25,606.97	27,983.98
Total number of minimum spanning trees (MSTs)	48	32
Area of MSTs (km^2): mean (SD)	1766.64 (1051.54)	287.47 (563.85)

Note that when the place prioritization algorithm is initialized with the existing NPAs ("NPA solution"), more land is required to represent 10% of each species' habitat and establish connectivity between conservation areas.

average area of 287.47 km^2 (SD = 563.85) or 0.23% of the area of the TVB are prioritized. This means that the amount of land required to construct paths to connect the conservation areas in the rarity solution is less than the land required for the NPA solution. The large standard deviation associated with each average MST area is due to the large variance in the number of conservation areas among components. The spatial configurations of the MSTs based on the rarity and NPA solutions were significantly different (Syrjala test, $p = 0.01$). For both the NPA and rarity solution, the median length of the sets of connectivity areas linking conservation areas was 4.24 km.

3.4. *Multi-criteria analysis*

The set of MSTs based on the NPA solution had three non-dominated solutions and the set of MSTs based on the rarity solution had four.

4. Discussion

Like previous studies (Alcérreca-Aguirre et al., 1988; Sánchez-Cordero et al., 2004; Villaseñor et al., 2005), this analysis demonstrates that the existing protected areas in the TVB do not represent biodiversity economically. When the site selection algorithm was initialized with the existing NPAs, 3833 km^2 more land was required to represent 10% of the distribution of each non-volant mammal than if the CAN was not so

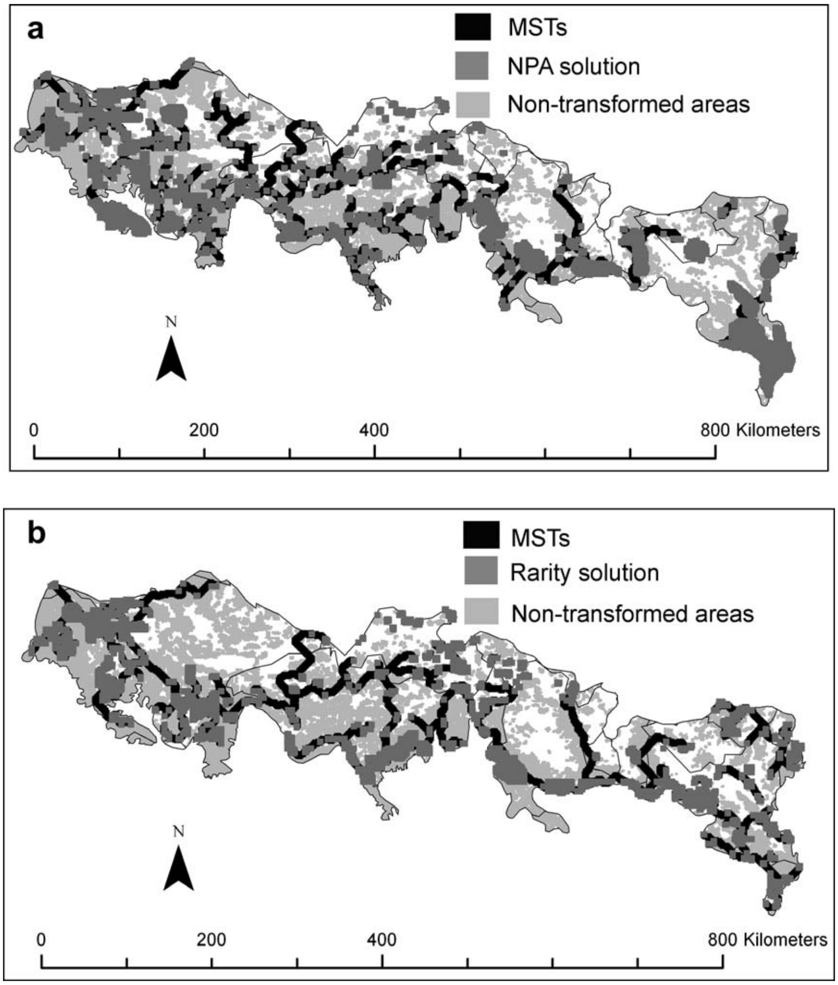

Fig. 4 – Conservation plans for the Transvolcanic Belt: (a) the NPA solution; (b) the rarity solution. Both plans are non-dominated solutions identified by the multi-criteria analysis.

initialized (Table 2). Among the first locations selected in both the NPA and rarity solution was a site in northern Veracruz containing more than 30 non-volant mammals. A conservation plan for the northeastern TVB using the same mammal database as the present plan (Ortega-Huerta and Peterson, 2004) also prioritized this site. This area should be an immediate priority for regional conservation.

The NPA solution is better connected than the rarity solution to the extent that the latter has more connected components. Human population may account for this difference in connectivity. The connectivity establishment procedure presented here constructs paths between conservation areas via sites with primary or secondary vegetation. It is plausible that a site with a high human population will lack such vegetation or be adjacent to sites without vegetation. The rarity solution contains about eight million more people than the NPA solution. Due to the high population of the rarity solution, many of its conservation areas may be surrounded by sites without vegetation, making it impossible to establish connectivity areas between them. Only when the MST based on the NPA solution was compared with the MST based on the rarity solution did the Syrjala detect significant differences in spatial configuration. In general, rejecting the null hypothesis of identical configurations is quite difficult with the Syrjala test (Sarkar et al., 2005). Therefore, the spatial differences between the MSTs must be quite strong. The MST for the NPA solution has extensive connectivity areas in central Jalisco that are not present in the MST for the rarity solution.

Though the biological importance of establishing connectivity between individual units of a CAN remains controversial (Noss, 1987; Simberloff et al., 1992), connectivity is known to be important for non-volant mammals in the TVB such as those in the genera *Peromyscus* and *Microtus*. In the case of *Peromyscus*, landscape connectivity influences population persistence to the extent that individuals are known to have better access to food in connected habitat patches (Orrock et al., 2003). In the case of *Microtus*, connectivity, rather than climatic fluctuations, affects population size and synchrony (Huitu et al., 2003). *Peromyscus* species are known to use linear landscape features such as strips of remnant habitat as corridors (Bolger et al., 2001). Of the 99 non-volant mammal species considered here, data on maximum dispersal distances were available for only 10 (Sutherland et al., 2000; Bowman et al., 2002). The dispersal distances for nine of these species exceeded the median length of the connectivity areas selected by the graph algorithms. This suggests that these small mammals would use the connectivity areas as dispersal corridors between conservation areas in the TVB. However, future studies should test the utility of these connectivity areas for mammals and other biological groups. In addition to their function as dispersal corridors, the connectivity areas could serve as sites for habitat restoration.

Were taxa other than non-volant mammals used to design the CAN, different places might be prioritized (though it is unlikely that sites selected here would not be selected at all). For example, the Tehuacán-Cuicatlán valley in southern Puebla has 365 endemic plants but its mammal species are both less diverse and less documented (Davila et al., 2002). Thus, when sites were selected to protect mammal habitat and the algorithm was not initialized with the existing natural protected areas, fewer sites in southern Puebla were selected. Quantifying the extent to which the plans presented here represent non-mammalian diversity requires formal surrogacy analysis (Sarkar et al., 2005), which is beyond the scope of this study. Irrespective of this, non-volant mammals are an important component of biodiversity that merit protection. The biodiversity value of a site can be defined as the number of features of the site that are not adequately protected elsewhere (Sarkar and Margules, 2002). By this definition, the biodiversity value of mammal habitat in the TVB is extremely high because the TVB has more endangered mammals than any other region of Mexico (Ceballos et al., 1998) and the existing protected areas do not represent this fauna adequately.

This conservation plan prioritizes many of the same sites as earlier plans for the TVB. A national plan for several hundred bird, mammal, and amphibian species in Mexico at the 0.25° scale prioritized northern Puebla and northern Michoacán (Brandon et al., 2005). The rarity solution (Fig. 4b) selects many sites in these areas. However, Brandon et al. (2005) also prioritize the western half of the state of Mexico. Most sites in the state of Mexico were excluded from the present plan because they lack primary or secondary vegetation. Pérez-Arteaga et al. (2005) designed a CAN for Mexican wildfowl that includes 12 conservation areas in the central highlands of the TVB, where the states of Guanajuato, Jalisco, and Michoacán meet. The NPA solution (Fig. 4a) proposes only 6 conservation areas in this region, but selects extensive connectivity areas there. However, the plans differ in scale since the wildfowl plan was carried out at the national scale. Velázquez et al. (2003) designed a CAN to protect 122 species of threatened and endangered amphibians, reptiles, birds, mammals, and vascular plants in Distrito Federal. They proposed sites along the southern and western borders of the state as “core areas” of the CAN. Although the NPA and rarity solutions (Figs. 4a and b) prioritize some of these same core areas, conservation and connectivity areas in Distrito Federal make up less than 1% of the present plan (Table 3); differences between the plans can be explained by scale to the extent that the present plan is for a region 1440 times larger (Velázquez et al., 2003). In addition, the plan presented here selects sites with high biodiversity content by means of an iterative selection procedure (Garson et al., 2002), whereas Velázquez et al. (2003) employed correspondence analysis and ordination.

Mammal species assemblages in the eastern TVB are dissimilar from the rest of the region, probably because the east has moist forests and cloud forests whereas the forests elsewhere in the TVB are mostly dry (Fa, 1989). The unique mammal fauna of the eastern TVB is represented in both of the CAN’s presented here. The plan initialized with the existing natural protected areas selects sites around the Tehuacán-Cuicatlán biosphere reserve in southern Puebla (Fig. 4a). The plan not initialized with the NPAs selected fewer sites in southern Puebla but more sites in the northern part of the state (Fig. 4b).

The planning method described here could be refined in several ways. Here, a two-stage method was used to select contiguity areas. First, the graph algorithms identified many sets of contiguity areas. Each set consisted of sites with high landscape quality that established connectivity between the

Table 3 – List of states and percent of conservation areas and connectivity areas included in the place prioritization algorithms for the Transvolcanic Belt

State	Conservation areas (%)	Connectivity areas (%)
Colima	0.0157 1.149	0.277 0.0376
Distrito Federal	0.141 0.238	0.99 0.827
Guanajuato	6.142 2.879	7.013 6.126
Hidalgo	0.768 0.311	0.04 0.113
Jalisco	37.59 32.101	28.922 38.858
Mexico	14.478 10.438	6.022 10.447
Michoacán	18.192 14.87	29.319 34.987
Morelos	1.802 4.483	2.219 0.789
Nayarit	0.517 0.632	0.713 0.827
Oaxaca	2.209 8.74	3.011 0.526
Puebla	15.544 19.0328	17.789 3.908
Queretaro	1.254 0.611	0.436 0
Tlaxcala	0.329 2.444	1.466 1.203
Veracruz	1.0184 1.957	1.783 1.278
Zacatecas	0 0.114	0 0.0752

The lower (upper) percentage is for the NPA (rarity) solution.

conservation areas. Second, the multiple-criteria synchronization procedure identified the sets with the smallest geographical areas and human populations. The landscape quality score served as an indicator of habitat suitability. Population served as a measure site vulnerability insofar as mammal habitat is more likely to be disturbed when the human population is high (Carroll et al., 2003). As an alternative to the two-stage method, a single utility function could be used to prioritize contiguity areas based on suitability and vulnerability simultaneously. However, such a function requires assigning arbitrary weights to the two criteria and assumes that they have a common quantitative scale (Sarkar and Garson, 2004). The multiple-criterion synchronization procedure presented here avoids the problems of arbitrariness and incommensurability because it generates an ordinal ranking of the sets of contiguity areas (based on area and population) rather than assigning numerical values to the two criteria.

Second, though the GIS model in this analysis used the same site sizes for the CANs and the connectivity areas, the graph algorithms described above permit different scales to be used. In Mexico, many NPAs are adjacent to expanding cities (Cantú et al., 2004). In this context, conservation planners may wish to use a fine spatial scale to model sites outside the NPAs in order to ensure that the connectivity areas that they select do not intersect with infrastructure such as roads. Moreover, the administrative boundaries of NPAs in Mexico are sometimes poorly defined (Bojórquez-Tapia et al., 2004) such that there is no clear delineation between a park and private lands. In such cases, it would be suitable to represent the CANs with a coarse spatial scale while using a fine spatial scale when selecting connectivity areas. In addition, though the analysis presented here did not calculate the cost of restoring transformed habitat in the TVB, conservation plans from other regions estimate that this can double the cost of the plan (Frazee et al., 2003). Calculating this cost would require data on the cost of buying and administrating sites adjacent to conservation areas and the cost of incentive-based agreements between land owners and CONABIO, such as tax breaks. Finally, the methodology presented establishes connectivity between conservation areas via MSTs using as few sites as possible so as to minimize the impact on the human population. However, planners may wish to establish multiple, redundant connections between conservation areas as a safeguard against future disturbances, such as changes in forest and life zone types in the TVB due to climate change (Villers-Ruíz and Trejo-Vázquez, 1998). This could be accomplished by placing all of the least-cost paths between conservation areas under protection rather than filtering the paths to find the MST(s). An alternative method to protect the CAN against future disturbance is to select sites here-and-now so as to minimize the expected cost of protecting species adequately in the future using stochastic optimization (Snyder et al., 2004).

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REFERENCES

Alcérreca-Aguirre, C., Consejo, J., Flores, O., Gutiérrez, D., Hentschel, E., Herzig, M., Pérez-Gil, R., Reyes, J.M., Sánchez-Cordero, V., 1988. Fauna Silvestre y Areas Naturales Protegidas. Fundación Universo Veintiuno, México D.F.

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.

Arita, H.T., Figueroa, F., Frisch, A., Rodriguez, P., Santos del Prado, K., 1997. Geographical range size and the conservation of Mexican mammals. Conservation Biology 11, 92–100.

Bocco, G., Velázquez, A., Siebe, C., 2005. Using geomorphological mapping to strengthen resource management in developing countries: the case of rural indigenous coummunities in Michoacán, Mexico. Catena 60, 239–253.

Bojórquez-Tapia, L.A., Cueva, H., Díaz, S., Melgarejo, D., Alcantar, G., Solares, M.J., Grobet, G., Cruz-Bello, G., 2004. Environmental conflicts and nature reserves: redesigning the Sierra San Pedro Mártir national park, Mexico. Biological Conservation 117, 111–126.

Bolger, D.T., Scott, T.A., Rotenberry, J.T., 2001. Use of corridor-like structures by bird and small mammal species. Biological Conservation 102, 213–224.

Bowman, J., Jaeger, J.A.G., Fahrig, L., 2002. Dispersal distance of mammals is proportional to home range size. Ecology 83, 2049–2055.

Brandon, K., Gorenflo, L., Rodrigues, A., Waller, R., 2005. Reconciling conservation, people, protected areas, and agricultural suitability in Mexico. World Development 33, 1403–1418.

Briones-Salas, M., Sánchez-Cordero, V., Sánchez-Rojas, G., 2006. Multi-species fruit and seed removal in a tropical deciduous forest in Mexico. Canadian Journal of Botany 84, 433–442.

Brooke, A., Kendrick, D., Meeraus, A., Raman, R., 1998. GAMS: A User's Guide. GAMS Development Corporation, Washington, DC.

Bunn, A.G., Urban, D.L., Keitt, T.H., 2000. Landscape connectivity: a conservation application of graph theory. Journal of Environmental Management 59, 265–278.

Cantú, C., Wright, R.G., Scott, J.M., Strand, E., 2004. Assessment of current and proposed nature reserves of Mexico based on their capacity to protect geophysical features and biodiversity. Biological Conservation 115, 411–417.

Carroll, C., Noss, R.F., Paquet, P.C., Schumaker, N.H., 2003. Use of population viability analysis and reserve selection algorithms in regional conservation plans. Ecological Applications 13, 1773–1789.

Ceballos, G., Rodríguez, P., Medellín, R.A., 1998. Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemicity, and endangerment. Ecological Applications 8, 8–17.

Cerdeira, J.O., Gaston, K.J., Pinto, L.S., 2005. Connectivity in priority area selection for conservation. Environmental Modeling and Assessment 10, 183–192.

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. 2002. Metadata and Digital Map Library. http://conabioweb.conabio.gob.mx/metacarto/metadatos_ing.pl (last accessed 9.12.05).

Daily, G., Ceballos, G., Pacheco, J., Suzán, G., Sánchez-Azofeifa, A., 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conservation Biology 17, 1814–1826.

Davila, P., del Coro Arizmendi, M., Valiente-Banuet, A., Villaseñor, J.L., Casas, A., Lira, R., 2002. Biological diversity of the Tehuacán-Cuicatlán valley, Mexico. Biodiversity and Conservation 11, 421–442.

Escalante, T., Rodríguez, G., Morrone, J.J., 2004. The diversification of Nearctic mammals in the Mexican transition zone. Biological Journal of the Linnean Society 83, 327–339.

Fa, J., 1989. Conservation-motivated analysis of mammalian biogeography in the Trans-Mexican Neovolcanic belt. National Geographic Research 5, 296–316.

Fa, J., Morales, L., 1993. Patterns of mammalian diversity in Mexico. In: Ramamoorthy, T., Bye, R., Lot, A., Fa, J. (Eds.), Biological Diversity of Mexico: Origins and Distribution. Oxford University Press, Oxford, pp. 319–364.

Fischer, D.T., Church, R.L., 2003. Clustering and compactness in reserve site selection: an extension of the biodiversity management area selection model. Forestry Science 49, 555–565.

Frazee, S., Cowling, R., Pressey, R., Turkpie, J., Lindenberg, N., 2003. Estimating the cost of conserving a biodiversity hotspot. Biological Conservation 112, 275–290.

Fuller, T., Sarkar, S., 2005. LQGraph Version 1.0 Manual. University of Texas Biodiversity and Biocultural Conservation Laboratory, Austin, Texas. http://uts.cc.utexas.edu/~consbio/Cons/ResNet.html (last accessed 9.12.05).

Fuller, T., Sarkar, S., 2006. LQGraph: a software package for optimizing connectivity in conservation planning. Environmental Modeling and Software 21, 750–755.

Garcia, A., 2006. Using ecological niche modelling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. Biological Conservation 130, 25–46.

Garson, J., Aggarwal, A., Sarkar, S., 2002. ResNet Ver 1.2 Manual. University of Texas Biodiversity and Biocultural Conservation Laboratory, Austin, Texas. Available from: <http://uts.cc.utexas.edu/~consbio/Cons/ResNet.html>.

Gove, A., Majer, J., Rico-Gray, V., 2005. Methods for conservation outside of formal reserve systems: the case of ants in the seasonal dry tropics of Veracruz, Mexico. Biological Conservation 126, 328–338.

Grinnell, J., 1917. The niche-relationship of the Californian thrasher. Auk 43, 427–433.

Hall, E.R., 1981. The Mammals of North America, vols. 1 and 2. Ronald Press, New York.

Huitu, O., Norrdahl, K., Korpimäki, E., 2003. Landscape effects on temporal and spatial properties of vole population fluctuations. Oecologia 135, 209–220.

Illoldi-Rangel, P., Sánchez-Cordero, V., Peterson, A.T., 2004. Predicting distributions of Mexican mammals using ecological niche modeling. Journal of Mammalogy 85, 658–662.

ILOG, 2003. ILOG CPLEX 9.1. Gentilly Cedex, France.

Instituto Nacional de Geografía, Estadísitica e Informática, 2000. XII Censo General de Población y Vivienda 2000. http://www.inegi.gob.mx/est (last accessed 9.12.05).

Manly, B.F.J., 1997. Randomization, Bootstrap, and Monte Carlo Methods in Biology. 2nd ed. Chapman & Hall, London.

Margules, C.R., Nicholls, A.O., Usher, M.B., 1994. Apparent species turnover, probability of extinction and the selection of nature reserves: a case study of the Ingleborough limestone pavements. Conservation Biology 8, 398–409.

Mas, J.-F., Velazquez, A., Diaz-Gallegos, J.-R., Mayorga-Saucedo, R., Alcantara, C., Bocco, G., Castro, R., Fernandez, T., Pérez-Vega, A., 2004. Assessing land use/cover changes: a nationwide multidate spatial database for Mexico. International Journal of Applied Earth Observation and Geoinformation 5, 249–261.

McDonnell, M.D., Possingham, H.P., Ball, I.R., Cousins, E.A., 2002. Mathematical methods for spatially cohesive reserve design. Environmental Modeling and Assessment 7, 107–114.

Méndez-Larios, I., Villasenor, J.L., Lira, R., Morrone, J.J., Dávila, P., Ortiz, E., 2005. Toward the identification of a core zone in the Tehuacán-Cuicatlán biosphere reserve, Mexico, based on parsimony analysis of endemicity of flowering plant species. Interciencia 30, 267–274.

Moffett, A., Garson, J., Sarkar, S., 2004. MultCSync: a software package for incorporating multiple criteria in conservation planning. Environmental Modelling and Software 20, 1315–1322.

Moffett, A., Sarkar, S., 2006. Incorporating multiple criteria into the design of conservation area networks: a minireview with recommendations. Diversity and Distributions 12, 125–137.

Munguía, M., 2004. Representatividad Mastofaunística en Áreas Naturales Protegidas y Regiones Terrestres Prioritarias en el Eje Neovolcánico: un Modelo de Conservación. Tesis de licenciatura, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, D.F.

Nalle, D., Arthur, J.L., Sessions, J., 2002. Designing compact and contiguous reserve networks with a hybrid heuristic algorithm. Forestry Science 48, 59–68.

Noss, R.F., 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology 1, 159–164.

Onal, H., 2004. First-best, second-best, and heuristic solutions in conservation reserve site selection. Biological Conservation 115, 55–62.

Onal, H., Briers, R.A., 2002. Incorporating spatial criteria in optimum reserve network selection. Proceedings of the Royal Society of London B 269, 2437–2441.

Onal, H., Briers, R.A., 2003. Selection of a minimum-boundary reserve network using integer programming. Proceedings of the Royal Society of London B 270, 1487–1491.

Onal, H., Briers, R.A., 2005. Designing a conservation reserve network with minimal fragmentation: a linear integer programming approach. Environmental Modeling and Assessment 10, 193–202.

Orrock, J.L., Danielson, B.J., Burns, M.J., Levey, D.J., 2003. Spatial ecology of predator–prey interactions: corridors and patch shape influence seed predation. Ecology 84, 2589–2599.

Ortega-Huerta, M.A., Peterson, A.T., 2004. Modelling spatial patterns of biodiversity for conservation prioritization in North-eastern Mexico. Diversity and Distributions 10, 39–54.

Pérez-Arteaga, A., Jackson, S., Carrera, E., Gaston, K.J., 2005. Priority sites for wildfowl conservation in Mexico. Animal Conservation 8, 41–50.

Peterson, A.T., Holt, R.D., 2003. Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation. Ecology Letters 6, 774–782.

Peterson, A.T., Soberón, J., Sánchez-Cordero, V., 1999. Conservatism of ecological niches in evolutionary time. Science 285, 1265–1267.

Rodrigues, A.S., Gaston, K.J., 2002. Optimisation in reserve selection procedures – why not? Biological Conservation 107, 123–129.

Sánchez-Cordero, V., Martínez-Gallardo, R., 1998. Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. Journal of Tropical Ecology 14, 139–151.

Sánchez-Cordero, V., Munguía, M., Peterson, A.T., 2004. GIS-based predictive biogeography in the context of conservation. In: Lomolino, M., Heaney, L. (Eds.), Frontiers in Biogeography. Sinauer Press, Sunderland, MA, pp. 311–323.

Sánchez-Cordero, V., Cirelli, V., Munguía, M., Sarkar, S., 2005a. Place prioritization for biodiversity representation using species' ecological niche modelling. Biodiversity Informatics 2, 11–23.

Sánchez-Cordero, V., Illoldi-Rangel, P., Linaje, M., Sarkar, S., Peterson, A.T., 2005b. Deforestation and extant distributions of Mexican endemic mammals. Biological Conservation 126, 465–473.

Sánchez-Rojas, G., Sánchez-Cordero, V., Briones, M., 2004. Effect of plant species, fruit density, and habitat on post-dispersal fruit and seed removal by spiny pocket mice (*Liomys pictus*, Heteromyidae) in a tropical dry forest in Mexico. Studies on Neotropical Fauna and Environment 39, 1–6.

Sarkar, S., Margules, C., 2002. Operationalizing biodiversity for conservation planning. Journal of Biosciences 27, S299–S308.

Sarkar, S., 2003. Conservation area networks. Conservation and Society 1, v–vii.

Sarkar, S., 2005. Biodiversity and Environmental Philosophy: An Introduction. Cambridge University Press, New York.

Sarkar, S., Garson, J., 2004. Multiple criterion synchronization (MCS) for conservation area network design: the use of non-dominated alternative sets. Conservation and Society 2, 433–448.

Sarkar, S., Pappas, C., Garson, J., Aggarwal, A., Cameron, S., 2004. Place prioritization for biodiversity conservation using probabilistic surrogate distribution data. Diversity and Distributions 10, 125–133.

Sarkar, S., Justus, J., Fuller, T., Kelley, C., Garson, J., Mayfield, M., 2005. Effectiveness of environmental surrogates for the selection of conservation area networks. Conservation Biology 19, 815–825.

Siek, J., Lee, L.-Q., Lumsdaine, A., 2002. The Boost Graph Library: User Guide and Reference Manual. Addison-Wesley, Boston.

Simberloff, D., Farr, J., Cox, J., Melman, D., 1992. Movement corridors – conservation bargains or poor investments? Conservation Biology 6, 493–504.

Snyder, S.A., Haight, R.G., ReVelle, C.S., 2004. A scenario optimization model for dynamic reserve site selection. Environmental Modeling and Assessment 9, 179–187.

Soberón, J., Peterson, A.T., 2004. Biodiversity informatics: managing and applying primary biodiversity data. Philosophical Transactions of the Royal Society of London B 359, 689–698.

Stockwell, D.R.B., Peters, D., 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science 13, 143–158.

Stockwell, D.R.B., Peterson, A.T., 2002. Controlling bias in biodiversity data. In: Scott, J.M., Heglund, P.J., Morrison, M.L. (Eds.), Predicting Species Occurrences: Issues of Scale and Accuracy. Island Press, Washington, DC, pp. 537–546.

Sutherland, G.D., Harestad, A.S., Price, K., Lertzman, K.P., 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conservation Ecology 4, 16 [online] URL: http://www.consecol.org/vol4/iss1/art16.

Syrjala, S.E., 1996. A statistical test for a difference between the spatial distributions of two populations. Ecology 77, 75–80.

United States Geological Survey, 1998. GTOPO30 Global 30 Arc-second Digital Elevation Model. Reston: USGS. http://edc.usgs.gov/products/elevation/gtopo30/gtopo30.html (last accessed 9.12.05).

Urban, D., Keitt, T., 2001. Landscape connectivity: a graph-theoretical perspective. Ecology 82, 1205–1218.

Van Langevelde, F., Schotman, A., Claasen, F., Sparenburg, G., 2000. Competing land use in the reserve site selection problem. Landscape Ecology 15, 243–256.

Velazquez, A., Mas, J.F., Diaz-Gallegos, J.R., Mayorga-Saucedo, R., Alcantara, P.C., Castro, R., Fernandez, T., Bocco, G., Escurra, E., Palacios, J.L., 2001. Patrones y tasas de cambio de uso de suelo en México. Gaceta Ecológica Nueva Época No. 62. Instituto Nacional de Ecología y Secretaria del Medio Ambiente y Recursos Naturales, México D.F., México.

Velázquez, A., Bocco, G., Romero, F.J., Pérez-Vega, A., 2003. A landscape perspective on biodiversity conservation: the case of central Mexico. Mountain Research and Development 23, 240–246.

Villa, B., Cervantes, F.A., 2003. Los mamíferos de México. Instituto de Biología, UNAM- Grupo Editorial Iberoamérica, México, D.F.

Villaseñor, J.L., Ibarra-Manríquez, G., Meave, J.A., Ortiz, E., 2005. Higher taxa as surrogates for plant biodiversity in a megadiverse country. Conservation Biology 19, 232–238.

Villers-Ruíz, L., Trejo-Vázquez, I., 1998. Climate change on Mexican forests and natural protected areas. Global Environmental Change 8, 141–157.

Virolainen, K.M., Virola, T., Suhonen, J., Kuitunen, M., Lammi, A., Siikamaki, P., 1999. Selecting networks of nature reserves: methods do affect the long-term outcome. Proceedings of the Royal Society of London Series B-Biological Sciences 266, 1141–1146.

Williams, J.C., 1998. Delineating wildlife corridors with multiobjective programming. Environmental Modeling and Assessment 3, 77–86.