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Systematic conservation assessment for the Mesoamerica, Chocó, and Tropical Andes biodiversity hotspots: a preliminary analysis

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Abstract Using IUCN Red List species as biodiversity surrogates, supplemented with additional analyses based on ecoregional diversity, priority areas for conservation in Mesoamerica, Chocó, and the Tropical Andes were identified using the methods of systematic conservation planning. Species' ecological niches were modeled from occurrence records using a maximum entropy algorithm. Niche models for 78 species were refined to produce geographical distributions. Areas were prioritized for conservation attention using a complementarity-based algorithm implemented in the ResNet software package. Targets of representation for Red List species were explored from 10 to 90% of the modeled distributions at 10% increments; for the 53 ecoregions, the target was 10% for each ecoregion. Selected areas were widely dispersed across the region, reflecting the widespread distribution of Red List species in Mesoamerica, Chocó, and the Tropical Andes, which underscores the region's importance for biodiversity. In general, existing protected areas were no more representative of biodiversity than areas outside them. Among the countries in the region, the protected areas of Belize performed best and those of Colombia and Ecuador worst. A high representation target led to the selection of a very large proportion of each country except Colombia and Ecuador (for a 90% target, 83–95% of each country was selected). Since such large proportions of land cannot realistically be set aside as parks or reserves, biodiversity conservation in Mesoamerica, Chocó, and the Tropical Andes will require integrative landscape management which combines human use of the land with securing the persistence of biota.

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Introduction

Mesoamerica, Chocó, and the Tropical Andes, bounded in the north by the Isthmus of Tehuantepec (in southern Mexico), ending in the south and south–east in northern Colombia and Ecuador, and limited to the west and north–east by the Pacific Ocean and the Caribbean Sea, respectively, have long been recognized as being among the Earth's most important centers of species diversity and endemism (Myers et al. 2000; Calderón et al. 2004). Though this region occupies <0.5% of Earth's terrestrial surface, it is estimated to contain about 7–10% of its species (Miller et al. 2001). The area contains more than 20,000 plant species by most estimates, of which 20% are likely to be endemic to the region (CCAD 2002). Similarly, about a third of its >500 mammal species are endemic, and there are over 1,000 recorded bird species (CCAD 2002). There are several factors responsible for the high biodiversity of the region, starting with its geological origins as an archipelago near large species-rich continental landmasses (Hooghiemstra et al. 1992; Kappelle et al. 1992), and accentuated by the high environmental diversity within its boundaries. A large variation in precipitation (500–7,500 mm year^{-1}) is superimposed on discontinuous mountain chains (0–3,820 m; average annual temperature, 32.5–7.5°C) which separate the Pacific and Caribbean basins (Calderón et al. 2004). The soil is rich and volcanic, encouraging the proliferation of biota, and ever since Mesoamerica's Inter-Oceanic Channel was closed some 3–5 Mya with the formation of the Isthmus of Panama (Donnelly 1989), immigration from both the north and the south have led to the assembly of exceptional faunal and floral diversity in a relatively tiny amount of land (Raven and Axelrod 1974). This assembly was part of what has been called "the great American biotic interchange" (Stehli and Webb 1985).

Because of this high species richness and endemism, Mesoamerica, Chocó, and the Tropical Andes have been a major focus of biodiversity conservation interest for several decades (Jukofsky 1992; Miller et al. 2001). In spite of many well-publicized initiatives for conservation both nationally (Sarukhán et al. 1996; Sarukhán and Dirzo 2001; Evans 1999; Fandiño-Lozano and Wyngaarden 2005b) and trans-nationally (CCAD 1993; Illueca 1997; Miller et al. 2001; Calderón et al. 2004), the biodiversity of Mesoamerica is under continued threat from a variety of factors including a deforestation rate of about 1% year^{-1} from 2000 to 2005 (FAO 2005), a human population growth rate of over 2% year^{-1} (Miller et al. 2001), and the reliance of the majority of the human population on biological resources taken directly from the wild (Miller et al. 2001). According to some estimates, about 30% of the region's primary and secondary vegetation have been completely transformed to agricultural fields and urban settlements (Bryant et al. 1997). Other habitats, including coral reefs, mangroves, wetlands, and grasslands have suffered similar losses (Burke et al. 2000; Matthews et al. 2000; Revenga et al. 2000). Poverty is a major factor in maintaining threats to all habitats, with almost half the human population living below the poverty line, and much of it lacking access to basic health care, education, and safe water (Miller et al. 2001).

These threats, the high species richness, and the high level of endemism led to the designation of Mesoamerica, Chocó, and the Tropical Andes as three of the 25 global biodiversity "hotspots" (Myers et al. 2000). Conservation planning for this region as an integral whole has been a priority for several organizations for almost two decades. In 1990, the New York Zoological Society (which became the Wildlife Conservation Society in 1993) along with the Caribbean Conservation Corporation launched the Paseo Pantera initiative as a "cooperative agreement" with USAID (Jukofsky 1992). The aim of the project was to establish a forest corridor running from Panama to the Selva Maya at the intersection of Mexico, Guatemala, and Belize. This corridor was supposed to provide continuous habitat for potential dispersal of panthers throughout the region (Carr et al. 1994). More importantly, the initiative marked the return of peace to Mesoamerica and the potential for regional co-operation on environmental problems (Illueca 1997).

The Paseo Pantera initiative provided the background for the trans-governmental Mesoamerican Biological Corridor (MBC) project. As early as 1989, with the prospect of peace looming in the foreground, the heads-of-state of several countries in the region signed a "Charter Agreement for the Protection of the Environment" which established the Comisión Centroamericana de Ambiente y Desarrollo (CCAD 1989). Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama were full members, with Mexico having observer status (Miller et al. 2001). Following the adoption of the Rio Convention on Biodiversity in 1992, CCAD promoted several regional initiatives for forest management and establishment of priority areas for biodiversity conservation (CCAD 1993). Sustainable development was soon added to the agenda (CCAD 1994).

Between 1992 and 1997, through discussions primarily at the governmental level, the Paseo Pantera initiative was embedded into an agenda that integrated conservation and sustainable development in what was initially called the Central American Biological Corridor (Miller et al. 2001). Its geographical focus was eventually expanded to include the five southern states of Mexico (Campeche, Chiapas, Quintana Roo, Tabasco, and Yucatan) after which it was renamed as the Mesoamerican Biological Corridor (MBC). The MBC was endorsed by regional heads-of-state in 1997 and responsibility for planning and co-ordinating its implementation was assigned to the CCAD. By 1998 CCAD had prepared a proposal, "Program for the Consolidation of the Mesoamerican Biological Corridor," to submit for funding to the United Nations Development Program (UNDP)'s Global Environment Facility (GEF) and the German Gesellschaft für Technische Zusammenarbeit (GTZ) (Miller et al. 2001). Funding was approved in 1999, and an MBC Regional Office Coordinating Unit was opened in Managua; since then, additional funds have come from other sources, including the World Bank [see Global Transboundary Protected Area Network (http://www.tbpa.net/case_10.htm, last accessed 17 October 2008)].

Transnational non-governmental organizations (NGOs) have also begun developing regional conservation plans which are intended to complement the planning initiatives of the official MBC project. Conservation International (CI) has begun the process of identifying "Key Biodiversity Areas" (Conservation International 2004) on the basis of habitat requirements of critically endangered (CR) species and those with restricted ranges (Jaime Garcia-Moren, personal communication). In 2004, The Nature Conservancy (TNC) published a "portfolio" of both terrestrial and marine "action sites" for 27 terrestrial and five marine ecoregions (as defined by Olson et al. 2001) as well as coarser-scale "action areas" (Calderón et al. 2004). As biodiversity surrogates (which it calls "targets") TNC used 403 terrestrial, 25 freshwater, and 34 coastal-marine ecological communities and systems. The viability of the surrogates in each area was assessed by experts on the basis of size, condition, and landscape context (connectivity and intactness) following the methodology of Morris et al. (1999). Experts selected a network of priority sites so that the best occurrence and at least ten viable occurrences of each surrogate was achieved, resulting in a portfolio of 78 terrestrial, 50 freshwater, and 15 coastal-marine sites. These sites were then aggregated at a coarser spatial scale to identify 20 priority areas (Calderón et al. 2004).

The analysis reported here uses systematic conservation planning (SCP) methods (sensu, Margules and Pressey 2000; Cowling and Pressey 2003; Sarkar 2005; Margules and Sarkar 2007) to identify priority areas for conservation planning using IUCN Red List species and ecoregions as biodiversity surrogates. These priority areas are then compared to the existing protected areas of the region to assess the performance of the latter with respect to the inclusion of habitats of Red List species and the diverse ecoregions of Mesoamerica, Chocó, and the Tropical Andes. The analysis is limited to the terrestrial context, including freshwater and coastal but not marine habitats. The study region consists of 53 ecoregions (sensu, Olson et al. 2001). Species' distributions were modeled using a maximum entropy algorithm and the area prioritization used a complementarity-based algorithm. The use of such algorithms to supplement expert opinion and analysis is the main distinguishing feature of the SCP approach (Cowling et al. 2003; Margules and Sarkar 2007). This appears to be the first use of this approach in a trans-national context in Mesoamerica, Chocó, and the Tropical Andes. However, this analysis carries out a priority area identification only for a preliminary assessment of conservation goals and the performance of existing protected areas (PAs); it is not intended to prescribe management policies.

The SCP protocol envisions a set of stages to formulate a conservation plan for a region, including: stakeholder identification and involvement; data collection and assessment; modeling and corrective data treatment, when necessary; the choice of biodiversity surrogates, conservation targets, and goals; a review of existing conservation areas; prioritization of additional potential conservation areas; assessment of site viability; feasibility assessment of a conservation proposal weighed against competing demands for land; and the eventual implementation and periodic reassessment of a plan (Margules and Sarkar 2007). Since its purpose is assessment rather than the formulation of an implementation-oriented plan, this analysis does not include all stages of the SCP protocol. There is no explicit stakeholder involvement; however, preliminary identification of priority areas is important because it can guide the identification of potential stakeholders and help instigate their active involvement as more sophisticated implementation-oriented plans are developed. Feasibility assessment can only be performed with the full involvement of such stakeholders. Finally, biological viability analysis is only incorporated in this analysis in a rudimentary way by excluding anthropogenically transformed areas (see "Landscape GIS Models").

This analysis also differs from the past and ongoing transnational analyses of conservation in the region in including a larger study area than is customary, extending into Colombia and Ecuador. The delineation of the study area was based on the ecological definition of Mesoamerica, Chocó, and the Tropical Andes (as explained in "Study Region"). In contrast, the MBC project uses political boundaries because implementation must take place in political context. The World Resources Institute (WRI) also used the political delineation of the study area from the MBC project (Miller et al. 2001). While it is true that implementation depends on political boundaries, the presumption here is that ecological analyses should be based on ecological criteria and, after priority areas are identified in this way, the question of political implementation should be broached—this is the "feasibility assessment" stage of SCP. If political implementation of conservation plans is impractical in some areas, then the SCP process envisions the replacement of these areas with other (biologically) functionally equivalent areas with such areas also chosen using ecological criteria.

In contrast, TNC used ecoregions to delineate its study region but its analysis is restricted to a subset of the area analyzed here, ignoring parts of Mexico to the north and Colombia and Ecuador to the south. There are two additional and more important differences between

TNC's analysis and this one: (1) TNC chose to ignore species-level surrogates on the grounds that there were insufficient data on them. However, there is some good data available for a suite of Red List species and to ignore these altogether when identifying priority areas for conservation is unwarranted and TNC could have profitably supplemented their surrogate set with Red List species. Such a mixed strategy was followed by the Australian BioRap Project to develop a provisional conservation portfolio for Papua New Guinea when faced with sparse species-level data (Faith et al. 2001); and (2) even though TNC has advocated methods similar to SCP in other contexts (see Groves et al. 2002), its Mesoamerican analysis was based on expert judgment. Cowling et al. (2003) and others (Pressey 1994; Smith et al. 2006; Margules and Sarkar 2007) have pointed out the pitfalls of not using systematic (often algorithmic) methods to supplement expert opinion: systematic methods lead to repeatable analyses, permit detailed exploration of alternative choices of surrogates, targets, and goals, and enable explicit quantitative evaluation of results in meeting those targets and goals. Expert-based plans have also been known to produce plans that do not provide adequate representation of biodiversity surrogates and are often not optimal with respect to spatial economy (Sarakinos et al. 2001; Cowling et al. 2003). Good planning involves the use of both systematic methods and expert judgment; this analysis aims to provide some baseline results that may be evaluated by experts and then re-analyzed systematically. Expert judgment was used here to refine species' ecological niche models.

More specifically, the major aims of this analysis were (1) a broad identification of priority areas for Red List species in the Mesoamerica, Chocó, and Tropical Andes region, (2) an identification of priority areas that also represent the ecoregional diversity of Mesoamerica, Chocó, and the Tropical Andes; and (3) an analysis of the performance of existing protected areas (PAs) with respect to both these goals. A subsidiary goal was to analyze the portfolio produced by TNC. However, these results should not be interpreted as recommending individual areas for immediate protection. Rather, the analysis should form the basis for discussion with stakeholders about opportunities and constraints, and experts about appropriate surrogates, targets, and goals. Simultaneously, there must be significantly more data collection and assessment so that more sophisticated analyses geared towards producing implementation-oriented results can be performed.

Landscape features

Study region

For this study the Mesoamerica, Chocó, and Tropical Andes region was defined using the ecoregional classification of Olson et al. (2001), which is a refinement Dinerstein et al. (1995) and Ricketts et al. (1995). The study region consisted of 53 ecoregions in 10 countries (Fig. 1): Mexico, Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador. Marine habitats were excluded from consideration. Major islands were included: Isla Cozumel and Isla del Carmen in Mexico; Ambergris Caye and the Turneffe Islands in Belize; Isla de Roatán in Honduras; and Isla de Coiba and Isla del Rey (in the Archipelago de Las Perlas) in Panama. The Pacific Ocean and the Caribbean Sea define the western and north-eastern boundaries of the study region.

The northern boundary was delineated within the Isthmus of Tehuantepec in Mexico, including the Balsas depression and ecoregions associated with it because of their high biogeographic affinity with Mesoamerican biota (Morrone 2005; Escalante et al. 2007). This boundary marks the southern range limits of several Nearctic taxa and northern range limits

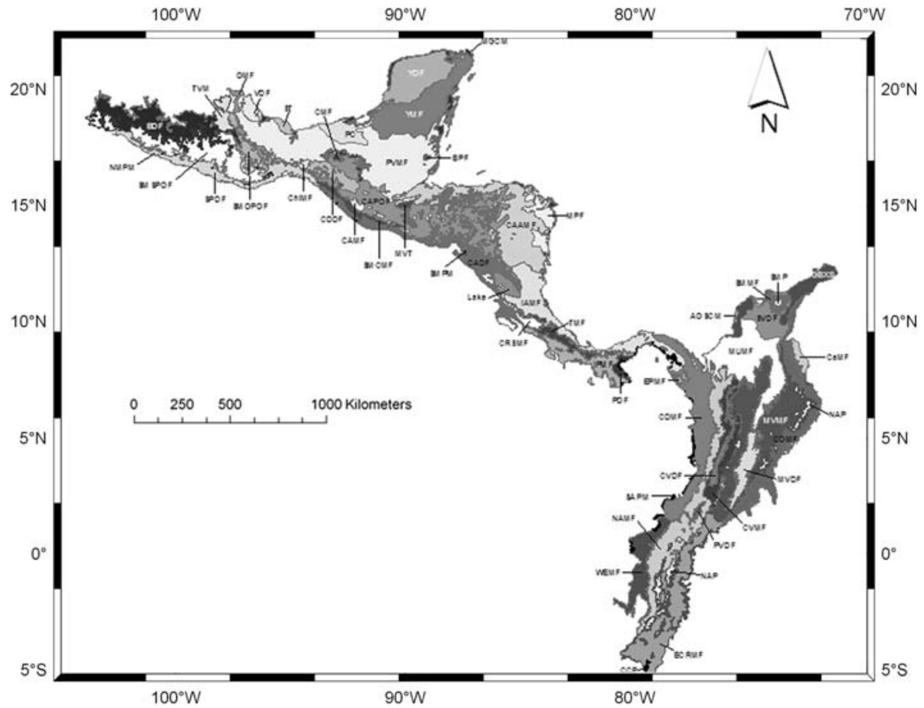


Fig. 1 Study region. AOSCM, Amazon-Orinoco-Southern Caribbean mangroves; BDF, Balsas dry forests; BPF, Belizian pine forests; CaMF, Catatumbo moist forests; CVDF, Cauca Valley dry forests; CVMF, Cauca Valley montane forests; CAAMF, Central American Atlantic moist forests; CADF, Central American dry forests; CAMF, Central American montane forests; CAPOF, Central American pine-oak forests; CDDF, Chiapas depression dry forests; CMF, Chiapas montane forests; ChiMF, Chimalapas montane forests; CDMF, Chocó-Darién moist forests; CCP, Cordillera Central páramo; COMF, Cordillera Oriental montane forests; CRSMF, Costa Rican seasonal moist forests; ECRMF, Eastern Cordillera real montane forests; EPMF, Eastern Panamanian montane forests; GBXS, Guajira-Barranquilla xeric scrub; IAMF, Isthmian-Atlantic moist forests; IPMF, Isthmian-Pacific moist forests; Lake, Lake; MVDF, Magdalena Valley dry forests; MVMF, Magdalena Valley montane forests; MUMF, Magdalena-Urabá moist forests; MGCM, Mesoamerican Gulf-Caribbean mangroves; MPF, Miskito pine forests; MVT, Motagua Valley thornscrub; NAP, Northern Andean páramo; NMPM, Northern Mesoamerican Pacific mangroves; NAMF, Northwestern Andean montane forests; OMF, Oaxacan montane forests; PDF, Panamanian dry forests; PC, Pantanos de Centla; PVDF, Patía Valley dry forests; PVMF, Petén-Veracruz moist forests; SMMF, Santa Marta montane forests; SMP, Santa Marta páramo; ST, Sierra de los Tuxtlas; SMCMF, Sierra Madre de Chiapas moist forests; SMOPOF, Sierra Madre de Oaxaca pine-oak forests; SMSPOF, Sierra Madre del Sur pine-oak forests; SVDF, Sinú Valley dry forests; SAPM, South American Pacific mangroves; SMPM, Southern Mesoamerican Pacific mangroves; SPDF, Southern Pacific dry forests; TMF, Talamancan montane forests; TVM, Tehuacán Valley matorral; VDF, Veracruz dry forests; WEMF, Western Ecuador moist forests; YDF, Yucatán dry forests; YMF, Yucatán moist forests

of several Neotropical taxa. Such Nearctic taxa consist of a wide range of floristic and faunistic groups including terrestrial vertebrates (Fa and Morales 1991; Escalante et al. 2007), lepidoptera (Peterson et al. 1999), cacti (Bravo et al. 1999), and composites and bryophytes (Delgadillo 2000; Delgadillo and Villaseñor 2002). The Neotropical taxa include mammals such as shrews, armadillo, muroid rodents (Briones and Sánchez-Cordero 2004), as well as amphibians, reptiles, and birds (Casas-Andreu et al. 1996; Peterson et al. 1993, 1999, 2004). From the west to the east, 11 ecoregions comprise the northern boundary: Balsas dry forests, Sierra Madre del Sur pine-oak forests, Oaxaca montane forests, Sierra

Madre de Oaxaca, Veracruz dry forests, Tehuacán Valley matorral, Mesoamerican Gulf-Caribbean mangroves, Sierra de los Tuxtlas, Petén-Veracruz moist forests, Pantanos de Centla, and Yucatan dry forests. Three other ecoregions could have potentially been included but were excluded because recent work, based on mammal distributions, has determined that these are part of a separate biogeographical region (Escalante et al. 2007): these are the Trans-Mexican volcanic belt, the Jalisco dry forests, and the Veracruz moist forest.

The southern and south-eastern boundaries were taken to lie in northern Ecuador and Colombia because the ranges of several Mesoamerican species, including endemic species of conservation concern, end there. These include mammal species, especially rodents such as heteromyids and peromiscines (Anderson et al. 2002a, b; Anderson 2003), bats (Albuja 1992, 1999), birds (Cracraft 1985; Best and Kessler 1995; Joseph and Stockwell 2002), and other terrestrial vertebrates (Albuja et al. 1980; Jarrín-V 2001). More importantly, this is where the Andes split into three separate ranges: Cordillera Occidental, Cordillera Central, and Cordillera Oriental. This topographical transition was used to define these boundaries. The ecoregions at the boundary are those that intersect with the three ranges emerging from the Andes. From west to east, the southern boundary ends with three ecoregions in Ecuador: the Eastern Cordillera Real montane forests, Northwestern Andean montane forests, and Western Ecuador moist forests. The south-eastern boundary continues in Ecuador and Colombia ending with three more ecoregions: Cordillera Oriental montane forests, Catatumbo moist forests, and Guajira-Barranquilla xeric scrub.

The study area includes 809 existing protected areas (PAs) as identified by the World Data Base on Protected Areas (http://www.unep-wcmc.org/wdpa/, last accessed 22 June 2007); 557 of these are classified by the World Conservation Union (IUCN) under one of their categories, I–VI, while 252 other PAs, although being so designated in the different countries, are yet to be placed under any of the IUCN categories. These other PAs and the PAs from all IUCN categories (I–VI) were included in the analysis with no distinction made between levels of protection since there was no information available at a regional scale on the relative performance of the different categories. While it is customary wisdom that strictly protected categories (I and II) perform better than the others, recent work in Mexico indicates that Biosphere Reserves (category VI) perform better than National Parks (Sánchez-Cordero and Figueroa 2007; Figueroa and Sánchez-Cordero 2008).

Table 1 shows the area and percentage area of each ecoregion in the total study area and the percentage of the ecoregion already in a protected area. Table 2 shows the area and percentage of each ecoregion present in each country, the percentage of each ecoregion represented within each country, and the percentage of that ecoregion protected within each country.

Biodiversity surrogates

SCP requires the identification of biodiversity surrogates, that is, quantifiable features of biodiversity on which data can be realistically obtained for use in planning protocols. In the terminology of Sarkar and Margules (2002) (see also, Sarkar 2002; Margules and Sarkar 2007), "true" surrogates are those such features that are themselves the components of biodiversity targeted for conservation; "estimator" surrogates are environmental or biological features which can be used to estimate the representation of true surrogates in conservation areas. In this study, species at risk of extinction, as identified by the IUCN Red List (http://www.iucnredlist.org, last accessed 21 June 2007), were taken as true surrogates which is uncontroversial. However, distributional data were available for only 9% of these species, and only 2% could be reliably modeled. Moreover, most of these were

Table 1 Ecoregions of Mesoamerica, relative prevalence, and representation in protected areas

Ecoregion	Area (km^2)	Area of Mesoamerica (%)	Ecoregion in protected areas (%)	Transformation (%)
Petén-Veracruz moist forests	148770.721	8.963	16.715	40.921
Central American pine-oak forests	111342.561	6.708	4.357	50.422
Magdalena Valley montane forests	105053.236	6.329	1.08	13.759
Central American Atlantic moist forests	89473.642	5.39	10.754	22.927
Northwestern Andean montane forests	81164.133	4.89	5.07	14.429
Magdalena-Urabá moist forests	76741.005	4.623	0.448	40.670
Eastern Cordillera real montane forests	76445.092	4.606	5.05	5.116
Chocó-Darién moist forests	72846.025	4.389	5.818	19.057
Yucatán moist forests	69533.519	4.189	4.011	8.916
Central American dry forests	67519.839	4.068	1.227	60.957
Balsas dry forests	62441.917	3.762	1.114	35.831
Sierra Madre del Sur pine-oak forests	61173.904	3.686	0.426	18.461
Cordillera Oriental montane forests	58681.511	3.535	4.676	5.753
Isthmian-Atlantic moist forests	57820.55	3.483	6.411	31.904
Yucatán dry forests	49723.833	2.996	0.366	16.653
Southern Pacific dry forests	41790.925	2.518	0.356	49.914
Western Ecuador moist forests	33886.716	2.042	0.661	17.801
Cauca Valley montane forests	32055.07	1.931	0.558	16.092
Northern Andean páramo	29635.932	1.785	3.988	2.729
Isthmian-Pacific moist forests	28955.537	1.744	1.556	49.568
Guajira-Barranquilla xeric scrub	27462.73	1.655	3.968	21.043
Sinú Valley dry forests	24980.499	1.505	0.388	44.107
Mesoamerican Gulf-Caribbean mangroves	21545.447	1.298	4.324	11.801
Magdalena Valley dry forests	19635.192	1.183	0.003	10.832
Miskito pine forests	18053.745	1.088	0.482	8.856
Pantanos de Centla	17082.886	1.029	1.865	58.292
Talamancan montane forests	16341.725	0.985	4.285	11.295
Sierra Madre de Oaxaca pine-oak forests	14345.454	0.864	0.323	26.423
Chiapas depression dry forests	14021.603	0.845	0.105	77.723
Central American montane forests	13299.105	0.801	1.368	42.736
Sierra Madre de Chiapas moist forests	11258.153	0.678	0.66	60.214
Costa Rican seasonal moist forests	10628.901	0.64	0.441	32.716
Tehuacán Valley matorral	9892.221	0.596	0.687	10.643
Lake	8014.42	0.483	0.121	1.183
Oaxacan montane forests	7600.825	0.458	0.001	47.172
Cauca Valley dry forests	7344.886	0.443	0	17.552
Catatumbo moist forests	6764.966	0.408	0.342	18.247
South American Pacific mangroves	6628.151	0.399	0.42	15.985
Veracruz dry forests	6610.969	0.398	0.001	60.874
Southern Mesoamerican Pacific mangroves	6281.579	0.378	0.881	24.155
Chiapas montane forests	5778.264	0.348	0.109	64.325

Table 1 continued

Ecoregion	Area (km^2)	Area of Mesoamerica (%)	Ecoregion in protected areas (%)	Transformation (%)
Panamanian dry forests	5070.623	0.305	0.065	84.418
Santa Marta montane forests	4784.658	0.288	1.467	0.381
Sierra de los Tuxtlas	3825.368	0.23	0.639	67.993
Eastern Panamanian montane forests	3044.012	0.183	0.914	59.566
Belizian pine forests	2830.694	0.171	0.423	16.648
Amazon-Orinoco-Southern Caribbean mangroves	2509.693	0.151	0.238	12.307
Motagua Valley thornscrub	2336.769	0.141	0.189	87.720
Patía Valley dry forests	2270.689	0.137	0	4.821
Chimalapas montane forests	2083.674	0.126	0.056	55.642
Santa Marta páramo	1243.629	0.075	0.53	0.000
Northern Mesoamerican Pacific mangroves	720.046	0.043	0.012	12.550
Cordillera Central páramo	500.16	0.03	0.051	0.219
Total	1659847.404	100	100	28.252

plants. To address this deficiency, the 53 ecoregions defined by Olson et al. (2001) were also added as estimator surrogates in a subsequent analysis. This assumes that representing the full variety of ecoregions in conservation areas will lead to the representation of the Red List species for which no modeled distributions were available (a more detailed classification into ecoregions—that is, one with more categories—which would be more desirable was not available at the regional scale).

For the 10 countries in the study region, the total number of species in the three categories of the IUCN Red List, CR, Endangered (EN), and Vulnerable (VU) are, for the four orders of vertebrates: Amphibians—CR 222, EN 286, VU, 184; Mammals—CR 19, EN 53 VU 67; Birds—CR 26, EN 62, VU 112; Reptiles—CR 13, EN 8, VU 22; and for Plants—CR 372, EN 916, VU 1271. In total there are 3,633 such species. Note that these numbers include areas outside the study region in the cases of Mexico, Colombia, and Ecuador. Table S1 lists the 333 species for which occurrence data are available in publicly accessible data bases (see "Acknowledgments"). It includes the number of geo-referenced data points available and the number of those points that are post-1980. Only post-1980 data were used to model species' distributions because the large-scale deforestation of the previous decades is known to have significantly altered the land cover of Mesoamerica (Utting 1997).

Methods of analysis

Landscape GIS models

Maps of ecoregions were obtained from the World Wide Fund for Nature (http://www.worldwildlife.org/science/data/terreco.cfm, last accessed 22 June 2007). The study region was divided into 0.02° × 0.02° longitude × latitude cells. This resulted in 343,383 cells with an average area of 4.818 km^2 (SD = 0.098; max = 4.946; min = 4.599). All point

Table 2 Percentage of country occupied by each ecoregion and the percentage of each ecoregion in a country

Ecoregion	Area (km^2)	Total country (%)	Total ecoregion in country (%)	Ecoregion in country's protected areas (%)	Transformation (%)
Belize	21829.006				18.022
Belizian pine forests	2825.374	13.114	99.812	12.158	16.525
Central American Atlantic moist forests	1.532	0.007	0.002	0.019	0.000
Mesoamerican Gulf-Caribbean mangroves	2434.81	9.886	11.301	5.4	9.105
Petén-Veracruz moist forests	16511.063	76.732	11.098	82.423	19.458
Yucatán moist forests	56.228	0.262	0.081	0	58.230
Colombia	510164.522				18.571
Amazon-Orinoco-Southern Caribbean mangroves	2509.693	0.492	100	0.994	12.307
Catatumbo moist forests	6764.966	1.326	100	1.428	18.247
Cauca Valley dry forests	7344.886	1.44	100	0	17.552
Cauca Valley montane forests	32055.07	6.283	100	2.328	16.092
Central American dry forests	8.683	0.002	0.013	0.005	0.000
Chocó-Darién moist forests	59479.251	11.659	81.651	15.753	14.669
Cordillera Oriental montane forests	58681.511	11.502	100	19.507	5.753
Eastern Cordillera real montane forests	10712.771	2.1	14.014	2.206	8.813
Eastern Panamanian montane forests	966.067	0.189	31.737	0.952	67.306
Guajira-Barranquilla xeric scrub	27462.73	5.383	100	16.553	21.043
Magdalena Valley dry forests	19635.193	3.849	100	0.013	10.832
Magdalena Valley montane forests	105053.236	20.592	100	4.503	13.759
Magdalena-Urabá moist forests	76741.005	15.042	100	1.869	40.670
Northern Andean páramo	14205.196	2.784	47.932	8.986	2.002
Northwestern Andean montane forests	48962.26	9.597	60.325	13.954	15.240
Patía Valley dry forests	2270.689	0.445	100	0	4.821
Santa Marta montane forests	4784.658	0.938	100	6.119	0.381
Santa Marta páramo	1243.629	0.244	100	2.21	0.000
Sinú Valley dry forests	24980.499	4.897	100	1.621	44.107
South American Pacific mangroves	3917.766	0.768	59.108	0.997	6.230
Western Ecuador moist forests	2384.764	0.467	7.037	0.002	14.726
Costa Rica	50531.604				24.963
Central American dry forests	5953.959	11.783	8.818	6.718	56.314
Costa Rican seasonal moist forests	8513.287	16.847	80.096	6.111	27.042
Isthmian-Atlantic moist forests	16687.546	33.024	28.861	25.566	21.071

Table 2 continued

Ecoregion	Area (km^2)	Total country (%)	Total ecoregion in country (%)	Ecoregion in country's protected areas (%)	Transformation (%)
Isthmian-Pacific moist forests	9166.819	18.141	31.658	16.425	26.206
Mesoamerican Gulf-Caribbean mangroves	271.807	0.538	1.262	1.61	3.919
Southern Mesoamerican Pacific mangroves	762.778	1.51	12.143	0.825	20.760
Talamancan montane forests	9175.409	18.158	56.147	42.745	9.499
Ecuador	146261.303				9.226
Cordillera Central páramo	500.16	0.342	100	0.575	0.219
Eastern Cordillera real montane forests	65732.321	44.942	85.986	50.815	4.513
Northern Andean páramo	15430.736	10.55	52.068	20.616	3.398
Northwestern Andean montane forests	32201.873	22.017	39.675	19.382	13.195
South American Pacific mangroves	894.262	0.611	13.492	1.191	8.139
Western Ecuador moist forests	31501.952	21.538	92.963	7.421	18.034
El Salvador	20601.449				56.337
Central American dry forests	8289.927	40.24	12.278	36.25	61.962
Central American montane forests	950.425	4.613	7.147	23.343	37.344
Central American pine-oak forests	10748.755	52.175	9.654	35.476	56.127
Sierra Madre de Chiapas moist forests	74.343	0.361	0.66	1.12	50.524
Southern Mesoamerican Pacific mangroves	537.998	2.611	8.565	3.811	8.203
Guatemala	109316.807				40.061
Central American Atlantic moist forests	8436.563	7.718	9.429	7.125	33.568
Central American dry forests	6610.744	6.047	9.791	0.262	66.542
Central American montane forests	5958.073	5.45	44.801	7.827	43.533
Central American pine-oak forests	29429.441	26.921	26.431	7.661	51.333
Chiapas depression dry forests	903.49	0.826	6.444	0	48.454
Chiapas montane forests	192.251	0.176	3.327	0.003	56.441
Mesoamerican Gulf-Caribbean mangroves	322.81	0.295	1.498	0.721	2.248
Motagua Valley thornscrub	2336.769	2.138	100	1.277	87.720
Petén-Veracruz moist forests	48160.639	44.056	32.372	74.229	23.493
Sierra Madre de Chiapas moist forests	5770.291	5.279	51.254	0.177	74.144
Southern Mesoamerican Pacific mangroves	1060.763	0.97	16.887	0.389	61.401

Table 2 continued

Ecoregion	Area (km^2)	Total country (%)	Total ecoregion in country (%)	Ecoregion in country's protected areas (%)	Transformation (%)
Yucatán moist forests	134.974	0.123	0.194	0.329	10.508
Honduras	111772.341				33.983
Central American Atlantic moist forests	33698.636	30.149	37.663	61.548	15.027
Central American dry forests	19081.171	17.071	28.26	1.354	58.241
Central American montane forests	5546.825	4.963	41.708	0	42.612
Central American pine-oak forests	44819.181	40.099	40.253	29.674	42.305
Mesoamerican Gulf-Caribbean mangroves	1914.746	1.713	8.887	2.686	5.152
Miskito pine forests	6038.202	5.402	33.446	3.444	4.419
Southern Mesoamerican Pacific mangroves	673.58	0.603	10.723	1.294	17.271
Mexico	488588.842				35.313
Balsas dry forests	62441.917	12.78	100	6.381	35.831
Belizian pine forests	5.321	0.001	0.188	0	81.657
Central American dry forests	3214.949	0.658	4.761	0.993	74.532
Central American pine-oak forests	15982.722	3.271	14.355	2.116	61.081
Chiapas depression dry forests	13118.113	2.685	93.556	0.598	79.739
Chiapas montane forests	5586.013	1.143	96.673	0.625	64.597
Chimalapas montane forests	2083.674	0.426	100	0.319	55.642
Mesoamerican Gulf-Caribbean mangroves	13103.022	2.682	60.816	17.814	15.536
Northern Mesoamerican Pacific mangroves	720.046	0.147	100	0.07	12.550
Oaxacan montane forests	7600.825	1.556	100	0.001	47.172
Pantanos de Centla	17082.886	3.496	100	10.685	58.292
Petén-Veracruz moist forests	84099.019	17.213	56.529	16.314	55.115
Sierra de los Tuxtlas	3825.368	0.783	100	3.662	67.993
Sierra Madre de Chiapas moist forests	5413.519	1.108	48.085	3.62	45.500
Sierra Madre de Oaxaca pine-oak forests	14345.454	2.936	100	1.853	26.423
Sierra Madre del Sur pine-oak forests	61173.904	12.521	100	2.441	18.461
Southern Mesoamerican Pacific mangroves	1431.826	0.293	22.794	1.728	16.317
Southern Pacific dry forests	41790.925	8.553	100	2.038	49.914
Tehuacán Valley matorral	9892.221	2.025	100	3.937	10.643
Veracruz dry forests	6610.969	1.353	100	0.002	60.874

Table 2 continued

Ecoregion	Area (km^2)	Total country (%)	Total ecoregion in country (%)	Ecoregion in country's protected areas (%)	Transformation (%)
Yucatán dry forests	49723.833	10.177	100	2.099	16.653
Yucatán moist forests	69342.317	14.192	99.725	22.704	8.873
Nicaragua	127729.399				32.076
Central American Atlantic moist forests	47336.911	37.06	52.906	47.455	26.655
Central American dry forests	24360.385	19.072	36.079	4.279	60.592
Central American montane forests	843.781	0.661	6.345	1.679	44.007
Central American pine-oak forests	10362.462	8.113	9.307	2.939	60.588
Costa Rican seasonal moist forests	2115.607	1.656	19.904	0.648	55.547
Isthmian-Atlantic moist forests	18590.544	14.555	32.152	31.321	22.219
Lake	8014.42	6.275	100	1.268	1.183
Mesoamerican Gulf-Caribbean mangroves	3179.198	2.489	14.756	5.679	4.824
Miskito pine forests	12015.543	9.407	66.554	2.019	11.086
Southern Mesoamerican Pacific mangroves	910.547	0.713	14.496	2.713	6.225
Panama	73052.102				48.378
Chocó-Darién moist forests	13366.774	18.298	18.349	29.061	38.584
Eastern Panamanian montane forests	2077.945	2.844	68.263	9.757	55.968
Isthmian-Atlantic moist forests	22542.46	30.858	38.987	26.246	47.911
Isthmian-Pacific moist forests	19788.718	27.088	68.342	7.624	60.390
Mesoamerican Gulf-Caribbean mangroves	319.054	0.437	1.481	0.765	4.835
Panamanian dry forests	5070.623	6.941	100	0.932	84.418
South American Pacific mangroves	1816.124	2.486	27.4	1.062	40.894
Southern Mesoamerican Pacific mangroves	904.087	1.238	14.393	1.366	28.416
Talamancan montane forests	7166.317	9.81	43.853	23.187	13.594

For Colombia, Ecuador, and Mexico, only that part which is within the study region is being considered (see "Methods")

occurrence data for the Red List species were resampled to this grid, reducing multiple records of a species in the same cell to one occurrence point. Land cover data for the study region was obtained from the Global Land Cover 2000 (Hansen et al. 2000). These data were classified into 60 categories (see Table 6 in the Supplementary Material). Cropland, intensive agriculture, and urban/built categories were interpreted as transformed areas while the rest of the categories were interpreted as being untransformed enough for potential inclusion within conservation areas as they are or for ecological restoration aimed at the persistence of biota. The Global Land Cover 2000 data had a resolution of $0.01° \times 0.01°$ which were resampled to a $0.02° \times 0.02°$ resolution. The percentage of transformation of each ecoregion is given in Table 1, and that for each ecoregion in each country is given in Table 2.

Data on the protected areas were obtained from the World Database of Protected Areas (WDPA; http://www.unep-wcmc.org/wdpa/, last accessed 22 June 2007) maintained by the United Nations Environment Programme and the World Conservation Monitoring Centre. Areas in Tables 1 and 2 were calculated using the equal area cylindrical projection (by using Projector! extension in ArcView 3.2).

Ecological niche models

Point occurrence data for animals and plants listed in the categories CR, EN and VU of the IUCN Red List were obtained from several scientific collections (see "Acknowledgments"). In order to reflect the current state of the habitat, only point occurrence data collected since 1980 were retained. Ecological niche models were then constructed for the 101 listed animal and plant species for which there were sufficient data (i.e., there were at least four occurrence records).

The Maxent software package (Version 2.2; Phillips et al. 2004, 2006) was used to construct ecological niche models. Maxent has been shown to be robust for modeling distributions from presence-only data (Elith et al. 2006). Following published recommendations, Maxent was run without the threshold feature and without duplicates so that there was at most one sample per pixel; linear, quadratic and product features were used (Phillips et al. 2004, 2006; Pawar et al. 2007). The convergence threshold was set to 1.0×10^{-5}, which is a conservative value based upon North American breeding bird survey data and small mammal data from Latin America (Phillips et al. 2004, 2006).

For climatic variables, 19 layers, each at a resolution of 30″ ($0.0083° \times 0.0083°$), were obtained from the WorldClim database (Hijmans et al. 2005; http://worldclim.org, last accessed 12 December 2006); These layers [Pawar et al. (2007) provide a complete list] were used along with elevation, slope, and aspect as the environmental variables. Elevation was obtained from the U. S. Geological Survey's Hydro-1K DEM data set (USGS 1998) and slope and aspect were derived from the DEM using the Spatial Analyst extension of ArcMap 9.0. All climate and spatial layers were clipped to an area bounded by 21° 30′ 30.27″ N by 5° 0′ 1.12″ S and 103° 30′ 52.49″ W by 71° 6′ 45.72″ W, a box containing the study region, and were resampled to a $0.02° \times 0.02°$ resolution in ArcGIS.

Niche model accuracy was evaluated by constructing the models using 75% of the available records, with the other 25% used for testing. At least four occurrence records are necessary to construct such a niche model. Model accuracy was determined using a receiver operating characteristic (ROC) analysis (Phillips et al. 2006). For all thresholds an ROC curve was produced with sensitivity plotted on the y axis and (1—specificity) plotted on the x-axis. The area under the curve (AUC) provides a measure of model performance. An optimal model would have an AUC of 1 while a model that predicted species occurrences at random would have an AUC of 0.5.

Following Pawar et al. (2007), only those niche models possessing an AUC >0.75 and a P-value of <0.05 (for the sensitivity and specificity tests) were retained for further use. Finally, the relative probabilities predicted by Maxent were converted into expected presences for a species by dividing all relative probabilities across the landscape by the highest relative probability achieved for that species. This normalization assumes that a species is at least present in the cell with the highest predicted relative probability of its occurrence.

Geographic projection of species' ecological niches must be modified to produce distributions because species may not occupy all regions ecologically suitable for them for a variety of reasons including barriers to dispersal and competition with other species (Soberón and Peterson 2005). Refinement removed from each model all cells with a predicted probability of <0.1. Stricter refinement protocols have sometimes been used; for instance, in many analyses by restricting to cells that are contiguous with those that have a reported occurrence of species (Soberón and Peterson 2005). However, because of the sparse available data for the study region, which is a result of inadequate sampling, such strict refinement is likely to exclude many areas in which a species is likely to be present. For the species used in this analysis, there is no suggestion of geographical barriers to their dispersal within Mesoamerica, Chocó, and the Tropical Andes. Expert knowledge was used to drop niche models which showed systematic over-prediction (see "Results").

Area prioritization and representation targets

Area prioritization was carried out with a heuristic complementarity-based algorithm implemented in the ResNet software package (Garson et al. 2002; Sarkar et al. 2002) because such algorithms are computationally fast while finding near-optimal solutions to problems (Csuti et al. 1997; Sarkar et al. 2004). The optimization problem to be solved is the minimum-area problem: finding the smallest set of areas in which all biodiversity surrogates meet their representation targets. ResNet selects areas to solve the minimum-area problem using a two-pass algorithm. In the version of ResNet that was used, the first pass uses complementarity to select the area with the largest total expected value for the presence of surrogates with unmet targets. Ties are broken by selecting one of the tied cells at random. Area selection terminates when the targeted representation for each species has been met. The second pass removes cells that may have become redundant with respect to achieving the representation targets due to later cell selection. Other versions of ResNet use both rarity and complementarity in the first pass; however, Sarkar et al. (2004) reported that using complementarity alone produces better results with probabilistic data.

The aim of this analysis was a broad identification of priority areas for Red List species and to analyze the performance of existing PAs, and not to recommend individual areas for immediate protection. Thus, a range of representation targets was used to identify priority areas without recommending a specific target. Those areas that are selected at low targets of representation of Red List species have higher priority values than those only selected at higher targets. Four prioritization scenarios were run in this analysis. Two different surrogate sets were used. In both, the Red List species were included, and targets of representation were set from 10 to 90% in 10% increments for each of the species. In the second, a uniform target of 10% was additionally set for the ecoregions. In general, targets of representation used in such prioritization protocols do not have full biological justification (Soulé and Sanjayan 1998; Margules and Sarkar 2007). Using a wide range of targets for the most important biodiversity surrogates in this analysis, the Red List species, avoids this problem. The 10% target for the ecoregions is also conventional (Margules and Sarkar 2007), though the Secretariat of the Convention on Biological Diversity (2002) set that target for each of the world's ecoregions. Hence the use of the 10% target here; it was assumed that higher targets for them would be unrealistic. Area prioritization was carried twice for each of these alternatives, once for the whole study area and once removing the transformed areas from the study region.

The effectiveness of each country's existing protected areas at representing biodiversity was estimated by calculating: (1) the proportion of the entire country selected by ResNet (hereafter p_c) and (2) the proportion of the country's protected areas so prioritized (hereafter p_{pa}). At each representation target, the following were computed: the point estimate of the difference in proportions ($p_c - p_{pa}$), the lower limit of the 95% confidence interval of the difference (hereafter L), and upper limit of the 95% confidence interval (hereafter U). If $p_c > p_{pa}$, $L > 0$, and $U > 0$, then the prioritized proportion of the entire country was significantly greater than the prioritized proportion of the country's protected areas. Conversely, if $p_c < p_{pa}$, $L < 0$, and $U < 0$, then the prioritized proportion of the country's protected areas was significantly greater than the prioritized proportion of the entire country.

The point estimate ($p_c - p_{pa}$) may be too liberal due to the non-independence of p_c and p_{pa} (Agresti 2002). To address this issue, separate contingency tables were constructed for the country and protected area data. In the former, cell$_{j1}$ represented the number of selected sites in country j and cell$_{j2}$ represented the number of unselected sites. In the latter, cell$_{j1}$ represented the number of selected sites in the protected areas of country j and cell$_{j2}$ represented the number of unselected sites in the protected areas. Pearson residuals >3 indicated that more sites were selected in a given category than expected (Simonoff 2003).

Results

Of the IUCN Red List species in the study region (that is, species that that are CR, EN, or VU), there was at least one occurrence record for 333 species in the accessible databases (see Table S1 of Supplementary Materials). However, at least four post-1980 occurrence records were only available for 101 species. Niche models were constructed for all of these; only 94 species had an AUC >0.75 (Table S1). Seven additional species were dropped because of large *P*-values. A further nine species were dropped from the analysis because of presumed overprediction, as described in "Ecological Niche Models". Whereas the modeled distribution predicted the species to be distributed across the entire study region, these species have restricted distributions as specified by IUCN Red List (http://www.iucnredlist.org, last accessed 21 June 2007): *Cyanolyca nana* is restricted in Mexico to Oaxaca, Queretaro, north Hidalgo, and central Veracruz; *Thorius narisovalis* is restricted in Mexico to north-central Oaxaca; *Lonchocarpus yoroensis* is restricted to Honduras, Mexico, and Nicaragua; *Mollinedia ruae* and *Lonchocarpus retiferus* are restricted to Honduras and Nicaragua; *Dendropanax sessiliflorus*, *Quararibea gomeziana*, and *Stenanona panamensis* are restricted to Costa Rica and Panama; and *Inga canonegrensis* is restricted to Costa Rica. For the other species, the two most common parameters producing the largest AUC when used independently (Explanatory Variable 1 in Table S1) were temperature seasonality (16 times) and precipitation of the wettest month (14 times) and the two most common parameters reducing the AUC most when excluded (Explanatory Variable 2 in Table S1) were altitude (24 times) and temperature (19 times). Table S1 shows these critical explanatory variables for all 78 species (5 CR; 21 EN; 52 VU) used in this analysis; there were 10 amphibian (3 CR; 5 EN; 2 VU), three bird (2 EN; 1 VU), three mammal (3 VU), and 62 plant (2 CR; 14 EN; 46 VU) species. This means 80% of the species used for the area prioritization were plants. We further refined our species list to 51 species that included 10 or more point locality records. The intersection between the set of sites prioritized to be put under a conservation plan when sites were selected to represent the 78 species with at least four records and the set of sites selected to represent the 51 species with at least 10 records was 81% on average (range: 74–92%;

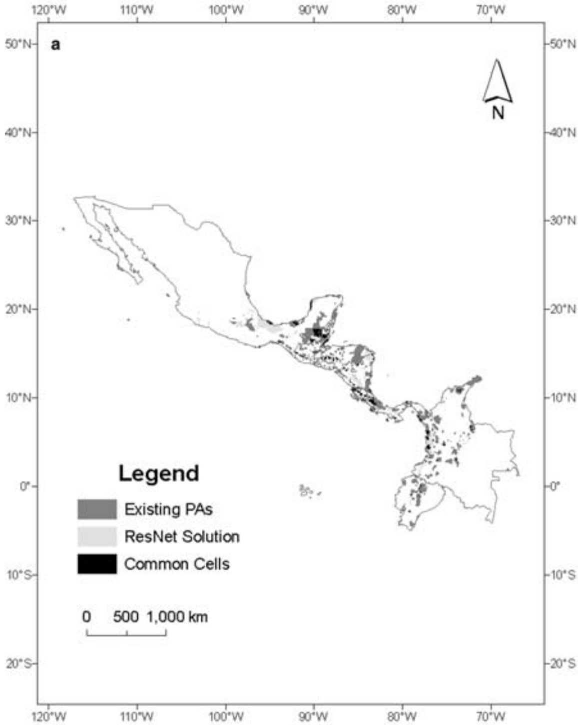
Supplementary Material Table S5). In light of this, the use of species with at least 10 records does not appear to result in a significantly different conservation area network than the use of species with at least four records.

Figures 2 and 3 shows the ResNet solutions for the different targets; the total selected area increases as the representation targets increase. In Fig. 2, only Red List species are used as surrogates. The percentage of total area selected varied from 5.1% for the 10% target to 82.04% for the 90% target. The percentage of overlap between the selected area and the PAs ranged between 6.46 and 87.7% for these two targets. Figure 3 corresponds to Fig. 2 when the ecoregions are also included as surrogates (with a uniform representation target of 10%). The percentage of total area selected was now 9.96% for the 10% target and 82.03% for the 90% target. The percentage of overlap between the selected area and the PAs ranged between 10.97 and 87.63%. In both these figures selected cells are widely dispersed across the region and, as expected, the amount of land selected increases monotonically with the target.

Figure 4 shows the percentage of untransformed area in each country selected at different targets, and Fig. 5 shows the percentage of the country selected in untransformed areas, both under two scenarios: Red List species as surrogates, and both Red List species and ecoregions as surrogates. Figure 6 shows the percentage of the existing PAs selected as a function of the representation target under the two scenarios. Throughout the analyses, the results for Mexico, Colombia, and Ecuador only refer to areas within the study region. What is striking is that similar patterns are seen for the percentage of the country′s untransformed area and that of the existing PAs that is selected at different targets. When Red List species alone are used as biodiversity surrogates, the PA network of Belize performs better than those of all other countries at all representation targets in the sense that a larger fraction of it was selected in the ResNet runs. When ecoregions are also included as surrogates, Costa Rica and El Salvador performs better than Belize (Fig. 6). The existing PA network of Ecuador performs worst using Red List species as surrogates, followed by Mexico, Honduras and Colombia. At the higher targets the same conclusion once again holds when ecoregions are included as surrogates (Fig. 6). However, for all countries except Colombia, Ecuador, and Mexico, protecting 90% of the modeled distribution for just these 78 species takes up 82.3–99.7% of each country's area. For Ecuador, Colombia, and Mexico, 65.8–79.7% is selected. (Figs. 3, 4).

The most important priority areas are those selected at the lowest representation targets for biodiversity surrogates because these areas are needed even to maintain minimal representation of species at risk. This fact can also be used to assess the performance of the existing PAs. Areas within 189 of the existing PAs were selected even at the lowest target used (10%). However, in most cases very few cells were selected (Figs. 2a, 3a). For each country in the study area, Table S2 of the Supplementary Materials lists the PAs which have at least one cell represented in a solution at the 10% species representation target. In addition, Table S2 lists the PAs that have some cells represented at the 10% species and ecoregion representation target, the 50% species representation target, and so on.

For prioritizations using only species, as well as for prioritizations that included both the species and the ecoregions, the prioritized proportion of Guatemala's protected areas was significantly greater than the prioritized proportion of the entire country at all representation targets [range of ($p_{\mathrm{pa}} - p_{\mathrm{c}}$): 4.08–26.29%]. Conversely, for Panama, the prioritized proportion of the entire country selected was significantly greater than the prioritized proportion of the protected areas [range of ($p_{\mathrm{c}} - p_{\mathrm{pa}}$): 2.4–14.75%]. For the species only prioritizations at each representation target, the null hypothesis that equal proportions of each country were selected was rejected ($\chi^2 \geq 4704.88$), as was the hypothesis that equal



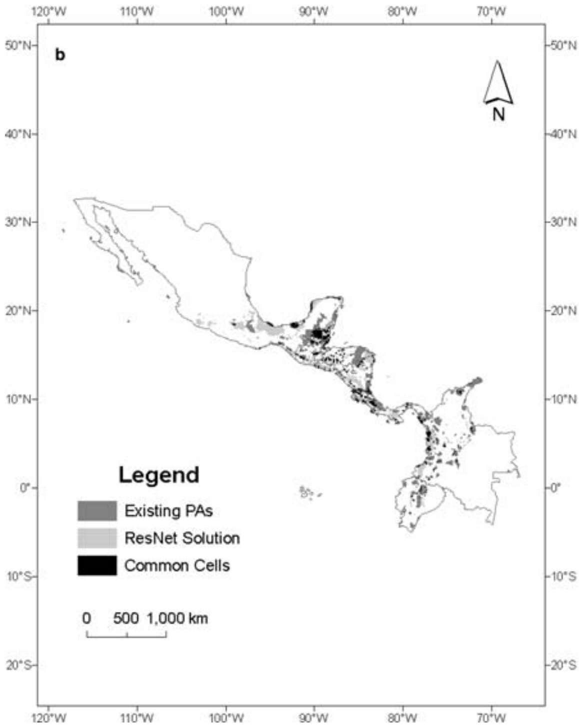
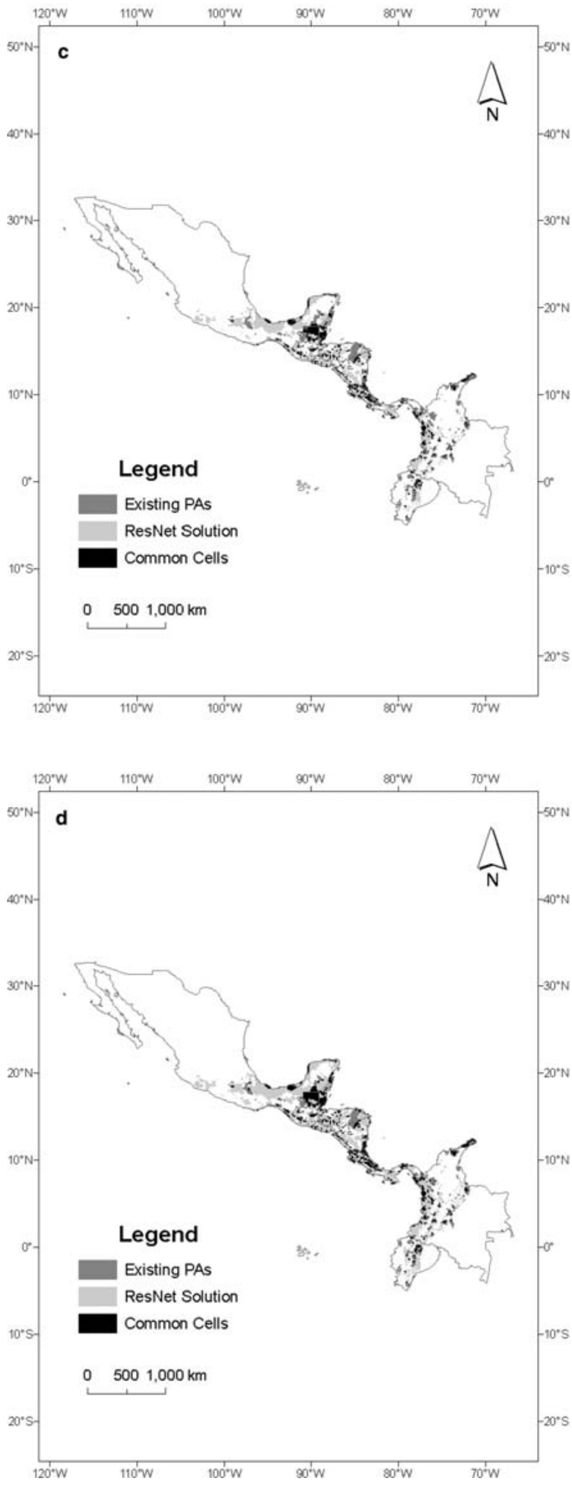


Fig. 2 Selected areas, Red List species as biodiversity surrogates: **a** target of representation for Red List species = 10%; **b** target = 20%; **c** target = 30%; **d** target = 40%; **e** target = 50%; **f** target = 60%; **g** target = 70%; **h** target = 80%; **i** target = 90%. *Black* areas correspond to cells that are common to the existing PAs and the ResNet solutions; the *dark grey* cells are the additional ones in the existing PAs; and the *light grey* cells are those in the ResNet solutions

Fig. 2 continued



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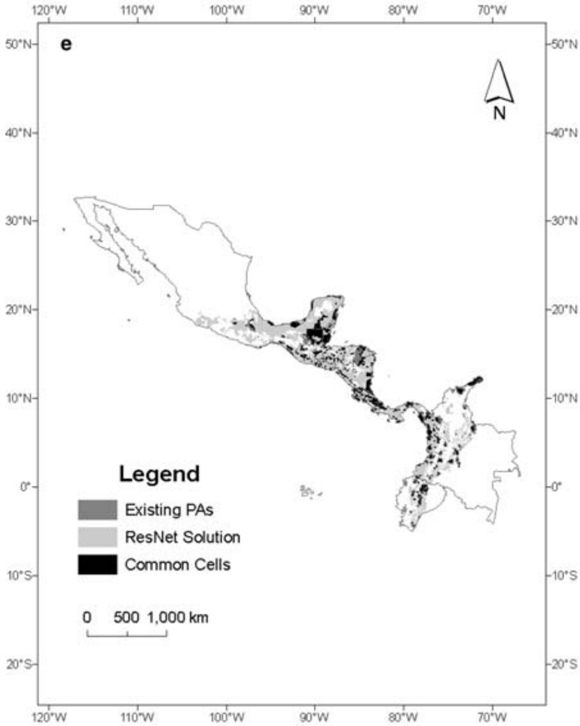

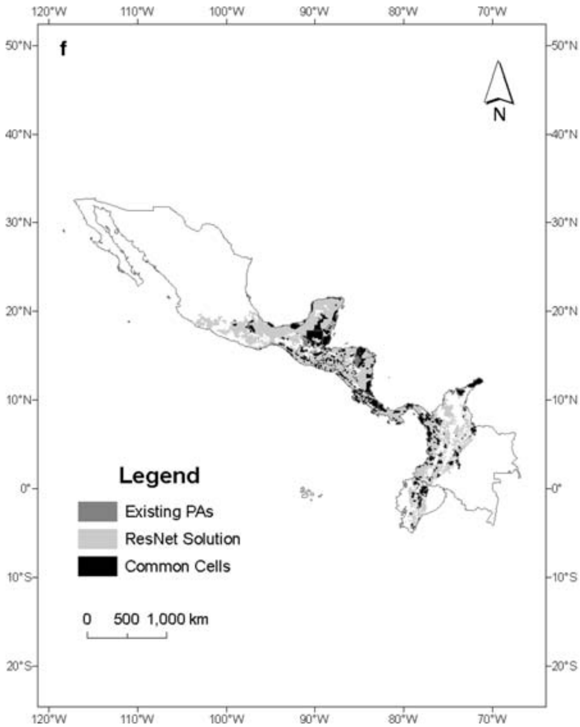

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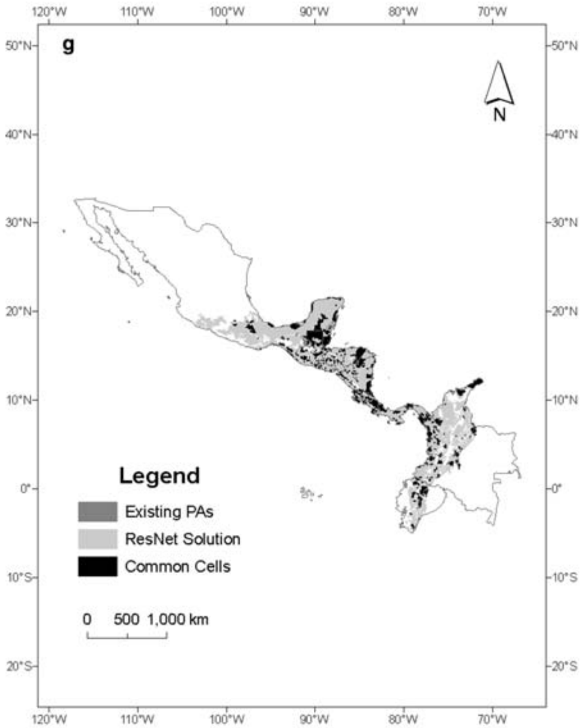

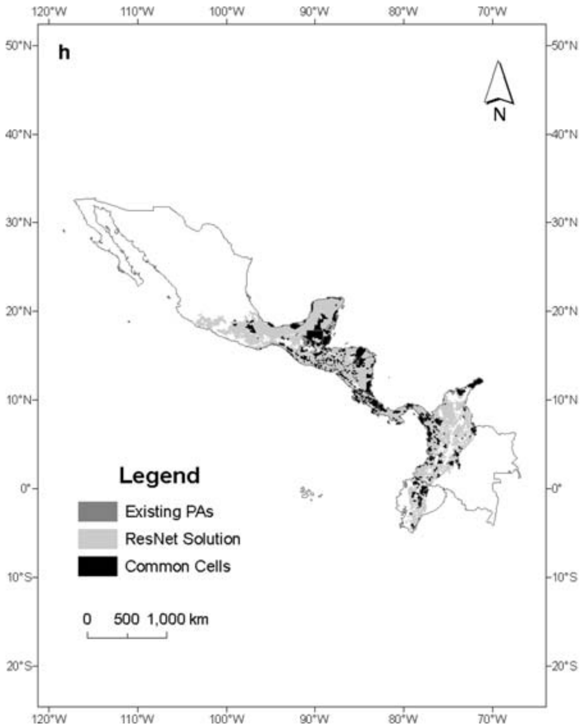

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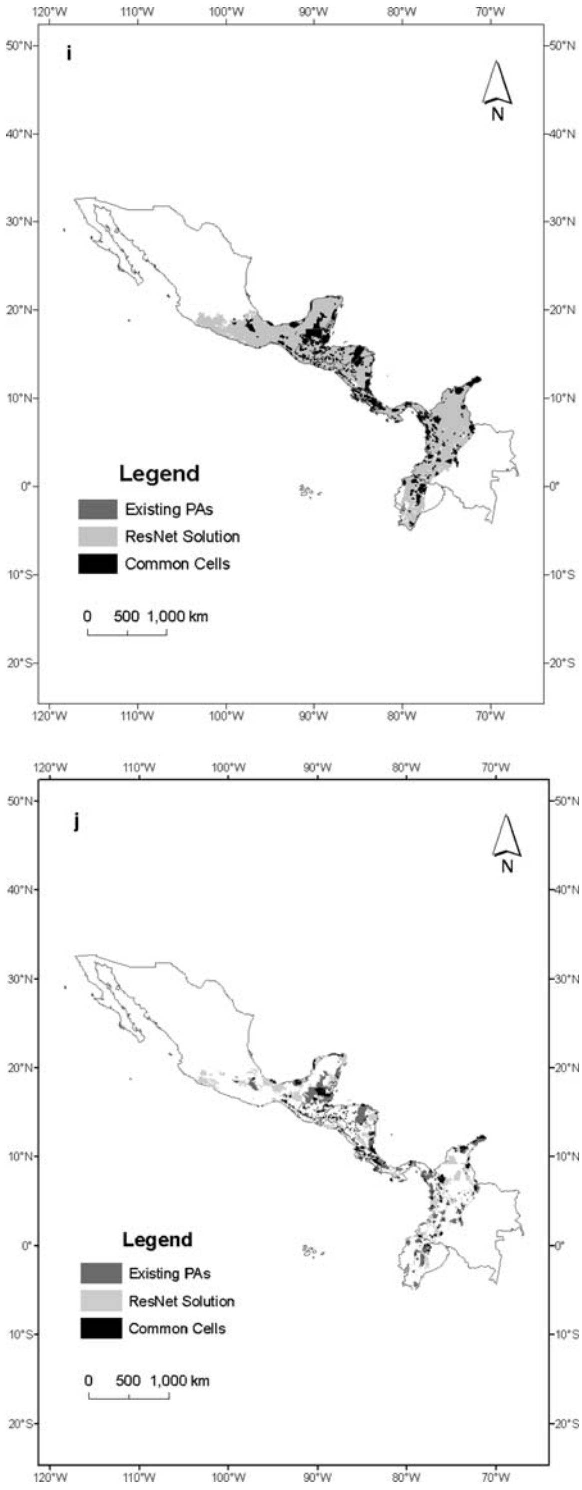


Fig. 3 Selected areas, Red List species and ecoregions as biodiversity surrogates: The target of representation was uniformly 10% of each ecoregion. For Red List species' targets and the interpretation of the cells, see the caption of Fig. 2

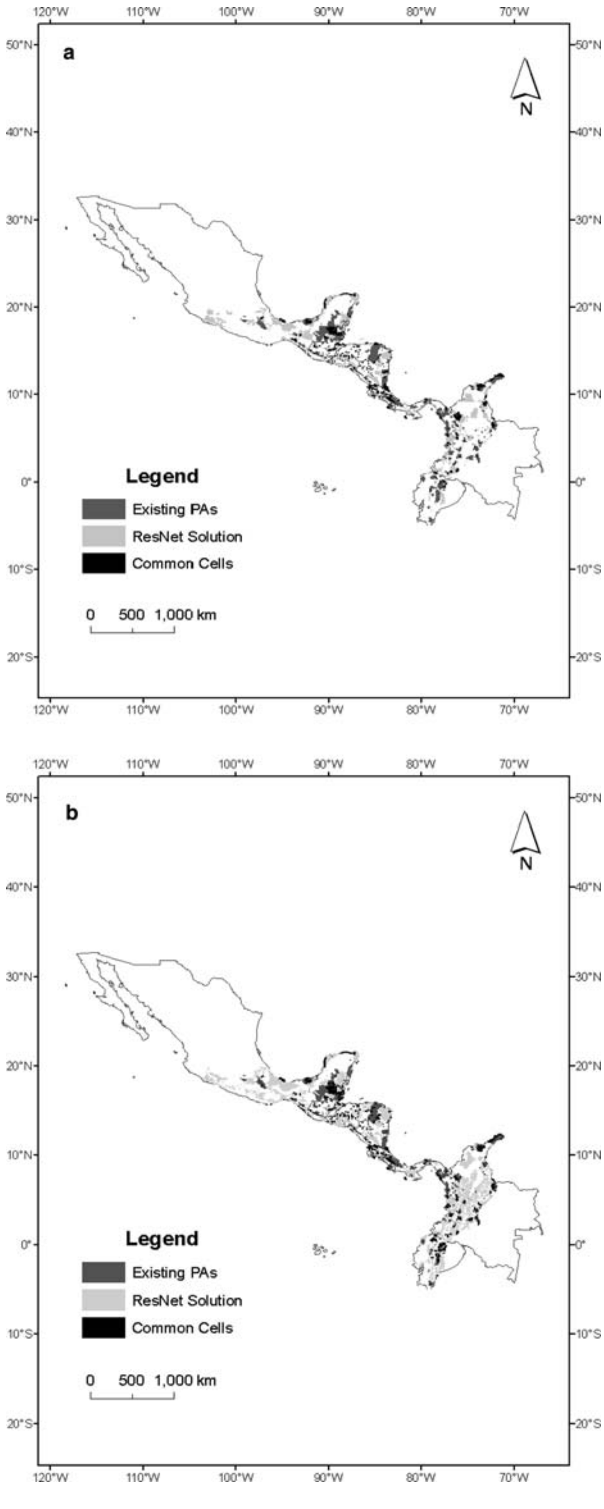


Fig. 3 continued

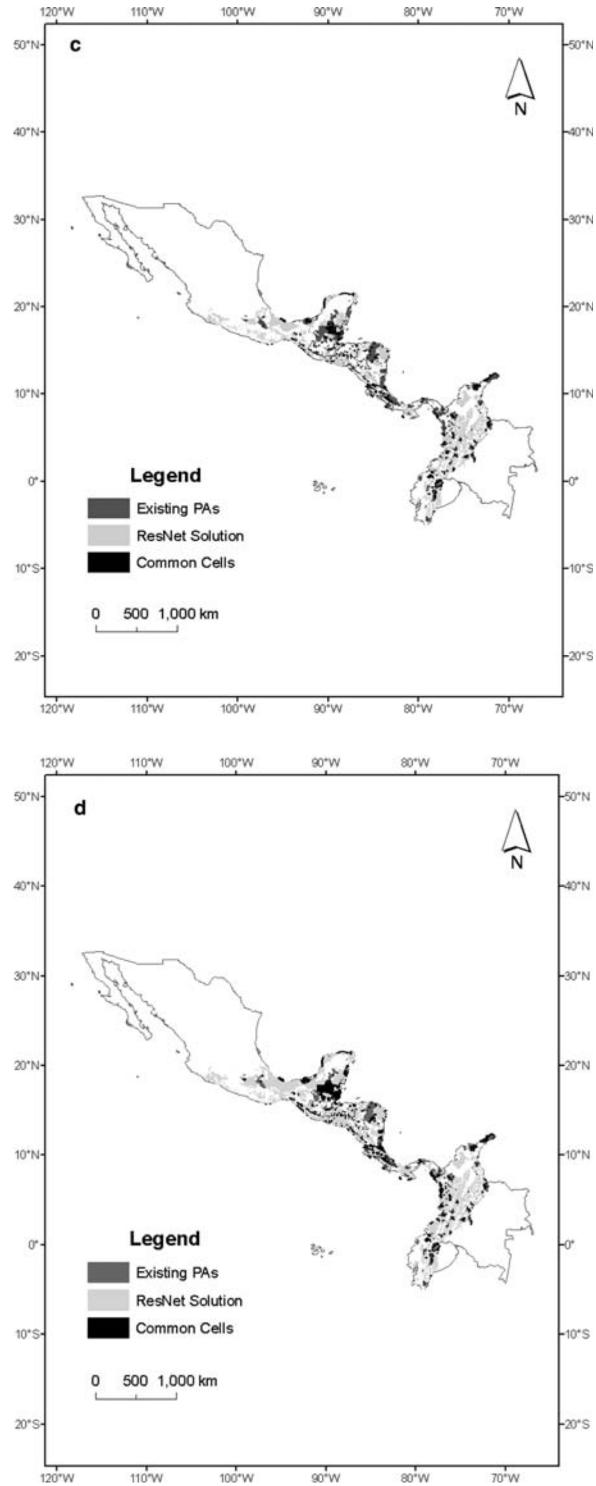
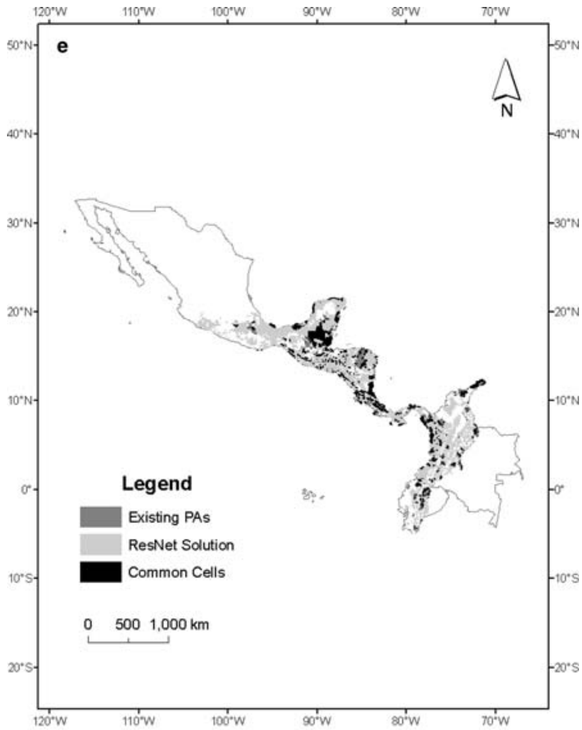
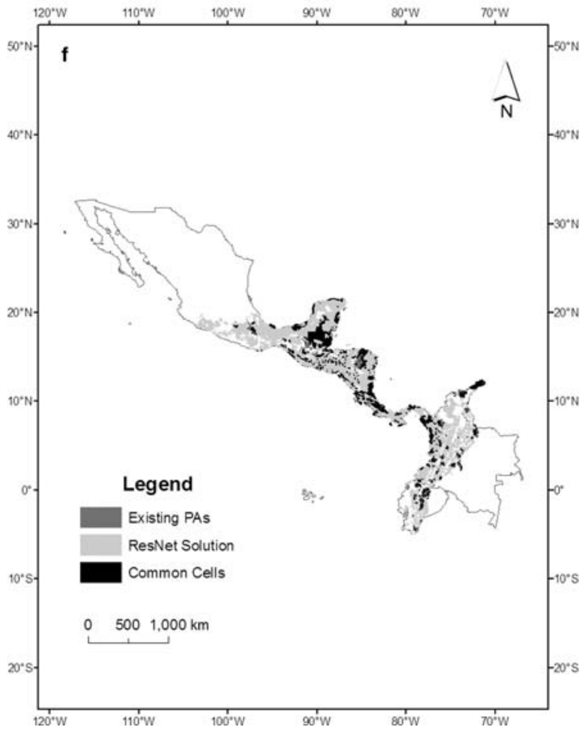


Fig. 3 continued





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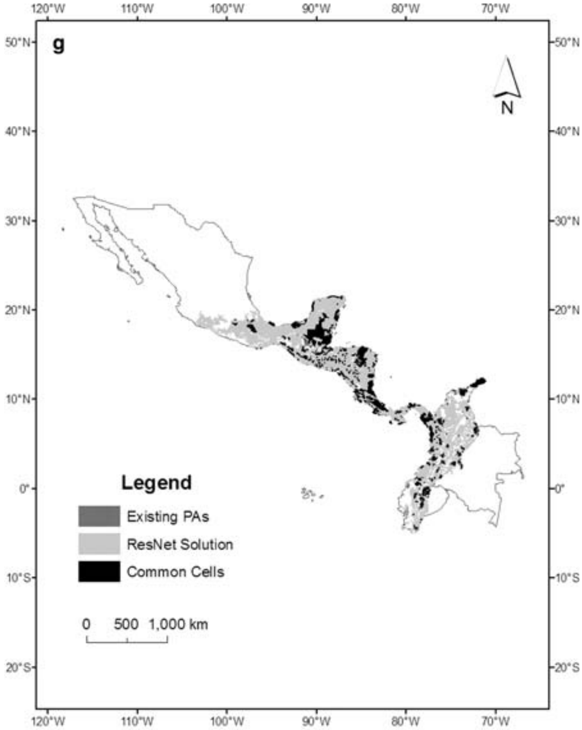

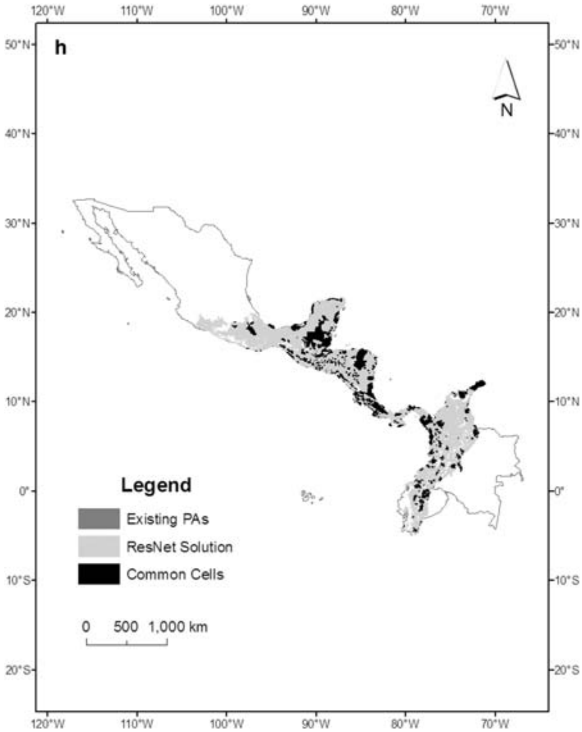

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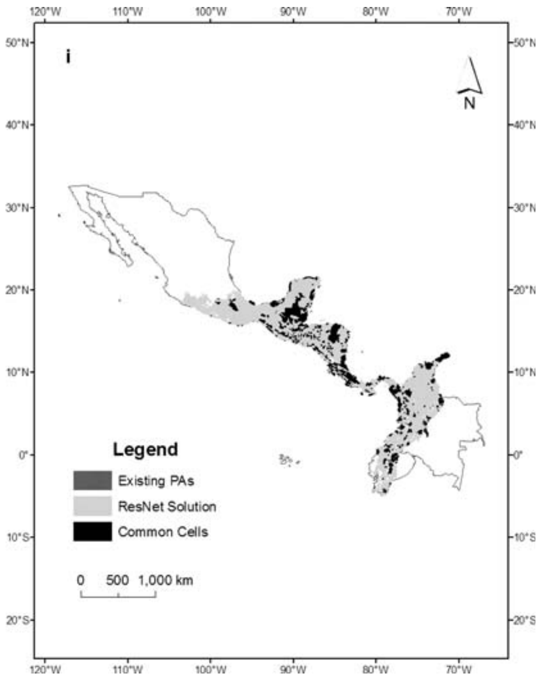

proportions of the protected areas of each country were selected ($\chi^2 \geq 1941.07$); in each case, $df = 9$ and $P < 2.2 \times 10^{-16}$. For all representation targets >10%, the surplus of selected sites in Guatemala was significantly greater than that of any other country (range of Pearson residuals: 19.59–48.36).

Discussion

The results obtained here are of relevance to other regional planning exercises for Mesoamerica, Chocó, and the Tropical Andes that are under way, for instance, as part of the MBC project even though those exercises are limited to a subset of the study region analyzed here. The larger landscape ecological context—which was adopted here on biogeographical grounds (see "Study Region")—helps place more restricted analyses in their proper regional context. Even at this larger scale, the most salient result obtained here is that, for all countries except Colombia, Mexico and Ecuador, protection of a large proportion of the distribution of only 78 Red List species takes up a very large proportion of the untransformed land: if the distribution representation target is 90%, the untransformed land needed amounts to 85–98% of each country. Including more species will only increase this area. The size of this area is a result of species at risk being widely distributed throughout Mesoamerica, Chocó, and the Tropical Andes which, in turn, underscores the region's importance for biodiversity. In the case of Colombia, Mexico and Ecuador, less area is probably being selected only because there were many fewer species' records (including those of endemic species) in the data set.

High representation targets are inevitable to ensure the persistence of species at risk (Sarakinos et al. 2001; Margules and Sarkar 2007). However, it is unreasonable to expect

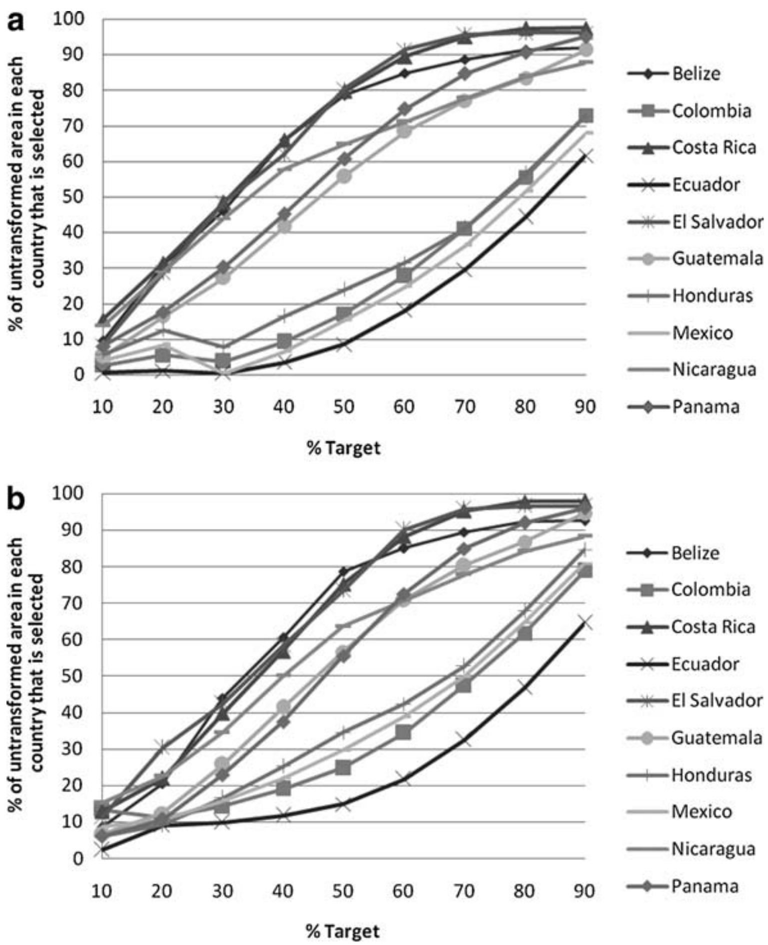

Fig. 4 Percentage of untransformed area selected in each country as a function of the representation target for Red List species: **a** only Red List species used as biodiversity surrogates; **b** both Red List species and ecoregions used as biodiversity surrogates

such large proportions of the land of any country to be set aside for conservation if that involves no human activity or use of the land. What this analysis shows is that, for biodiversity conservation to work in Mesoamerica, Chocó, and the Tropical Andes, an integrative approach to land use over the entire landscape must be developed. Exclusionary policies such as setting up National Parks or "absolute" biological reserves may have far less a role to play than land management through ecologically sound practices as, for instance, encouraged in Biosphere Reserves (Figueroa and Sánchez-Cordero 2008). This means that planning must involve human stakeholders from the beginning as envisioned in the SCP protocol.

It is encouraging that 189 of the 809 existing PAs (see Table S1) are selected when Red List species are surrogates, and the target is only 10%, which is a very modest target for such species. This seems to suggest that, unlike the ad hoc selection of existing PAs in many areas of the world (Pressey 1994; Pressey et al. 1996), those in Mesoamerica, Chocó, and the Tropical Andes were better selected to represent its biodiversity. However, what Figs. 4, 5, and 6 shows is that only a slightly higher fraction of the area within existing PAs

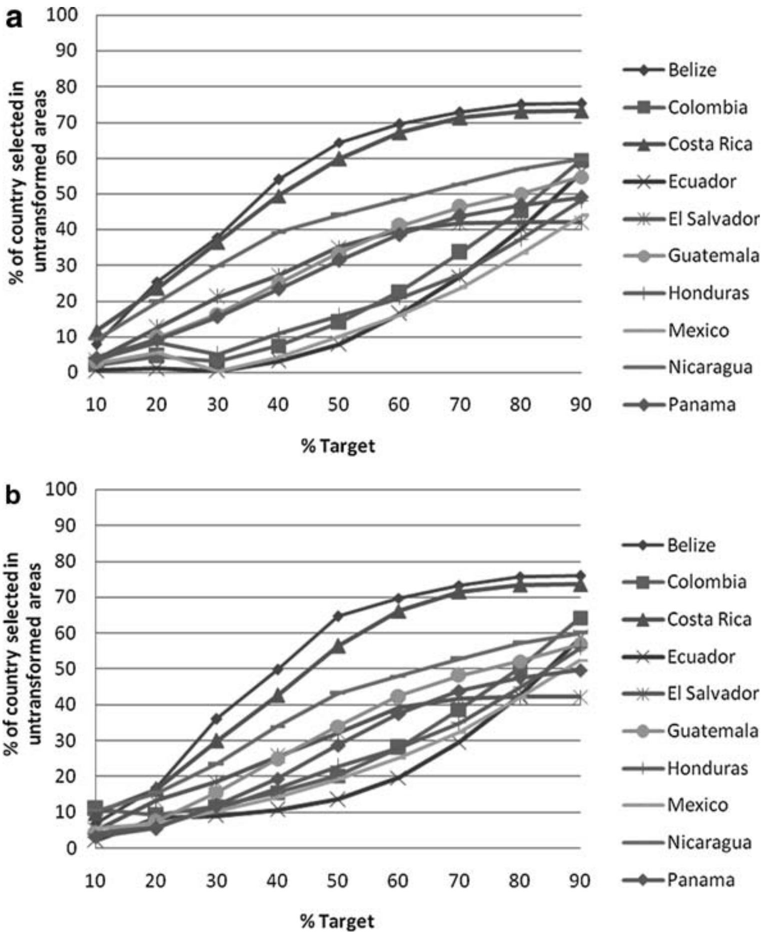

Fig. 5 Percentage of country's untransformed area selected as a function of the representation target for Red List species: **a** only Red List species used as biodiversity surrogates; **b** both Red List species and ecoregions used as biodiversity surrogates

is selected at any target compared to the fraction of the area of each country that is selected at that target. Thus, areas within the existing PAs are doing little better than areas outside with respect to representing biodiversity. In Figs. 4, 5, and 6 this conclusion is particularly obvious in the case of Colombia, Mexico, and Ecuador. The goal of SCP is to avoid this problem of inappropriate land allocation by prioritizing the most representative areas for conservation action.

Turning to individual countries, it is striking that all analyses show the existing PA network of Guatemala outperforming those of the other Mesoamerican countries. However, this is only true because those regions of Guatemala that were considered consisted of the remaining anthropogenically untransformed areas. Similarly, this analysis shows that the protected areas of Panama performing poorly compared to the other countries, once again when we restrict attention to the untransformed areas. Though there was no uniform statistical trend across all representations targets, Colombia and Ecuador also perform poorly in terms of the representativeness of their existing PAs which confirms

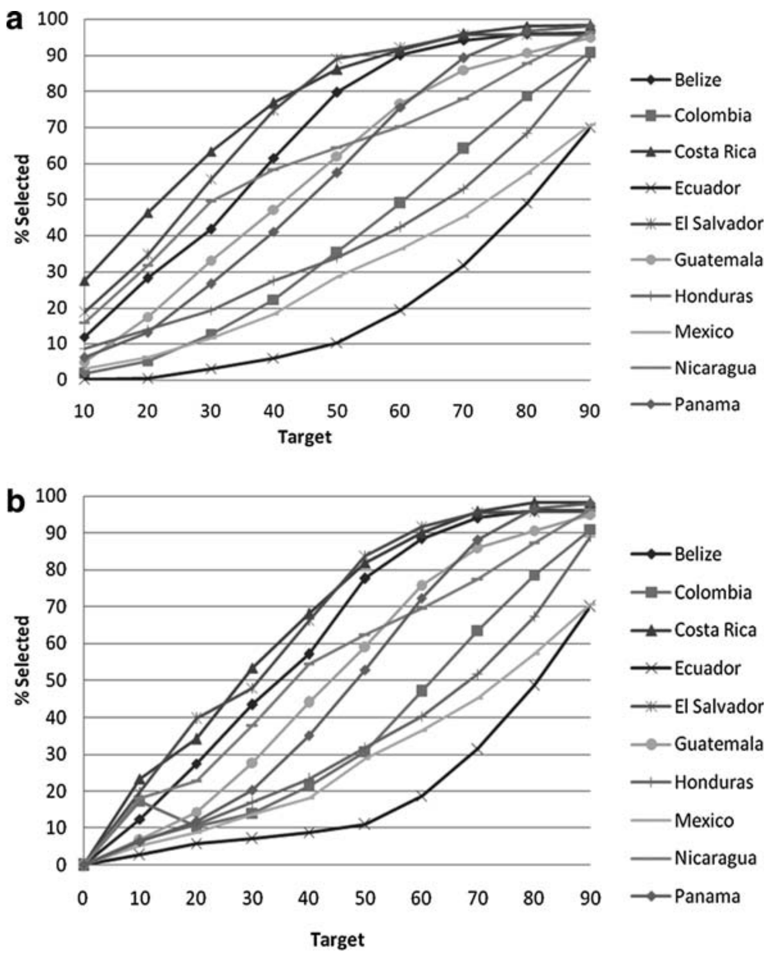

Fig. 6 Percentage of protected areas selected as a function of the representation target for Red List species. The entire area were available for selection. **a** Only Red List species used as biodiversity surrogates; **b** both Red List species and ecoregions used as biodiversity surrogates

the results of earlier analyses. Sierra et al. (2002) noted that, though more than 14% of Ecuador's terrestrial area falls within existing PAs, some habitat types, especially ecosystems on the coast and in the western Andes were under-represented. In this analysis, these ecosystems, when they fall within the study area, were selected at even low targets, using either the Red List species or both species and ecoregions as surrogates (Figs. 2a, 3a). Similarly, Fandiño-Lozano (1996) noted that though almost 10% of Colombia's habitat falls within PAs, 47.2% of the habitat types were unprotected. In both countries it is likely that excessive attention to tropical wet forests has led to their over-representation in the existing PA network at the expense of other habitats.

The results obtained here should be compared to those from other area prioritization efforts in the region both in order to identify areas that are assigned high priority by all methods (so that these areas receive special attention) and to see whether SCP techniques make any unique contribution. The methodology followed by CI in designating priority areas is very similar to the one used here; indeed in some regions of the world such as Melanesia, CI is using SCP techniques (Chris Margules 2007, personal communication). It is therefore quite likely that CI's results will be similar to those obtained here when they are made public. However, it is particularly instructive to compare these results to the portfolio published by the Nature Conservancy because the methodology used by Calderón et al. (2004), with its reliance only on environmental (non-taxonomic) surrogates and expert judgment is very different from the one used here. TNC distinguished its "portfolio" which consisted of 143 nominal conservation areas from 20 more coarse-grained "conservation action areas" (Calderón et al. 2004).

At a coarse spatial resolution TNC's portfolio and this analysis identify similar priority areas, for instance, the Lacandon-Maya forest in Mexico, the Maya Mountains of Belize, the Cordillera Central of Costa Rica, and the Bosque San Blas Darién of Panama. For Costa Rica there is very good concordance between TNC's portfolio and the results of this exercise, probably reflecting the high level of expertise readily available on Costa Rica's biodiversity (Evans 1999). At finer spatial resolutions, there are important differences: uniformly, this analysis selects a small fraction of the areas in TNC's portfolio even in the same region (especially for the 10 and 20% targets), thus providing a more fine-tuned identification of priority areas. This suggests that SCP methods can be usefully deployed to refine that portfolio. Moreover, there were some major differences: (1) in Honduras, TNC's portfolio prioritizes the Bosawar—Río Plátano area which does not emerge as important in this analysis for targets <70%; (2) in Nicaragua, TNC prioritized the Mahogany area which this analysis does not; and (3) this analysis identified some of the tropical deciduous forests of Panama as priority areas even at 10 and 20% targets, whereas TNC's portfolio ignores them. These forests should probably be part of any conservation portfolio, but the differences between TNC's portfolio and these SCP results merit further detailed analysis.

Turning to TNC's conservation action areas, these are concentrated to the north–east of the region (at the Mexico-Guatemala border and in Guatemala and Honduras) and to the south (Costa Rica and Panama). Each such area is large and an SCP analysis could be used to specify conservation areas within them more exactly. However, some important habitat types are not included in any TNC conservation action area. For instance, tropical dry forests of Costa Rica and Nicaragua (the Central American Dry Forest ecoregion) are not in an action area, in spite of being one of the most threatened ecotypes in the region (see that percentages of protection and transformation in Table 1). Similarly the Sierra Madre de Oaxaca pine-oak forests are not targeted even though they are not adequately protected (Table 1). These habitats were selected in this analysis at targets as low as 10 and 20% with either surrogate set. TNC's conservation action areas should be treated with caution.

Colombia and Ecuador were not part of TNC's analysis. For Colombia, at the national level, Fandiño-Lozano and van Wyngaarden (2005b) have recently carried out an SCP exercise using the Focalize (Fandiño-Lozano and van Wyngaarden 2005a) and C-Plan (Pressey 1999; Ferrier et al. 2000) software packages. As surrogates they used 337 topological and 62 chorological types that were established using remote-sensed data (Landsat images). Representation targets were set individually for each topological type based on the estimated area needed for minimal viable populations of four mammal species, *Panthera onca*, *Puma concolor*, *Tapirus terrestris* and *Tapirus pinchaque*. When the target here was 10 or 20%, areas selected here were similar to those prioritized by Fandiño-Lozano and van Wyngaarden (2005b) in much of the area within the study region. However, they prioritize areas between the Sanquianga and the Farallones de Cali PAs as well as an area between the Muchique and Galeras PAs in the southwest part of the country. These do not emerge as priority areas in this analysis. Moreover, this analysis does prioritize areas in the extreme west of the Cordillera de los Picachos PA as well as an area between the Laguna de Cocha, the Purace, and the Alto Fragua Indi Wasi PAs, an area south of Los Colorados and areas in the extreme north of the Western Ecuador Moist Forests which Fandiño-Lozano and van Wyngaarden (2005b) analysis excludes.

Finally, six limitations of this analysis should also be noted: (1) the most important limitation is that it was based on modeled distributions of only 78 species which is a mere 2% of the Red List species of the Mesoamerica, Chocó, Tropical Andes region. Moreover, 62 or 80% of the species used were plants. Efforts are now under way to collate and systematize data from many regional museums, universities, and other repositories to create a comprehensive public database for the region. It is hoped that the publication of this preliminary analysis will encourage local and regional scientists to share data by showing how useful these data can be in generating an adequate conservation plan for the region. This analysis will be repeated every year with additional data so that results become increasingly relevant towards the design of an implementation-oriented plan; (2) this analysis only used species deemed to be at risk by IUCN. These should be supplemented by subregional—for instance, national—priority lists of species at risk. However, other species are also of strong conservation concern, for instance, species that are endemic to the region even if they are not at present at risk. Future analyses will try to include as many of these as possible; (3) the land cover data set used was coarse and may not indicate all anthropogenically transformed areas that should not be regarded as candidate areas for conservation. Efforts are also under way to use remote-sensed data to generate a finer-resolution and more accurate land cover map so that all biologically unviable land can be excluded when developing a conservation plan; (4) the classification of the study area into only 53 ecoregions was also coarse. Future work will have to use a finer classification which will have to be created for the region. While such classifications exist for many of the countries individually, for instance, Mexico (CONABIO 1998), Costa Rica (Holdridge 1967), and Colombia (Fandiño-Lozano and van Wyngaarden 2005b), a regional classification is still lacking; (5) there was no attempt at all to incorporate spatial criteria such as size, shape, connectivity, dispersion, replication, and alignment into the priority area network designed here. These are obviously important for the persistence of biota (Sarkar et al. 2006; Margules and Sarkar 2007) and should be included in future analysis; and (6) the analysis performed here is still quite far from one that can produce an implementation-oriented plan. For that purpose stakeholders must be brought in as decision-makers and the analysis must take into full account sociopolitical opportunities and constraints.

Acknowledgments Animal species data were obtained from MaNIS (http://manisnet.org, last accessed 4 April 2007), HerpNET (http://www.herpnet.org/, last accessed 4 April 2007), ORNIS (http://olla.berkeley.edu/ornisnet/, last accessed 4 April 2007), and REMIB (Red Mundial de Información sobre Biodiversidad; http://www.conabio.gob.mx/remib/doctos/remib_esp.html, last accessed 4 April 2007). Additional records were obtained from Smithsonian National Museum of Natural History (http://www.mnh.si.edu/rc/, last accessed 4 April 2007). Plant species data were obtained from the University of Missouri Botanical Garden, W^3TROPICOS (http://mobot.mobot.org/W3T/Search/vast.html, last accessed 22 January 2007)—thanks are due to Nancy Shackelford for processing these data. MCL thanks the Consejo Nacional de Ciencia y Tecnología (CONACyT) for support and J. Nicolás Urbina-Cardona for assistance with the preparation of the Tables and Figures and for comments on an earlier draft. This work was supported by NSF Grant No. SES-0645884, 2007–2009 ("From Ecological Diversity to Biodiversity," PI: SS). TF acknowledges support from the Marion Elizabeth Eason Endowed Scholarship for the Study of Biology and the University Continuing Fellowship from the University of Texas.

References

Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken
Albuja VL (1992) Mammal list; July trip. In: Parker TA III, Carr JL (eds) Status of forest remnants in the Cordillera de la Costa and adjacent areas of southwestern Ecuador. Conservation International Rapid Assessment Program Working Papers, Vol 2
Albuja VL (1999) Murciélagos del Ecuador, 2nd edn. Cicetrónic Compañía Limitada, Quito
Albuja VL, Ibarra M, Urgilés J et al (1980) Estudio preliminar de los vertebrados ecuatorianos. Escuela Politécnica Nacional, Quito
Anderson RP (2003) Real vs. artefactual absences in species distributions: tests for *Oryzomys albigularis* (Rodentia: Muridae) in Venezuela. J Biogeogr 30:591–605
Anderson RP, Peterson AT, Gómez-Laverde M (2002a) Using GIS-based niche modeling to test geographic predictions of competitive exclusion and competitive release in South America pocket mice. Oikos 98:3–16
Anderson RP, Gómez-Laverde M, Peterson AT (2002b) Geographical distributions of spiny pocket mice in South America: insights form predictive models. Glob Ecol Biogeogr 11:131–141
Best BJ, Kessler M (1995) Biodiversity and conservation in Tumbesian Ecuador and Peru. BirdLife International, Cambridge, UK
Bravo H, Scheinvar H, Scheinvar L (1999) El interesante mundo de las cactáceas, 2nd edn. Fondo de Cultura Económica, México
Briones M, Sánchez-Cordero V (2004) Diversidad de mamíferos del estado de Oaxaca. In: García-Mendoza A, Ordónez MJ, Briones-Salas M (eds) Diversidad biológica del estado de Oaxaca. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, and World Wildlife Fund
Bryant D, Nielsen D, Tangley L (1997) The last frontier forests. Issues Sci Technol 14:85–87
Burke L, Kura Y, Kassem K et al (2000) Pilot analysis of global ecosystems: coastal ecosystems. World Resources Institute, Washington
Calderón R, Boucher T, Bryer M et al (2004) Setting biodiversity conservation priorities in Central America. The Nature Conservancy, Arlington
Carr MH, Lambert JD, Zwick PD (1994) Mapeo de la potencialidad de un corredor biológico continuo en América Central/Mapping of continuous biological corridor potential in Central America. Paseo Pantera. University of Florida, Gainesville
Casas-Andreu G, Méndez de la Cruz FR, Camarillo-Rangel JL (1996) Anfíbios y reptiles de Oaxaca: lista, distribución y conservación. Acta Zoológica Mexicana 69:1–35
CCAD (Comisión Centroamericana de Ambiente y Desarrollo) (1989) Central American agreement for the protection of the environment. CCAD, San Isidro
CCAD (Comisión Centroamericana de Ambiente y Desarrollo) (1993) Plan de acción forestal tropical para Centroamerica. CCAD, Guatemala City
CCAD (Comisión Centroamericana de Ambiente y Desarrollo) (1994) Central American alliance for sustainable development. CCAD, San José
CCAD (Comisión Centroamericana de Ambiente y Desarrollo) (2002) Nature, people, and well being. World Bank and CCAD, Paris
CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) (1998) La diversidad biológica de México: estudio de país. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City
Conservation International (2004) Conserving earth's living heritage: a proposed framework for designing biodiversity conservation strategies. Conservation International, Washington
Cowling RM, Pressey RL (2003) Introduction to systematic conservation planning in the cape floristic region. Biol Conserv 12:1–13
Cowling RM, Pressey RL, Sims-Castley R et al (2003) The expert or the algorithm?—comparison of priority conservation areas in the cape floristic region identified by park managers and reserve selection software. Biol Conserv 112:147–167
Cracraft J (1985) Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. In: Buckley PA, Foster MS, Morton ES et al (eds). Neotropical ornithology. Ornithological Monographs. American Ornithologists' Union, Washington, DC, Vol 36
Csuti B, Polasky S, Williams PH et al (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. Biol Conserv 80:83–97
Delgadillo MC (2000) Mosses and the Caribbean connection between North and South America. Bryologist 103:82–86
Delgadillo MC, Villaseñor JL (2002) The status of the South American *Grimmia herzogii* (Musci). Taxon 51:123–129

Dinerstein E, Olson DM, Graham DJ (1995) A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. World Bank, Washington, DC

Donnelly TW (1989) Geologic history of the Caribbean and Central America. In: Bally AW, Palmer AR (eds) Geological Society of America decade of North American geology, Vol. A, The geology of North America: an overview. Geological Society of America, Boulder

Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29(2):129–151

Escalante T, Sánchez-Cordero V, Morrone JJ et al (2007) Parsimony analysis of endemicity, Goloboff fit, and areas of endemism in Mexico: a case study using species' ecological niche modelling of terrestrial mammals. Interciencia 32(3):151–159

Evans S (1999) The green republic: a conservation history of Costa Rica. University of Texas Press, Austin

Fa JE, Morales LM (1991) Mammals and protected areas in the Trans-Mexican Volcanic Belt. In: Mares MA, Schmidly DJ (eds) Latin American Mammalogy: History, Biodiversity, and Conservation. University of Oklahoma Press, Norman, Oklahoma

Faith DP, Margules CR, Walker PA (2001) A biodiversity conservation plan for Papua New Guinea based on biodiversity trade-offs analysis. Pac Conserv Biol 6:304–324

Fandiño-Lozano M (1996) Framework for ecological evaluation oriented at establishment and management of protected areas. Dissertation, University of Amsterdam

Fandiño-Lozano M, van Wyngaarden W (2005a) Focalize software. Grupo ARCO, Bogotá

Fandiño-Lozano M, van Wyngaarden W (2005b) Prioridades de consevación biológica para Colombia. Grupo ARCO, Bogotá

FAO (United Nations Food and Agriculture Association) (2005) State of the world's forests. United Nations Food and Agriculture Association, Rome

Ferrier S, Pressey RL, Barrett TW (2000) A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. Biol Conserv 93:303–325

Figueroa F, Sánchez-Cordero V (2008) Effectiveness of natural protected areas to prevent land use and land cover change in Mexico. Biodivers Conserv 17:3223–3240

Garson J, Aggarwal A, Sarkar S (2002) ResNet Ver 1.2 manual. University of Texas Biodiversity and Biocultural Conservation Laboratory, Austin

Groves CR, Jensen DB, Valutis LL et al (2002) Planning for biodiversity conservation: putting conservation science into practice. BioScience 52:499–512

Hansen M, DeFries R, Townshend JRG et al (2000) Global land cover classification at 1 km resolution using a decision tree classifier. Int J Remote Sens 21:1331–1365

Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San Jose

Hooghiemstra H, Cleef AM, Noldus G et al (1992) Upper quaternary vegetation dynamics and palaeoclimatology of the La Chonta Bog Area (Cordillera de Talamanca, Costa Rica). J Quart Sci 7:205–225

Illueca J (1997) The paseo pantera agenda for regional conservation. In: Coates AG (ed) Central America: a natural and cultural history. Yale University Press, New Haven

Jarrín-V P (2001) Mamíferos en la niebla: Otonga, un bosque nublado del Ecuador. Publicaciones Especiales, Museo de Zoología, Centro de Biodiversidad y Ambiente. Pontificia Universidad Católica del Ecuador 5:1–244

Joseph L, Stockwell D (2002) Climatic modeling of the distribution of some *Pyrrhura parakeets* of northwestern South America with notes on their systematics and special reference to *Pyrrhura caeruleiceps* Todd, 1947. Ornithol Neotrop 13:1–8

Jukofsky D (1992) Path of the panther. Wildlife Conserv 95(5):18–24

Kappelle M, Cleef AM, Chaverri A (1992) Phytogeography of Talamanca montane *Quercus* forests, Costa Rica. J Biogeogr 19:299–315

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:242–253

Margules CR, Sarkar S (2007) Systematic conservation planning. Cambridge University Press, Cambridge

Matthews E, Payne R, Rohweder M et al (2000) Pilot analysis of global ecosystems: forest ecosystems. World Resources Institute, Washington

Miller K, Chang E, Johnson N (2001) Defining common ground for the Mesoamerican biological corridor. World Resources Institute, Washington

Morris W, Doak D, Groom M et al (1999) A practical handbook for population viability analysis. The Nature Conservancy, Arlington

Morrone JJ (2005) Cladistic biogeography: identity and place. J Biogeogr 32:1281–1284

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Olson DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial ecoregions of the worlds: a new map of life on Earth. Bioscience 51:933–938

Pawar S, Koo MS, Kelley C et al (2007) Conservation assessment and prioritization of areas in northeast India: priorities for amphibians and reptiles. Biol Conserv 136:346–361

Peterson AT, Flores-Villela O, León-Paniagua L et al (1993) Conservation priorities in northern Middle America: moving up in the world. Biodivers Lett 1:33–38

Peterson AT, Soberón J, Sánchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. Science 285:1265–1267

Peterson AT, Caneco-Márquez L, Contreras Jiménez JL et al (2004) A preliminary biological survey of Cerro Piedra Larga, Oaxaca, Mexico: birds, mammals, reptiles, amphibians, and plants. An Inst Biol, Univ Nac Aut Méx, Serie Zool 75(2):439–466

Phillips SJ, Dudik M, Shapire RE (2004) A maximum entropy approach to species distribution modeling. In: Greiner R, Schuurmans D (eds) Proceedings of the twenty-first international conference on machine learning. ACM, New York, pp 655–662

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Pressey RL (1994) Ad hoc reservations: forward or backward steps in developing representative reserve systems. Conserv Biol 8:662–668

Pressey RL (1999) Applications of irreplaceability analysis to planning and management problems. Parks 9:42–51

Pressey RL, Ferrier S, Hager TC et al (1996) How well protected are the forests of north-eastern New South Wales? analyses of forest environments in relation to formal protection measures, land tenure, and vulnerability to clearing. For Ecol Manag 85:311–333

Raven PH, Axelrod DI (1974) Angiosperm biogeography and past continental movement. Ann Mo Bot Gard 61:539–673

Revenga C, Brunner J, Henninger N et al (2000) Pilot analysis of global ecosystems: freshwater systems. World Resources Institute, Washington

Ricketts TH, Dinerstein E, Olson DM et al (1995) Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington, DC

Sánchez-Cordero V, Figueroa F (2007) La efectividad de las Reservas de la Biosfera en México para contener procesos de cambio en el uso del suelo. In: Halffter G, Guevara S (eds) Hacia una cultura de conservación de la diversidad biológica Sociedad Entomológica Aragonesa, CONABIO, CONANP, CONACyT, Instituto de Ecología, A. C., MAB-UNESCO. Ministerio de Medio Ambiente-Gobierno de España, Zaragoza

Sarakinos H, Nicholls AO, Tubert A et al (2001) Area prioritization for biodiversity conservation in Québec on the basis of species distributions: a preliminary analysis. Biodivers Conserv 10:1419–1472

Sarkar S (2002) Defining 'biodiversity': assessing biodiversity. Monist 85:131–155

Sarkar S (2005) Biodiversity and environmental philosophy: an introduction to the issues. Cambridge University Press, Cambridge, UK

Sarkar S, Margules CR (2002) Operationalizing biodiversity for conservation planning. J Biosci 27(S2): 299–308

Sarkar S, Aggarwal A, Garson J et al (2002) Place prioritization for biodiversity content. J Biosci 27(S2): 339–346

Sarkar S, Pappas C, Garson J et al (2004) Place prioritization for biodiversity conservation using probabilistic surrogate distribution data. Divers Distrib 10:125–133

Sarkar S, Pressey RL, Faith DP et al (2006) Biodiversity conservation planning tools: present status and challenges for the future. Ann Rev Environ Res 31:123–159

Sarukhán J, Dirzo D (2001) Biodiversity rich countries. In: Levin SA (ed) Encyclopedia of biodiversity. Academic Press, San Diego, pp 419–436

Sarukhán J, Soberón J, Larson J (1996) Biological conservation in a high beta-diversity country. In: di Castri F, Younes T (eds) Biodiversity, science and development. Towards a new partnership. CAB International—IUBS, Paris, pp 246–263

Secretariat of the Convention on Biological Diversity (2002) Global strategy for plant conservation. Secretariat of the Convention on Biological Diversity, Montreal. http://www.bgci.org/files/7/0/global_strategy.pdf. Cited 24 June 2007

Sierra R, Campos F, Chamberlin J (2002) Conservation priorities in continental Ecuador: a study based on landscape and species level biodiversity patterns. Landsc Urban Plan 59:95–110

Simonoff JS (2003) Analyzing categorical data. Springer, Berlin

Smith RJ, Goodman PS, Matthews WS (2006) Systematic conservation planning: a review of perceived limitations and an illustration of the benefits, using a case study from Maputaland, South Africa. Oryx 40:400–410

Soberón J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Inform 2:1–10

Soulé ME, Sanjayan MA (1998) Conservation targets—do they help? Science 279:2060–2061

Stehli FG, Webb SD (eds) (1985) The great american biotic interchance. Plenum, New York

The IUCN Species Survival Commission (2007) IUCN Red List of threatened species. http://www.iucnredlist.org/. Cited 26 May 2008

USGS (U. S. Geological Survey) (1998) GTOPO30 Global 30 arc-second digital elevation model. USGS, Reston. http://edcdaac.usgs.gov/gtopo30/gtopo30.html. Cited 31 May 2007

Utting P (1997) Deforestation in Central America: historical and contemporary dynamics. In: de Groot JP, Ruben R (eds) Sustainable agriculture in Central America. St. Martin's, New York, pp 9–29

WDPA Consortium (2007) World database on protected areas 2007. Available via World Conservation Union (IUCN) and UNEP-World Conservation Monitoring Centre (UNEP-WCMC). http://sea.unep-wcmc.org/wdbpa/index.htm. Cited 26 May 2008