Ecology Letters, (2003) **6**: 818–824 doi: 10.1046/j.1461-0248.2003.00503.x

LETTER

Present patterns and future prospects for biodiversity in the Western Hemisphere

Sandy J. Andelman[1]* and Michael R. Willig[2]
[1]*National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA*
[2]*Ecology Program, Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, TX 79409-3131, USA*
**Correspondence: E-mail: andelman@nceas.ucsb.edu*

Abstract

Creating networks of nature reserves to protect areas rich in biodiversity from the adverse impacts of anthropogenic change is a critical and urgent task. We illustrate the skewed geographical and size distributions of protected areas in the Western Hemisphere. For instance, 811 of 1413 reserves in the Western Hemisphere are smaller than 10 km^2, and 35% of the total area of these reserves is in Alaska. We compile ranges for all bats in the continental Western Hemisphere and find that 82% of threatened and small-range species are not protected adequately. Many of the most vulnerable species occur in the areas of highest human density. We provide maps delineating areas where conservation investments may have the greatest impact in preventing biodiversity losses.

Keywords

Biodiversity, protected areas, Chiroptera, conservation planning, macroecology, biogeography, human population density.

Ecology Letters (2003) 6: 818–824

INTRODUCTION

Land-use change is predicted to be the primary driver of terrestrial species extinctions and changes in global biodiversity during the next century (Sala *et al.* 2000). Thus, creating reserves to protect ecologically representative areas and areas rich in biodiversity is a cornerstone of conservation strategies (Dobson *et al.* 1997; Scott *et al.* 2001). Identifying an effective and efficient set of areas for conservation investments requires information on patterns of species diversity, the distribution of existing protected areas, and the distribution of threats to species in different areas (Dobson *et al.* 2001). Although several global or continental schemes have been proposed for prioritising biodiversity conservation investments (Mittermeier *et al.* 1998; Olson & Dinerstein 1998; Myers *et al.* 2000; Burgess *et al.* 2002), these have not explicitly considered the extent to which biodiversity is already protected within existing conservation areas. Moreover, although systematic evaluations of biodiversity patterns and the adequacy of existing protected areas have been the focus of several reviews, most have focused on only a single country (Hunter & Yonzon 1993; Pressey 1995; Kiester *et al.* 1996; Dobson *et al.* 1997; Jennings 2000; Margules & Pressey 2000; Scott *et al.* 2001). Previous analyses have not explicitly examined the geographical distribution and ecological representation of protected areas at hemispheric or global scales and relatively little attention has been given to comprehensive assessment of the imminence of threats to unprotected elements of biodiversity. Here we systematically review the extent and adequacy of protected areas for conserving species-level biodiversity throughout the Western Hemisphere and consider the relative significance of different areas for conservation investments.

Our data include the ranges of all bats in the continental New World, not a sample of them. Thus, our results are complete at the hemispheric scale, and are subject only to the uncertainties in measurements of species ranges, taxonomic synonymies, and to inadequate species discovery, especially in the tropics (May & Nee 1995; Patterson 1996). Ideally, one would consider patterns of species diversity for all taxa, but such data currently are not available. Previous analyses have used mammals as indicators of the conservation status of the Earth's biota, because of their taxonomic diversity and the spectrum of ecological niches that they exploit (Ceballos & Ehrlich 2002). Bats are a crucial component of mammalian biodiversity, comprising 23% of mammalian species in the Western Hemisphere, and 20% globally (Patterson 1994). The spatial distribution of chiropteran species richness parallels that of mammals in general (Willig *et al.* 2003). Bats reflect a wide spectrum of the ecological niches exploited by mammals, including both aerial and ground-based insect-, fruit-, nectar-, fish-, and blood-feeding habits. Moreover, globally, almost a fourth of all bat species are threatened (IUCN 2000; Hutson *et al.* 2001; Jones *et al.* 2003). Evaluating the representation of bat species within reserves is thus a reasonable step in assessing the adequacy of current conservation efforts (Medellin *et al.* 2000; Andelman & Willig 2002).

MATERIAL AND METHODS

We used two types of data to assess the extent and adequacy of protected area coverage for species conservation. We obtained data on the locations and sizes of protected areas from the UNEP World Conservation Monitoring Centre Protected Areas Programme (http://www.unep-wcmc.org/protected_areas/data), the most comprehensive source of global-scale data on protected area status. We also developed a GIS database containing the distributional ranges of 249 of the 255 currently recognized bat species (Koopman 1982, 1993) in the continental Western Hemisphere (Hall 1981; Eisenberg 1989; Redford & Eisenberg 1992; Koopman 1993a,b; Eisenberg & Redford 1999). The remaining six species (*Anoura latidens*, *Artibeus amplus*, *A. fimbriatus*, *A. glaucus*, *A. obscurus* and *Sturnira luisi*) were excluded from analyses because distributional records were insufficient to provide the basis for plotting range maps. Using ArcGIS, we superimposed the ranges to create synthetic maps of bat species occurrence and species richness in 250 km by 250 km quadrats.

We considered areas classified by IUCN as category I (strict nature reserves or wilderness areas managed for scientific research or wilderness protection) or category II (national parks managed for ecosystem protection and recreation that is environmentally responsible) management areas (http://www.unep-wcmc.org/protected_areas/data) to be reserves. Although conservation also will occur in other types of managed areas, category I and II areas are primarily dedicated to biodiversity conservation. For each quadrat, we summed the areas of all reserves to obtain a measure of the total area in reserves. We considered a quadrat to be adequately protected if at least 10% of its total area was contained within reserves. In reality, the minimum percentage of an area required to be in reserves, such that all species in that area are represented, will vary, and likely will depend on the diversity and endemism of the taxa of interest, as well as on the size of selection units (Rodrigues & Gaston 2001). It has been recommended that at least 10–50% of terrestrial ecosystems should be protected within reserves (IUCN 1993; Soule & Sanjayan 1998). Thus our threshold for considering a quadrat protected is likely to be a lower bound.

To systematically prioritize areas for future conservation investments, we used a complementarity-based (Vane-Wright *et al.* 1991; Faith 1994) simulated annealing algorithm (Andelman *et al.* 1999) to quantify the number of unrepresented species potentially protected through conservation investments in each quadrat. The potential contribution of an area to any conservation goal is dynamic, and depends on the extent to which conservation targets for each species have been met within existing protected areas, and on the compositional distinctiveness of each area, relative to other areas. We used measures of irreplaceability (Ferrier *et al.* 2000) to estimate the conservation value of each quadrat in the context of four conservation scenarios defined by the conservation goal (protect each species in one vs. three quadrats) and by the status of current reserves (considering or ignoring the status of existing reserves). High irreplaceability should translate into high payoffs for unrepresented species from conservation investments in those quadrats.

For each conservation scenario, we ran the reserve selection algorithm 200 times. The level of irreplaceability is indicated by the percentage of times an area was selected within a scenario. For example, an area selected in all 200 simulations would be completely irreplaceable in that the specified conservation goal could not be achieved without conservation investments in that area. In contrast, a site never selected by the algorithm would have a 0% irreplaceability value.

We generated eight irreplaceability scenarios, four of which we present here. For the other four scenarios, we stratified species geographically into northern temperate species, equatorial species, and southern temperate species, and set conservation goals within each stratum. The goals were to conserve either one or three occurrences of each species within a stratum in which it occurred. We did this in two ways: ignoring existing reserves, and forcing solutions to include existing reserves. The results of the geographically stratified scenarios were qualitatively indistinguishable from those without geographical stratification, and the conclusions derived from stratified and unstratified scenarios were identical. Thus, for simplicity, we present irreplaceability scenarios only for the unstratified scenarios.

RESULTS

We find that the distribution of reserves in the Western Hemisphere is skewed, both geographically and in terms of size. There are 1413 reserves distributed among 435 quadrats in the Western Hemisphere (Fig. 1a). They range in size from less than 0.01 km^2 to over 36000 km^2; however, most are small, with a median size of only 4.86 km^2 (Fig. 1b). Eighty-three percent of reserves in the Western Hemisphere are <100 km^2 in area, and 57% are <10 km^2 (Fig. 1b). Only 23 quadrats have at least 10% of their area protected within reserves (hereafter protected quadrats), and 11 of these are in Alaska (Fig. 1c). Alaskan reserves comprise 35% of the total 602 675 km^2 of all reserves within the entire hemisphere (Fig. 1d).

Although the distribution of reserves is skewed towards northern latitudes (Fig. 1a,d), bats, like most organisms

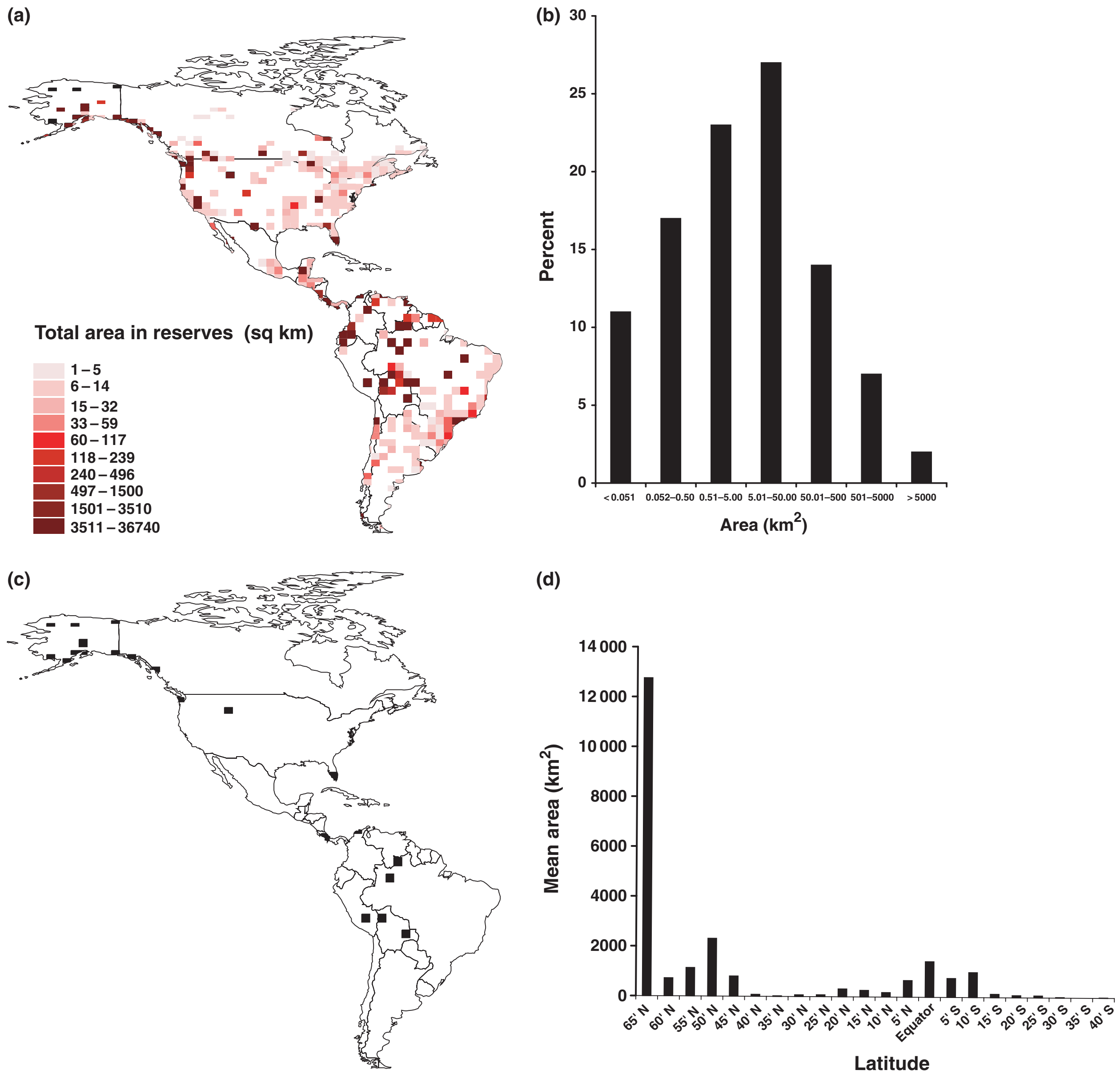

Figure 1 (a) Map showing distribution of reserves (IUCN Category I and II protected areas) in the Western Hemisphere at the scale of 250 km × 250 km quadrats (n = 1413 reserves). (b) Distribution of reserve sizes in the Western Hemisphere (n = 1413 reserves). (c) Distribution of quadrats with at least 10% of their area within reserves (n = 40 reserves distributed among 23 quadrats). (d) Distribution of reserve area by latitudinal band. Data from (http://www.unep-wcmc.org/protected_areas/data).

(Willig *et al.* 2003), exhibit a strong latitudinal gradient of increasing species richness toward the tropics (Fig. 2a). Regions of high species richness are concentrated in northwestern South America, particularly in association with the Andes, and in MesoAmerica. From a conservation perspective, species known to be at risk of extinction and species with small geographical ranges are of most immediate concern. In the continental Western Hemisphere, 21% of bat species are considered to be threatened by IUCN (IUCN 2000; Hutson *et al.* 2001). To identify small-range species, we partitioned species into range size quartiles (RSQs). Small-range species are those in the lowest RSQ. Threatened and small-range species (hereafter referred to as species of concern) are concentrated in coastal Peru and Ecuador, and southern Mexico (Fig. 2b). Secondary concentrations of species of concern occur in MesoAmerica, the Guiana Shield, Colombia and the temperate Andes (Fig. 2b,c). Thus, at the species level, the degree of

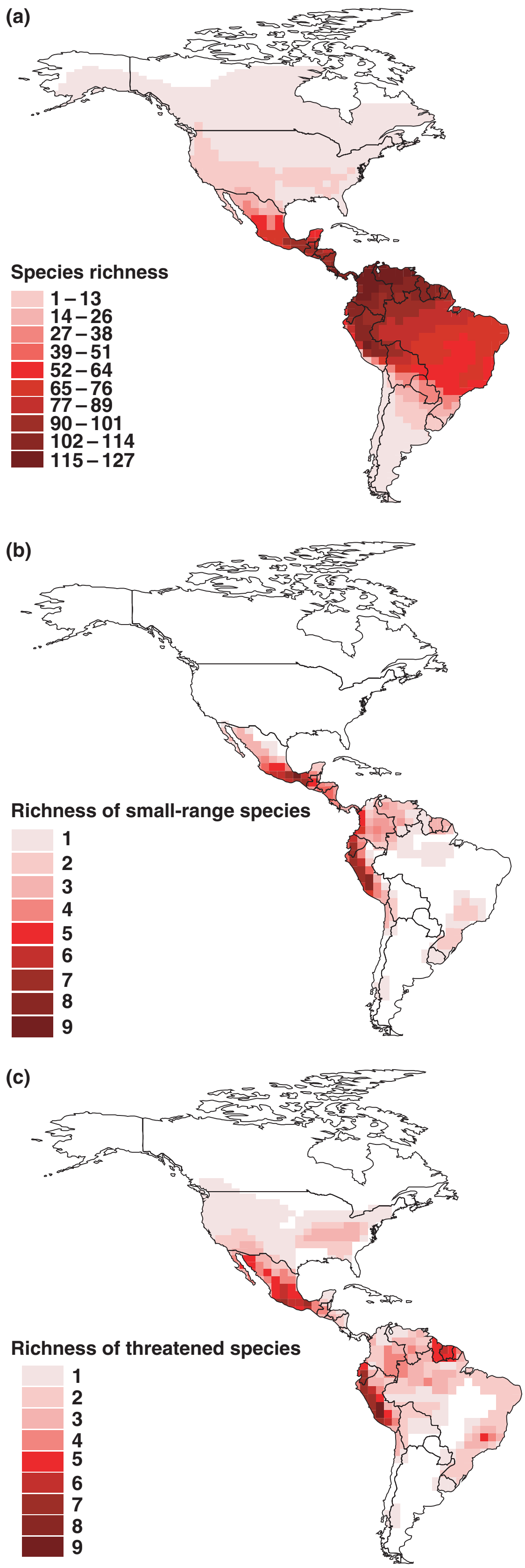

Figure 2 (a) Map showing pattern of continental bat species richness in the Western Hemisphere at the scale of 250 km × 250 km quadrats ($n = 249$ species). (b) Map showing pattern of species richness for small-range species (i.e. those in the lowest range size quartile) ($n = 61$ species). (c) Map showing pattern of species richness for threatened species (i.e. those listed as critically endangered, endangered or vulnerable on the IUCN Red List) (IUCN 2000; Hutson *et al.* 2001) ($n = 52$ species).

protection afforded by existing reserves is biased: quadrats containing the highest concentrations of species of concern contain some of the lowest concentrations of reserves. Fifteen of 23 protected quadrats contain no species of concern, and the remainder have five or fewer species of concern. Moreover, 82% of the species of greatest conservation concern (i.e. threatened and small-range species) are inadequately protected by existing reserves. In contrast, all species with large ranges (i.e. those occurring within the largest RSQ) occur within at least one protected quadrat, and 92% of large-range species occur in at least five protected quadrats.

Across the range of conservation scenarios we considered, ten areas consistently emerge as high priorities for conservation investment based on irreplaceability analysis (Fig. 3): subtropical Mexico, MesoAmerica, Tropical Andes, Choco-Darien Region, Brazilian Cerrado, Baja California, Venezuelan Llanos, the southern Andes of Argentina and Chile, the Amazon Basin, and Guiana Shield.

DISCUSSION

Although it is common knowledge that the distribution of protected areas is highly skewed relative to the distribution of biodiversity, the pattern has not previously been quantified at hemispheric or global scales. Our results suggest that 82% of threatened and small range bat species are not adequately represented within reserves. Areas with high concentrations of threatened and small-range species indicate where population, and potentially species extinctions are most likely to occur. Although our analyses included only bats, spatial patterns of bat species diversity are representative of mammal species diversity more generally (Willig *et al.* 2003). Moreover, areas of high irreplaceability for bats correspond reasonably well to those identified as hotspots based on analyses of endemic plant species (Myers *et al.* 2000).

Ceballos & Ehrlich (2002) recently found that mammalian population extinctions are concentrated where there are high human population densities, or where human impacts, such as intensive agriculture, grazing and hunting have been severe. Our analyses suggest that areas with the highest concentrations of species of conservation concern have

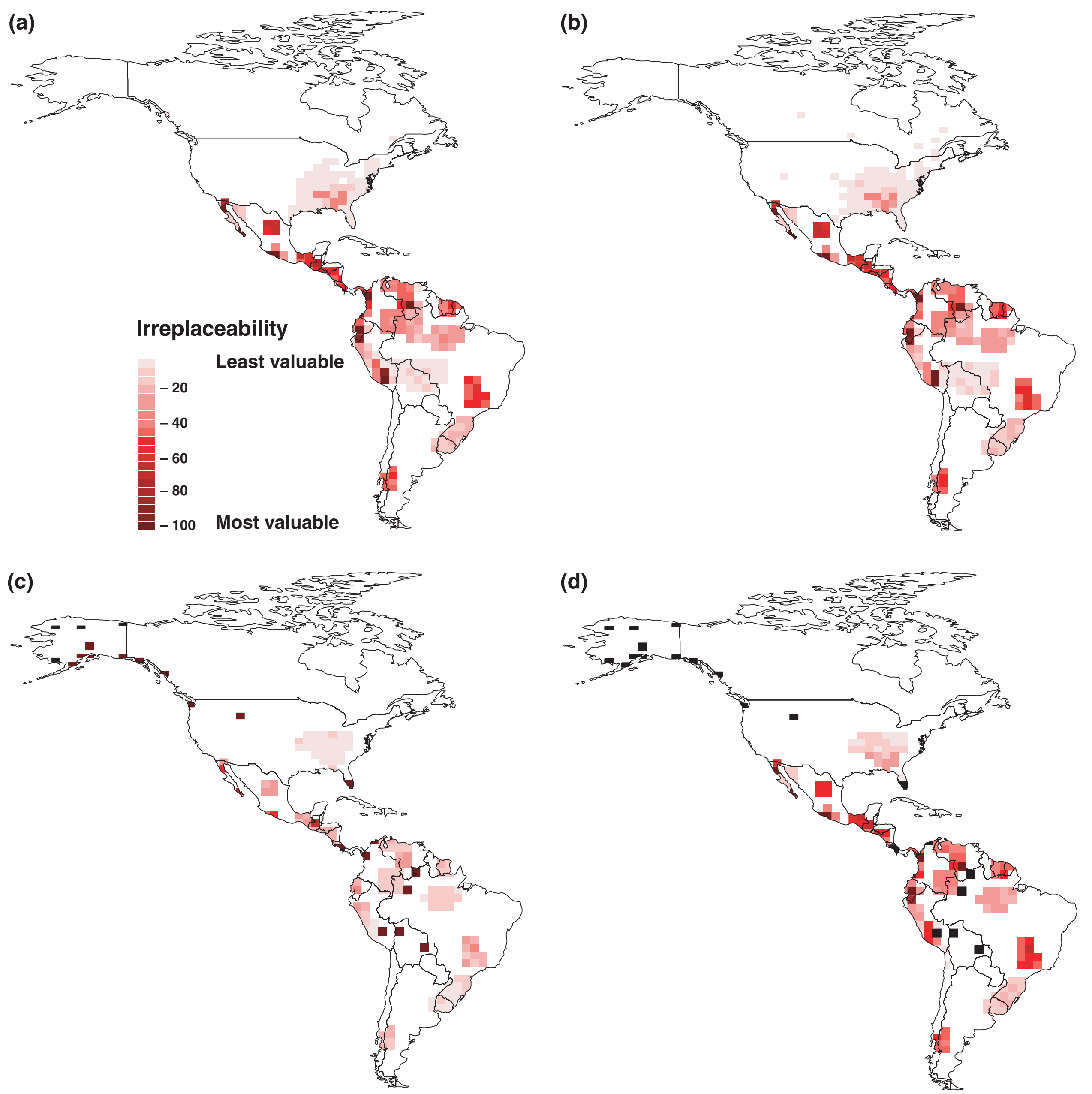

Figure 3 Irreplaceability (Ferrier *et al.* 2000) surfaces in which the goal is to protect at least (a) one or (b) three occurrence of each species, ignoring the status of existing reserves; and to protect (c) one or (d) three occurrences of each species, with existing reserves (black squares) locked into the reserve network.

some of the lowest concentrations of reserves. Further, our assessment also reveals a striking correspondence between areas in MesoAmerica and South America with many species of concern and few or no reserves, and areas with dense and expanding human populations (Fig. 4). Five of the areas we identified as high priorities for conservation have previously been identified as highly threatened by anthropogenic activities (i.e. subtropical Mexico, MesoAmerica, Tropical Andes, Choco-Darien Region, and Brazilian Cerrado). Three priority regions for bats are moderately threatened (i.e. Baja California, Venezuelan Llanos, and southern Andes of Argentina and Chile), and two are relatively secure (i.e. Amazon Basin and Guiana Shield) (Dinerstein *et al.* 1995).

Some caution is needed in interpreting our results. Although the UNEP–WCMC database is the most

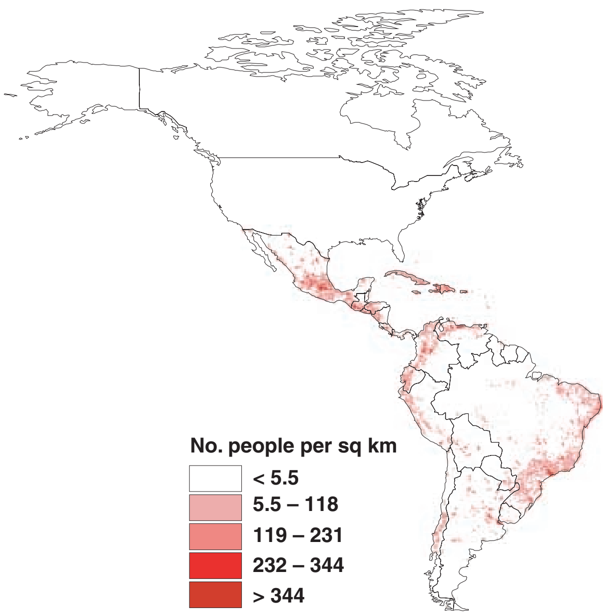

Figure 4 Human population density in Latin America and the Carribean. Data from UNEP/GRID Latin America population database. http://grid2.cr.usgs.gov/datasets/datalist.php3.

comprehensive source of data on the global distribution of protected areas, it almost certainly is incomplete. In addition, our analysis considered only IUCN category I and II management areas. Undoubtedly, particularly in the Neotropics, significant biodiversity conservation efforts will occur in other types of reserves, such as sustainable development reserves, or indigenous reserves. Thus, from this perspective, our assessment of levels of protection for bats may be a worst case scenario. On the other hand, our analyses addressed only the criterion that reserves should represent the full range of biodiversity. Larger areas are needed to ensure the viability or long-term persistence of species.

To prevent species extinctions and loss of associated phylogenetic diversity and ecological function, additional conservation investments are urgently needed, particularly in areas with both high densities of species of conservation concern and high levels of threat. Comparable hemispheric or global-scale synthesis and analysis of the spatial dynamics of other taxa, and more comprehensive data on the distribution of reserves and other managed areas, particularly in the tropics, would create an even more compelling assessment of priorities for conservation investments.

ACKNOWLEDGMENTS

We thank D. Camuso for GIS assistance. G. da Fonseca, B. Fenton, T. Kunz, R. Medellin, B. Patterson, and J. M. Scott provided useful comments. The work was supported by NSF grant DEB-0074676 (SJA), the National Center for Ecological Analysis and Synthesis (NCEAS) through NSF grant DEB-0072909, the University of California, and the Santa Barbara campus, and by Department of Biological Sciences, Texas Tech University, especially J. Zak.

REFERENCES

Andelman, S.J. & Willig, M.R. (2002). Alternative configurations of conservation reserves for Paraguayan bats: considerations of spatial scale. *Cons. Biol.*, 16, 1352–1363.

Andelman, S.J., Ball, I., Davis, F. & Stoms, D. (1999). *Sites v. 1.0: An Analytical Toolbox for Designing Ecoregional Conservation Portfolios*. The Nature Conservancy, Arlington, VA.

Burgess, N.D., Rahbek, C., Larsen, F.W., Williams, P. & Balmford, A. (2002). How much of the vertebrate diversity of sub-Saharan Africa is catered for by recent conservation proposals? *Biol. Conserv.*, 107, 327–339.

Ceballos, G. & Ehrlich, P.R. (2002). Mammal population losses and the extinction crisis. *Science*, 296, 904–907.

Dinerstein, E., Olson, D.M., Graham, D.J., Webster, A.L., Primm, S.A., Bookbinder, M.P. & Ledec, G.A. (1995). *Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean*. WWF, The World Bank, Washington, DC.

Dobson, A.P., Rodriguez, J.P., Roberts, W.M. & Wilcove, D.S. (1997). Geographic distribution of endangered species in the United States. *Science*, 275, 550–553.

Dobson, A.P., Rodriguez, J.P. & Roberts, W.M. (2001). Synoptic tinkering: integrating strategies for large-scale conservation. *Ecol. Appl.*, 11, 1019.

Eisenberg, J.F. (1989). *Mammals of the Neotropics. The Northern Neotropics*, Vol. 1. University of Chicago Press, Chicago, IL.

Eisenberg, J.F. & Redford, K.H. (1999). *Mammals of the Neotropics. The Central Tropics*, Vol. 3. University of Chicago Press, Chicago, IL.

Faith, D.P. (1994). Phylogenetic pattern and the quantification of organismal biology. *Philos. Trans. R. Soc. B.*, 345, 45–58.

Ferrier, S., Pressey, R.L. & Barrett, T.W. (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. Cons.*, 93, 303–325.

Hall, E.R. (1981). *The Mammals of North America*, 2nd edn. Wiley, New York.

Hunter, M.L. & Yonzon, P. (1993). Altitudinal distribution of birds, mammals, people, forests and parks in Nepal. *Cons. Biol.*, 7, 420–423.

Hutson, A.M., Mickleburgh, S. & Racey, P.A. (2001). *Michrochiropteran Bats: Global Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland.

IUCN (1993). *Parks for Life: Report of the IVth World Congress on National Parks and Protected Areas*. IUCN, Gland, Switzerland.

IUCN (2000). *Red List of Threatened Species*. IUCN, Gland, Switzerland.

Jennings, M.D. (2000). Gap analysis: concepts, methods and recent results. *Landscape Ecol.*, 15, 5–20.

Jones, K.E., Purvis, A. & Gittleman, J.L. (2003). Biological correlates of extinction risk in bats. *Am. Nat.*, 161, 601–614.

Kiester, A.R., Scott, J.M., Csuti, B., Noss, R.F., Butterfield, B., Sahr, K. & White, D. (1996). Conservation prioritization using GAP data. *Cons. Biol.*, 10, 1332–1342.

Koopman, K.F. (1982). Biogeography of the bats of South America. In: *Mammalian Biology in South America* (eds Mares, M.A. & Genoways, H.H.). Special Publication Series No. 6, Pymatuning Laboratory of Ecology, University of Pittsburgh, pp. 273–302.
Koopman, K.F. (1993). Order Chiroptera. In: *Mammal Species of the World: A Taxonomic and Geographic Reference* (eds Wilson, D.E. & Reeder, D.M.). Smithsonian Institution Press, Washington, DC, pp. 137–241.
Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature*, 405, 243–253.
May, R.M. & Nee, S. (1995). Taxonomy – the species alias problem. *Nature*, 378, 447–448.
Medellin, R.A., Equiha, M. & Amin, M.A. (2000). Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Cons. Biol.*, 14, 1666–1675.
Mittermeier, R.A., Myers, N., Thompsen, J.B., da Fonseca, G.A.B. & Olivieri, S. (1998). Global biodiversity hotspots and major tropical wilderness areas. *Conserv. Biol.*, 12, 516–520.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
Olson, D. & Dinerstein, E. (1998). The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conserv. Biol.*, 12, 502–515.
Patterson, B.D. (1994). Accumulating knowledge on the dimensions of biodiversity: Systematic perspectives on Neotropical mammals. *Biodiv. Lett.*, 2, 79–86.
Patterson, B.D. (1996). The species alias problem. *Nature*, 380, 589.
Pressey, R.L. (1995). Crown jewels or leftovers? *Search*, 26, 47–51.
Redford, K.H. & Eisenberg, J.F. (1992). *Mammals of the Neotropics. The Southern Cone*, Vol. 2. University of Chicago Press, Chicago, IL.
Rodrigues, A.S.L. & Gaston, K.J. (2001). How large do reserve networks need to be? *Ecol. Lett.*, 4, 602–609.
Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. *et al.* (2000). Biodiversity – global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.
Scott, J.M., Davis, F.W., McGhie, R.G., Wright, R.G., Groves, C. & Estes, J. (2001). Nature reserves: do they capture the full range of America's biological diversity? *Ecol. Appl.*, 11, 999–1007.
Soule, M.E. & Sanjayan, M.A. (1998). Ecology – conservation targets – do they matter? *Science*, 279, 2060.
Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991). What to protect – systematics and the agony of choice. *Biol. Cons.*, 55, 235–254.
Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Ann. Rev. Ecol. Syst.*, in press.

Editor, M. Hochberg
Manuscript received 6 June 2003
First decision made 13 June 2003
Manuscript accepted 18 June 2003

Fast track submitted and reviewed