

24 **Incorporating Connectivity into Conservation Planning: A Multi-Criteria**
25 **Case Study from Central Mexico**

26
27 **Abstract**

28
29 The interdigitation of the Nearartic and Neotropical biogeographic zones in the
30 Transvolcanic Belt (TVB) of central Mexico provides the region with high faunal
31 richness and endemism. Biodiversity conservation in the TVB must
32 accommodate the region's human population of more than 40 million. The
33 current study presents conservation plans for the TVB intended to protect 99
34 non-volant mammal species while minimizing the impact on the human
35 population. A rarity-complementarity algorithm was used to select a
36 conservation area network (CAN) from sites with untransformed vegetation to
37 represent 10 % of each species' habitat. In addition, a new method was
38 developed for augmenting the connectivity of CANs using graph theory.
39 External sites were assigned quality scores based on the frequency with which
40 they were selected at different targets of representation for species. Graph
41 algorithms identified the highest-quality sites needed to link all conservation
42 areas in an economical manner. These connectivity areas can facilitate
43 migration or egress of biota in the event of local environmental stress. The
44 network initialized with existing protected areas occupied 9.13 % of the TVB
45 whereas the network built from scratch occupied 6.02 %. In both cases, an
46 additional area of only about 1.5 % of the region was required to link all
47 conservation areas in the network. Finally, a multiple criterion synchronization
48 technique was used to select those connected networks which minimized both
49 total area and human population impact.

50
51 **Keywords:** conservation; ecological restoration; graph theory; Mexican
52 Transvolcanic Belt; natural protected areas; reserve selection.

53 **Introduction**

54

55 A central tenet of conservation planning is that fragmented and isolated
56 conservation areas are inadequate for the long term persistence of biodiversity,
57 especially if turnover in the conservation areas is high (Margules et al., 1994;
58 Virolainen et al., 1999). Place prioritization algorithms have attempted to
59 address this by minimizing the perimeter length of the network of conservation
60 areas (McDonnell et al., 2002; Nalle et al., 2002; Onal and Briers, 2002) or the
61 total distance between the areas (Fischer and Church, 2003; Onal and Briers,
62 2003). However, this does not ensure that a contiguous path of protected sites
63 links the conservation areas. Several methods have been proposed for
64 selecting such paths, which are intended to serve primarily as dispersal
65 corridors for animals (Williams, 1998; van Langevelde et al., 2000; Cerdeira et
66 al., 2005; Onal and Briers, 2005). A shortcoming of these methods is that they
67 are intractable for the large biodiversity datasets being made available through
68 species' ecological niche modeling (Soberón and Peterson, 2004). In addition to
69 incorporating connectivity, conservation plans for populous regions must
70 address the needs of the human population using multicriteria decision-making
71 methods (reviewed in Moffett and Sarkar, 2006).

72 The objective of this study is to develop a framework for conservation
73 planning that integrates ecological niche modeling, the selection of conservation
74 areas, connectivity establishment, and multicriteria methods. What is novel
75 about the approach presented here is the combination of these four techniques
76 (Figure 1) and the connectivity establishment procedure, which is able to handle
77 much larger data sets than previous algorithms (Fuller and Sarkar, 2006). The

78 framework is illustrated by developing a conservation plan for the Transvolcanic
79 Belt (TVB) of central Mexico.

80 The TVB is particularly suited for a multicriteria method because it has a
81 high population but also high faunal endemism. In particular, the TVB contains
82 all of the known endemic non-volant mammalian genera in Mexico and half of
83 known endemic non-volant mammal species, most of which are small mammals
84 (Fa and Morales, 1993; Escalante et al., 2004). Significant threats to
85 biodiversity in the TVB include high deforestation and other forms of habitat
86 transformation to satisfy the needs of a human population of nearly 40 million
87 (Instituto Nacional de Geografía, Estadística e Informática, 2000; Velázquez et
88 al., 2001). The TVB contains a large number of decreed natural protected
89 areas (NPAs) most of which are small, with areas less than 10 km.² (Figure 2).
90 Some of these NPAs were among the first decreed in the country but most were
91 selected on the basis of political or scenic criteria rather than biological content
92 (Alcérreca et al., 1988). For example, even vascular plant inventories are
93 available for less than one-third of the NPAs, suggesting that they were not
94 designated based on known biodiversity content (Villaseñor et al., 2005). As a
95 result, these NPAs are known to be collectively inadequate for conserving the
96 TVB's high biodiversity (Sánchez-Cordero et al., 2004). One option to address
97 these problems would be to increase the size of the NPAs. However, due to the
98 high deforestation, development, and consequent habitat fragmentation in the
99 TVB, almost all the NPAs cannot be enlarged to include more relatively intact
100 biological habitats (Munguía, 2004; Sanchez-Cordero et al., 2005a, b).

101 An alternative strategy to avoid the negative effects of the small size of
102 individual protected areas is to use relatively intact or restorable habitat to

103 establish connectivity between units of a conservation area network (CAN). A
104 CAN is defined as a set of areas managed for the persistence of biodiversity
105 into the future (Sarkar, 2003). The term “conservation area” is preferred over
106 the more traditional “reserve” because the latter term has the connotation that
107 almost all human activity is banned in the protected areas (Sarkar, 2003).
108 Whereas conservation areas should consist of habitat already suited for the
109 long-term persistence of biodiversity features, the connectivity areas may
110 consist of less “high quality” areas. The connectivity areas may have some
111 degree of human-induced transformation but retain secondary vegetation and
112 are suitable for the migration mammal species or as a temporary refuge.
113 Connectivity areas may also comprise areas that are degraded but potentially
114 restorable; restoration to reasonably adequate habitat is much more easily
115 achievable (both in terms of scientific knowledge and economic resources) than
116 restoration into the high quality habitat required for a conservation area (Daily et
117 al., 2003; Gove et al., 2005). Existing protected areas in the TVB have small
118 human populations engaged in agriculture, forestry, and mineral extraction
119 (Bocco et al., 2005; Méndez-Larios et al., 2005). The appropriate policy for each
120 conservation or connectivity area must be determined by local context. It can
121 include human exclusion, habitat restoration, sustainable resource extraction, or
122 even some types of agricultural production (Sarkar, 2005).

123 The aim of this work is to propose a regional landscape-scale plan for the
124 TVB using all 99 non-volant mammals that occur in the region. Potential clients
125 for the plan include the Mexican governmental agencies Comisión Nacional
126 Para el Conocimiento y Uso de la Biodiversidad (CONABIO) and Comisión
127 Nacional de Áreas Naturales Protegidas (CONANP) or nongovernmental

128 organizations in Mexico such as PRONATURA. Non-volant mammals are used
129 because of their high regional extinction risk in the TVB (Sánchez-Cordero et
130 al., 2005a, b), high endemism, high species richness, and their role as
131 important seed-dispersers in the ecosystem (Sánchez-Cordero and Martínez-
132 Gallardo, 1998; Sánchez-Rojas et al., 2004; Briones-Salas et al., 2006). In
133 Mexico, non-volant mammals are also one of the best known biological groups
134 nationwide, and the species' distributions are well documented (Fa and
135 Morales, 1993; Arita et al., 1997; Villa and Cervantes, 2003).

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

140

141 **Methods**

142 *Biogeographic Region*

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

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

166 *Modeling Species' Distributions*

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

178 Modeled species' distributions were constructed with the Genetic
179 Algorithm for Rule-set Prediction software package (GARP; Stockwell and
180 Peters, 1999). GARP uses ecological-environmental abiotic and biotic variables
181 of known species' occurrence points to produce coarse-grained species'
182 ecological niche models ("Grinnelian" models; Grinnell, 1917) projected as
183 potential distributions. In GARP, occurrence points are divided evenly into
184 training and testing data sets. An iterative algorithm consisting of rule selection,
185 evaluation, testing, and subsequent incorporation or rejection is used to "evolve"
186 a most predictively accurate set of rules from an original set of possibilities (e.g.,
187 logistic regression, bioclimatic rules). The algorithm runs for 1 000 iterations or
188 until convergence (see Stockwell and Peterson, 2002). The final rules are then
189 used to predict the total distribution for each species.

190 GARP has proven a robust tool for predicting species' geographic
191 distributions for mammals (Illoldi-Rangel et al., 2004) and other taxa in Mexico
192 (Garcia, 2006). Because GARP does not produce a unique solution, its use
193 here followed published recommendations for the construction of optimal
194 subsets of replicate models (Anderson et al., 2003). For each analysis 100
195 replicate models at a $0.01^\circ \times 0.01^\circ$ resolution were produced, the 20 models
196 with lowest omission error were initially retained, and the ten models with
197 commission errors close to the median finally adopted for subsequent use.
198 Further modeling refinement consisted of rejecting obvious over-predictions for
199 microendemics (for example, disjunction distributions) based on Hall (1981).
200 Species' extant distributions were then calculated by overlaying the Inventario
201 Nacional Forestal 2000 map (Mas et al., 2004) and excluding only areas holding

202 highly transformed habitat (type (iii) sites). The extant distribution models were
203 used for the connectivity analyses (see below).

204 *Place Prioritization Protocols*

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

220 *Landscape Quality Score*

221 Suppose planners wish to protect an at-risk species subject to the
222 following constraints: at most 1 % of the habitat of each species can be
223 protected or at most 99 % of the habitat can be protected. A site first selected
224 when the first constraint is in effect is more critical for the species’ persistence
225 than one first selected under the latter constraint. This assumption was used to
226 score sites in the TVB such that sites first selected at low targets of

227 representation earned higher quality scores than those first selected at higher
228 targets. ResNet was used to prioritize places to represent species' habitat in the
229 TVB at 20 target levels (5 – 100% at increments of 5%). 100 replicates of each
230 of the 20 place prioritizations were generated. Each replicate used a different
231 random reshuffling of the rows of input file. Since ResNet uses a heuristic
232 algorithm in which ties are broken by selecting a site at random, this could result
233 in different solutions in each replicate. The final site quality scores were
234 weighted by the frequency of selection at a given target level so that sites
235 selected frequently at low targets had the highest scores.

236 *Graph-theoretical Connectivity Protocols*

237 The second stage, that is, the establishment of connectivity in the
238 networks by linking conservation areas, required the development of some new
239 techniques. The connectivity areas were selected with graph algorithms, which
240 select paths that directly link conservation areas via high-quality sites that are
241 not currently part of the conservation areas. This permits organisms, particularly
242 mobile animals, in one conservation area to disperse to another using a path of
243 contiguously protected sites. Graphs have previously been used for
244 conservation planning but only for one or two species at a time (Bunn et al.,
245 2000; Urban and Keitt, 2001). This analysis extends these techniques to an
246 arbitrary number of species and other biodiversity surrogates. Both type (i) and
247 type (ii) sites were used for selecting the connectivity areas. Type (ii) sites are
248 less intact than those of type (i) but still potentially restorable to adequate
249 habitat for the relevant species. Thus, type (ii) sites were considered suitable for
250 connecting conservation areas, but not adequate as sites for conservation
251 areas themselves.

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

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

271 Random graphs ($n = 1000$; Siek et al., 2002) were generated to provide
272 a null model for comparing connectivity properties of the graphs corresponding
273 to the NPA and rarity solutions. In the random graphs, the number of vertices
274 equaled the number of conservation areas in the NPA and rarity solutions but
275 edges were assigned at random between the vertices. Finally, spatial statistics

276 (Syrjala 1996) were used to assess whether the NPA and rarity solutions had
277 the same configurations and whether their MSTs were spatially similar.

278 *Multi-Criteria Analysis*

279
280 The third stage used multi-criteria analysis to select the conservation plan with
281 the minimal area and human impact (measured as the human population of
282 sites in the plan). LQGraph finds all MSTs of a CAN. Alternative MSTs are
283 interchangeable with respect to their connectivity properties but may differ in
284 other criteria relevant for biodiversity conservation. All the MSTs were ordered
285 by their area and human population. Population data were obtained from
286 CONABIO (2002; www.conabio.gob.mx) and Instituto Nacional de Geografía,
287 Estadística e Informática (2000; www.inegi.gob.mx). The GIS model provided
288 data on areas (km.²).

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

300

301 **Results**

302 *Species*

303 The species used in this study were 99 non-volant mammal species consisting
304 of 14 species endemic to the TVB, 24 species endemic to Mexico, and 61 non-
305 endemic species. Extant species' distributions ranged from 50 - 52 770 km.²
306 (0.04 - 42.77% of the total area) for the endemics to the TVB, 1290 - 69 000
307 km.² (1.05 - 55.93% of the total area) for the endemics to Mexico, and 1070 -
308 54 970 km.² (0.87 - 44.56% of the total area) for the non-endemics (Table 1).

309 *Conservation Areas and Landscape Quality Analyses*

310 The 39 existing protected areas had a total area of 9 179 km.² or 7.4 %
311 of the TVB. More than half of the decreed NPAs have areas less than 100 km.²
312 and only two are larger than 1 000 km.² The NPA-initialized solution contained 9
313 658 sites with a total area of 11 264.4 km.² or 9.13 % of the TVB, whereas the
314 rarity-initialized solution contained 6 382 sites with an area of 7 431.32 km.² or
315 6.02 % of the TVB. Both solutions were at most 0.04 % suboptimal. In the
316 conservation planning literature, a solution within 1% of the optimum is
317 generally considered optimal (Onal 2004). These results confirm previous
318 findings that the rarity-complementarity algorithm implemented in ResNet is
319 competitive with optimal solution methods (Sarkar et al. 2004). The graph-
320 based representation of the NPA solution had 442 conservation areas, 4 823
321 paths between conservation areas, and 25 components (Table 2). The graph
322 corresponding to the rarity solution had 409 conservation areas, 4 030 paths,
323 and 39 components.

324 *Connectivity Analyses*

325 The least cost paths between the conservation areas occupied 20.76 %
326 of the TVB in the NPA solution and 22.66 % in the rarity solution, which is too
327 large a portion of the landscape to be included in a conservation plan in such a

328 populous region (Table 2). Thus, the least cost paths were filtered to find MSTs.
329 The MSTs established connectivity among conservation areas using only 6.9 %
330 and 1.02 % of the area of the least cost paths in the respective solutions. Thus,
331 connectivity can be established via MSTs more economically than via least-cost
332 paths.

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

341 In the MSTs based on the NPA solution, on average an additional
342 1520.97 (SD = 905.49) sites (in addition to the CAN sites) with an average area
343 of 1766.64 (SD = 1051.54) km.² or 1.43 % of the area of the TVB are prioritized
344 (Figure 4). In the MSTs based on the rarity solution, on average an additional
345 247 (SD = 485.46) sites (in addition to the CAN sites) with an average area of
346 287.47 (SD = 563.85) km.² or 0.23 % of the area of the TVB are prioritized. This
347 means that the amount of land required to construct paths to connect the
348 conservation areas in the rarity solution is less than the land required for the
349 NPA solution. The large standard deviation associated with each average MST
350 area is due to the large variance in the number of conservation areas among
351 components. The spatial configurations of the MSTs based on the rarity and
352 NPA solutions were significantly different (Syrjala test, $p = 0.01$). For both the

353 NPA and Rarity solution, the median length of the sets of connectivity areas
354 linking conservation areas was 4.24 km.

355 *Multi-Criteria Analysis*

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

358 **Discussion**

359 Like previous studies (Alcérreca-Aguirre et al., 1989; Sánchez-Cordero et
360 al., 2004; Villaseñor et al., 2005), this analysis demonstrates that the existing
361 protected areas in the TVB do not represent biodiversity economically. When
362 the site selection algorithm was initialized with the existing NPAs, 3 833 km.²
363 more land was required to represent 10 % of the distribution of each non-volant
364 mammal than if the CAN was not so initialized (Table 2). Among the first
365 locations selected in both the NPA and rarity solution was a site in northern
366 Veracruz containing more than 30 non-volant mammals. A conservation plan for
367 the northeastern TVB using the same mammal database as the present plan
368 (Ortega-Huerta and Peterson, 2004) also prioritized this site. This area should
369 be a priority for regional conservation.

370 The NPA solution is better connected than the rarity solution to the extent
371 that the latter has more connected components. Human population may
372 account for this difference in connectivity. The connectivity establishment
373 procedure presented here constructs paths between conservation areas via
374 sites with primary or secondary vegetation. It is plausible that a site with a high
375 human population will lack such vegetation or be adjacent to sites without
376 vegetation. The rarity solution contains about eight million more people than the
377 NPA solution. Due to the high population of the rarity solution, many of its

378 conservation areas may be surrounded by sites without vegetation, making it
379 impossible to establish connectivity areas between them. Only when the MST
380 based on the NPA solution was compared with the MST based on the rarity
381 solution did the Syrjala detect significant differences in spatial configuration. In
382 general, rejecting the null hypothesis of identical configurations is quite difficult
383 with the Syrjala test (Sarkar et al., 2005), so the spatial differences between the
384 MSTs must be quite strong. The MST for the NPA solution has extensive
385 connectivity areas in central Jalisco that are not present in the MST for the rarity
386 solution.

387 Though the biological importance of establishing connectivity between
388 individual units of a CAN remains controversial (Noss, 1987; Simberloff et al.,
389 1992), connectivity is known to be important for non-volant mammals in the TVB
390 such as those in the genera *Peromyscus* and *Microtus*. In the case of
391 *Peromyscus*, landscape connectivity influences population persistence to the
392 extent that individuals are known to have better access to food in connected
393 habitat patches (Orrock et al., 2003). In the case of *Microtus*, connectivity,
394 rather than climatic fluctuations, affects population size and synchrony (Huitu et
395 al., 2003). *Peromyscus* species are known to use linear landscape features
396 such as strips of remnant habitat as habitat linkages and corridors (Bolger et al.,
397 2001). Of the 99 non-volant mammal species considered here, data on
398 maximum dispersal distances were available for only ten (Sutherland et al.,
399 2000; Bowman et al., 2002). The dispersal distances for nine of these species
400 exceeded the median length of the connectivity areas selected by the graph
401 algorithms. This suggests that these small mammals would use the connectivity
402 areas as dispersal corridors between conservation areas in the TVB. However,

403 future studies should test the utility of these connectivity areas for mammals
404 and other biological groups. In addition to their function as dispersal corridors,
405 the connectivity areas could serve as sites for habitat restoration.

406 Were taxa other than non-volant mammals used to design the CAN,
407 different places might be prioritized (though it is unlikely that sites selected here
408 would be deselected). For example, the Tehuacán-Cuicatlán valley in southern
409 Puebla has 365 endemic plants but its mammal species are both less diverse
410 and less documented (Davila et al., 2002). Thus, when sites were selected to
411 protect mammal habitat and the algorithm was not initialized with the existing
412 natural protected areas, fewer sites in southern Puebla were selected.

413 Quantifying the extent to which the plans presented here represent non-
414 mammalian diversity requires formal surrogacy analysis (Sarkar et al., 2005),
415 which is beyond the scope of this study. Irrespective of this, non-volant
416 mammals are an important component of biodiversity that merit protection. The
417 biodiversity value of site can be defined as the number of features of the site
418 that are not adequately protected elsewhere (Sarkar and Margules 2002). By
419 this definition, the biodiversity value of mammal habitat in the TVB is extremely
420 high because the TVB has more endangered mammals than any other region of
421 Mexico (Ceballos et al., 1998) and the existing protected areas of the do not
422 represent this fauna adequately.

423 This conservation plan prioritizes many of the same sites as earlier plans
424 for the TVB. A national plan for several hundred bird, mammal, and amphibian
425 species in Mexico at the 0.25° scale prioritized northern Puebla and northern
426 Michoacán (Brandon et al., 2005). The rarity solution (Figure 4 b) selects many
427 sites in these areas. However, Brandon et al. (2005) also prioritize the western

428 half of the state of Mexico. Most sites in the state of Mexico were excluded from
429 the present plan because they lack primary or secondary vegetation. Pérez-
430 Arteaga et al. (2005) designed a CAN for Mexican wildfowl that includes 12
431 conservation areas in the central highlands of the TVB, where the states of
432 Guanajuato, Jalisco, and Michoacán meet. The NPA solution (Figure 4a)
433 proposes only 6 conservation areas in this region, but selects extensive
434 connectivity areas there. However, the plans differ in scale since the wildfowl
435 plan was carried out at the national scale. Velázquez et al. (2003) designed a
436 CAN to protect 122 species of threatened and endangered amphibians, reptiles,
437 birds, mammals, and vascular plants in Distrito Federal. They proposed sites
438 along the southern and western borders of the state as “core areas” of the CAN.
439 Although the NPA and rarity solutions (Figures 4a and 4b) prioritize some of
440 these same core areas, conservation and connectivity areas in Distrito Federal
441 make up less than 1 % of the present plan (Table 3); differences between the
442 plans can be explained by scale to the extent that the present plan is for a
443 region 1440 times larger (Velazquez et al., 2003). In addition, the plan
444 presented here selects sites with high biodiversity content by means of an
445 iterative selection procedure (Garson et al., 2002), whereas Velazquez et al.
446 (2003) employed correspondence analysis and ordination.

447 Mammal species assemblages in the eastern TVB are dissimilar from the
448 rest of the region, probably because the east has moist forests and cloud
449 forests whereas the forests elsewhere in the TVB are dry (Fa, 1989). The
450 unique mammal fauna of the eastern TVB is represented in both of the place
451 prioritizations presented here. The plan initialized with the existing natural
452 protected areas selects sites around the Tehuacán-Cuicatlán biosphere reserve

453 in southern Puebla (Figure 4a). The plan not initialized with the NPAs selected
454 fewer sites in southern Puebla but more sites in the northern part of the state
455 (Figure 4b).

456 The planning method described here could be refined in several ways.
457 Here, a two-stage method was used to select contiguity areas. First, the graph
458 algorithms identified many sets of contiguity areas. Each set consisted of sites
459 with high landscape quality that established connectivity between the
460 conservation areas. Second, the multiple-criteria synchronization procedure
461 identified the sets with the smallest geographical areas and human populations.
462 The landscape quality score served as an indicator of habitat suitability.
463 Population served as a measure site vulnerability insofar as mammal habitat is
464 more likely to be disturbed when the human population is high (Carroll et al.,
465 2003). As an alternative to the two-stage method, a single utility function could
466 be used to prioritize contiguity areas based on suitability and vulnerability
467 simultaneously. However, such a function requires assigning arbitrary weights
468 to the two criteria and assumes that they have a common quantitative scale
469 (Sarkar and Garson, 2004). The multiple-criterion synchronization procedure
470 presented here avoids the problems of arbitrariness and incommensurability
471 because it generates an ordinal ranking of the sets of contiguity areas (based
472 on area and population) rather than assigning numerical values to the two
473 criteria.

474 Second, though the GIS model in this analysis used the same site sizes
475 for the CANs and the connectivity areas, the graph algorithms described above
476 permit different scales to be used. In Mexico, many NPAs are adjacent to
477 expanding cities (Cantú et al., 2004). In this context, conservation planners may

478 wish to use a fine spatial scale to model sites outside the NPAs in order to
479 ensure that the connectivity areas that they select do not intersect with
480 infrastructure such as roads. Moreover, the administrative boundaries of NPAs
481 in Mexico are sometimes poorly defined (Bojórquez-Tapia et al., 2004) such
482 that there is no clear delineation between a park and private lands. In such
483 cases, it would be suitable to represent the CANs with a coarse spatial scale
484 while using a fine spatial scale when selecting connectivity areas. In addition,
485 though the analysis presented here did not calculate the cost of restoring
486 transformed habitat in the TVB, conservation plans from other regions estimate
487 that this can double the cost of the plan (Frazee et al., 2003). Calculating this
488 cost would require data on the expense of buying and administrating sites
489 adjacent to conservation areas and the cost of incentive-based agreements
490 between land owners and CONABIO, such as tax-breaks. Finally, the
491 methodology presented establishes connectivity between conservation areas
492 via MSTs using as few sites as possible so as to minimize the impact on the
493 human population. However, planners may wish to establish multiple, redundant
494 connections between conservation areas as a safeguard against future
495 disturbances, such as changes in forest and life zone types in the TVB due to
496 climate change (Villers-Ruíz et al., 1998). This could be accomplished by
497 placing all of the least-cost paths between conservation areas under protection
498 rather than filtering the paths to find the MST(s). An alternative method to
499 protect the CAN against future disturbance is to select sites here-and-now so as
500 to minimize the expected cost of protecting species adequately in the future
501 using stochastic optimization (Snyder et al., 2004).

502

503 **Acknowledgments**

504 We thank A. Estrada, J. Justus, T. Keitt, H. Önal, R. Palasek, R. Plowes, and P.
505 Wright for discussions. J. Soberón and G. Halffter provided useful comments
506 on an earlier draft of this work. VS-C thanks the Secretaría del Medio Ambiente
507 y Recursos Naturales and Consejo Nacional de Ciencias y Tecnología
508 (SEMARNAT-CONACyT C01-314-A1) for partially funding this research. The
509 following museum collections were consulted to built the mammal database:
510 Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México;
511 Colección de Mamíferos, Universidad Autónoma Metropolitana-Iztapalapa;
512 Centro Interdisciplinario de Investigación y Desarrollo Regional de Oaxaca;
513 University of Kansas Natural History Museum; American Museum of Natural
514 History, New York; National Museum of Natural History, Washington, D.C.;
515 Field Museum of Natural History, Chicago, Illinois; Museum of Zoology,
516 University of Michigan, Ann Arbor; Michigan State University Museum, East
517 Lansing; Museum of Vertebrate Zoology, University of California, Berkley;
518 Texas Tech University Museum, Lubbock; Texas Cooperative Wildlife
519 Collections, Texas A&M University, College Station, and at MaNIS,
520 <http://elib.cs.berkeley.edu/manis>.

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842

843 **Figure Captions**

844

845 Figure 1: Flowchart of the conservation planning framework for the
846 Transvolcanic Belt.

847

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

851

852 Figure 3: Natural protected areas of the Transvolcanic Belt (black) with state
853 names. "D. F." stands for "Distrito Federal".

854

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

858

859 Table 1.
 860 List of non-volant mammals in the Transvolcanic Belt (TVB) of central Mexico,
 861 consisting of 61 non-endemics to Mexico (NE), 24 endemics to Mexico (E), and
 862 14 microendemics to the TVB (M). Actual distribution predictions were
 863 produced by including only remnant untransformed habitat based on the
 864 Inventario Nacional Forestal 2000 within the species' potential distributions (see
 865 Methods for details).
 866
 867

Species	Actual Distribution (km.²)	Geographic position
Rodentia		
<i>Glaucomys volans</i>	52 350	NE
<i>Sciurus aureogaster</i>	50 320	NE
<i>Sciurus colliaei</i>	25 940	E
<i>Sciurus deppei</i>	37 560	NE
<i>Sciurus nayaritensis</i>	43 750	NE
<i>Sciurus oculatus</i>	17 310	E
<i>Spermophilus adocetus</i>	19 270	E
<i>Spermophilus mexicanus</i>	41 110	NE
<i>Spermophilus perotensis</i>	11 030	M
<i>Spermophilus variegatus</i>	48 910	NE
<i>Spermophilus pilosoma</i>	12 190	NE
<i>Cratogeomys gymnurus</i>	44 440	M
<i>Cratogeomys merriami</i>	53 050	E
<i>Cratogeomys tylorhynchus</i>	52 770	M
<i>Pappogeomys alcorni</i>	130	M
<i>Pappogeomys bulleri</i>	24 140	E
<i>Thomomys umbrinus</i>	52 870	NE
<i>Zygogeomys trichopus</i>	7 740	M
<i>Dipodomys phillipsii</i>	53 350	E
<i>Liomys pictus</i>	41 740	NE
<i>Liomys irroratus</i>	53 300	NE
<i>Liomys spectabilis</i>	17 030	M
<i>Perognatus flavus</i>	1070	NE
<i>Baiomys musculus</i>	43 560	NE
<i>Baiomys taylori</i>	44 280	NE
<i>Habromys simulatus</i>	12 410	E
<i>Hodomys alleni</i>	25 000	E
<i>Nelsonia neotomodon</i>	18 590	M
<i>Neotoma albigula</i>	14 070	NE
<i>Neotoma mexicana</i>	47 900	NE
<i>Neotoma nelsoni</i>	50	M
<i>Neotomodon alstoni</i>	47 900	E
<i>Nyctomys sumichrasti</i>	47 180	NE
<i>Oligoryzomys fulvescens</i>	49 260	NE
<i>Oryzomys couesi</i>	43 030	NE
<i>Oryzomys alfaroi</i>	50 170	NE
<i>Oryzomys melanotis</i>	30 090	E
<i>Osgoodomys banderanus</i>	40 620	E
<i>Peromyscus aztecus</i>	49 200	NE

<i>Peromyscus bullatus</i>	280	M
<i>Peromyscus difficilis</i>	69 000	E
<i>Peromyscus furvus</i>	40 910	E
<i>Peromyscus leucopus</i>	23 830	NE
<i>Peromyscus maniculatus</i>	39 310	NE
<i>Peromyscus mekisturus</i>	1290	E
<i>Peromyscus melanophrys</i>	24 390	E
<i>Peromyscus melanotis</i>	52 880	NE
<i>Peromyscus mexicanus</i>	42 940	NE
<i>Peromyscus pectoralis</i>	39 060	NE
<i>Peromyscus spicilegus</i>	38 370	E
<i>Peromyscus truei</i>	50 910	NE
<i>Reithrodontomys chrysopsis</i>	50 670	M
<i>Reithrodontomys fulvescens</i>	35 690	NE
<i>Reithrodontomys hirsutus</i>	14 700	M
<i>Reithrodontomys megalotis</i>	52 400	NE
<i>Reithrodontomys mexicanus</i>	39 540	NE
<i>Reithrodontomys microdon</i>	32 330	NE
<i>Reithrodontomys sumichrasti</i>	50 640	NE
<i>Sigmodon hallen</i>	37 680	E
<i>Sigmodon fulviventer</i>	37 020	NE
<i>Sigmodon hispidus</i>	45 110	NE
<i>Sigmodon leucotis</i>	43 270	E
<i>Sigmodon mascotensis</i>	43 190	E
<i>Microtus mexicanus</i>	51 680	NE
<i>Microtus quasiater</i>	48 750	M
Carnivora		
<i>Urocyon cinereoargenteus</i>	52 870	NE
<i>Canis latrans</i>	30 090	NE
<i>Bassariscus astutus</i>	54 970	NE
<i>Nasua narica</i>	42 410	NE
<i>Procyon lotor</i>	40 400	NE
<i>Conepatus mesoleucus</i>	37 640	NE
<i>Mephitis macroura</i>	47 050	NE
<i>Spilogale putorius</i>	42 040	NE
<i>Spilogale pygmaea</i>	13 870	E
<i>Mustela frenata</i>	53 440	NE
<i>Lontra longicaudis</i>	37 210	NE
<i>Taxidea taxus</i>	9810	NE
<i>Puma concolor</i>	35 780	NE
<i>Leopardus wiedii</i>	23 340	NE
<i>Lynx rufus</i>	42 460	NE
Insectivora		
<i>Cryptotys goldmani</i>	53 140	NE
<i>Cryptotys mexicana</i>	53 060	E
<i>Cryptotys parva</i>	50 300	NE
<i>Megasorex gigas</i>	35 580	E

<i>Notiosorex crawfordi</i>	27 490	NE
<i>Sorex emarginatus</i>	5480	E
<i>Sorex macrodon</i>	12 330	M
<i>Sorex saussurei</i>	50 510	NE
	5930	NE
Lagomorpha		
<i>Lepus californicus</i>		
<i>Lepus callotis</i>	42 320	NE
<i>Sylvilagus audubonii</i>	8950	NE
<i>Sylvilagus cunicularis</i>	49 180	E
<i>Sylvilagus floridianus</i>	50 500	NE
<i>Romerolagus diazii</i>	20 350	M
Didelphimorphia		
<i>Didelphis marsupialis</i>	49 730	NE
<i>Didelphis virginianus</i>	43 670	NE
Artiodactyla		
<i>Odocoileus virginianus</i>	42 090	NE
<i>Tayassu tajacu</i>	38 040	NE
Xenathra		
<i>Dasypus novemcinctus</i>	42 260	NE

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872 Table 2.
 873 Statistics of graph models for establishing conservation area networks (CAN) in
 874 the Transvolcanic Belt. Note that when the place prioritization algorithm is
 875 initialized with the existing NPAs ("NPA solution"), more land is required to
 876 represent 10 % of each species' habitat and establish connectivity between
 877 conservation areas.
 878

	NPA solution	Rarity solution
CAN Area (km. ²)	11 264.4	7 431. 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	4 283	4 030
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)	1 766.64 (1 051.54)	287.47 (563.85)

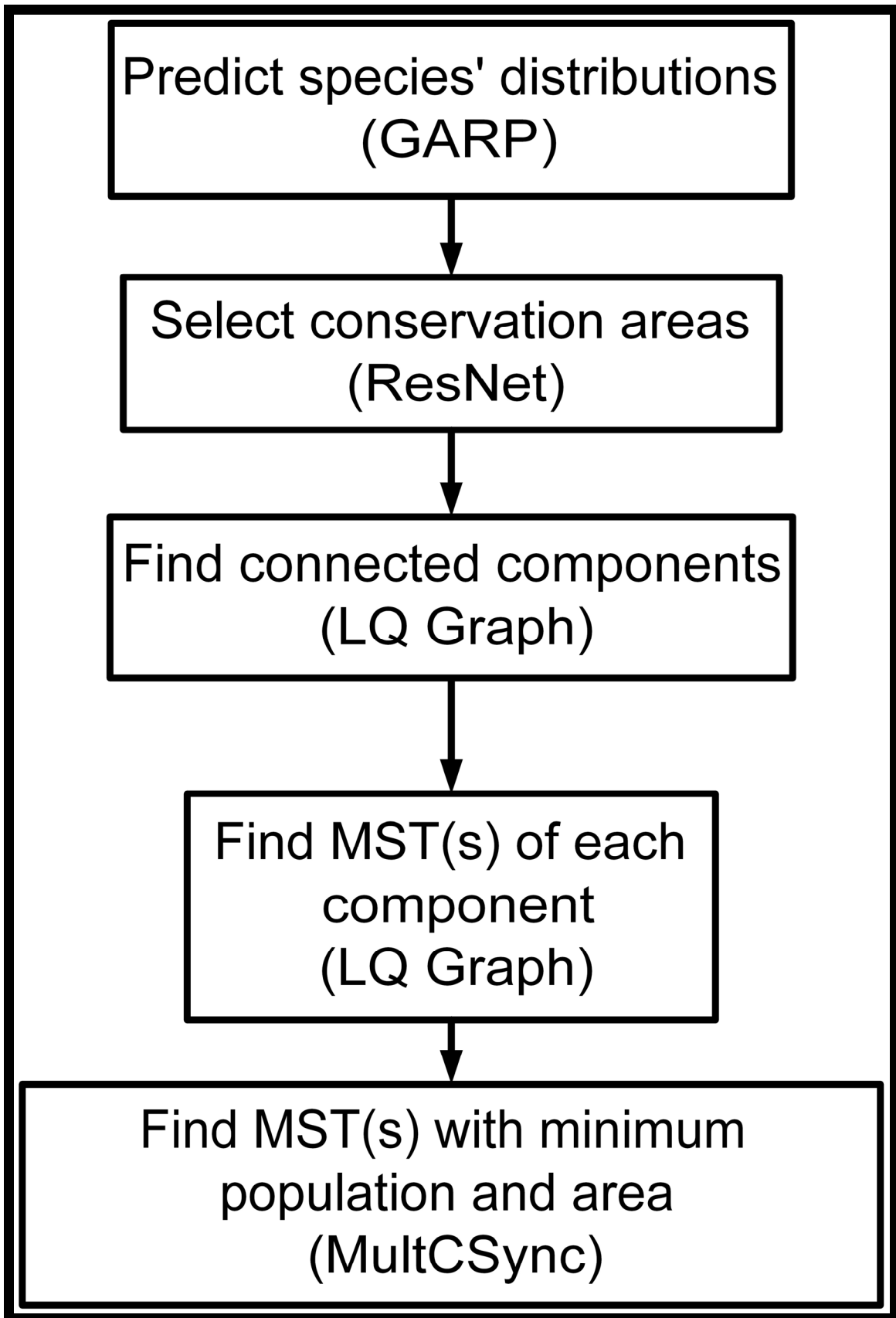
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887 Table 3
 888 List of States and percent of conservation areas and connectivity areas included
 889 in the place prioritization algorithms for the Transvolcanic Belt. The lower
 890 (upper) percentage is for the NPA (rarity) solution.
 891

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

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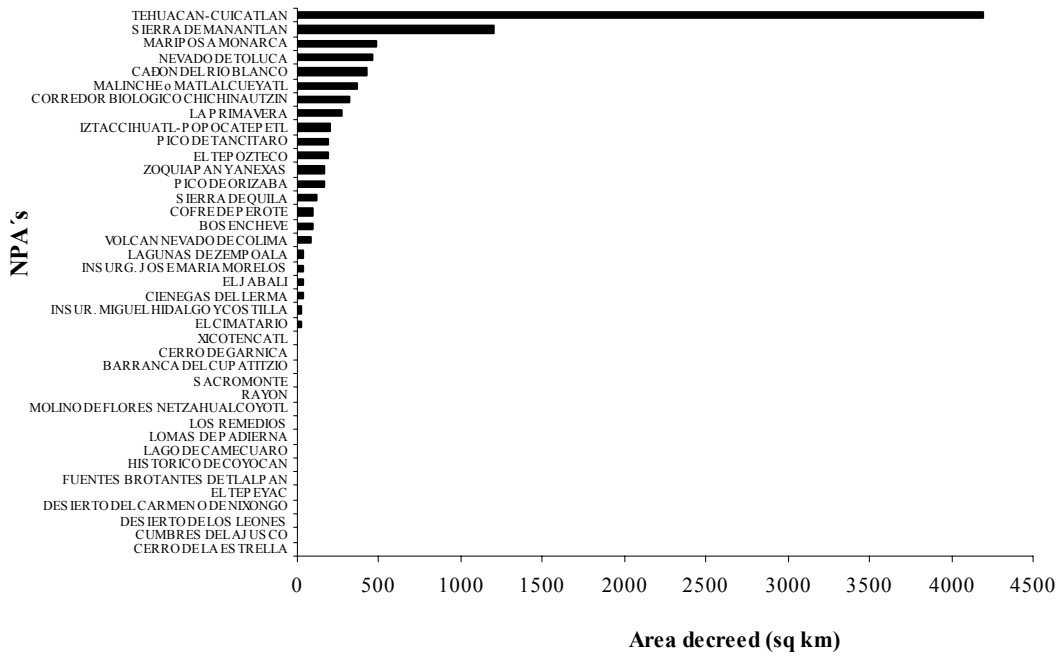
Figure 1



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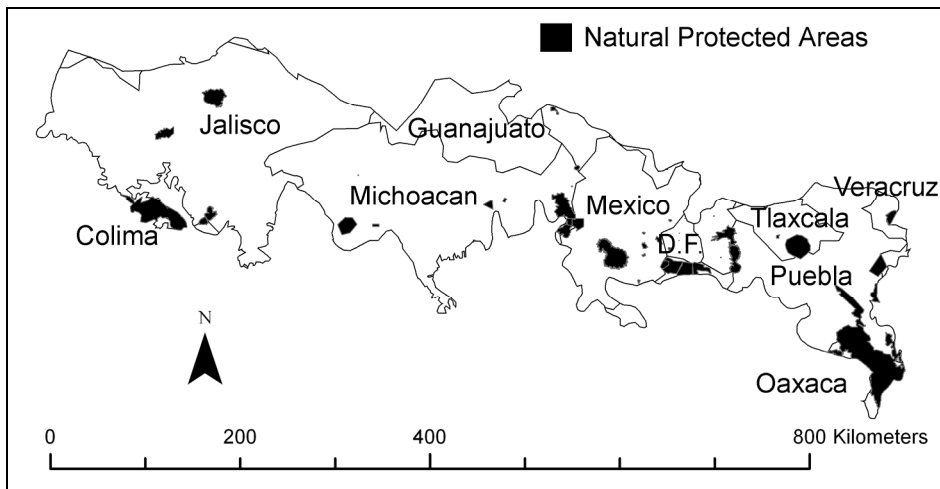
Figure 2



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Figure 3

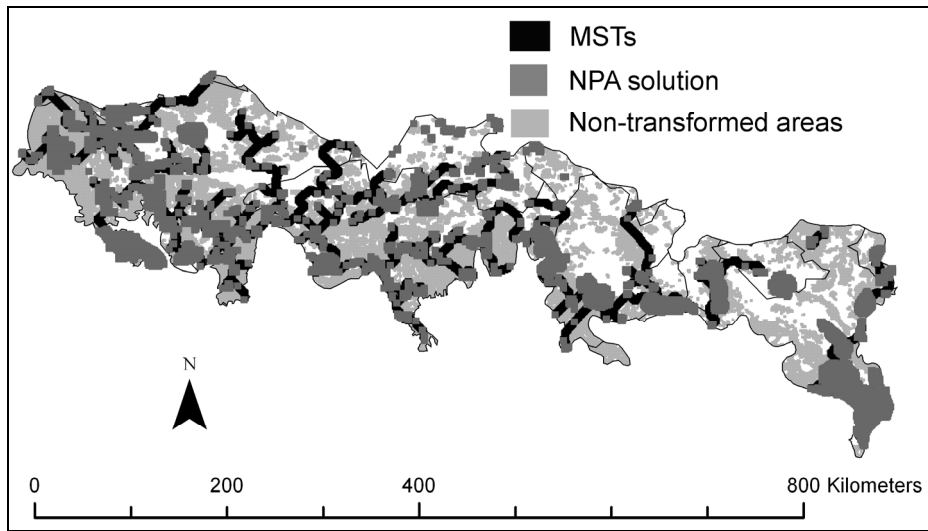


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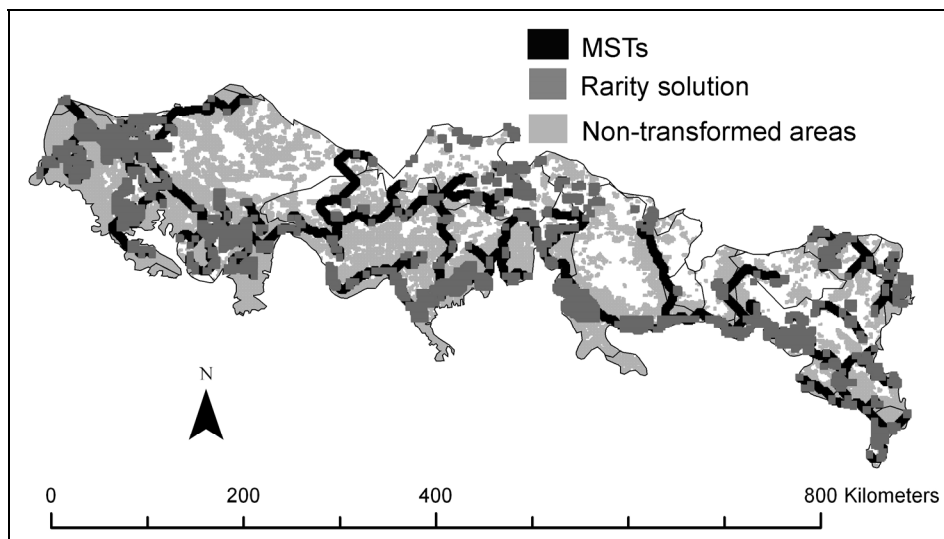
Figure 4

(a)



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(b)



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