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BIODIVERSITY RESEARCH

Solving the maximum representation problem to prioritize areas for the conservation of terrestrial mammals at risk in Oaxaca

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ABSTRACT

Oaxaca, located in south-west México within the Mesoamerican biodiversity hotspot, holds exceptionally high biodiversity for several taxa, including mammals. It has four decreed natural protected areas (NPAs) covering 5% of its total area, but only three of these, covering only 0.2% of the area, are strictly protected as National Parks. The current study develops ecological niche models for 183 terrestrial mammals for use as biodiversity surrogates in a systematic conservation planning exercise. Forty-five of these species were selected on the basis of their being either endangered or threatened or otherwise listed under the Mexican Red List or because they were endemic to either Oaxaca or to Mexico. The niche models were constructed with a machine-learning algorithm (GARP, Genetic Algorithm for Rule-Set Prediction) and refined by restricting each model to sites with suitable vegetation and habitat patches contiguous with known occurrences of the species. If the entire predicted geographical distribution of each of the 45 species listed above is put under protection, the entire state of Oaxaca gets included. Therefore, we imposed different constraints on the maximum area that can be put under protection (5–30% of the area of Oaxaca) and selected nominal conservation area networks based on different percentage representation targets for the species' modelled distributions based on their conservation status (10–100%). The area selection utilized a rarity- and complementarity-based algorithm (in the ResNet software package). The goal was to have as many as possible of the 45 species at risk meet their specified representation targets in the budgeted area. The methods developed here combine ecological niche modelling and area prioritization algorithms for integrated conservation planning in a protocol that is suitable for other highly biodiverse regions.

Keywords

Conservation area network, endemic species, mammal conservation, maximum representation problem, Oaxaca.

INTRODUCTION

México, a megadiverse country because of its species richness and the high endemicity of its flora and fauna (Espinosa-Organista *et al*., 2001; Ceballos *et al*., 2002; Mittermeier & Robles, 2002; Vergara & Ayala, 2002; Escalante *et al*., 2003, 2004), ranks second globally in mammal richness (Fa & Morales, 1993; Arita *et al*., 1997; Ceballos *et al*., 1998; Villa & Cervantes, 2003). However, this high biological diversity is unevenly distributed in the country, with greater richness and endemicity in the Neotropical southern states (Escalante *et al*. in press). The state of Oaxaca in south-west México (Fig. 1) contains exceptionally high biodiversity among the regions of México and Mesoamerica (Sánchez-Cordero, 2001; Peterson *et al*., 2003b; García-Mendoza *et al*., 2004), which can be attributed in part to its location in a transition zone between the Nearctic and Neotropical biogeographical regions (Halffter, 1965; Ortega & Arita, 1998). As part of the Mesoamerican hotspot of vascular plant endemism (Myers *et al*., 2000), Oaxaca also contains three global centres of plant endemism recognized by the WWF/IUCN: the Sierra de Juárez, Tehuacán-Cuicatlán, and Uxpanapa-Chimalapa (Davis *et al*., 1997).

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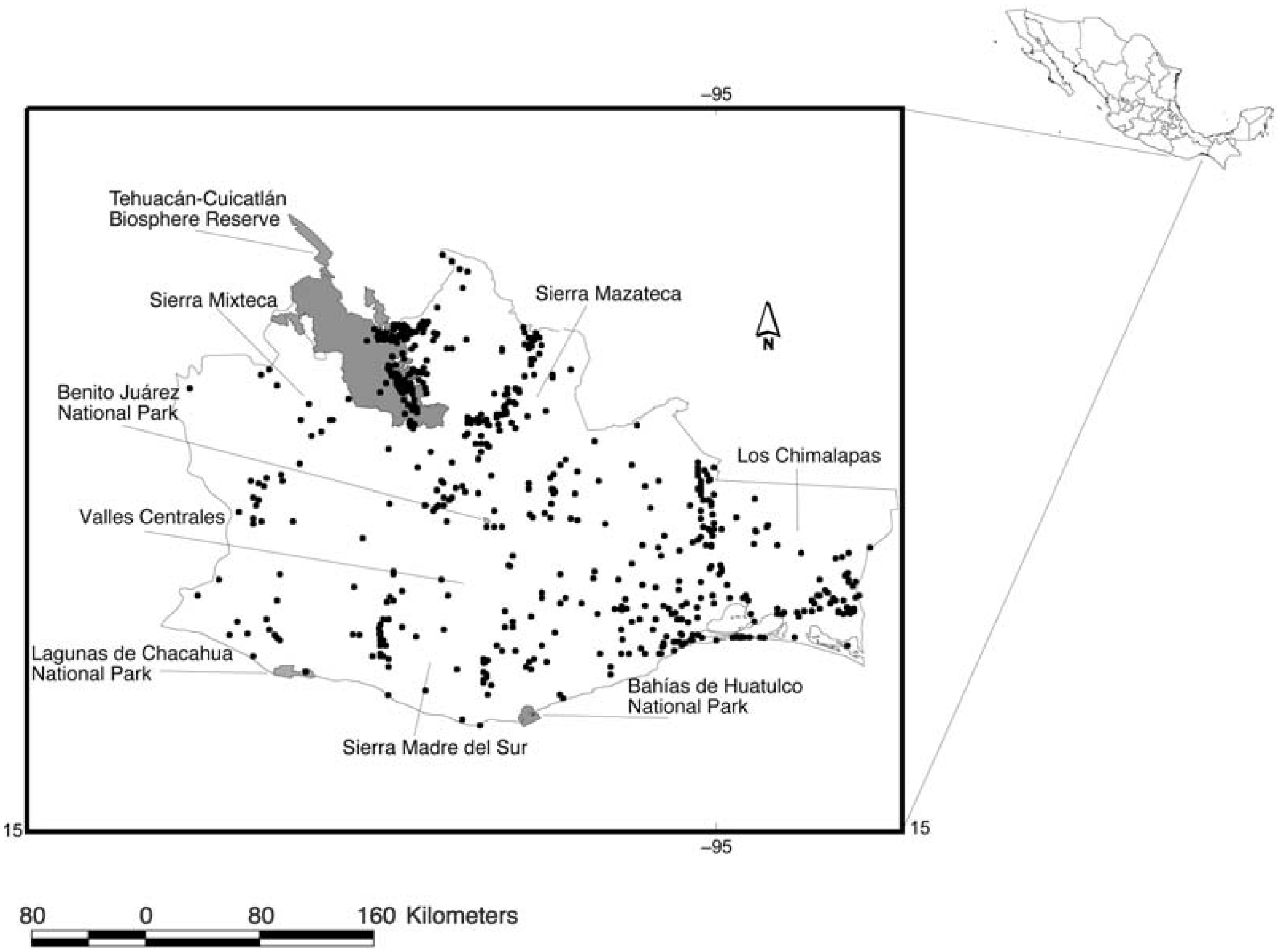

Figure 1 The state of Oaxaca, depicting the decreed Natural Protected Areas and the most important Sierras that cross the state, as well as the central valleys. The hatched area is the Tehuacán-Cuicatlán Biosphere Reserve. Black sites represent recorded occurrences of terrestrial mammals.

Though Oaxaca consists of only 5% of the area of México, it contains 50% of México's vascular plant species, 35% of its amphibian species, 26% of its reptile species, 63% of its bird species, and 55% of its terrestrial mammal species (Flores-Villela & Gerez, 1994; Briones-Salas & Sánchez-Cordero, 2004). All 10 orders of terrestrial mammals found in México occur in Oaxaca, as well as 77% (27) of the families, and 66% (40) of the genera (Goodwin, 1969). 183 terrestrial mammal species have been recorded in Oaxaca (Briones-Salas & Sánchez-Cordero, 2004), 45 of which fall under some protection category according to the official Mexican list of protected species (Norma Oficial Mexicana, NOM-059-Ecol-2001; Székely *et al.* 2005). Of these 45 species, 19 are endangered, nine others are at an elevated risk of extinction, and the remaining 17 are subject to special protection at the federal level because they may become threatened. Ten of Oaxaca's terrestrial mammal species are endemic to the state and six of these are included under some protection category (see Table 1).

Despite its disproportionately high biodiversity, Oaxaca has only four federal Natural Protected Areas (NPAs): Tehuacán-Cuicatlán Biosphere Reserve (which includes portions of the states of Puebla and Oaxaca, with 490,187 ha in Oaxaca), Lagunas de Chacahua National Park (14,187 ha), Bahías de Huatulco National Park (11,891 ha; of which 6000 ha is terrestrial – Gordon *et al.*, 2006) and Benito Juárez National Park (2737 ha). Together these NPAs cover 5% of the state's area. However, the three more strictly protected national parks comprise only 0.2% of Oaxaca. Moreover, though Oaxaca has three million hectares of forests, which occupy one-third of its total area (López-Arzola, 2005), the state suffers from high deforestation having had 23.8% of its natural habitat anthropogenically transformed to habitats such as agrosystems and urban settlements between 1990 and 2000 (Velázquez *et al.*, 2003; Gordon *et al.*, 2004; Mas *et al.*, 2004). Consequently, proposals for additional priority areas required for conserving Oaxaca's exceptional biodiversity are urgently needed. This study develops such a proposal.

Several methods exist for selecting areas with a high biodiversity value. Species richness has been used in the past but reflects neither the abundance of species nor the presence of rare and endemic species or those at risk of extinction. It also does not lead to spatial economy (efficiency) in the selection of conservation area networks (Margules *et al.*, 1988; Csuti *et al.*, 1997; Margules & Pressey, 2000; Faith, 2004; Sarkar, 2004). For these reasons, instead of species richness, measures such as rarity and complementarity (or differences between sites) and spatial criteria, such as the size and shape of individual conservation areas,

Table 1 Distributional and conservation status of 183 species of mammals of Oaxaca. EM: endemic to Mexico; Pr: under special protection; EO: endemic to Oaxaca; T: threatened; E: endangered. Here, restricted means the total habitat where actual data points have been collected.

Species	Number of unique point localities	Distributional Status	Conservation Status	Percentage of Habitat in Oaxaca	Percentage of Habitat in Existing Protected Areas of Oaxaca	Percentage of Restricted Habitat in Oaxaca	Percentage of Restricted Habitat in Existing Protected Areas
Agouti paca	5			7.19	0.12	0.26	0.00
Anoura geoffroyi	16			91.45	87.77	25.29	50.78
Antrozous dubiaquercus	6			77.62	55.57	0.03	0.00
Artibeus hartii	8			2.34	0.06	0.03	0.03
Artibeus hirsutus	5	EM		1.10	5.43	0.03	1.10
Artibeus intermedius	13			85.90	73.20	31.38	20.52
Artibeus jamaicensis	47			99.23	98.49	79.68	83.75
Artibeus lituratus	14			95.12	88.44	23.73	42.03
Ateles geoffroyi	5	Not endemic	E	58.00	25.57	11.62	2.17
Baiomys musculus	29			93.88	96.71	42.04	47.53
Balantiopteryx io	6			25.23	7.30	12.94	2.18
Balantiopteryx plicata	36			77.81	50.25	38.69	44.79
Bassariscus astututs	16	EM	T	98.94	96.16	1.46	5.77
Bassariscus sumichrasti	8	Not endemic	Pr	76.14	58.79	33.91	12.09
Caluromys derbianus	5			48.88	8.34	0.03	0.00
Canis latrans	14			93.30	91.76	0.46	7.14
Carollia subrufa	20			23.57	0.21	20.28	0.21
Carollia brevicauda	22			17.85	0.00	15.86	0.00
Carollia perspicillata	30			24.14	6.04	17.24	3.62
Centronycteris maximiliani	6	Not endemic	Pr	37.41	18.86	0.03	0.00
Centurio senex	10			87.41	64.81	23.49	1.45
Chiroderma villosum	4			50.25	47.27	0.06	0.77
Choeroniscus godmani	4			29.67	1.08	0.22	0.00
Choeronycteris mexicana	10	Not endemic	T	67.44	91.31	12.96	41.21
Conepatus mesoleucus	5			95.61	85.84	6.88	31.39
Cryptotis goldmani	7	EM	Pr	38.83	28.42	0.91	0.00
Cryptotis magna	15	EO	E	4.14	0.58	2.11	0.58
Cryptotis mexicana	21	EM	E	79.61	47.24	35.98	57.40
Cryptotis parva	7		Pr	88.86	81.60	25.44	31.57
Cyclopes didactylus	4			60.56	47.62	0.65	0.00
Dasyprocta mexicana	5	EM		33.46	23.50	0.15	0.00
Dasypus novemcintus	5			79.64	38.91	0.59	1.73
Dermanura azteca	9			70.25	54.13	2.33	4.94
Dermanura phaeotis	18			91.91	85.09	32.81	43.03
Dermanura tolteca	18			90.72	89.66	40.25	25.91
Desmodus rotundus	59			99.35	98.52	65.53	76.10
Diclidurus albus	2			66.10	53.86	0.06	0.00
Didelphis marsupialis	5			14.74	4.51	0.03	0.00
Didelphis virginiana	21			98.16	93.77	45.94	42.68
Diphylla ecaudata	4			6.94	0.00	0.75	0.00
Dipodomys phillipsii	5	EM	E	83.49	72.40	0.03	0.77
Eira barbara	8	Not endemic	E	82.44	73.63	12.03	7.96
Eptesicus fuscus	12			57.16	75.96	1.77	47.66
Eumops auripendulus	4			82.21	52.85	0.03	0.00
Eumops underwoodi	5			37.23	29.18	0.03	0.00
Galictis vittata	3	Not endemic	T	3.56	0.00	0.03	0.00
Glaucomys volans	4	Not endemic	T	57.08	79.61	0.16	4.14
Glossophaga commissarisi	8			56.77	12.97	12.34	6.97
Glossophaga leachii	6			82.72	46.18	1.05	4.03
Glossophaga morenoi	10			39.21	10.50	6.88	1.83
Glossophaga soricina	53			87.21	77.82	44.68	39.01
Habromys chinanteco	4	EO		78.90	87.27	0.34	0.92
Habromys lepturus	12	EO		3.27	0.58	0.26	0.58

Table 1 *Continued.*

Species	Number of unique point localities	Distributional Status	Conservation Status	Percentage of Habitat in Oaxaca	Percentage of Habitat in Existing Protected Areas of Oaxaca	Percentage of Restricted Habitat in Oaxaca	Percentage of Restricted Habitat in Existing Protected Areas
Herpailurus yaguarondi	7	Not endemic	T	82.59	60.23	12.50	13.70
Heteromys desmarestianus	31			15.35	0.49	11.87	0.49
Hylonycteris underwoodi	4			79.44	45.59	0.25	0.65
Idionycteris phyllotis	4			0.67	8.77	0.03	1.69
Lasiurus blossevillii	5			35.33	6.32	0.37	3.75
Lasiurus cinereus	7			99.20	96.62	3.47	19.13
Lasiurus ega	4			22.86	11.95	0.06	0.00
Lasiurus intermedius	5			98.34	93.16	36.15	22.32
Leopardus pardalis	5	Not endemic	E	20.63	6.19	2.76	1.05
Leopardus wiedii	9	Not endemic	E	98.58	95.24	16.21	18.59
Leptonycteris curasoae	10	Not endemic	T	90.10	71.77	23.61	19.54
Lepus californicus	5			65.22	73.14	0.06	1.32
Lepus callotis	6			7.16	26.15	0.04	6.29
Lepus flavigularis	13	EO	E	3.67	0.19	0.26	0.06
Liomys irroratus	109			61.04	85.22	44.39	68.75
Liomys pictus	39			42.59	6.93	28.95	6.53
Lonchorhina aurita	5	Not endemic	T	25.06	3.83	0.59	0.00
Lontra longicaudis	2	Not endemic	T	90.99	89.45	0.06	0.00
Lynx rufus	5			68.99	75.73	0.71	3.28
Macrotus waterhousii	21			90.98	86.75	8.06	52.41
Marmosa canescens	10	EM		72.27	77.91	10.55	65.15
Marmosa mexicana	5			60.25	18.37	9.83	5.50
Mazama americana	6			74.02	54.90	2.02	5.98
Megadonthomys cryophyllus	14	EM		79.87	95.30	44.10	72.26
Megadonthomys thomasi	5	EM	T	2.26	45.27	0.07	10.61
Mephitis macroura	6			11.77	6.19	1.50	0.00
Micronycteris brachyotis	5	Not endemic	T	3.96	0.00	0.04	0.00
Micronycteris megalotis	12			94.47	90.46	30.33	20.18
Microtus mexicanus	23			40.66	60.59	6.03	32.23
Microtus oaxacensis	5	EO	T	4.59	0.77	0.09	0.00
Microtus quasiater	5	EM	E	46.32	44.03	0.15	36.95
Microtus umbrosus	6	EO	E	18.91	15.95	0.56	3.28
Mimon bennettii	5	Not endemic	E	19.00	0.89	0.63	0.34
Molossops greenhalli	4	Not endemic	Pr	3.25	1.50	0.03	0.00
Molossus ater	4			85.59	69.09	18.45	15.66
Molossus molossus	7			84.43	69.03	22.21	4.74
Mormoops megalophylla	11			97.91	96.28	27.89	58.00
Mustela frenata	5			78.58	73.36	0.19	10.57
Myotis californicus	7			78.33	89.17	0.37	19.81
Myotis fortidens	4			78.50	56.70	1.88	0.00
Myotis nigricans	5		Pr	98.07	93.50	2.14	6.63
Myotis thysanodes	5			27.42	16.32	1.18	2.02
Myotis velifer	10			60.19	81.97	2.88	41.90
Nasua narica	14			98.30	87.68	50.72	45.26
Natalus stramineus	7			91.96	83.14	5.74	9.07
Neotoma mexicana	17			99.21	96.96	64.51	59.08
Noctilio leporinus	4			29.30	11.53	0.19	4.06
Nyctinomops aurispinosus	4			5.56	10.61	0.06	2.36
Nyctinomops laticaudatus	5			1.54	0.00	0.03	0.00
Nyctomys sumichrasti	10			36.25	16.96	17.01	7.73
Odocoileus virginianus	14			71.75	62.67	1.83	57.76
Oligoryzomys fulvescens	18			99.39	98.86	68.16	84.48
Orthogeomys cuniculus	4	EO	T	6.12	3.06	0.50	0.00
Orthogeomys grandis	18			52.81	34.18	30.15	34.18

Table 1 *Continued.*

Species	Number of unique point localities	Distributional Status	Conservation Status	Percentage of Habitat in Oaxaca	Percentage of Habitat in Existing Protected Areas of Oaxaca	Percentage of Restricted Habitat in Oaxaca	Percentage of Restricted Habitat in Existing Protected Areas
Orthogeomys hispidus	5			7.36	8.28	0.02	0.25
Oryzomys alfaroi	29			99.31	98.52	71.79	47.71
Oryzomys chapmani	30			99.37	98.86	60.58	92.18
Oryzomys couesi	40			48.92	60.81	35.64	49.23
Oryzomys melanotis	4			1.28	0.34	0.03	0.00
Oryzomys rostratus	3			9.83	0.80	0.03	0.00
Osgoodomys banderanus	4	EM		65.09	61.10	0.03	0.00
Panthera onca	4	Not endemic	E	54.40	49.93	0.06	0.00
Pecari tajacu	5			75.82	16.23	0.09	2.63
Peromyscus aztecus	41	EM		27.50	12.28	8.36	7.79
Peromyscus boylii	5			86.56	74.75	0.56	2.67
Peromyscus difficilis	6			41.10	63.76	2.57	14.62
Peromyscus furvus	8	EM		0.94	0.83	0.16	0.64
Peromyscus gratus	6			1.57	0.00	0.04	0.00
Peromyscus leucopus	12			33.05	47.14	14.27	41.69
Peromyscus levipes	23			99.30	98.86	34.74	79.10
Peromyscus maniculatus	8			19.16	56.50	1.41	15.73
Peromyscus megalops	16	EM		31.67	29.34	8.18	22.66
Peromyscus melanocarpus	34	EO		16.19	59.13	8.22	42.35
Peromyscus melanophrys	37	EM		99.33	98.86	36.58	80.17
Peromyscus melanurus	4	EO		22.06	19.07	0.33	0.00
Peromyscus mexicanus	72			99.37	98.80	82.67	86.76
Peromyscus pectoralis	4			20.60	23.01	0.06	2.79
Peromyscus truei	4			31.74	28.05	0.03	0.03
Peropteryx kappleri	3	Not endemic	Pr	76.67	63.18	0.03	0.00
Peropteryx macrotis	4			62.14	35.75	4.09	0.00
Philander opossum	7			19.74	0.00	3.29	0.00
Phyllostomus discolor	6			11.00	0.40	0.22	0.12
Pipistrellus subflavus	5			5.13	0.00	0.03	0.00
Platyrrhinus helleri	4			92.57	81.49	16.70	16.11
Potos flavus	11	Not endemic	Pr	95.03	88.56	29.21	15.69
Procyon lotor	14			95.02	91.07	35.13	32.01
Promops centralis	5			62.42	35.20	4.64	7.39
Pteronotus davyi	8			74.15	54.05	5.17	7.72
Pteronotus parnellii	26			89.41	49.05	6.25	13.99
Pteronotus personatus	9			88.29	46.00	14.25	4.21
Puma concolor	4			58.76	53.26	0.03	0.00
Reithrodonthomys fulvescens	19			51.87	72.05	42.04	58.90
Reithrodonthomys megalotis	11			76.98	90.85	27.09	46.64
Reithrodonthomys mexicanus	16			89.35	92.11	47.23	61.66
Reithrodonthomys microdon	4	Not endemic	T	38.84	48.13	1.46	11.50
Reithrodonthomys sumichrasti	17			47.47	42.96	13.94	36.15
Rheomys mexicanus	4	EO	T	3.64	0.19	0.18	0.00
Rhogeessa alleni	5	EM		2.20	4.14	0.03	0.00
Rhogeessa gracilis	4	EM		85.62	83.85	0.19	8.25
Rhogeessa parvula	6			72.75	47.05	0.09	2.29
Rhogeessa tumida	7			13.08	0.43	0.52	0.00
Rhynchonycteris naso	4	Not endemic	Pr	80.83	16.41	0.03	0.00
Saccopteryx bilineata	19			96.75	95.46	46.01	12.99
Sciurus aureogaster	52			98.19	75.22	81.20	62.22
Sciurus deppei	12			24.58	1.04	16.07	0.40
Scotinomys teguina	2	Not endemic	Pr	1.79	0.00	0.09	0.00
Sigmodon alleni	7	EM		45.50	23.63	0.19	0.00
Sigmodon hispidus	30			76.44	85.01	45.11	74.22

Table 1 *Continued.*

Species	Number of unique point localities	Distributional Status	Conservation Status	Percentage of Habitat in Oaxaca	Percentage of Habitat in Existing Protected Areas of Oaxaca	Percentage of Restricted Habitat in Oaxaca	Percentage of Restricted Habitat in Existing Protected Areas
Sigmodon mascotensis	6	EM		89.84	65.43	0.12	2.55
Sorex oreopolus	4			2.06	2.48	0.03	0.00
Sorex saussurei	15	EM	Pr	49.03	68.76	4.19	14.38
Sorex veraepacis	7	EM	E	48.31	59.53	4.61	20.73
Sphiggurus mexicanus	8			42.72	8.96	0.99	4.70
Spilogale putorius	15			98.84	94.57	37.30	35.93
Spilogale pygmaea	3	EM	T	37.64	26.72	0.06	0.00
Sturnira lilium	47			99.31	98.86	80.16	79.42
Sturnira ludovici	47			99.36	96.47	75.22	87.48
Sylvilagus brasiliensis	5			18.42	8.43	0.09	0.00
Sylvilagus cunicularius	5			88.30	84.07	1.17	18.63
Sylvilagus floridanus	25			98.59	92.58	71.63	44.80
Tadarida brasiliensis	15			98.81	98.18	52.08	63.92
Tamandua mexicana	11			97.76	82.55	4.16	48.43
Tapirus bairdii	5	Not endemic	E	54.91	29.24	0.12	0.00
Tayassu pecari	4			5.19	0.00	0.12	0.00
Trachops cirrhosus	12	Not endemic	T	21.86	0.06	7.99	0.06
Tylomys nudicaudus	12			72.29	42.78	35.64	6.10
Urocyon cinereoargenteus	43			98.96	98.25	54.86	69.21
Uroderma bilobatum	4			68.44	50.58	0.03	0.00
Vampyrodes caraccioli	4			5.58	0.00	0.03	0.00
Vulpes velox	5	Not endemic	T	3.53	2.26	0.09	0.00

and the connectivity between them, are now typically used in designing conservation area networks (Williams *et al.*, 1996; Griffiths *et al.*, 1999; Margules & Pressey, 2000; Sarkar & Margules, 2002; Margules & Sarkar, 2007).

The Oaxacan NGO Grupo Autónomo de Investigaciones Ambientales (GAIA), recently established a 10,000 ha system of protected areas in the seasonal dry forests on the state's Pacific coast (Gordon, 2006; Gordon *et al.*, 2006); however, these areas were selected without systematic conservation planning methods (*sensu* Margules & Pressey, 2000). Throughout Mexico, the failure to use systematic planning methods has resulted in protected areas that lack spatial economy and represent the country's biodiversity inadequately (Cantú *et al.*, 2004a; Brandon *et al.*, 2005). One contribution of this paper is to provide an example of systematic planning in Oaxaca that can serve as a model for the establishment of future protected areas elsewhere in Mexico and other regions. An algorithm based on rarity and complementarity is used to select such conservation areas.

The other contribution is to develop systematic area prioritization methods which take into account constraints on how much land can be designated for conservation. Area prioritization is typically done using a variety of optimal or heuristic algorithms. The input to such protocols is a set of sites with habitat quality sufficiently high to be potential candidates for conservation, and a list of biodiversity surrogates present at each site. Selection algorithms use explicit targets of representation for each surrogate. In general, prioritization is carried out with two types of goal (Sarkar, 2004; Sarkar *et al.*, 2006; Margules & Sarkar, 2007): (i) a minimum area goal, so that all surrogates meet their specified representation targets in as small an area as possible, with no restriction on the size of that total area; and (ii) a maximum representation goal, which aims to have as many surrogates as possible meet their representation targets within a specified area that cannot be exceeded, typically because of budget constraints.

Most practical past work in area prioritization has adopted the first method though both methods have been the subject of extensive theoretical work (Margules & Sarkar, 2007; Chapter 8). (Out of 30 analyses surveyed, only 14 attempted to select sites to achieve the maximum representation goal – see Appendix S8 of Supplementary Materials.) However, the second method of carrying out prioritization is more faithful to real world conservation decision scenarios, which almost always involve budget constraints. For targets of representation for biodiversity surrogates, if species are used as those surrogates, 10% of the original range of each species is widely used, though species at high risk of extinction obviously warrant higher targets (Sarakinos *et al.*, 2001). Different targets are advisable for the representation of endemic, protected, and nonlisted mammals (Table 2).

Of 14 previous articles about the maximum representation goal, six did not require targets of representation (Rothley, 1999; Polasky & Solow, 2001; Camm *et al.*, 2002; Arthur *et al.*, 2004; Moilanen, 2005; Tole, 2006), five assumed that a single occurrence of each species was adequate (Camm *et al.*, 1996; Arthur *et al.*, 1997; Church *et al.*, 2000; Juutinen *et al.*, 2004; O'Hanley *et al.*, 2007), and three allowed general targets (Appendix S8). Of

Table 2 Percentage of modelled mammal distributions used for selecting conservation area networks in Oaxaca. Risk categories are as defined in the Mexican Red List (Székely *et al.*, 2005).

Risk category	Target Set 1	Target Set 2	Target Set 3	Target Set 4
Endemics of Oaxaca listed	100	100	100	100
Endemics of Oaxaca not listed	100	100	100	50
Endemics of México	10	50	50	25
Endangered	10	100	100	100
Threatened	10	50	50	50
Species under special protection	10	25	50	25
Other mammals	10	10	10	10

these three articles, one presented no computational results on the maximum representation goal (Sarkar *et al.*, 2005), one presented results for random data sets only (Onal, 2003), and one analysed biological data sets (Fuller *et al.*, 2007). None of these three articles included spatial criteria in the area prioritization. In contrast with the current study, Fuller *et al.*'s analysis was at a much coarser resolution (0.05° × 0.05°, approximately 30 km^2) for the entire country of Mexico and was not intended to prioritize conservation areas at the scale of individual states. Thus, the present study constitutes the first application of the maximum representation goal with general targets and spatial criteria (see '*Selection of Conservation Area Networks*') at a resolution sufficiently fine to inform the practice of area prioritization at the state or regional scales.

The main focus of the present study is on endemic species because these can only be protected by conservation action within Oaxaca. The plans developed here are constrained by the total area that can be put under conservation; in the analysis below, this ranges from 5 to 30% of Oaxaca. The lower figure is probably uncontroversial in any context and more than 30% of any state in México is highly unlikely to be designated for conservation. The commonly used area targets of 10% (IUCN, 1983) and 12% (Hummel, 1995; World Commission on Environment and Development, 1997) fall within this range. Thus, the area constraints used here represent a realistic set of policy options for conservation planning in this region.

Oaxaca has a long tradition of mammalian inventories (Goodwin, 1969; Sánchez-Cordero, 1993), which permits combining historic and recent records as baseline information on collecting localities. Recent studies have used this information to model and verify species' ecological niches (Illoldi-Rangel *et al.*, 2004; Sánchez-Cordero *et al.*, 2005b). Mammals appear to be poorly represented in the existing NPAs of Oaxaca (Briones-Salas & Sánchez-Cordero, 2004) and therefore merit special attention. Because of the availability of these data and results, mammal species of Oaxaca are used here as biodiversity surrogates and their distributions are identified using field data and niche modelling. Specifically, niche modelling was used because it allows extrapolation from different biotic and abiotic parameters associated with a species' known occurrences to identify habitat where a species has not been recorded but is likely to occur.

METHODS

Study region

Located in the Isthmus of Tehuantepec (latitude: 18°39′ – 15°39′ N; longitude: 93°52′ – 98°32′ W), Oaxaca, with an area of 95,364 km^2, is the fifth largest state in México (Fig. 1). Oaxaca's high topographic diversity is due to the three mountain ranges that converge in the state: the Sierra Madre del Sur, which rises from the west and stretches along the coast; the inland Sierra Madre de Oaxaca, which originates at the centre of the country; and the mountain ranges that meet at the centre of the state to form the Valles Centrales in which the city of Oaxaca is located. In eastern Oaxaca, the climate is hot and dry (García-Mendoza *et al.*, 2004). As much as 80% (17) of the main vegetation types of México occur in Oaxaca, including temperate humid montane forests, pine, pine-oak, and oak forests, tropical dry and humid forests, and xeric vegetation (Velázquez *et al.*, 2003; Mas *et al.*, 2004). This environmental and topographic complexity contributes to Oaxaca's exceptionally high biodiversity, in particular, to its mammal species richness, which is the highest in México (Ceballos *et al.*, 1998; García-Mendoza *et al.*, 2004).

Models of species' distributions

A shortcoming of traditional methods for delimiting species' distributions is that geographical and taxonomic biases in biological inventories typically exclude areas where species are potentially present (Stockwell & Peters, 1999; Dennis & Thomas, 2000; Peterson, 2004; Soberón & Peterson, 2004). Ecological niche modelling avoids this by extrapolating from climatic, geological, and vegetation parameters associated with a species' known occurrences to identify habitat where a species has not been recorded but is likely to occur. This approach, as implemented in the Genetic Algorithm for Rule-set Prediction software package (GARP; Stockwell and Peters 1999), has been demonstrated to provide accurate coarse-scale predictions for México's herpetofauna (García, 2006), mammals (Illoldi-Rangel *et al.*, 2004; Sánchez-Cordero *et al.*, 2004; Sanchez-Cordero *et al.*, 2005b) and birds (Peterson *et al.*, 2000; Peterson *et al.*, 2002; Peterson *et al.*, 2006). In the case of mammals, GARP predictions were successfully tested in Oaxaca for 17 of the species used in this analysis (Illoldi-Rangel *et al.*, 2004).

A recent comparative analysis of niche models has found GARP, used with supervision as described below, was among the three best niche modelling methods in a tropical landscape (Elith *et al.*, 2006). Because of the tropical nature of the study area and especially because of the specific past success of predicting mammal distributions in Oaxaca with GARP (Illoldi-Rangel *et al.*, 2004), this niche modelling method was used to identify species distributions in this study. In ongoing work, other niche-modelling techniques (Maxent and RandomForest) are being tested and compared with GARP results.

Models of the ecological niches of the 183 terrestrial mammal species of Oaxaca (Hall, 1981; Briones-Salas & Sánchez-Cordero, 2004; see Table 1) were constructed from point occurrence data

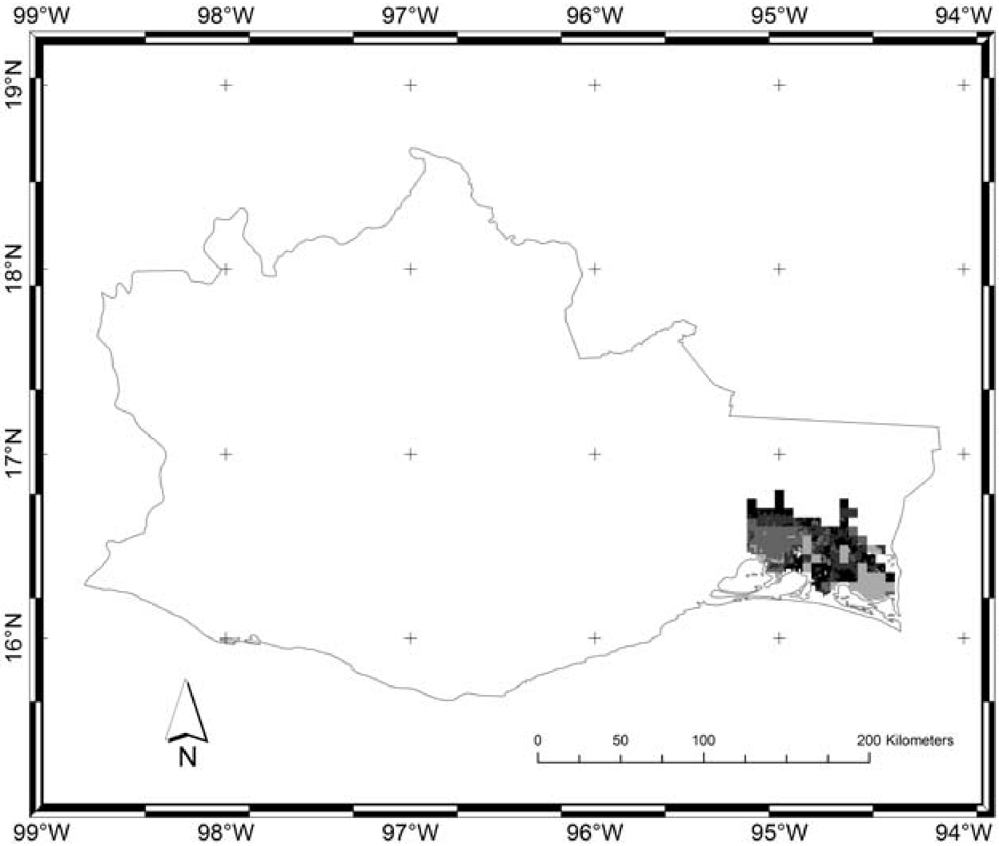

Figure 2 The modelled distribution of *Rheomys mexicanus*, an Oaxacan endemic mammal classified as threatened. Sites in grey are potential habitat (derived from the niche model) that have primary or secondary vegetation. Black sites are patches of potential habitat contiguous with known occurrences of the species.

compiled from national and international scientific collections (see Acknowledgements) and geo-referenced to the nearest 0.01° of longitude and latitude with 1 : 250,000 topographic maps. To characterize species' ecological niches, 10 environmental data layers were used (at a 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); and climatic parameters including mean annual precipitation, minimum daily precipitation, maximum daily precipitation, minimum and maximum daily temperature, and mean annual temperature (USGS, 1998).

Because GARP does not produce a unique solution, 100 replicate models were produced for each species. Of these, the 10 models with lowest omission error and with values close to the median of commission errors were retained following the protocol recommended by Anderson *et al.* (2003). The niche models were refined by excluding any site in which a species was predicted to be present if the site lacked primary or secondary vegetation (Mas *et al.*, 2004) and by restricting the modelled distribution to habitat patches contiguous with known occurrences of the species (Fig. 2). Model refinement utilized the National Forest Inventory, a recent digital map of the vegetation of México that distinguishes between primary and secondary vegetation (Velázquez *et al.*, 2003). For the terrestrial mammals considered here, habitats transformed into agrosystems and rural or urban settlements were assumed not to be able to support populations without immigration from adjacent natural habitats (Peterson & Holt, 2003; Sánchez-Cordero *et al.*, 2005a,b); these were excluded from the analysis.

Selection of conservation area networks

Oaxaca was divided into 78,511 sites with an average area of 1.18 km^2 (SD = 0.0041 km^2) at the 0.01 × 0.01 longitude × latitude scale. 11.36% of the sites were excluded from further analysis because they included human settlements or agricultural areas; this left 69,592 sites. The probabilistic expectation of finding a species at a site was defined as the percentage of the 10 best GARP models that classified the species as present in the site (Stockwell & Peterson, 2002; Anderson *et al.*, 2003). Area prioritization was carried out with a rarity-complementarity algorithm in the ResNet software package (Sarkar *et al.*, 2002), because such algorithms are known to find near-optimal solutions to maximum representation problems rapidly (Csuti *et al.*, 1997; ReVelle *et al.*, 2002). ResNet selects areas to solve the maximum representation problem using a hierarchical, two-pass algorithm. The first pass sorts the surrogates with unmet targets in nonincreasing order of rarity. The area containing the rarest such surrogate is selected for inclusion in the conservation area network. Ties with respect to rarity are disambiguated via complementarity by selecting the area with the largest number of surrogates with unmet targets. Ties with respect to complementarity are potentially broken based on adjacency by selecting an area spatially contiguous with previously selected areas; this rule leads to larger individual conservation areas. Remaining ties are broken by selecting an area at random. Area selection terminates when the land budget is exceeded (the contrast, here, is with a minimum area algorithm which terminates only when all surrogates have achieved their representation targets). The second pass removes sites whose deletion does not take the representation of a surrogate below the targeted level if it had originally met that target.

Targets of representation were defined based on the conservation status of each species (Burgman *et al.*, 2001; Sarakinos *et al.*, 2001; Pressey *et al.*, 2003; Pérez-Arteaga *et al.*, 2005). Mammal species were assigned to risk categories as defined by the Norma Oficial Mexicana 059-ECOL-2001, a technical standard issued by the Mexican government on the conservation status of endemic plants and wildlife (Székely *et al.*, 2005). Highest targets were assigned to mammal species that were in the highest risk categories and endemic to Oaxaca. Table 2 lists the target sets used in this analysis. Area selection was carried out by initializing the algorithm with the site containing the rarest species. Existing protected areas were ignored in the results presented here because early runs showed that initializing solutions with them made no difference. The percentage of sites selected in each of the 10 World Wide Fund for Nature (WWF) ecoregions in Oaxaca was also determined (Olson *et al.*, 2001), because they have served as the basis for previous analyses of biodiversity in México (Escalante *et al.*, 2003). These regions are the Balsas dry forests, Chimalapas montane forests, Northern Mesoamerican Pacific mangroves, Oaxacan montane forests, Petén/Veracruz moist forests, Sierra Madre de Oaxaca pine-oak forests, Sierra Madre del Sur pine-oak forests, Southern Mesoamerican Pacific mangroves, Southern Pacific dry forests, and the Tehuacán Valley matorral.

RESULTS

Endemicity affected the percentage of species' habitat in the existing NPAs (ANOVA $F_{2,180} = 4.49$, $P = 0.0125$); in particular, endemics to Oaxaca had less habitat in the NPAs than endemics to México (Tukey's HSD: $P = 0.013$) or nonendemics (Tukey's HSD: $P = 0.012$). Mexican endemic mammals and nonendemics are represented at the same levels in the existing NPAs. The null hypothesis that endangered species, threatened species, species under special protection, and nonlisted species have the same percentage of their habitat in the existing NPAs could not be rejected (at the 5% confidence level). Including the entire habitat of all six endemic species in a conservation area network took 10,841 sq km or 11.36% of the area of Oaxaca. This area was included in every solution obtained below at area targets above 10%.

After site prioritization, conservation area networks were selected to represent a range of targets for the 183 mammal species (Table 1) subject to land budgets of 5–30% of the area of Oaxaca. When the species' targets were held constant, the size of the conservation area network increased monotonically with the budget, from 4768 to 28,609 sq km. Appendix S1 in the Supplementary Materials gives the details of the solutions indicating the achieved representation target (as a percentage of the modelled habitat) for each species. The solutions (the black sites in Fig. 3; see Appendix S3 – S6 of Supplementary Materials for all the solutions) consist largely of sites in the Sierra Mazateca, Sierra Mixteca, Sierra Madre del Sur, Valles Centrales and portions of the Pacific lowlands (Fig. 1). Thus, these regions are particularly important for the conservation of Oaxaca's rarest mammals. Only some portions of the Tehuacán-Cuicatlán Biosphere Reserve were selected; the three national parks were not selected at all. However, solutions initialized by the existing NPAs (results not shown) contain a few scattered areas in the Sierras and the Pacific lowlands. These solutions were not significantly different from the rarity solutions and will not be further discussed. With increasing land budgets, a substantial increase of the number of selected areas in the Sierra Norte, Sierra Mixteca, Sierra Madre del Sur, and Pacific lowlands was observed (see the grey sites in Fig. 3). At the 30% land budget, areas were selected in the Uxpanapa-Chimalapas region in eastern Oaxaca (16°46′ N, 94°15′ W), which is a global centre of plant endemism (Davis *et al.*, 1997). Among the largest tropical moist forests in México, Chimalapas contains habitat for the Dwarf Jay (*Cyanolyca nana*) and the Keel-billed motmot (*Electron carinatum*), which are classified as vulnerable as by the IUCN (Castilleja, 1995; Wege & Long, 1995).

Turning to the WWF-defined ecoregions, no site from the Tehuacán Valley matorral was selected in the rarity or NPA solutions (see Appendix S2 in Supplementary Materials). The percentage of the ecoregion represented in the prioritized areas depended on the target type as defined in Table 2 for only three ecoregions (Balsas dry forest: $F_{1,27} = 4.567$, $P = 0.0418$; Northern Mesoamerican Pacific mangroves: $F_{1,27} = 27$, $P < 0.0001$; and Petén-Veracruz moist forest: $F_{1,27} = 14.405$, $P < 0.0008$). For the remaining six ecoregions, the same percentage of the ecoregion was selected irrespective of the target utilized in the area prioritization. However, the representation of these six ecoregions in the selected areas varied with the land budget (Chimalapas montane forest: ANCOVA $F_{1,27} = 53.209$, Oaxacan montane forest: $F_{1,27} = 299.694$, Sierra Madre de Oaxaca pine-oak forest: $F_{1,27} = 473.973$, Sierra Madre del Sur pine-oak forest: $F_{1,27} = 384.339$, Southern Mesoamerican Pacific mangroves: $F_{1,27} = 20.25$, and Southern Pacific dry forest: $F_{1,27} = 170.851$; $P < 0.001$ in all cases). Oaxacan montane forest is the ecoregion represented at the highest percentage at all land budgets, followed by Sierra Madre de Oaxaca pine-oak forests (Fig. 4; Target Set 4 is shown; results are similar for the other target sets).

DISCUSSION

Conservation planning exercises at the state (Peterson *et al.*, 2000; Cantú *et al.*, 2003, 2004a), regional (Ortega-Huerta & Peterson, 2004), and national scales (Cantú *et al.*, 2004b) in

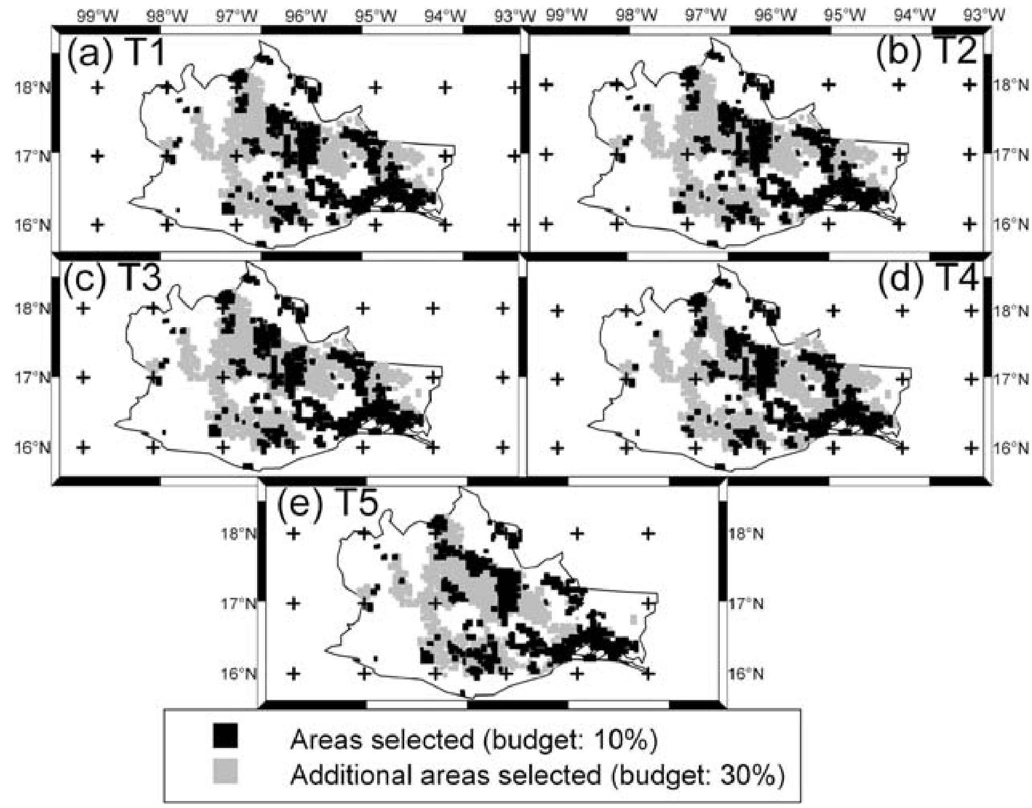

Figure 3 The effect of species' targets on conservation area networks for Oaxacan mammals. Species' targets (as defined in Table 1) varied between successive runs as follows: (a) target 1 (b), target 2 (c), target 3 (d), target 4, and (e) target 5. Black areas were selected with a rarity-based algorithm subject to a budgetary constraint of 10% of Oaxaca's area. The selection of grey areas was initialized with the decreed NPAs and restricted to 30% of Oaxaca's area.

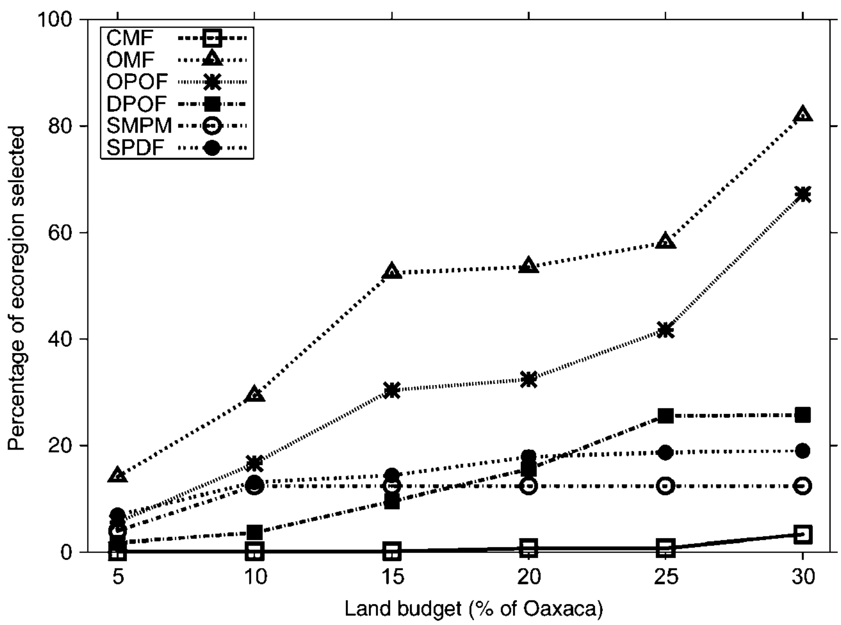

Figure 4 The effect of the land budget on the percentage of Oaxacan ecoregions selected (target 4 is shown). CMF = Chimalapas montane forest, OMF = Oaxacan montane forest, OPOF = Sierra Madre de Oaxaca pine-oak forest, DPOF = Sierra Madre del Sur pine-oak forest, SMPM = Southern Mesoamerican Pacific mangroves, SPDF = Southern Pacific dry forest.

Mexico have typically been based on expanding or refining the existing NPAs. However, as elsewhere in the world (Pressey, 1994), many decreed NPAs in Mexico were established based on scenic or political criteria and not because of their biodiversity content (Peterson *et al.*, 2000; Sánchez-Cordero *et al.*, 2004; Fuller *et al.*, 2007). This suggests that existing NPA systems must typically be supplemented by additional units to protect biodiversity adequately. The present analysis provides an example of how this can be done in the case of Oaxaca even though some biological criteria were used in their designation (see below). Results indicate that Oaxaca's existing NPAs equally represent habitat for nonlisted mammals, such as the white-footed deer mouse (*Peromyscus leucopus*), and endangered mammals, such as the jaguar (*Panthera onca*), rather than preferentially list species of known conservation concern. Additionally, the existing NPAs significantly favour more habitat for mammals not endemic to México or to the state of Oaxaca than Oaxaca's endemic mammals. The conservation area networks proposed for Oaxaca here would better represent the state's endemic mammal fauna. This study only considered federal protected areas because there is just one state protected area Oaxaca, Hierve el Agua, which has the relatively small area of 41.29 km^2. Moreover, it is actively used for recreation by tourists and local people and does not serve any significant conservation goal. It was, therefore, excluded from this analysis.

The nominal conservation areas identified by our protocol were budget-constrained because if the entire range of all 45 listed mammal species is included then the entire state of Oaxaca becomes a nominal conservation area. Progressively increasing targets of representation were therefore imposed to prioritize species from higher risk categories. A variety of target sets were used since no such method of using increasing representation targets is canonical (Margules & Sarkar, 2007). In all cases a uniform lower target of 10% of the modelled habitat was used for the other 138 species. It is also probably an unfortunate constraint in many other areas of the world that not all the habitat even for species at risk can be put under conservation management. It remains an open question whether the variable target method used here (and by others (Sarakinos *et al.*, 2001; Pressey *et al.*, 2003)) can be replaced by one that has better justification.

As noted earlier, ecoregional representation differed between the low (5%) and high (30%) land budgets. At the 5% budget, the largest proportion of selected areas consisted of Oaxacan montane forests, followed by the South Pacific dry forests (see Appendix S7 of Supplementary Materials for exact locations of these ecoregions). Montane forests (Velázquez *et al.*, 2003) and dry tropical forests (Gordon *et al.*, 2004) are conservation priorities in Oaxaca because they are disappearing at high annual rates and occupy less than a third of their pre-Columbian range. The Oaxaca montane forests, Sierra Madre de Oaxaca pine-oak forests, and Sierra Madre del Sur pine-oak forests were represented at the highest levels in the 30% area solution. In addition to mammals, avifauna (Peterson *et al.*, 2003a,b; Peterson, 2004), vascular plants (García-Mendoza *et al.*, 2004), and herpetofauna (García, 2006) are concentrated in these ecoregions.

The area selection prioritized the southern and eastern sections of the Tehuacán-Cuicatlán Biosphere Reserve (Fig. 3) because these areas have high quality habitat for terrestrial mammals. However, the Biosphere Reserve has a high human population and allows many different types of land use, not all of them compatible with biodiversity conservation (Méndez-Larios *et al.*, 2005). In this area prioritization, Oaxaca's three national parks were not selected. Thus, these areas are not of high priority for the conservation of terrestrial mammals. In addition, because of their small sizes (14,187 ha, 11,891 ha, and 2737 ha) these three NPAs are probably too small to ensure long-term persistence of mammal populations.

Adequate representation of rare mammals can be ensured by adding to the NPAs areas selected here. The present analysis identifies candidate sites for this purpose, such as those in the four Sierras (Mazateca, Mixteca, Madre del Sur, and Los Chimalapas; Fig. 1). As higher land budgets were incorporated in the area selection, increasing portions of these highlands were selected, as were the Pacific and Valles Centrales lowlands (Fig. 3). Similar portions of these regions were also included in the conservation area networks initialized with the existing NPAs (data not shown), highlighting the importance of this habitat for mammal conservation. Previous studies also proposed these regions as conservation priorities when the biodiversity surrogates used were mammals (Ceballos *et al.*, 1998; Sánchez-Cordero, 2001), plants (García-Mendoza *et al.*, 2004), and birds (Bojórquez-Tapia *et al.*, 1995).

Diversity gradients for terrestrial vertebrates in Oaxaca are typically correlated with elevational gradients with richness peaking at intermediate elevations and endemicity concentrated at high elevations (Sánchez-Cordero, 2001). Thus, protecting highland mammal habitat may also confer protection on other taxa, though this must be confirmed via explicit surrogacy analysis (Sarkar *et al.*, 2005) which is yet to be attempted for any region of Mesoamerica. Taxa other than mammals should be taken into account during a full-fledged conservation planning exercise, but adequate plans must include areas important for mammals. Thus, the present analysis may not select all priority areas for adequate biodiversity conservation, but the areas identified here will generally remain part of any more comprehensive plan.

Oaxaca's decreed NPAs exclude almost all highland habitats with a high endemicity of mammals and other faunistic groups (Peterson *et al.*, 1993, 2003b; García-Mendoza *et al.*, 2004). Some biological criteria were used to select the decreed NPAs, but these did not include the diversity of mammals and other vertebrates. For example, the Tehuacán-Cuicatlán Biosphere Reserve was selected based on the distribution of endemic cacti (UNAM, 1993; Dávila *et al.*, 2002). The Lagunas de Chacagua and Bahías de Huatulco National Parks are located on the Pacific coast, where the presence of tropical dry forest was the (appropriate) biological rationale for their designation.

Several aspects of the nominal conservation plans for Oaxaca presented here also have national importance for México and global significance for forest biodiversity. The largest ecoregions by percent area selected by the plans are Oaxacan montane forest and pine-oak forests (Fig. 4). With 70 species, Oaxaca has the highest oak richness in México (Kappelle, 2006). The Sierra Norte of Oaxaca is the world's greatest centre of endemism for the genera *Pinus* and *Quercus* (Gómez-Mendoza *et al.*, 2006). Pine-oak forests are important sources of medicines (Chapela, 2005; Kappelle & Juárez, 2006) and provide other ecosystem services such as carbon sequestration (Helmer & Brown, 2000; Chapela, 2005). By protecting pine-oak forests in Oaxaca, the nominal conservation areas proposed here would likely reduce deforestation and land cover change, which generate 23% of México's CO_2 emissions (Gómez-Mendoza *et al.*, 2006). The montane forests represented in the nominal conservation plans presented here are also critical ecosystems for water production (Chapela, 2005; Barrantes-Moreno, 2006; Kappelle, 2006). Water production and purification are crucially important issues in México because the area of irrigated land in the country increased five-fold to 6×10^6 ha during the second half of the twentieth century, placing enormous demands on water availability (Bray, 1996). Water borne diseases and water contamination with pesticides are a problem nationwide (Whiteford & Bernal, 1996). Though it represents only one-fifth of México's territory, south-east México (including Oaxaca) has more than half of the water resources in the country (Bray, 1996). The present plans would contribute to the protection of these resources because the selected areas represent up to 82% of the montane forest ecoregion (Fig. 4).

In the context of the variety of nominal plans developed here, the large percentage of pine-oak forests prioritized by the plans is also noteworthy because Oaxaca has a strong tradition of communal management of these forests. As much as 90% of Oaxaca's forests are controlled by communal forestry enterprises (Merino-Pérez & Segura-Warnholtz, 2005). The 15 or more indigenous groups of Oaxaca play a prominent role in communal forestry and comprise 40% of the state's population (Fox & Aranda, 1996; Chapela, 2005; López-Arzola, 2005). In the Sierra Norte region, communal forestry enterprises are highly organized and maintain community protected areas to preserve pine forests and other elements of biodiversity (Asbjornsen & Ashton, 2002a). Recently, such enterprises in Ixtlán de Juárez in the Sierra Norte collaborated with WWF to create a green forestry certification program (Mitchell, 2005). The successful implementation of conservation plans for Oaxaca, such as those developed in this analysis, will require support from these communal forestry enterprises (López-Arzola, 2005; Barrance *et al.*, 2006).

Community interests and traditions (including existing management methods) can be used to assess the prognosis for implementation of the various nominal plans developed in this analysis. It is unlikely than any single plan developed here will be implementable in its entirety. However, if a set of high priority areas as identified by any of the plans developed here can be selected for implementation, then the analysis can be re-iterated with those areas already selected and this process can be repeated until budgets are exhausted. This is an important way in which this analysis can be used in the field.

Highly organized communal enterprises, such as indigenous forestry groups, are becoming increasingly active in conservation planning throughout the world (Western & Wright, 1994). Indeed, since 1992, the 10 top forestry countries have transferred ownership of 215 million ha of forests to indigenous communities (White & Martin, 2002). If effective techniques can be developed in the Oaxacan context for involving communal enterprises in conservation planning, then these techniques could be applied to planning in other regions where communal enterprises are emerging as important participants in biodiversity conservation, such as the Pacific North-west in the US and Great Himalayan National Park in India (Asbjornsen & Ashton, 2002b). In this way, the biodiversity conservation area identification protocols developed here may be relevant in other regions with communal ownership of forests (López-Arzola, 2005).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Coverage of the surrogates in cells selected for each Target Set at different spatial constraints. For identification of species, see Table 1. For interpretation of Target Sets, see Table 2.

Appendix S2 Percentage of each ecoregion represented for each Target Set. For interpretation of Target Sets, see Table 2.

Appendix S3 Representation of species for Target Set 1 (as defined in Table 2). Areas were selected subject to an area constraint of: (a) 5%; (b) 10%; (c) 15%; (d) 20%; (e) 25%; and (f) 30%.

Appendix S4 Representation of species for Target Set 2 (as defined in Table 2). Areas were selected subject to an area constraint of: (a) 5%; (b) 10%; (c) 15%; (d) 20%; (e) 25% and (f) 30%.

Appendix S5 Representation of species for Target Set 3 (as defined in Table 2). Areas were selected subject to an area constraint of: (a) 5%; (b) 10%; (c) 15%; (d) 20%; (e) 25% and (f) 30%.

Appendix S6 Representation of species for Target Set 4 (as defined in Table 2). Areas were selected subject to an area constraint of: (a) 5%; (b) 10%; (c) 15%; (d) 20%; (e) 25% and (f) 30%.

Appendix S7 Ecoregions represented in the state of Oaxaca, according to Olson *et al*. (2001).

Appendix S8 Optimization Problems Analysed in Conservation Planning Exercises. The Web of Science data base was searched for articles in the primary literature about the topics 'reserve selection' and 'optimization'. Since the current study concerns planning in a single time stage for multiple species at risk, articles about multistage planning and single species were excluded from consideration. The 30 articles below are those that remained after this exclusion.

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