PLACE PRIORITIZATION FOR BIODIVERSITY REPRESENTATION USING SPECIES' ECOLOGICAL NICHE MODELING

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Abstract.—Place prioritization for biodiversity representation is essential for conservation planning, particularly in megadiverse countries where high deforestation threatens biodiversity. Given the collecting biases and uneven sampling of biological inventories, there is a need to develop robust models of species' distributions. By modeling species' ecological niches using point occurrence data and digitized environmental feature maps, we can predict potential and extant distributions of species in untransformed landscapes, as well as in those transformed by vegetation change (including deforestation). Such distributional predictions provide a framework for use of species as biodiversity surrogates in place prioritization procedures such as those based on rarity and complementarity. Beyond biodiversity conservation, these predictions can also be used for place prioritization for ecological restoration under current conditions and under future scenarios of habitat change (e.g., deforestation) scenarios. To illustrate these points, we (1) predict distributions under current and future deforestation scenarios for the Mexican endemic mammal *Dipodomys phillipsii*, and show how areas for restoration may be selected; and (2) propose conservation areas by combining nonvolant mammal distributional predictions as biodiversity surrogates with place prioritization procedures, to connect decreed natural protected areas in a region holding exceptional biodiversity: the Transvolcanic Belt in central Mexico.

Key words: biodiversity content, conservation, deforestation, ecological niche, endemic mammals, Mexico, place prioritization, restoration.

Resumen.—La selección de áreas prioritarias de conservación es fundamental en la planeación sistemática de la conservación, particularmente en países de mega-diversidad, en donde la alta deforestación es una de las amenazas a la biodiversidad. Debido a los sesgos taxonómicos y geográficos de colecta de los inventarios biológicos, es indispensable generar modelos robustos de distribución de especies. Al modelar el nicho ecológico de especies usando localidades de colecta, mapas digitales de variables ambientales y sistemas de información geográficos, se proyecta las distribuciones potencial y actual en hábitat transformados y no transformados por la deforestación. Estas hipótesis de distribución proveen un marco teórico para predecir presencia y ausencia de especies, como indicadores de la biodiversidad existente en áreas prioritarias seleccionadas con base en los principios de rareza y complementariedad. Para ilustrar esto, se muestran dos ejemplos; (1) se modeló el nicho ecológico de un roedor endémico *Dipodomys phillipsii*, proyectando su distribución en escenarios de deforestación actuales y a futuro. La predicción de la distribución de especies puede ser útil en la selección de áreas prioritarias para la conservación y la restauración, bajo escenarios actuales y futuros de deforestación, permitiendo una planeación sistemática adecuada de la conservación de la biodiversidad, y (2) proponer áreas de conservación, usando predicciones de distribuciones de mamíferos no voladores y procedimientos de selección de áreas prioritarias, como corredores que conecten las áreas naturales prioritarias decretadas en el Eje Neovolcánico, una región de alta biodiversidad.

Palabras clave: áreas prioritarias, contenido de biodiversidad, deforestación, mamíferos endémicos, México, nicho ecológico, restauración.

An emerging goal of conservation biology is to prioritize places for conservation and management on the basis of biodiversity value (Margules and Pressey 2000; Sarkar and Margules 2002). Traditionally, priority areas for conservation have involved natural protected areas (NPAs), which have usually been decreed in regions where no previous rigorous quantitative place prioritization was performed (Pressey et al. 1996a; Sarkar 1999). This is particularly the case for most countries holding exceptionally rich biodiversity, where use of criteria such as scenic value, wilderness quality, or mere availability leads to the practice of *ad hoc* reservation (Alcérreca et al. 1989; Pressey 1994).

Recent efforts involve adding new areas to NPA systems to improve biodiversity conservation, including worldwide (Rodriguez et al. 2004), continental (Andelman and Willig 2004), national and regional approaches (Pressey et al. 1993, 1996b). Selection of priority conservation areas uses large occurrence data sets for particular biological groups of conservation interest. For example, Williams et al. (1996) identified priority areas for bird conservation in the United Kingdom, based on an exhaustive database of species distribution of more than 170,000 records. They proposed areas holding high species richness (richness hotspots), endemism (rarity hotspots), and sets of areas showing maximal species representation for birds in the United Kingdom (Williams et al. 1996). Further steps for selection of priority areas for biodiversity conservation require inclusion of as many floristic and faunistic groups as possible, given that richness and rarity hotspots do not necessarily coincide geographically between such groups (Saetersdal et al. 1993; Williams 1998; Egbert et al. 1999; Peterson et al. 2000). Recent studies proposing networks of conservation areas for improving biodiversity conservation include plants and birds in Norway (Saetersdal et al. 1993), plants (Willis et al. 1996), and birds (Godown and Peterson 2000; Fairbanks et al. 2001) in South Africa and the United States, and terrestrial vertebrates in the United States (Csuti et al. 1997).

More complex approaches include probabilistic methods to identify reserve networks representing greatest expected numbers of species (Polasky et al. 2000; Sarkar et al. 2004), and incorporation of optimization procedures such as flexibility (ability to incorporate crucial information on real conservation problems), efficiency (ability to maximize species richness at the minimum cost), and accountability (solution transparency), identified as key attributes for prioritizing areas for biodiversity conservation (Nichols and Margules 1993; Pressey et al. 1996a; Williams 1998; Rodrigues et al. 2004; Sarkar et al. 2004). Further noteworthy efforts for multi-taxa selection of priority areas for biodiversity conservation involve both governmental and academic participation. For example, the Mexican National Commission for the Conservation and Use of Biodiversity (CONABIO) has launched one of the most prominent efforts for prioritization and regionalization of areas for conservation in conjunction with decreed NPAs at the national level, where taxonomic experts play a major role in identifying richness and rarity hotspots for a wide range of biological groups for terrestrial and marine environments (Arriaga et al. 2000a,b; Challenger 1998; CONABIO 1998; CONABIO and SEMARNAT 2000).

Recently, Margules and Pressey (2000) proposed a synthetic framework for systematic conservation planning which involves place prioritization as one of its central goals; this framework was extended by Sarkar (2004). It consists of a number of stages starting from compilation of information about biodiversity distribution and explicit conservation goals for a region. To achieve this, four problems for biodiversity planning and management must be solved (Sarkar et al. 2002; Sarkar 2004):

(i) *Surrogate selection*: surrogates form the explicit focus of conservation (species, vegetation types, ecosystem types, etc.), and the task of finding adequate surrogates is referred to as the "surrogacy problem". The most common surrogates are distributions of well-known species, and environmental parameters such as average rainfall, average temperature, and soil type, since these are often the only data available (Margules et al. 1995; Nix et al. 2000). However, if total species diversity is the explicit conservation goal, whether or not these surrogates are adequate indicators or good predictors has not been solved theoretically (Sarkar et al. 2002; Sarkar 2004). This is particularly relevant and challenging for regions holding exceptionally high diversity, such as the so-called megadiverse countries;

(ii) *Place prioritization*: once surrogates have been chosen, selected places are ordered hierarchically according to their biodiversity content; this is referred to as the "place prioritization problem" and is discussed in more detail below;

(iii) *Viability of biota at prioritized places*: for each place selected, projected future scenarios for biological entities (populations, species, communities, ecosystems) must be taken into account. This is usually referred as the "viability problem," and is perhaps the most difficult stage of the planning protocol to execute in practice. Viable areas must be estimated for all surrogates selected *and* the broader biota for which they are surrogates (Sarkar et al. 2002; Sarkar 2004). Such analyses will result in re-ordering of prioritized areas, taking into account degrees of future viability. Selected areas with low viabilities are ranked lower in the place prioritization than those with high viability; place prioritization for restoration requires further analyses. It should be emphasized that such a priority ranking of selected places must reflect their biodiversity value, a primary goal for place prioritization. There are a number of methodologies for estimating viabilities of these biological entities, from conducting stochastic population viability analysis (PVA) for small and restricted populations (Boyce 1992; Burgman et al. 1993), to estimating viability of selected places based on risk of habitat conversion particularly into agrosystems (Pressey et al. 1996a);

(iv) *Final selection of appropriate places for management plan implementation*: selection of appropriate places for management practices and sustainable use of natural resources should presumably start with those areas with highest biodiversity value. Subsequently, socioeconomic, social, and political factors central to launching adequate management practices must also be incorporated into a conservation plan. This is usually referred as the "feasibility problem."

It should be noted that the solution of the last two problems requires reliable and frequent feedback, given that management practices can alter significantly the viability of biotas at selected places. Human-induced changes in land use and viability of biota at selected places must be considered in the context of overall conservation and management practices and policies for entire regions.

Deforestation threatens biodiversity conservation and increasing human pressure for land conversion to agrosystems and urban settlements results in fewer extensive areas potentially devoted to biodiversity conservation. Consequently, urgent action for conservation planning based on systematic place prioritization criteria is urgently needed. In particular, deforestation can impact biodiversity distributions significantly (Sánchez-Cordero et al. 2004), requiring proper adjustment or re-analysis of management plans. Such "adaptive management" involves recurrent evaluation of place prioritizations for conservation content (Meffe and Carroll 1997; Sarkar et al. 2002; Sarkar 2004).

In this contribution, we will focus only on the surrogacy and place prioritization problems. We propose the use of ecological niche modeling, by which presences or absences of species are interpreted into potential distributional areas. These modeled distributions provide a theoretical framework for use of species as surrogates for overall biodiversity content. We describe a place prioritization protocol, emphasizing selection of places containing rare surrogates (the principle of "rarity") and places that add as many underrepresented surrogates as possible to a set of selected places (the principle of "complementarity"), and discuss fruitful options not only for systematic conservation, but also for restoration planning. This protocol combines ecological niche modeling with place prioritization for biodiversity representation under current and future deforestation scenarios.

MODELING SPECIES' ECOLOGICAL NICHES

Natural history museum collections store massive amounts of information on biodiversity, containing primary information on species' geographic occurrences for documenting biodiversity worldwide. This information can be compiled into databases containing species' records and georeferenced collecting localities gathered from national and international institutions (Soberón 1999). However, given the uneven and biased taxonomical and geographical nature of museum collections, tools for extrapolating from what is *known* to a more general prediction of species' distributions are necessary.

Several efforts have advocated modeling species' ecological niches, based on a Grinnellian geographic niche concept (Grinnell 1917; MacArthur 1972), which are then projected as potential distributional maps (Peterson et al. 1999; Sánchez-Cordero et al. 2001, 2004). One such approach is based on use of a genetic algorithm, in combination with occurrence data sets and digitized maps of environmental features. In particular, the Genetic Algorithm for Rule-set Prediction (GARP[1], Stockwell and Peters 1999) uses an evolutionary computing approach to compute niche models that can be projected as potential geographic distributions of species (Peterson et al. 1999; Stockwell and Peters 1999). GARP has proven a robust method for modeling species' ecological niches for large numbers of taxa (Peterson 2001; Peterson et al. 1999; Peterson and Kluza 2003; Illoldi-Rangel et al. 2004; Sánchez-Cordero et al. 2004).

While ecological niche modeling predicts potential geographic distributions of species, certain areas may not be occupied currently, given effects of other factors external to the model, such as historical constraints, species interactions, and changes in land use patterns (Anderson et al. 2003; Peterson et al. 1999; Sánchez-Cordero et al. 2001, 2004). One such factor is deforestation, which leads to reduction and fragmentation of natural habitats, limiting species' realized distributions to subsets of their potential distributions. We can quantify reductions of species' distributions by constructing potential niche models based on climate, topography, and reference vegetation maps, and then overlaying these maps on actual land use/land cover maps. Extant distributions of species are taken as areas holding untransformed natural habitats *within* potential distributions, assuming that deforested areas probably constitute inviable ecological conditions (Sánchez-Cordero et al. 2004). Our approach to modeling species' extant distributions based on current land-use patterns provides a testable framework for predicting where species are present, as well as regions in which populations are reduced or extirpated by loss of natural habitats. Predictions of potential and actual distributions of species serve to indicate effects of scenarios of habitat transformation on biodiversity; these distributions can then be used to plan for conservation and restoration.

To illustrate this approach, we show potential scenarios of changes in species' distributions due to deforestation. The heteromyid *Dipodomys phillipsii* is an endemic rodent associated with arid and semi-arid habitats and occurring on the Mexican Plateau, the Transvolcanic Belt and Oaxaca (Hall 1981). We modeled the ecological niche of *D. phillipsii* using GARP, point occurrence data georeferenced to the nearest 0.01° of longitude and latitude for each locality using 1:250,000 topographic maps (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO 1998[2]), and 10 environmental data layers (0.04 × 0.04° pixel resolution), including potential vegetation type (Rzedowski 1986); elevation, slope, and aspect (from the U.S. Geological Survey's Hydro-1K data set[3]); and climatic parameters including mean annual precipitation, mean daily precipitation, maximum daily precipitation, minimum and maximum daily temperature, and mean annual temperature (CONABIO 1998). We then overlayed transformed areas due to human-induced habitat conversion, based on satellite imagery resulting in a land use/land cover map for 1980 and 2000 (Velázquez et al. 2001).

All point occurrence data from collecting localities (*N* = 73) for this species are dated before 1970 (Hall 1981); as such, specimens were collected in natural habitats prior to the 1980 land use habitat transformation within its range (Hall 1981). Transformed areas converted into agrosystems and urban areas are presumed to represent non-viable ecological conditions for this rodent (Sánchez-Cordero et al. 2004). This assumption based on hypotheses of general niche conservatism tested for diverse taxa in Mexico (Peterson et al. 1999; Peterson and Holt 2003) assumes that rapid adaptation to new environments produced by human-induced habitat transformation is unlikely, particularly without recurrent immigration from adjacent natural habitats (Peterson and Holt 2003). These hypotheses are particularly likely to hold for locally-adapted endemic species.

We found extensive transformed areas, particularly in the Transvolcanic Belt (TVB), as well as in the northwestern and southern portions of the distribution of this species (Figure 1). Moreover, habitat conversion from untransformed to transformed uses, when the species' potential and actual distributions are compared (based on the Inventario Nacional Forestal 1980 and 2000, respectively), showed that areas already fragmented are more likely to suffer additional reduction due to human-induced habitat

[1] http://www.lifemapper.org/desktopgarp.

[2] http://www.conabio.gob.mx.

[3] http://www.usgs.gov.

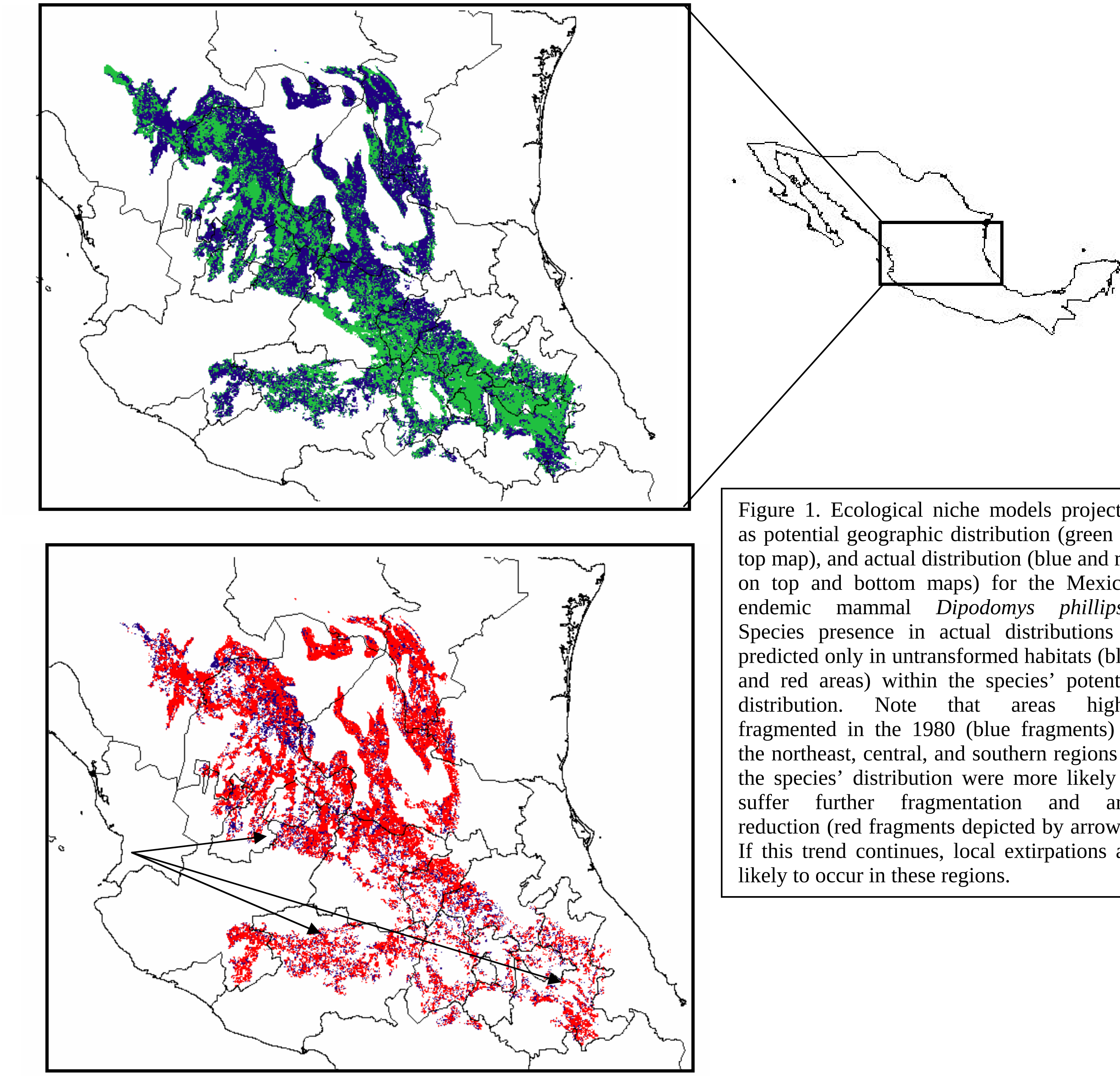


Figure 1. Ecological niche models projected as potential geographic distribution (green on top map), and actual distribution (blue and red on top and bottom maps) for the Mexican endemic mammal *Dipodomys phillipsii*. Species presence in actual distributions is predicted only in untransformed habitats (blue and red areas) within the species' potential distribution. Note that areas highly fragmented in the 1980 (blue fragments) in the northeast, central, and southern regions of the species' distribution were more likely to suffer further fragmentation and area reduction (red fragments depicted by arrows). If this trend continues, local extirpations are likely to occur in these regions.

degradation (Figure 1). If such a trend continues, fragments remaining in the TVB, and in the northwestern and southern parts of the species' range will suffer further severe reductions or will simply disappear. As a consequence, these areas are predicted at being of high risk of population extirpations, and should be selected for restoration. (Obviously, such distributional scenarios should first be validated in the field.)

PLACE PRIORITIZATION PROCEDURES

We will briefly discuss the place prioritization procedures incorporated in the ResNet software package[4] (Sarkar et al. 2002; Aggarwal et al. 2000). Algorithms in ResNet belong to the family of algorithms introduced by Margules et al. (1988; Nicholls and Margules 1993), but add a novel dynamic memory allocation scheme that results in no constraints on size of the data set. Several recent studies of regional planning for conservation purposes use ResNet (Sarakinos et al. 2001; Sarkar et al. 2004; Tognelli, in press).

The operational procedure starts when a region is divided into a set of places on the basis of geographical coordinates, ecoregions, or biogeographic regions, and the algorithm orders those places by their biodiversity content. The algorithm assumes either that an explicit target has been set for adequate representation of each surrogate (e.g., number of selected places at which a surrogate must be present), or that a maximum allowed area or a maximum allowed cost of a proposed set of priority places has been specified. The goal of all such algorithms is to achieve the target as economically as possible, by selecting as few places as possible for reaching the conservation goal (Margules et al. 1988; Sarkar et al. 2004).

Three rules are incorporated into the algorithms of ResNet: (i) *Rarity*: surrogates are first ordered inversely by their frequency of appearance in the data set. Then, places are ordered according to whether they contain the rarest surrogate, the next rarest surrogate, and so on, iteratively. (ii) *Complementarity*: places are ordered based on numbers of surrogates that have not met their targeted representation. (iii) *Richness*: places are ordered based on number of surrogates present; however, richness is used only in initial step (selecting the first place), since it has been shown previously that reliance on richness results in inefficient place selection (Williams et al. 1996; Csuti et al. 1997). In ResNet, three criteria may be used to initialize the prioritization procedure: rarity, richness, or from a set of pre-selected places (e.g., existing protected areas). For both initialization and iterative place selection, ties are broken arbitrarily by selecting the first place on the list, so a unique place is chosen. Further refinement of place prioritization can be achieved by introducing adjacency considerations, by which areas neighboring already-selected areas are given preference over others, resulting in larger and more contiguous areas. Iterations continue until the target is met—that is, that all surrogates are adequately represented or the maximum allowed area or cost is exceeded. If no explicit target is set, the procedure continues until all places are selected (Sarkar et al. 2002). The order in which places are selected produces a ranking of places based on their biodiversity content. Biodiversity content is thus implicitly defined by the algorithm, and the intuition behind this approach is that diversity is adequately captured by rarity and complementarity (Sarkar 2002; Sarkar and Margules 2002). As expected, depending on initialization and iteration criteria chosen, a number of different solutions can be achieved (Sarkar et al. 2002).

CURRENT CHALLENGES AND AN EXAMPLE

The two techniques—ecological niche modeling and place prioritization—merge to form a synthetic protocol in the emerging field of biodiversity informatics, with potentially extensive applicability to conservation planning. Ecological niche modeling facilitates inclusion of more taxa than would otherwise be possible, providing a framework for incorporation of large numbers of species, including those with high conservation priority, as biodiversity surrogates (Egbert et al. 1999; Peterson et al. 2000; Rojas-Soto et al. 2004). This is particularly true in megadiverse countries, despite controversies about whether the surrogates commonly employed are true indicators of biodiversity (Margules and Pressey 2000; Sarkar et al. 2002). As a consequence, place prioritization for biodiversity content using criteria of rarity and complementarity can be implemented readily based on robust models of species' geographic distributions. We envision a challenging research program for applying these approaches to prioritization challenges in megadiverse countries worldwide (Rodrigues et al. 2004). Current

[4] http://uts.cc.utexas.edu/~philsci/sarkar/main.html.

proposals from international conservation organizations such as IUCN and World Park Commission[5] encourage governments worldwide to include at least 10% of their land into reserves for launching conservation programs; these potential natural protected areas can be selected following methodologies described herein and elsewhere (Margules and Pressey 2000; Sarkar et al. 2002). Recent studies using ecological niche modeling of multiple taxa, and place prioritization procedures hold promising for identifying additional areas devoted for conservation (Egbert et al. 1999; Peterson et al. 2000).

Deforestation ranks among the major threats to biodiversity conservation worldwide, making place prioritization for biodiversity content urgent. In many countries, institutional and governmental efforts on bioinformatics are making available massive amounts of information from natural history museum specimens and digital environmental data on the Internet (CONABIO, INBIO[6], MaNIS[7]). Modeling ecological niches projected as potential and actual distributional hypotheses provide a framework for understanding species' distributions across current untransformed and transformed landscapes (Sánchez-Cordero et al. 2001, 2004), useful for assigning probabilities of presence of surrogates in place prioritization procedures for biodiversity content. Species' actual distributions based on ecological niche models where only untransformed habitats are included can be further used as baseline distribution hypotheses for inclusion in place prioritization procedures (Figure 1) (Munguía 2003; Sánchez-Cordero et al. 2004).

We illustrate this point by combining species' actual distributions (e.g., Figure 1, bottom panel) with place prioritization procedures using terrestrial nonvolant mammals in the TVB as biodiversity surrogates to identify priority areas for connecting decreed natural protected areas (NPAs; Fig. 2; see Munguía 2003; Munguía et al. in prep.). This region holds exceptionally rich biodiversity, but rampant deforestation threatens its conservation. Conversely, the TVB holds many decreed NPAs, including 39 NPAs of 1000 ha or more (Munguía 2003; Sánchez-Cordero et al. 2004; Fuller et al. submitted).

Searching among already-existing areas, we selected 13 priority areas based on endemicity, species richness, and complementarity: Reserva de la Biósfera Sierra de Manantlán, Parque Nacional Volcán Nevado de Colima, Parque Nacional La Primavera, and Parque Nacional Sierra de Quila, in the western region; Reserva de la Biosfera Corredor Biológico Chichinautzin, Parque Nacional El Tepozteco-Zempoala, Reserva de la Biosfera Mariposa Monarca, and Parque Nacional El Cimatario, in the central region; and Parque Nacional La Malinche, Reserva de la Biosfera Valle de Tehuacán-Cuicatlán, and Parque Nacional Cofre de Perote, in the eastern region, of the TVB (Figure 2). We then proposed connecting these NPAs by choosing remnant untransformed habitats, based on the 2000 land use/land cover map (CONABIO), lying along straight paths, as follows: for the western region, corridors connected Sierra de Manantlán with Volcán de Colima, Sierra de Quila, and La Primavera; for the central region, corridors connected Izta-Popo with Corredor Biológico Chichinautzin, El Tepozteco-Zempoala, Mariposa Monarca, and El Cimatario; for the eastern region, corridors connected La Malinche with Valle de Tehuacán-Cuicatlán, Pico de Orizaba, and Cofre de Perote (Fig. 2) (Munguía 2003; Munguía et al. in prep.). A further refinement of this analysis using actual distributions of 99 terrestrial nonvolant mammals as biodiversity surrogates, place prioritization procedures, and graph theory for identifying priority areas in the TVB is presented elsewhere (Fuller et al. submitted).

Future projections of deforestation can also be incorporated into the niche modeling framework to generate predictions of potential distributional areas under forecasts of habitat transformation scenarios. Such distributional models can be used as surrogates in place prioritization procedures to identify priority areas under current and future scenarios of deforestation (Sánchez-Cordero et al. 2001, 2004). Deforestation has major impacts on species' distributions (Sánchez-Cordero et al. 2004), so efforts to combine niche modelling with place prioritization procedures offer an extremely useful tool for planning current and future conservation strategies in megadiverse countries.

Place prioritization for biodiversity content also enables inclusion of selection of areas for habitat restoration based on comparison of potential and actual distributions in transformed and

[5] http://www.iucn.org.
[6] http://www.inbio.ac.cr.
[7] http//elib.cs.berkeley.edu/manis/.

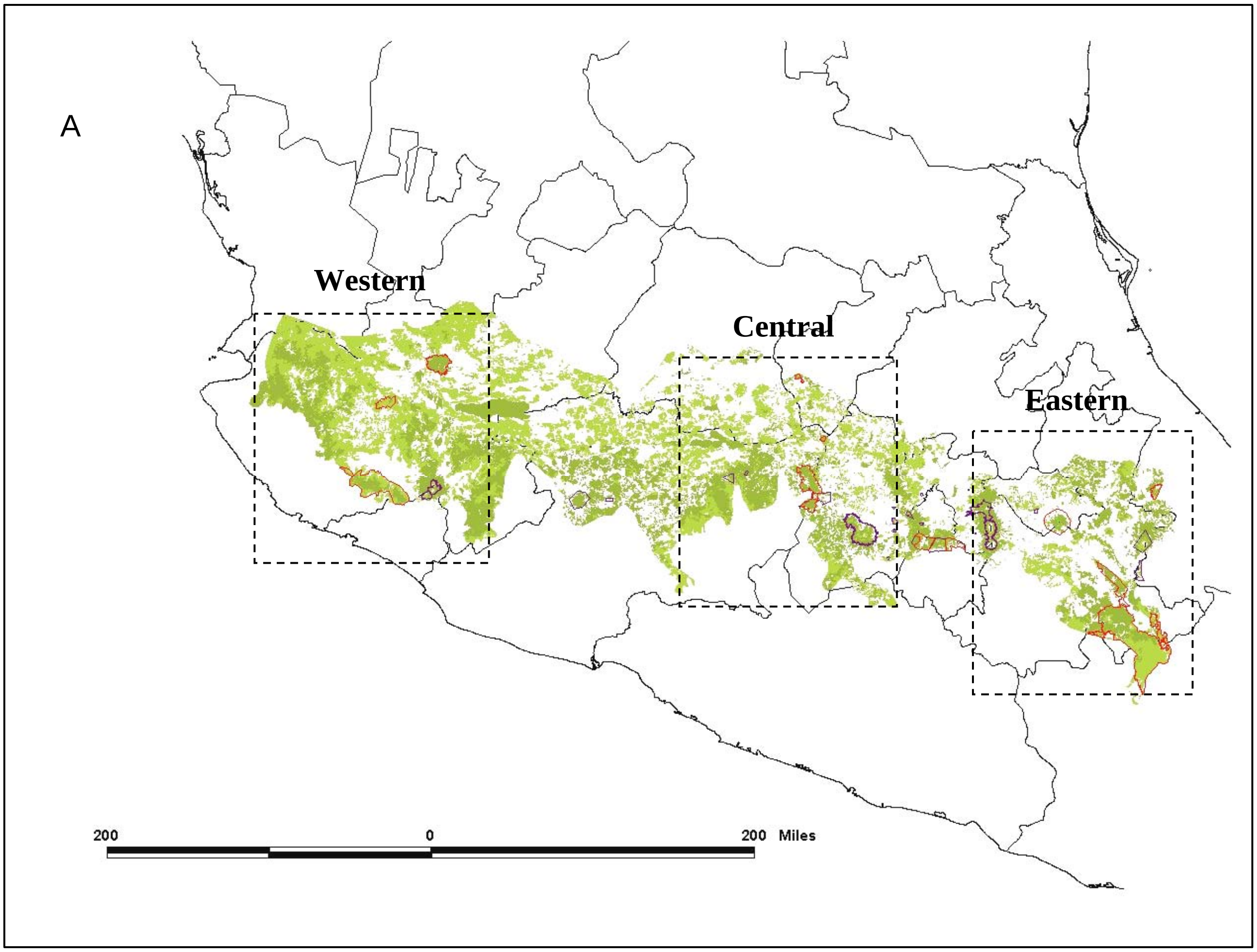
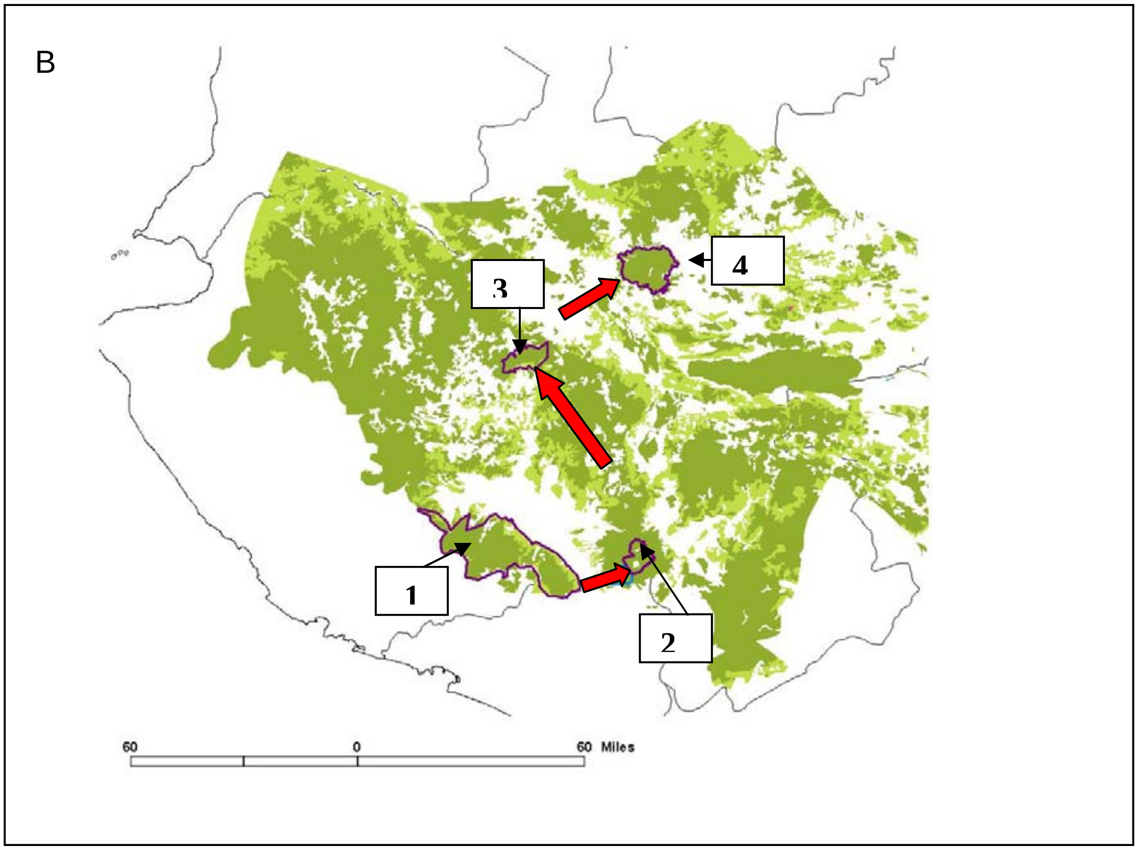


Figure 2. Proposed areas connecting decreed priority natural protected areas (NPAs) in the Transvolcanic Belt of central Mexico, a region of exceptional biodiversity. Priority NPAs were selected based on richness of endemism, species richness, and complementarity (Munguía 2004; Munguía et al, in prep.). (A) Overview of the TVB, depicting remnant untransformed natural habitats based on 2000 land use/land cover map (green area), and selected priority decreed NPAs (delineated polygons). (B) Selected areas identified as corridors (see arrows) of remnant untransformed habitat connecting priority NPAs for the western, central, and eastern regions of the TVB. Priority NPAs shown are: (1) Reserva de la Biósfera Sierra de Manantlán, (2) Parque Nacional Nevado de Colima, (3) Parque Nacional La Primavera (4) Parque Nacional Sierra de Quila, (5) Parque Nacional Izta-Popo, (6) Reserva de la Biosfera Corredore Biológico Chichinautzin, (7) Parque Nacional El Tepozteco-Zempoala, (8) Reserva de la Biosfera Mariposa Monarca, (9) Parque Nacional El Cimatario, (10) Parque Nacional la Malinche, (11) Reserva de la Biosfera Valle de Tehuacan-Cuicatlán, (12) Parque Nacional Pico de Orizaba, and (13) Parque Nacional Cofre de Perote. (3 pages)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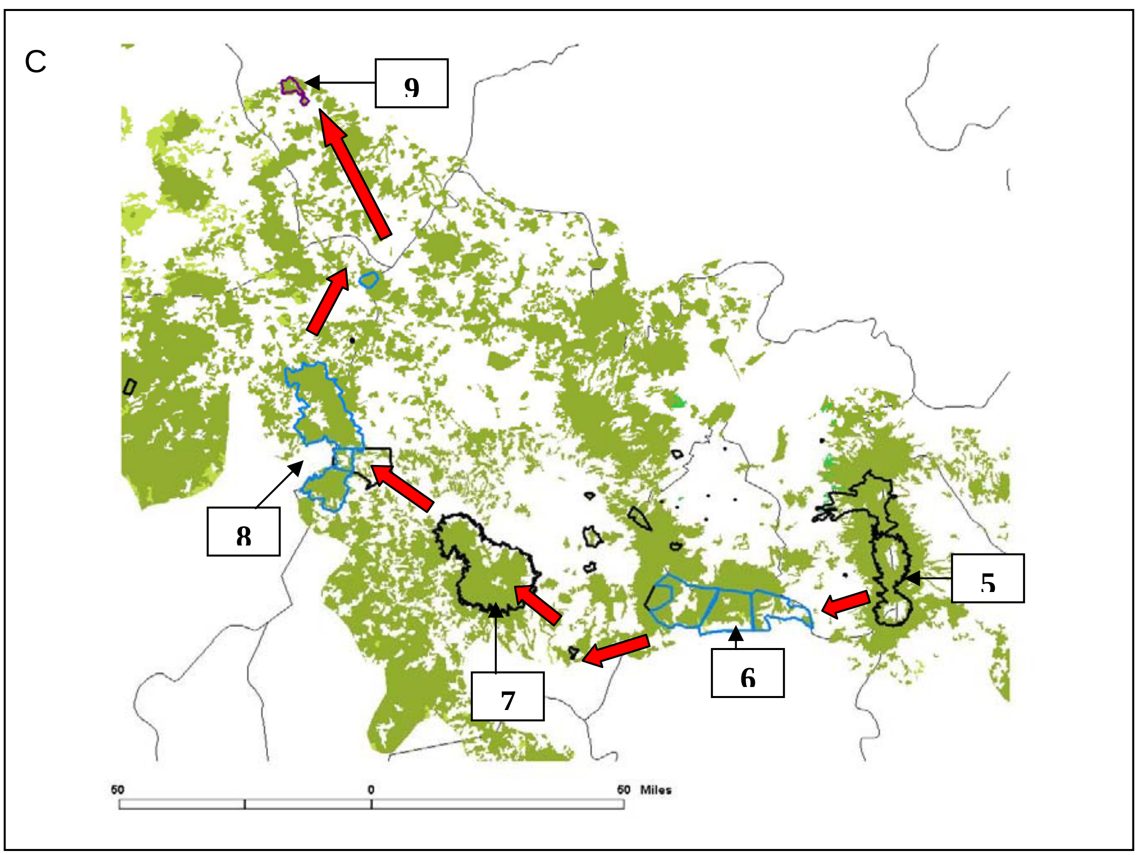
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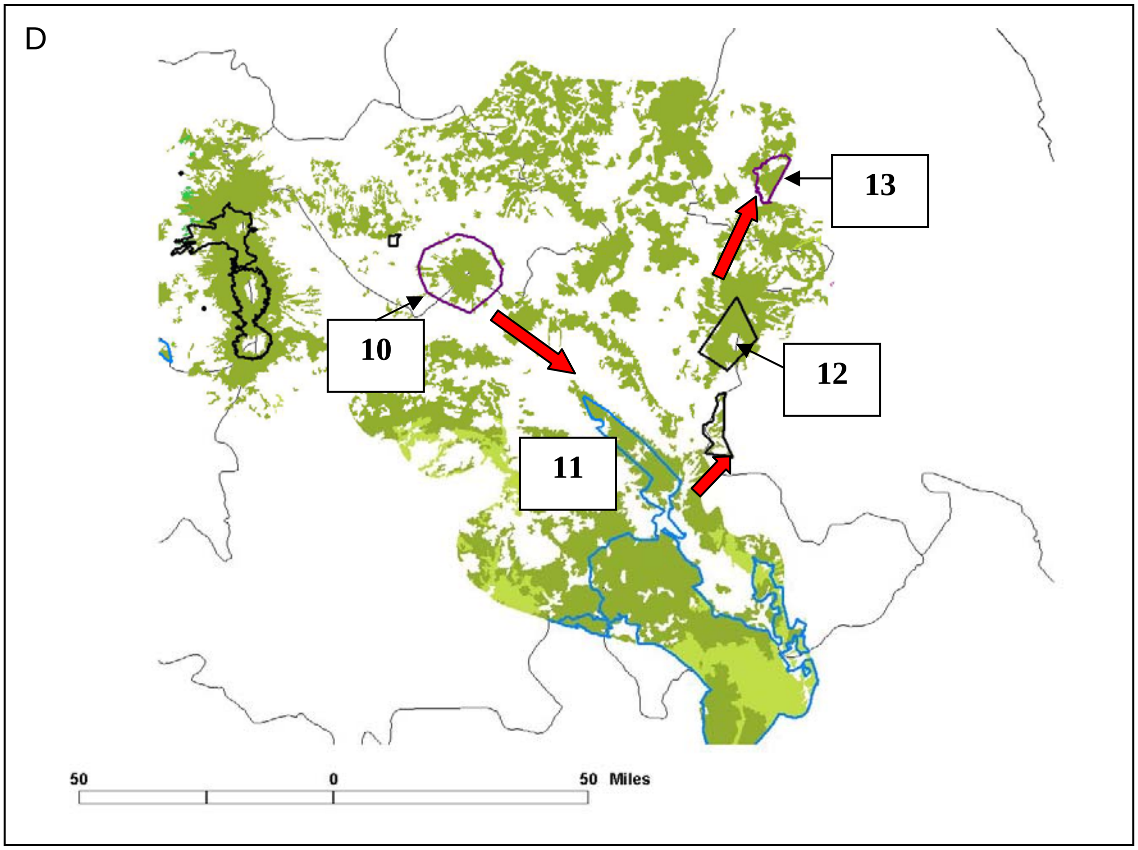
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untransformed landscapes (Fuller et al. submitted). Our distributional models computing potential and actual distributions in untransformed and transformed landscapes can provide baseline information for selection of priority areas for restoration. For example, transformed areas within the potential distributions of priority species are potential areas for restoration from transformed habitats to the original untransformed natural habitat. The above approaches of ecological niche modelling, reconstructing actual distributions, and incorporation into place prioritization procedures results in robust analytical tools for improving systematic conservation planning protocols for conservation and restoration sites (Margules and Pressey 2000; Sarkar 2004).

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