Global Gap Analysis: Priority Regions for Expanding the Global Protected-Area Network

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Protected areas are the single most important conservation tool. The global protected-area network has grown substantially in recent decades, now occupying 11.5% of Earth's land surface, but such growth has not been strategically aimed at maximizing the coverage of global biodiversity. In a previous study, we demonstrated that the global network is far from complete, even for the representation of terrestrial vertebrate species. Here we present a first attempt to provide a global framework for the next step of strategically expanding the network to cover mammals, amphibians, freshwater turtles and tortoises, and globally threatened birds. We identify unprotected areas of the world that have remarkably high conservation value (irreplaceability) and are under serious threat. These areas concentrate overwhelmingly in tropical and subtropical moist forests, particularly on tropical mountains and islands. The expansion of the global protected-area network in these regions is urgently needed to prevent the loss of unique biodiversity.

Keywords: conservation planning, conservation priorities, global gap analysis, irreplaceability, protected areas

The *in situ* conservation of viable populations in natural ecosystems is widely recognized as a fundamental requirement for the maintenance of biodiversity (CBD 1992). Accordingly, governments worldwide have invested in the creation of more than 100,000 protected areas in 227 countries or territories, occupying 11.5% of the planet's land surface area (Chape et al. 2003). However, little is known of the extent to which this global network fulfills one of its major goals—namely, protecting species biodiversity—or of the regions where protection is most lacking. This information is needed to guide the strategic expansion of the network and the effective allocation of scarce conservation resources to maximize the persistence of biodiversity on the planet.

In a previous study, we provided the global gap analysis assessing the effectiveness of protected areas in representing species diversity (Brooks et al. 2004, Rodrigues et al. 2004). That analysis revealed more than 1400 "gap species" of terrestrial vertebrates (12% of all species analyzed) that were not

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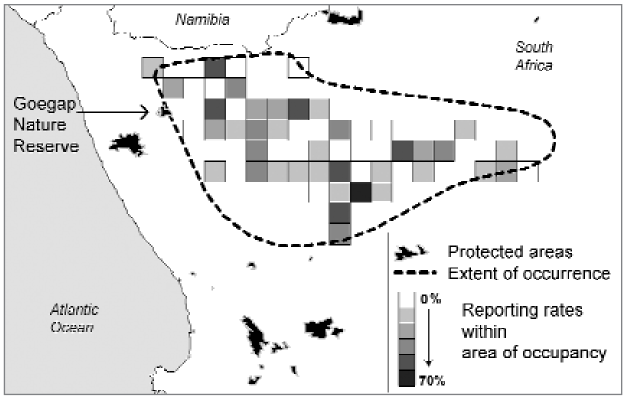

Figure 1. An example of commission errors obtained when overlapping species range maps with protected areas. The red lark, **Certhilauda burra,** *is classified as vulnerable and is endemic to South Africa. Its extent of occurrence, mapped by BirdLife International (2000), marginally overlaps the Goegap Nature Reserve, giving the impression that the species occurs in a protected area. However, this is a species whose habitat is naturally patchy, and most of this habitat has been overgrazed and degraded. It is estimated that the species occupies only about 1000 km^2 out of its 72,000 km^2 extent of occurrence (BirdLife International 2000). Data from a different source provide further insights. The area of occupancy (Gaston 1994) of this species has been obtained at quarter-degree resolution by the Southern African Bird Atlas Project (Harrison et al. 1997). These data confirm that most of the species' extent of occurrence is not occupied, and indicate that the species is likely to be absent from Goegap Nature Reserve. The variability in reporting rates (i.e., in the percentage of all visits made to a cell in which the species was recorded, positively related to the species' relative abundance across its range) demonstrates that the species' conservation value is uneven even within its area of occupancy.*

covered by protected areas in any part of their range. While this result clearly demonstrated that the global protected-area network is far from complete, we cautioned that this figure is a major underestimate of the numbers of gap species. "Covered species" were defined as those whose range is overlapped by any protected area (mapped as extent of occurrence; Gaston 1994), regardless of the size and characteristics of that area or the fraction of the range covered. In practice, large parts of the extents of occurrence of many species are unsuitable for their conservation (figure 1), and the management of many protected areas is not effective in ensuring their ecological integrity (Brandon et al. 1998). Consequently, a map of the distributions of gap species provides only a partial picture to guide investment in the expansion of the global protected-area network, as it is not an accurate guide to conservation requirements. This is particularly true for regions with small and scattered protected areas. In such regions, only species with very small ranges will not overlap with at least one such protected area, but many more species will, in practice, have only a very small proportion of their range included in protected areas (figure 2). Further, such a map does not incorporate a dimension of temporal threat (i.e., information regarding the likelihood of biodiversity loss in the future), which is a fundamental variable in defining which regions require the most urgent conservation investment (Margules and Pressey 2000).

Here we build on our earlier work to provide a pragmatic assessment of species coverage by the existing global protected-area network, which we hope will serve as guidance for the expansion of the network. We refine the criteria for considering a species covered, and we use this information to calculate the irreplaceability value (Pressey et al. 1994) of unprotected sites in complementing the global protected-area network. We combine the irreplaceability value with information on threat (Pressey and Taffs 2001) to highlight regions of the world that are current priorities for the expansion of this network.

Species and protected-area data

The data sets used in this analysis are described in detail elsewhere (Brooks et al. 2004, Rodrigues et al. 2004), and thus only a brief overview is presented here. Data on the global distribution of protected areas were obtained from the World Database on Protected Areas, or WDPA (2003). We used all records in the WDPA except (a) point records without geographic location (zero latitude and longitude), (b) records that did not seem to correspond to established protected areas, (c) point records for which no data on area were available, and (d) records corresponding to areas smaller than 100 hectares (ha). This 100-ha threshold is well below most estimates of the minimum area needed to support intact communities of vertebrate species (Gurd et al. 2001), and so it serves to exclude protected areas that are likely to be largely irrelevant for the conservation of the analyzed vertebrate species (although they may play other important conservation roles). Excluding protected areas smaller than 100 ha, and those for which no area was known, eliminated 54% of the protected-area records (mostly in Europe) but made little change in the overall area protected (only reducing it from 11.5% of the terrestrial surface to 10.9%). The WDPA records (2003) were used irrespective of their IUCN classification (IUCN 1994), which means that areas not traditionally considered as formal protected areas (e.g., indigenous reserves) were included in the analysis.

Distribution maps were obtained for 11,633 species of terrestrial vertebrates (Brooks et al. 2004): 4735 terrestrial mammals, compiled by the IUCN Global Mammal Assessment; 1171 globally threatened birds, compiled by BirdLife International (2000); 273 freshwater turtles and tortoises, based on the EMYSystem World Turtle Database (Iverson et al. 2003); and 5454 amphibians, compiled by the Global Amphibian Assessment (Stuart et al. 2004). These maps represent the extent of occurrence (Gaston 1994), and therefore their area is typically a large overestimate of the true area of occupancy of each species and an even larger overestimate of the area that is adequate for the protection of each species

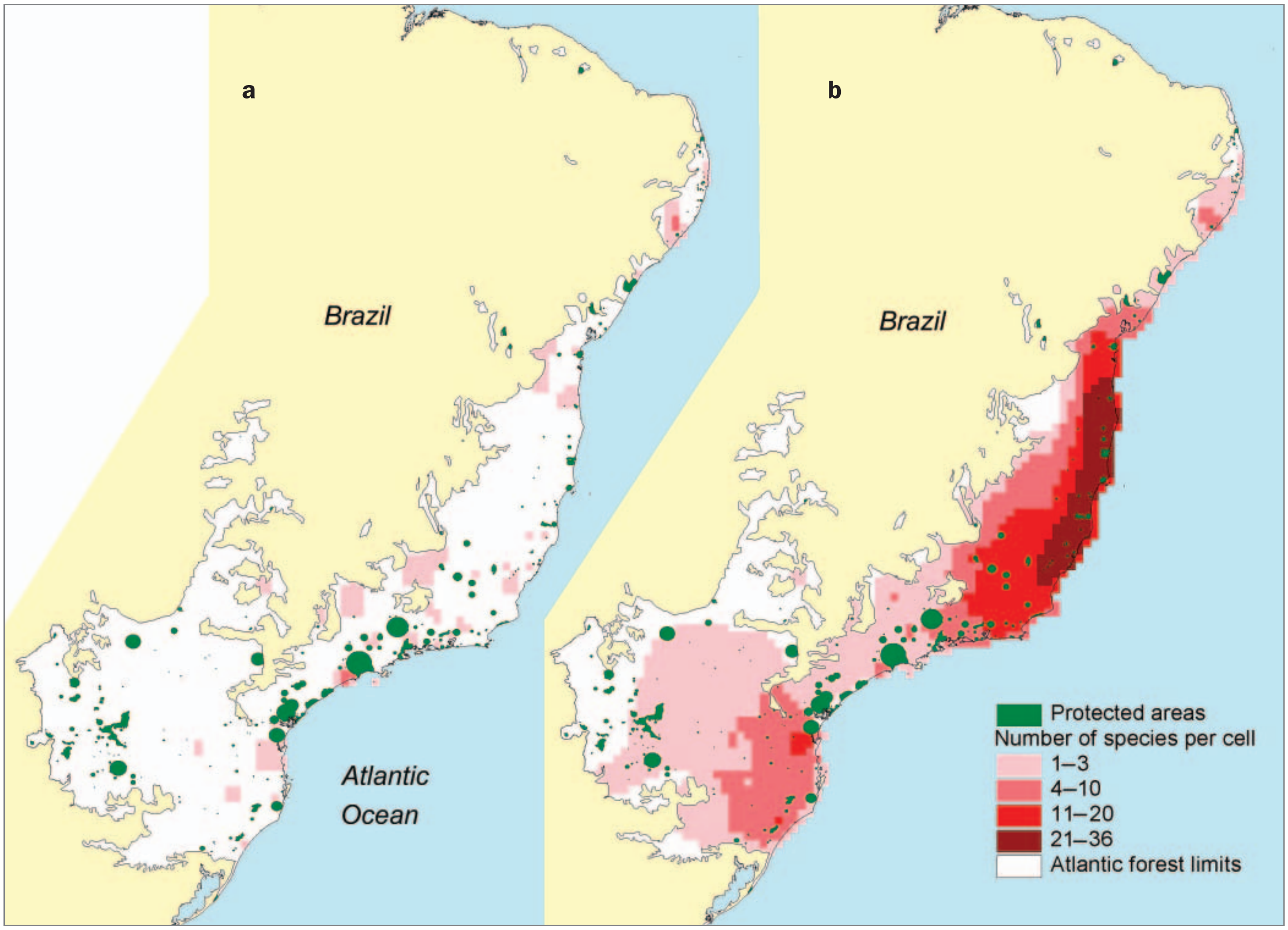

Figure 2. Coverage in protected areas of mammal, amphibian, turtle, and threatened bird species endemic to the Atlantic Forest hotspot (Myers et al. 2000). Endemic species were defined as those with at least 90% of their global range confined to the hotspot. (a) Density (per quarter-degree grid cell) of the 59 endemic species that fall completely outside protected areas (16% of the 375 endemic species analyzed). (b) Density (per quarter-degree grid cell) of the 136 endemic species that have less than 5% of their range in the hotspot covered by protected areas (36% of the total endemic species). The latter species are mainly concentrated in regions with small, scattered protected areas, and hence are not detected by a simple approach focusing on species that overlap no protected areas at all.

(figure 1). The species data also include assessments of threat status, with 1063 mammals, 1171 birds, 119 turtles, and 1543 amphibians already listed (IUCN 2003) or to be listed (Global Amphibian Assessment) as globally threatened by the IUCN Red List.

Identifying priorities for expanding the protected-area network

Gap analysis is a planning approach based on the assessment of the comprehensiveness of existing protected-area networks and the identification of gaps in coverage (Scott et al. 1993). The methodology used here has roots in two research lines: (1) the gap analysis approach applied by the US Geological Survey's Gap Analysis Program, or GAP (Jennings 2000), among others; and (2) systematic conservation planning methods for the selection of networks of protected areas (Margules and Pressey 2000).

Criteria for distinguishing gap species from covered species. The results of any gap analysis depend critically on the criteria applied to distinguish between a gap species and a covered species. In theory, the minimum requirement for a species to be considered covered by the global protected-area network is the inclusion within the network of at least one viable population. This requirement includes not only a minimum number of individuals sufficient to prevent the effects of genetic and demographic stochasticity (Soulé 1987) but also all the ecological infrastructure necessary for species persistence in the long term, with allowance made for the natural variability of environmental conditions (environmental stochasticity) and for natural or anthropogenic changes (such as climate change). These prerequisites for survival vary considerably among species. In practice, the data that are currently available on species and protected areas at the global scale (extent of species occurrence and polygons of protected areas) do not allow such complexity to be considered. Therefore, any criterion applied to these data to distinguish between covered and gap species is inevitably an approximation.

When data on species and on protected areas are overlaid, two types of error are obtained: *omission errors,* in which a species is considered absent from a protected area in which it is present, and *commission errors,* in which a species is considered present in a protected area where it is absent. While both are an inevitable consequence of limitations in the data, commission errors are likely to predominate (Rodrigues et al. 2004), particularly given the coarse representation of the extent of occurrence of many species (figure 1) and the fact that maps of the extent of occurrence by definition overestimate true occurrences. In addition, species may be present in protected areas but not effectively protected, if the management is not adequate to ensure the species' long-term persistence. Nevertheless, the larger the proportion of a species' range that is overlapped by protected areas, the higher the likelihood that the species is truly covered. While in our earlier analysis (Rodrigues et al. 2004) a species was considered covered if any portion of its range overlapped any portion of a protected area, the approach adopted in this analysis was to establish a target for representation of each species. Such a target was defined as the percentage of the species' extent of occurrence that must overlap protected areas for the species to be considered covered. A species not represented in any protected area is considered a gap species, while a species that meets only a portion of its representation target is considered a partial gap species.

More demanding representation targets (a larger percentage of the range) were set for species with more restricted ranges (figure 3). The exact thresholds used in this analysis necessarily have a degree of arbitrariness, but they were decided according to the following rationale. A constant representation target would bias the results toward widespread species (e.g., 15% of a wide range is still a large area, whereas 15% of a small range could be inadequate for the species' persistence). Furthermore, species with small ranges tend to be rare, not only in terms of range size but also in terms of local abundance (Gaston et al. 1997). This results in a "double jeopardy" for rare species (Lawton 1993): The number of individuals protected in 15% of the range of a narrow endemic species, for example, is disproportionately smaller than the number protected in the same fraction of the range of a widespread species. Species with small ranges tend to be more vulnerable to adverse natural events and anthropogenic activities, resulting in the well-known negative relationship between species' range size and their extinction risk (Gaston 2003). A 100% representation target was set for those species (18%) with very small ranges, smaller than 1000 square kilometers (km^2). Given the spatial resolution used in this analysis (one-half-degree cells), we could treat these species only as either 100% protected or fully unprotected. In practice, it makes sense that as species' ranges approach the size of functional protected areas, the species tend to be either totally covered or totally absent from protected areas. The 10% representation target for very widespread species means that these species are, on average, neutral to the analysis, as 10% is approximately the total area of the planet covered by protected areas (Chape et al. 2003). The 250,000-km^2 threshold is arbitrary, but it corresponds to one-third of all species.

Representation targets for migratory bird species were defined separately for their breeding and nonbreeding ranges, given that each of these may have different conservation requirements. For example, the target for the breeding range of the hooded crane *Grus monacha* (approximately 1,600,000 km^2 in southeastern and south-central Siberia, Russia) is 10%, while for the nonbreeding range (approximately 135,000 km^2 in Japan, South Korea, and China), it is 22%. The main threat to this species, which is classified as vulnerable, is habitat destruction in its nonbreeding grounds (BirdLife International 2000). If comprehensive data were available, a similar approach would have been appropriate for other taxa, such as congregatory mammal species (Mittermeier et al. 2003).

Prioritizing areas for the expansion of the global protected-area network. To investigate which areas are priorities for the expansion of the existing protected-area network, we used a half-degree geographic projection grid to divide the world's land area outside protected areas into nonoverlapping spatial units (hereafter referred to as "sites"). The resulting 105,086 unprotected sites have variable shapes and sizes, with a maximum area of approximately 3090 km^2 for a fully unprotected half-degree cell around the equator.

We calculated the percentage of each species' range that overlaps with each unprotected site. Combining this percentage with the representation target and the percentage of each species' range that was already protected, we calculated the irreplaceability value of each site (Pressey et al. 1993, Margules and Pressey 2000). The irreplaceability value of a site is the likelihood that it would be included in an expanded protected-area network that represented all species to their representation targets. Conversely, irreplaceability may be considered as the extent to which options for achieving these targets would be reduced if the site were not protected (Pressey et al. 1994). It ranges from 0% (a site that is not needed to achieve target goals) to 100% (a site for which there are no replacements; targets cannot be achieved without its protection). Sites with progressively lower irreplaceability therefore have progressively more options for replacement. Irreplaceability was estimated using a statistical predictor (Ferrier et al. 2000) implemented by C-Plan software (NSW NPWS 2001).

Site threat, or vulnerability, is a measure of the likelihood that biodiversity values in a site will be lost (Pressey and Taffs 2001). Threat information is frequently applied to assessing conservation priority, either through measures of human impact (e.g., lost habitat [Myers et al. 2000] and the potential for agriculture or forestry [Pressey and Taffs 2001]) or through a combined (multispecies) assessment of the probability of species loss (Root et al. 2003). There are advantages and drawbacks in any specific measure (see Gaston and colleagues [1997] for a discussion). Here, we adopted the latter

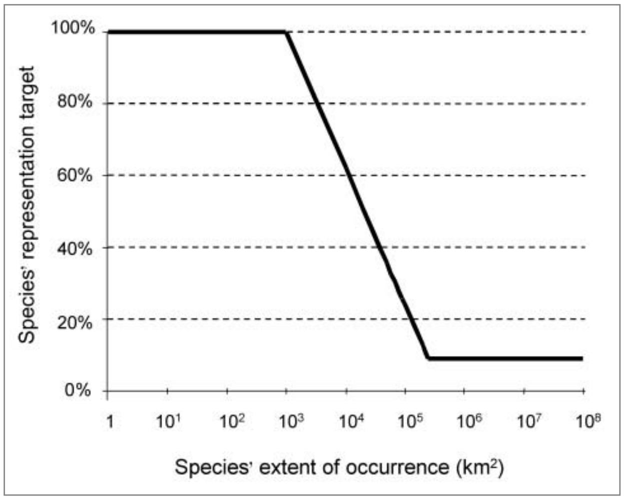

Figure 3. Relationship between each species' extent of occurrence and its representation target (percentage of range that must be overlapped by protected areas in order for the species to be considered covered). For very narrowly distributed species (extent of occurrence < 1000 square kilometers [km^2]), the representation target is 100% of the range; for very widespread species (< 250,000 km^2), the target is 10%. For species with ranges of intermediate size, the target was interpolated between these two extremes.

approach, which combines the IUCN threat categories of the different species in each site. This has two main advantages: The threat assessments producing the risk categorization are made by people who understand the life histories, population trends, and specific threats of the species; and the assessments can integrate detailed information across threatening processes, some of which are impossible to map even at a regional scale, let alone globally. In this analysis, threat levels were calculated using the extinction risk indicator (Butchart et al. 2004), which is based on the number of species in each Red List category (IUCN 2001), multiplied by a weight that represents the extinction risk of a species in that category. The weights were determined as 0.5 for critically endangered, 0.05 for endangered, and 0.005 for vulnerable species. These weights are based on thresholds in the IUCN (2001) criteria for extinction probability (criterion E), number of mature individuals (criteria C1 and D), range or extent of occurrence (criterion B1), and area of occupancy (criterion B2). First, a different set of weights was calculated for each criterion. For example, weights based on extinction probabilities over three generations were calculated assuming both a constant annual risk of extinction and a sigmoid extinction curve (cumulative probability of extinction as a function of time). Weights based on criteria B1, C1, and D fixed the risk of extinction for critically endangered species at 0.5, and assumed that the population size and range measures were inversely related to the risk of extinction. Then the weights based on different criteria were combined by taking their geometric average. Details of the calculation of the weights are given by Butchart and colleagues (2004).

Neither irreplaceability nor threat alone adequately predicts which areas should be given priority in the allocation of conservation resources. A site with high irreplaceability and low threat, while important, is not necessarily the highest priority for investment, because options for conservation will still be available in the future. Likewise, a site with high threat and low irreplaceability is not a high priority, because other spatial options are available for the conservation of the same biological values. Sites of high irreplaceability and high threat are those where options for replacement are not available either spatially or temporally; hence, these sites require immediate conservation attention to prevent the loss of unique biodiversity values. These correspond, therefore, to the highest priorities for conservation action (Margules and Pressey 2000, Pressey and Taffs 2001). The highest-priority sites for the expansion of the global protected-area network were identified as those that fall simultaneously into the higher classes of irreplaceability value (0.9 or greater) and threat value (the top 5% in values of the extinction risk indicator).

Species coverage and geography of priority areas for expanding the protected-area network

This analysis identified 1483 species (13% of all species analyzed) with zero coverage in protected areas, including 276 mammals (153 threatened), 940 amphibians (422 threatened), 23 turtles (14 threatened), and 244 birds (all threatened; an additional species had zero protection in its breeding range). The overall number of gap species is 4% larger than that reported in our earlier study (Rodrigues et al. 2004); this difference corresponds to species that are covered only by protected areas that are smaller than 100 ha or that are represented as point records. Significantly, the overwhelming majority (74%) of species do not achieve their representation targets (figure 4). Threatened species are even less well covered: 89% are either gap species (21%) or partial gap species (68%). Of the most threatened (critically endangered) species, 92% are either gap species (43%) or partial gap species (49%).

These results indicate that amphibians are markedly less well covered than other taxa, with mammals the best-covered group, followed by turtles and threatened birds (figure 4). The most likely explanations for this pattern include (a) differences in range size (much smaller in amphibians; Rodrigues et al. 2004), as species of restricted distribution have a higher probability of falling through the network; and (b) taxonomic bias, as few protected areas have been created with specific consideration of amphibians, while birds and mammals are more frequently taken into consideration. Both of these explanations are supported by differences within taxa. For example, 6% of all mammals, and 14% of all threatened mammals, are gap species. Yet these gap species do not include any carnivore (typically with large range sizes and in the spotlight of conservation attention), while in contrast, 7% of all rodents (23% of threatened species) are gap species.

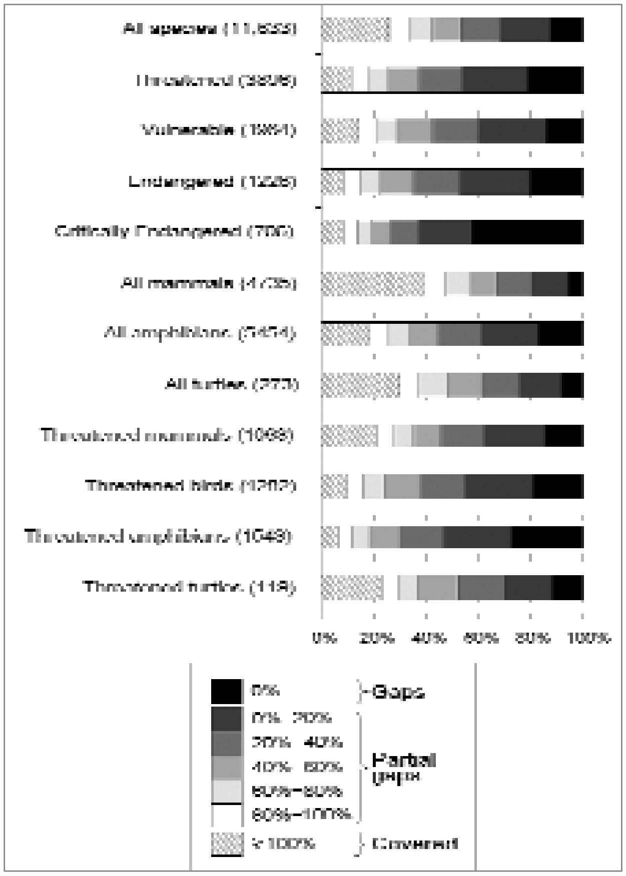

Figure 4. Proportions of gap, partial gap, and covered species across different taxa and different threat categories. Numbers in parentheses correspond to numbers of species, except for threatened birds, in which breeding and nonbreeding ranges are considered separately. Percentage values are the fraction of each species' representation target covered in protected areas.

Overall, the sites identified as urgent priorities for the expansion of the network of protected areas (figure 5) fall overwhelmingly in the tropics (which make up 85% of the priority area for protection, although they account for only 39% of the world's land area), especially in tropical and subtropical moist forests (65% of the priority area, compared with 14% of total land area). They are also disproportionately located on islands (31%, compared with 5% of total land area; islands are defined as all landmasses smaller than Australia). Those priority sites that lie on continents are generally located in regions of high topographic complexity (tropical mountains).

Asia emerges as an extremely high-priority region for new protected-area investment. In South Asia, the specific priority regions are the Western Ghats, Sri Lanka, and the eastern Himalayas. In East Asia, southern and eastern China and the Japanese Nansei-Shoto islands (or Ryukyu Islands) are the highest priorities. However, the most dense concentrations of sites requiring urgent new investment are in Southeast Asia, especially in Vietnam, in northern Thailand, in peninsular Malaysia, and on nearly all of the major Philippine and Indonesian islands. To the east, New Guinea, many Pacific islands (the Solomon Islands, Samoa, Fiji, French Polynesia, and Hawaii), New Zealand, and Australia's Queensland wet tropics emerge as major priorities for the establishment of new protected areas.

For Africa, the highest-priority sites for new conservation investment lie almost exclusively in the mountains, including upper Guinea, the Cameroonian highlands, the Albertine rift, the Ethiopian highlands, the Kenyan highlands, the Eastern Arc Mountains, the coastal forests of eastern Africa, Maputaland-Pondoland, and the Cape Floristic region. Madagascar is extremely important. Islands emerge as uniformly urgent, largely because of their threatened birds; notably high-priority islands are São Tomé, the Seychelles, Mauritius and Réunion, and the Comoros. The lack of priority sites in the Congo basin and the miombo–mopane woodlands of southern Africa is a reflection of the relatively broad distributions of species in these areas and, to a lesser extent, their existing protected-area coverage.

In the Western Hemisphere, four main regions are highlighted as urgent priorities for the establishment of new protected areas. The Andes and the neighboring lowland Pacific forests of the Chocó and Tumbes are extremely important, as are the Atlantic Forest, the Caribbean, and Central America. Although the Guayana Shield and the Amazon are noted centers of endemism, the lack of priority sites there reflects their extensive networks of protected areas and the relatively wide ranges of most of their species.

Although overall the map of priority sites for the expansion of the network of protected areas (figure 5) is similar to that of the density of gap species in our earlier study (Rodrigues et al. 2004), there are important differences. The most common discrepancy relates to regions that have increased in prominence, such as the Atlantic Forest of South America and the Western Ghats of India. These are regions that frequently include a network of small and scattered protected areas, which prevents more species from being identified as gap species (figure 2), but that are appropriately highlighted for their high irreplaceability and threat (Myers et al. 2000) when partial gap species are also considered.

On the other hand, some regions highlighted earlier (Rodrigues et al. 2004) for the presence of gap species have decreased in importance for expanding the global protected-area network (figure 5). These include regions of the Amazon and Congo basins, where threat is low, even if local irreplaceability is high at some points (although some of these are artifacts of higher sampling). Relatively low irreplaceability also contributes to the reduction in prominence of Somalia in the Horn of Africa; gap species there are relatively widespread (e.g., the beira, *Dorcatragus megalotis,* with a 78,000-km^2 extent of occurrence mainly restricted to Somalia), and consequently few individual sites are highlighted as highly irreplaceable. The most serious absences from the map of priorities for expanding the global network are small tropical islands, and this omission reflects a drawback of the threat measure applied. Indeed, such islands have typically high

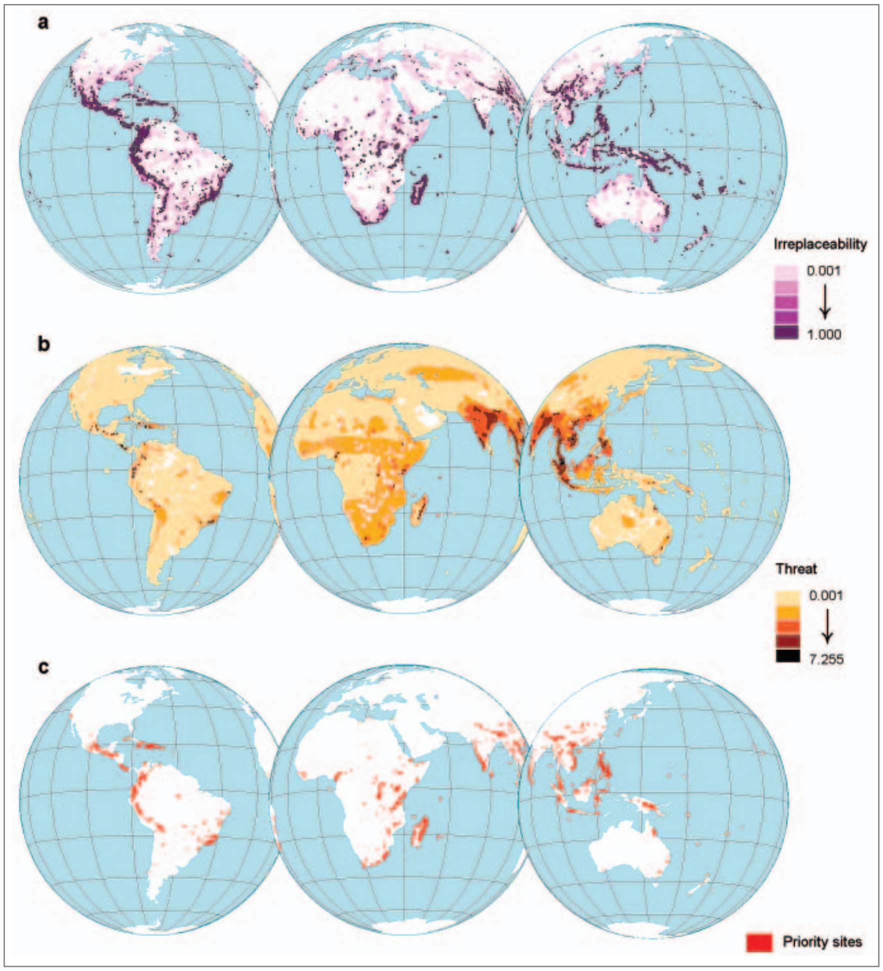

Figure 5. Global distribution of (a) irreplaceability, (b) threat, and (c) priority sites for the expansion of the global protected-area network, based on data for species of mammals, amphibians, turtles, and threatened birds.

levels of endemism (and hence high irreplaceability), their faunas are frequently highly threatened, and many have no protected areas at all (e.g., Príncipe Island in the Gulf of Guinea). However, small islands are naturally species-poor ecosystems (frequently aggravated by high past extinction rates; Pimm et al. 1995), and as such tend to have low absolute numbers of threatened species, even if these are a high proportion of their entire fauna. This artifact may be avoided in future analyses if threat levels are based on the percentage of all species in a given area that are threatened, and not only on absolute numbers of threatened species (this was not possible in this analysis, given that data on nonthreatened birds were not available globally).

Conservation implications

The sites highlighted in this analysis are urgent priorities for the expansion of a global network that covers vertebrate species comprehensively, but they are not the full set of sites that require conservation attention. Conversely, if a given site has not been highlighted as a priority, that does not mean it should not be considered for further protection. Only a limited number of species have been considered here, and while these are legitimate conservation targets in their own right, this analysis cannot claim to address all biodiversity. In particular, plants and invertebrates were not considered, and the network of marine protected areas is even less comprehensive than the terrestrial one (Roberts 2003), while freshwater ecosystems are some of the most threatened and neglected of all (Abell 2002). As information on additional taxa is being compiled (Brooks et al. 2004), the modeling approach explored by Ferrier and colleagues (2004) is another promising way of addressing broader biodiversity in a global gap analysis.

As more and better data become available, future assessments will include not only additional taxa but also more refined information on the range boundaries for those species analyzed, as well as the variations in population structure within those boundaries, to reflect more accurately regions where long-term viability can be ensured. Better data on protected areas will include information on management type and effectiveness, to enable improved evaluation of which species are likely to be adequately protected in which protected areas.

Interpretation of the results of the present analysis also needs to take into account that measures of threat and irreplaceability are scale dependent, and that they are determined by the parameters used in this analysis regarding species representation targets and extinction risk. Likewise, the final priority map depends on the criteria used to select the top sites in terms of irreplaceability and threat. Preliminary sensitivity analyses demonstrate that as these thresholds are relaxed (e.g., considering the top 10% of threatened species instead of the top 5%, or cells with irreplaceability greater than 0.8 instead of 0.9), a larger overall number of sites are identified as priority areas. While this affects the identity of the particular sites identified, it does not affect the global pattern of the results: The same regions stand out globally. Similar robustness was found in analyses of sensitivity to changes in other parameters. For example, if the weights used to calculate site threat are changed to give less relative value to the categories of higher threat (e.g., weights of 0.005, 0.05, and 0.5, rather than 1, 2, and 3, for vulnerable, endangered, and critically endangered species, respectively), some of the smaller islands disappear (those with lower species richness but in which faunas have higher threat levels), but the global patterns remain stable in terms of priority regions identified. Nevertheless, this reinforces the caveat that the results of this analysis cannot be considered as a binary distinction between important and unimportant sites.

Finally, the sites identified as urgent priorities for the expansion of the global network are not a useful guide to the location of the boundaries of new protected areas. Indeed, the spatial units considered here for unprotected sites are an artificial partition of the unprotected surface of the planet, created purely for analytical purposes. These sites are, on average, much larger than the vast majority (92%) of the world's protected areas; they do not correspond to meaningful units for land management; and they typically include a diverse array of habitats and land uses, of variable levels of conservation value. Given the coarse scale of this analysis, and the associated spatial uncertainty, our main recommendation is therefore that the areas highlighted become urgent priorities for finer-scale assessments. These assessments should investigate the feasibility and viability of expanding the global protected-area network to protect the species in each site that trigger high values of irreplaceability and threat. These assessments may reveal that other species-focused conservation tools besides formal protected areas are the most appropriate in some regions, including community management areas. The "key biodiversity areas" approach discussed by Eken and colleagues (2004) presents an appropriate framework for the identification of fine-scale conservation priorities within the larger-scale regions highlighted in this global gap analysis. Their approach, also based on irreplaceability and threat, incorporates much more detailed information on different species' conservation needs and on the adequacy of particular areas for the conservation of each species.

The global gap analysis is certainly not the first global assessment of priorities for conservation action. Previous studies, mainly led by international nongovernmental organizations, include endemic bird areas (Stattersfield et al. 1998), the Global 200 ecoregions (Olson and Dinerstein 1998), and biodiversity hotspots (Myers et al. 2000). The contribution of our analysis toward this composite picture comes from two characteristics that distinguish it from previous assessments at the global scale: (1) It is based on relatively detailed spatial data on the distribution of thousands of species, covering four classes of vertebrates; and (2) it explicitly accounts for the existing global protected-area network in defining priorities for future action that are complementary to existing conservation efforts. These differences in data and methods could have resulted in a quite divergent set of results, but they did not. On the contrary, the similarities between the present results and previously recommended priorities are striking: 97% of the priority area overlaps with at least one of the three global priority schemes mentioned above, 89% overlaps with at least two, and 59% overlaps with all three schemes. This demonstrates the need for expanding the protected-area network in regions that are widely regarded as global conservation priorities.

Although these results reinforce the importance of particular regions as global priorities, the vast majority of these regions are in low-income countries in the tropics, which can least afford the costs (especially the opportunity costs) of establishing and enforcing protected areas (James et al. 1999). Indeed, many of the existing protected areas in these regions are struggling because of the lack of resources needed to ensure that they can fulfill their conservation role (Brandon et al. 1998). Thus, our recommendation for the rapid and strategic establishment of protected areas in the regions highlighted as urgent priorities comes hand in hand with the recommendation that the existing protected areas be reinforced to ensure their effectiveness, and that the costs (Bruner et al. 2004) be borne largely by the global community, as represented by foundations, private corporations, bilateral and multilateral institutions, and individuals (Balmford and Whitten 2003).

Massive efforts to establish protected areas over the last few decades (Chape et al. 2003) have already contributed substantially to the conservation of global biodiversity. Yet the global protected-area network still falls short of minimally covering even terrestrial vertebrates, the best known and typically the most popular group of species (Rodrigues et al. 2004). If the planet is to conserve its living biodiversity heritage, a greatly increased and strategically placed investment in establishing new protected areas must be made as soon as possible. This gap analysis is a first attempt to establish a global framework to guide decisions for doing so.

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