Global mammal distributions, biodiversity hotspots, and conservation

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Hotspots, which have played a central role in the selection of sites for reserves, require careful rethinking. We carried out a global examination of distributions of all nonmarine mammals to determine patterns of species richness, endemism, and endangerment, and to evaluate the degree of congruence among hotspots of these three measures of diversity in mammals. We then compare congruence of hotspots in two animal groups (mammals and birds) to assess the generality of these patterns. We defined hotspots as the richest 2.5% of cells in a global equal-area grid comparable to 1° latitude × 1° longitude. Hotspots of species richness, ''endemism,'' and extinction threat were noncongruent. Only 1% of cells and 16% of species were common to the three types of mammalian hotspots. Congruence increased with increases in both the geographic scope of the analysis and the percentage of cells defined as being hotspots. The within-mammal hotspot noncongruence was similar to the pattern recently found for birds. Thus, assigning global conservation priorities based on hotspots is at best a limited strategy.

hotspot congruence | birds | patterns of species distribution | endemism | threatened species

Few topics in conservation biology have received as much attention as hotspots of species diversity. Hotspots have been widely used to determine priority areas for conservation at different geographic scales, and in recommending concentrating resources in those regions to maximize the number of protected species (1, 2). Hotspots are defined as either the top sites in terms of species diversity or as the most threatened and most diverse sites (1, 3, 4). In these definitions, identifying hotspots requires a measure of species diversity, which often is species richness, number of restricted-range (e.g., endemic) species, or number of species at risk, and a measure of threat, which often is human population density or land converted to agriculture (5, 6). A critical assumption of the use of hotspots for conservation that has not been widely tested at a global level is how much congruence or overlap there is among hotspots of species richness, endemic species, or species at risk. Wide overlap among these three types of hotspots implies the selection of fewer sites to represent all species and the possibility of using one of them as a surrogate for the others.

In this paper we assessed the distribution of 4,818 nonmarine mammal species (excluding cetaceans, sirenians, and pinnipeds; list available from G.C. on request) to make a general evaluation of the utility of hotspots for determining conservation priorities for the mammals of the World. Global patterns of species distribution were assessed by comparing the distribution of all mammal species in 17,800 equal-area terrestrial cells of 100 × 100 km (5, 7). Using this database, we evaluated (*i*) mammalian species richness, endemism (hereafter, more accurately, restricted–range species or "narrow-ranging" species (8), and threatened species: (*ii*) hotspots for those three aspects of mammal diversity, defined as the top 2.5% of cells in each category: (*iii*) congruence among the three kinds of hotspots and comparisons with published data on bird hotspots; (*iv*) sensitivity of results to hotspot definitions (i.e., geographic area covered by the hotspot and the percentage of cells considered as hotspot cells); and (*v*) efficiency of hotspots for conservation of mammalian species diversity.

Results and Discussion

The global distribution of overall mammalian species richness, restricted-range species, and threatened species is summarized in Fig. 1. As we expected on the basis of a plethora of studies, species richness of mammals is concentrated in tropical regions throughout the world (9, 10). What our analysis has added is the identification of particular regions with high species diversity at a fine scale throughout the World. The highest concentrations being found in northern South America, especially in the Amazonian lowlands, the Andes, East Africa, and Southeast Asia (Fig. 1*A*). In contrast, although restricted-range species are found on all continents, they are concentrated in relatively few regions containing many islands, peninsulas, or island-like habitats such as mountaintops (Fig. 1*B*). In the Americas there are relatively continuous concentrations of restricted-range species in a large region extending from central Mexico to the northern and central Andes, and in the Atlantic forests of Brazil. In Africa, restricted-range species are found commonly in the tropical lowlands of Cameroon in the west, in the inland and coastal forests of East Africa, in the Ethiopian highlands, and on Madagascar. Restricted-range species in Asia are frequent in southern India and Sri Lanka, southwestern China, Vietnam, Taiwan, Malaysia, Indonesia, Philippines, New Guinea, and northern Australia. As expected, the occurrence of centers of threatened species is concentrated in regions with high-impact human activities, and it follows to a certain extent the patterns of species richness. Threatened species are found throughout the world, with higher concentrations in tropical regions of the Western Hemisphere, Africa, and Asia (Fig. 1*C*).

Our second objective, the identification of hotspots, defined as the top 2.5% of cells in each category, showed that hotspots are concentrated in very few places. It was unexpected that mammalian hotspots of species richness were found in only two primary regions (Fig. 2*A*): (*i*) Central America and northern South America and (*ii*) equatorial Africa, especially in the east. In contrast, restricted-range species showed hotspots, as expected, in limited areas scattered in Mexico, Central America, northern South America, Madagascar, Sri Lanka, Indonesia, New Guinea, the Philippines, and Taiwan (Fig. 2*B*). The lack of hotspots for restricted-range species in Africa is notable, especially when considering the high concentration of species richness hotspots there, and both the high number of restricted-range species and identified hotspots of restricted-range species in continent-wide analyses (11). Hotspots of threatened species

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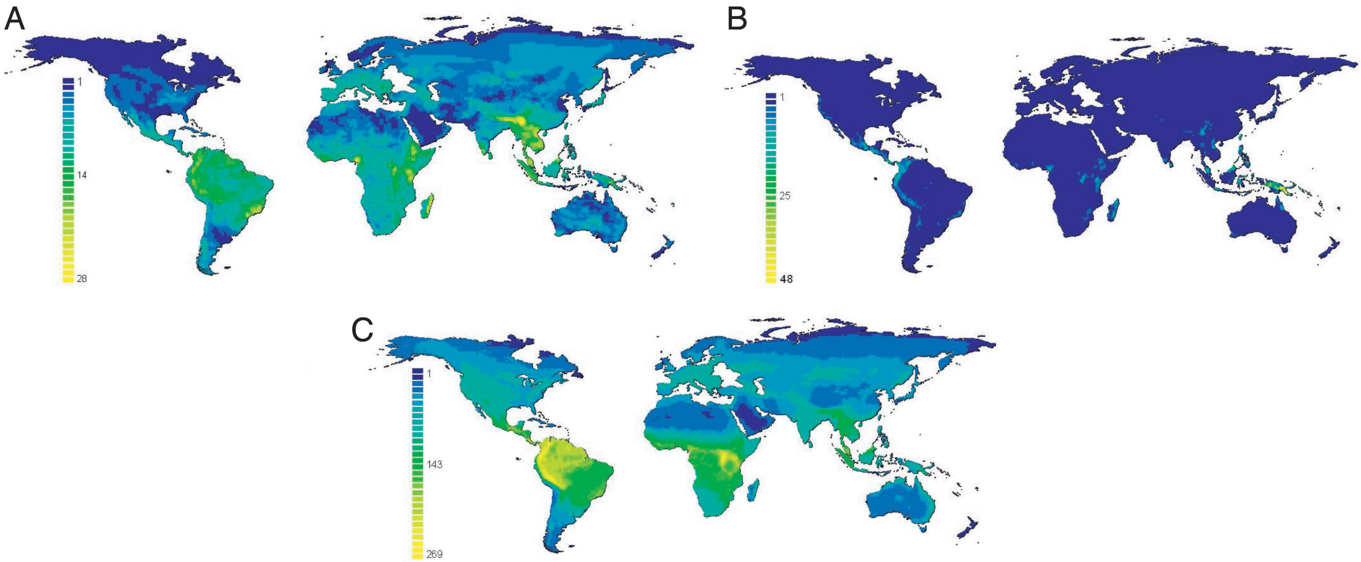

Fig. 1. Patterns of species distribution of mammals throughout the world, showing species richness (*A*), restricted-range species (*B*), and threatened species (*C*). All scales are in terms of number of species per 10,000-km^2 grid cell. (See *Materials and Methods* for further details.)

are found in a scattering of locations occupying roughly a quarter of the area of the Western Hemisphere species richness hotspot, but also include the Atlantic forests in Brazil, about a third of the equatorial Africa species richness hotspot, plus much of Madagascar and part of western Africa, and the western Ghats in India, parts of Sumatra, Borneo, Sulawesi and Papua New Guinea, and the Himalayan foothills southward to Singapore (Fig. 2*C*). The total number of mammal species found in the three types of 2.5% hotspots is surprisingly high (n = 2,833, or 59% of all species, Table 1), but there is a lot of variation. The number of species represented in the species-richness hotspots was only 26% of all mammal species, whereas the restricted-range and threatened hotspots contained 32% and 47%, respectively (Table 1). Although seemingly contradictory, these results are expected on the basis of the average area of distribution of mammals (5). All restricted-range species and many threatened species have very narrow, little-overlapping geographic ranges. The 2.5% restricted-range and threatened species hotspots are therefore more extensively distributed, covering more species because they lack the high species overlap of the richness hotspots.

The broad patterns in mammalian distributions are remarkably similar to those in birds (4), the main difference being the higher species richness in the mammal hotspots despite the higher global species richness of birds (>9,000 species). There are, however, some clear differences in detail. There are hotspots of bird species richness in Asia, but none for mammals. But there are mammalian hotspots for restricted-range and threatened species in Papua New Guinea and Madagascar, where none were found for birds.

Cumulatively, the three types of mammalian hotspots included 859 grid cells (Fig. 3 and Table 2). Those grid cells are equivalent to ≈5% of Earth's ice-free land surface.

How much congruence is there among hotspots? Under the 2.5% criterion, only 1% of cells were common to all three types

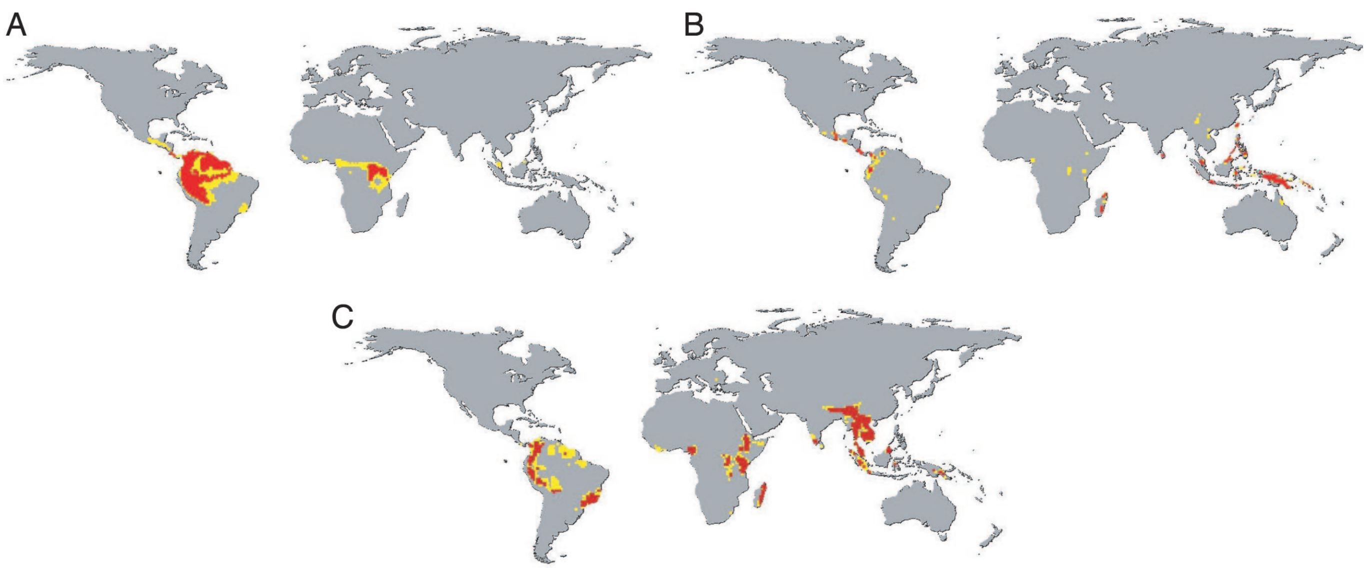

Fig. 2. Hotspots of species richness (*A*), restricted-range species (*B*), and threatened species (*C*). The 2.5% hotspots are shown in red, and the 5% hotspots are shown in yellow and red.

Table 1. Representation of mammalian species richness, restricted-range species, and threatened species in the 2.5% and 5% hotspots

Hotspots	Total species*	Species (%) 2.5% criterion	Species (%) 5% criterion
Richness	4,818	1,265 (26)	1,919 (40)
Restricted	1,520	1,525 (32)	2,565 (53)
Threatened	1,116	2,257 (47)	2,630 (55)
Total in all hotspots		2,833 (59)	3,274 (68)

The first column indicates the number of species in that category; e.g., ''restricted-range species'' is the total number of mammal species with narrow ranges (>250,000 km^2). The first numbers (''Species'') in columns 3 and 4 (''2.5% criterion'' and ''5% criterion'') indicate the total numbers of species represented in the different hotspots, and the numbers in parentheses show the percentages of species represented with respect to total number of nonmarine species richness *on the planet* (''Global total,'' 4,818 species).
*Global total (total richness = all species in study, 4,818).

Table 2. Results of the 2.5% defined hotspots under three different types of diversity measure

2.5% defined hotspots	Area in 10,000 km^2 (% total land mass)	Number of species (% total mammal spp.)
Richness	443 (2.4)	1,265 (26)
Restricted	128 (1)	1,525 (32)
Threatened	409 (2.3)	2,257 (47)
Total in all hotspots	859 (4.7)	2,833 (59)

The number of 10,000-km^2 grid cells defined as hotspots and the number of mammal species represented in those cells are tabulated. Note the different numbers of cells in each type of hotspot, with the most in richness, as explained in the text.

of hotspots of mammalian diversity (Tables 2 and 3). Similarly, the number of mammal species found in cells that were common to all three types of hotspots was small (16%, 444 species) and varied from 2% to 23% in cells shared by just two types of hotspots (Fig. 3). The number of species exclusive to each hotspot type varied from 4% to 19% and was 12% on average. The equivalent numbers for birds (4) varied from 23% to 32%, respectively (Fig. 4). Interestingly, 38% (1,063) of the mammalian species were exclusively found in one type of hotspot; for example, 24% (536) species were represented only in the hotspots of threatened species, although they may, of course, be found outside of hotspots. In addition, for both birds and mammals the aspect of diversity that gives the greatest number of species in a single cell is overall richness (birds 959, mammals 269), followed by restricted-range species (birds 89, mammals 48), and then by threatened species (birds 31, mammals 28). However, both restricted-range and threatened species hotspots represent a larger proportion of both mammalian and avian (4) species richness than species-richness hotspots (Fig. 4).

The little congruence in detail among hotspots based on richness, restricted-range species, and threatened species was expected for three reasons: (*i*) broad scale patterns of species richness are strongly influenced by widespread species, (*ii*) the roles of ecological and evolutionary processes in determining geographic ranges of widespread and restricted-range species, are frequently different, and (*iii*) the differential environmental correlates of species richness, restricted-range species, and threatened species, among many other factors (12, 13). Although no information is available for mammals at a broad geographic scale, an instructive example is found in African birds. In this case primary productivity is a good predictor of overall species richness and relatively unimportant for restricted-range species, whereas topographic heterogeneity is the most important predictor for restricted-range species and of negligible relevance for widespread species (12).

In relation to our fourth objective, we predicted that congruence would rise with increasing the threshold for defining the hotspots (i.e., by increasing the percentage of cells considered as hotspots) and by enlarging the geographic scale (i.e., by increasing the size of the cells from 10,000 km^2). This prediction arises from the patterns of species distribution of overall species richness, restricted-range species, and threatened species, where the probability of including more species is directly related to area (3, 4, 9, 10, 14). We found that even small increments in these factors, i.e., the percentage of cells considered as hotspots and the size of the cell area, drastically increase the congruence among the three aspects of biodiversity. Our sensitivity analysis moving from a 2.5% criterion to 5%, 20%, and 40% of grid cells criteria showed the expected increase in the number of species represented in the hotspots (Fig. 5*A*). For example, the 5% hotspots expand to include 1,482 cells (i.e., 58% more cells than in the 2.5% hotspot criterion), with additional grid cells in the species richness hotspots America and Africa as well as some in the Malay Peninsula and Borneo (Fig. 2 and Table 1). In the case of both restricted-range and threatened species, additional cells are found on all continents (Fig. 2). Similarly, the number of species represented in the hotspots showed a large increment and included 68% of the total terrestrial mammal fauna. Of those species, the number represented in all three types of hotspots increased from a mere 16% to 42%, and the number of species found exclusively in one type of hotspot dropped from only 23% to 19%. Increasing the percentage of cells considered as hotspots

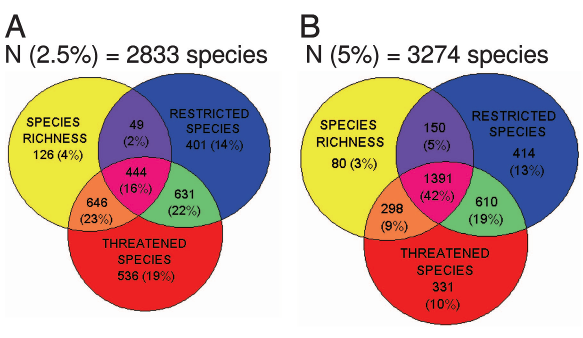

Fig. 3. Congruence of mammalian species richness, restricted-range species, and threatened species in the 2.5% (*A*) and 5% (*B*) hotspot grid cells. Note the relatively high number of species shared by all grid cells in the 5% hotspots. Percentages are of total number of mammal species represented in three types of hotspots (see Table 2).

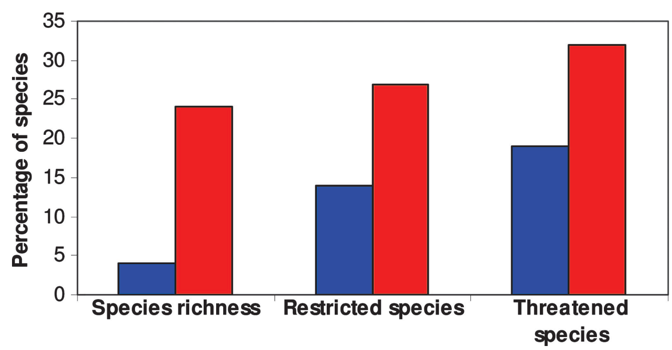

Fig. 4. Comparison of the percentage of species represented in the three types of hotspots of diversity between mammals (blue bars) and birds (red bars, data from ref. 4).

Table 3. Congruence among the hotspots

	Congruence of hotspots, %		
	Richness	Restricted-range species	Threatened species
Richness	0.0001	2	23
Restricted-range species	1	0.0001	22
Threatened species	10	2	0.0001

The overlap in species (above diagonal) and cells (below diagonal) is shown. The statistical significance of comparing overlap versus random is indicated in the diagonal.

even more, to 20% and 40%, markedly increased the congruence among the three aspects of biodiversity, from 16% to 83% (Fig. 5). Comparable trends have been recently reported for birds (4), indicating the possibility that this is a general trend. A sensitivity analysis also showed that increasing the size of the cell strongly improved the congruence among hotspots determined on the basis of richness, restricted-range, and threat (Fig. 5*B*). Our largest cell size (300 × 300 km) are slightly smaller to the average size of the ecoregions used for recent comparison of congruence among vertebrate distributions (8). At that level of resolution, as congruence increases endemism becomes a useful surrogate for species richness and threat.

Finally, we tested the efficiency of hotspots for conservation of mammalian diversity in two ways; by using a complementarity analysis (that is, determining networks of sites that complement each other in their species composition) and by comparing the number of species represented in the three types of hotspots. The

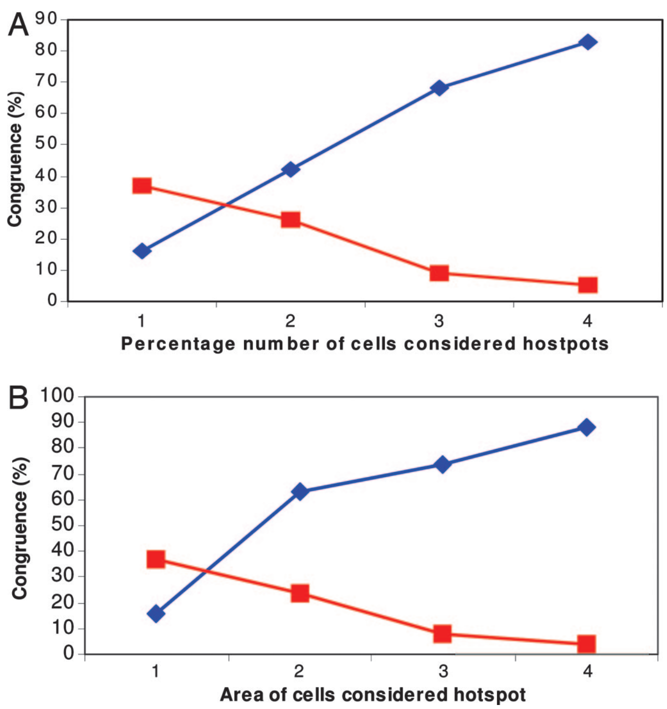

Fig. 5. Congruence of mammalian species richness, restricted-range species, and threatened species clearly increases as a function of both the number of cells considered as hotspots (*A*) and the area covered by the hotspots (*B*). In *A*, the percentages of cells considered hotspots, 2.5%, 5%, 20%, and 40%, are represented as 1, 2, 3, and 4, respectively, on the *x* axis. In *B*, the areas covered by the hotspots, 10,000, 20,000, 40,000, and 90,000 km^2, are represented as 1, 2, 3, and 4, respectively, on the *x* axis. The blue line indicates the percentage of species shared by the three types of hotspots; the red line indicates the percentage of species found in only one of the three types of hotspots.

complementarity analysis revealed, as expected, considerable overlap in the three aspects of species diversity in contiguous hotspot grid cells, because adjacent cells could even have identical faunas and still be included in the hotspot. Overall, only 17% of all of the 443 species richness hotspot grid cells selected on the 2.5% criterion were required to represent all of the species found in those hotspots in at least one cell; i.e., there is a very large overlap in species composition among hotspot cells. In the Western Hemisphere only 4% of the hotspot cells were needed to represent all species, whereas in Africa such species representation required 30% of the cells. Using an optimization framework such as complementarity can greatly improve the efficiency of hotspots in representing the maximum number of species in the minimum number of cells. Several other papers, including one of ours evaluating conservation priorities of mammals throughout the world (5), have demonstrated that complementarity analysis is an efficient tool for selection of sites for conservation (2, 3, 5, 15).

Our comparison of the ability of the different hotspots (under the 2.5% criterion) to include the largest number of species showed, as we expected, that hotspots of species richness contained fewer species than hotspots of restricted-range or threatened species (Table 2 and Fig. 3). Hotspots of restricted-range species represented only 68% of the species present in the hotspots of threatened species. But they encompassed many fewer cells, 31% of the number considered hotspot cells for threatened species (Table 2). A straightforward implication is that at a global scale the use of hotspots of restricted-range species and/or threatened species for selecting priority sites for conservation is more appropriate than using hotspots of species richness. This is true, however, only if our goal is to maximize the number of species conserved without consideration of the number of populations or percent range of each protected (5). Similar conclusions have been reached by other studies at smaller geographic scales (3).

Of course, one must carefully consider critical issues related to this kind of global evaluation when reaching conclusions about its application to conservation. First, the use of rough geographic range maps such as the ones used here has to be taken into account. These range maps depict what is call the *extent of occurrence*, which is the area defined by the outer limits of the range, instead of the *area of occupancy*, the total area of sites in which one can actually encounter individuals of the species (9, 15). At the moment, we have little choice, but it is clear that this decision is nonconservative, because some of the cells considered to contain species will in fact occur within the extent of occurrence but not the area of occupancy (as shown, for example, in butterflies, e.g., ref. 16). Our results show general patterns, but for actual selection of sites for conservation more detailed information about distributions at a finer scale is highly desirable (G.C., J. Pacheco, G. C. Daily, A. Sanchez-Azofeifa, and P.R.E., unpublished work).

Additionally, there is no particular reason to expect that areas of species richness, range restriction, and threat should overlap greatly, considering the ecological and evolutionary histories underlying the geographic distribution of species and factors generating anthropogenic threats. For instance, the greatest center of avian species richness is on the eastern slopes of the Andes, whereas various islands are centers for bird restriction and threat (4). The archipelagos and adjacent land mass areas of Southeast Asia contain no centers of avian species richness, but high concentrations of both restriction and threat. So, as we show here, the entire "hotspot" approach based exclusively on species composition, which was extremely valuable in focusing attention on species diversity in the past, now requires more detailed analyses to be really useful. A combination of threat estimation (1) and complementarity evaluation (2, 15) is clearly a solid approach that greatly improves the usefulness of the hotspot approach.

Hotspots evaluated at the ecoregion level (8) have widely recognized limitations in conservation planning because essentially the entire biosphere has now been altered by human actions and units as large as ecoregions will contain many areas that are not suitable habitat (17). There are no fully "pristine" areas to preserve outside of some deep in Earth's crust that harbor bacterial communities, and determination of areas of relative conservation value at smaller geographic scales is therefore necessary. In addition, most of biodiversity lies within developing countries, often threatened because of political endemism (18), and what reserves might have already been established in hotspots frequently are "paper parks" (19) or subject to local human population pressures. The likelihood of species migrations in response to global climate change (20) adds further complexity to the development of conservation strategies, and further limits the present usefulness of the classic hotspot approach.

Smaller-scale analyses are now part of the protocol of countryside biogeography (21), which focuses on the evaluation and enhancement of the hospitability of substantial human-disturbed areas to biodiversity and ways to enhance it. It pays attention to the combined problems of preserving both biodiversity and ecosystem services at local and regional scales (22, 23). This paradigm requires a shift away from an exclusive focus on preservation of species to that of populations. Populations supply the critical services, are substantially more threatened than species themselves (18, 24), and generally have much more restricted distributions than species. Of course, the continuing erosion of population diversity bodes ill for species diversity as well. Therefore, future evaluations of hotspots should involve criteria beyond congruence of patterns of cell occupancy. One such criterion is the need for preserving substantial numbers of populations in or out of hotspots (18)—the sort of issue addressed by the "ten percent of range criterion" used in a recent estimation of global extinction threats to land mammals (5). Others, of great importance to conservation planners, are complementarity, connectivity, disturbance, and buffering (25, 26), all of which must be added to the consideration of even the relatively small-scale cells used in this study. Finally, it is important to evaluate how socio-economic data can be incorporated into this kind of macroecological and biogeographic analysis (27, 28).

Conclusions

Conservation biologists and managers must carefully reconsider conservation priorities. They must wrestle with difficult questions not included when efforts are focused solely on hotspots of species diversity, however they are defined. The crucial issue is balancing allocation of effort to conservation of species diversity with protection of population diversity and ecosystem services, especially when the elements to be conserved occur in "coldspots" (29). That means acquiring information on complementarity within and between groups that can be used in making difficult judgments about trade-offs between redundancy and diversity at the species level. For instance, two species of predatory insect may undergo population increases and maintain a pest-control service as a species of insectivorous bat declines. How should the joint distributions of the three be evaluated? This involves the vexed issue of trade-offs between preservation of existence values and ecosystem services, and further problems related to accelerating climate change. Making judgments on ecosystem services involves a similar series of issues at the population level. Indeed, conservation biologists will soon be converging on economists with a strong focus on "elasticity of substitution" (30).

Considering how little is known about the distribution and ecology of most organisms—indeed, of even the best-known groups such as mammals, birds, and butterflies—it is clear that time, funds, and personnel will not be available in the foreseeable future to illuminate these issues in detail except for a small sample of systems. Even the results here, for the mammals, whose distributions are known in more detail than most of the biota, will likely need revision as new biogeographic information becomes available. Therefore research effort must be concentrated on carefully selected test systems. In addition, all conservation biologists should be attempting to find ways of reducing the basic drivers of biodiversity loss: population growth, overconsumption by the rich, and the use of faulty technologies and socio-economic-political systems (30).

Materials and Methods

We developed a geographic information system including ArcView 3.1 shapefiles for each species (5, 9). The files contain the known geographic range depicted by a boundary map (extent of occurrence) (9). Species richness was defined as the total number of mammal species in a single cell. Restricted-range species referred to the total number of species in each cell having a geographic range less than or equal to 250,000 km^2. Threatened species in each cell were all species considered threatened, endangered, or critically endangered by the International Union for the Conservation of Nature and Natural Resources (IUCN) (31). Finally, we carried out an optimization analysis using a complementarity algorithm (MARXAN) to assess the efficiency of hotspots in representing the three different aspects of mammal diversity. The analysis selects the minimum number of grid cells required to represent all species in each category in the three kinds of hotspots (2, 15).

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