may result from straightforward geometrical constraints. This variation may thus be expected in more realistic, numerical simulations of the geodynamo and may provide an important constraint on those models[12–14]. □

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# Effectiveness of the global protected area network in representing species diversity

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**The Fifth World Parks Congress in Durban, South Africa, announced in September 2003 that the global network of protected areas now covers 11.5% of the planet's land surface[1]. This surpasses the 10% target proposed a decade earlier, at the Caracas Congress[2], for 9 out of 14 major terrestrial biomes[1]. Such uniform targets based on percentage of area have become deeply embedded into national and international conservation planning[3]. Although politically expedient, the scientific basis and conservation value of these targets have been questioned[4,5]. In practice, however, little is known of how to set appropriate targets, or of the extent to which the current global protected area network fulfils its goal of protecting biodiversity. Here, we combine five global data sets on the distribution of species and protected areas to provide the first global gap analysis assessing the effectiveness of protected areas in representing species diversity. We show that the global network is far from complete, and demonstrate the inadequacy of uniform—that is, 'one size fits all'—conservation targets.**

Systematic approaches to conservation planning have been developed over the last two decades to guide the efficient allocation of the scarce resources available for protecting biodiversity[6]. Gap analysis is a planning approach based on assessment of the comprehensiveness of existing protected area networks and identification of gaps in coverage[7,8]. It has also been developed into a formal method now applied by the US Geological Survey National Gap Analysis Program[9] and others. Numerous gap analyses at regional scales reveal that coverage of biodiversity by existing networks of protected areas is inadequate[10,11]. Furthermore, many such networks are

  

Table 1 **Numbers of gap species in the current protected area network and in randomly selected networks**

| Taxon | Median range size (km$^2$) | Numbers of gap species | | | | |
|---|---|---|---|---|---|---|
| | | Current network (all PAs) | Current network (PAs >1,000 ha and IUCN I–IV) | Model I (equal area sites) | Model II (variable area sites) | Model III (tropical bias) |
| All species | | | | | | |
| Mammals ($n = 4,735$) | 247,341 | 258 (5.5%) | 644 (13.5%) | 297.7 (6.3%) | 342.3 (7.2%) | 226.6 (4.8%) |
| Turtles ($n = 273$) | 309,172 | 21 (7.7%) | 48 (17.6%) | 24.6 (9.0%) | 26.5 (9.7%) | 23.8 (8.7%) |
| Amphibians ($n = 5,454$) | 7,944 | 913 (16.7%) | 1,718 (31.5%) | 1,230.2 (22.6%) | 1,507.8 (27.7%) | 804.2 (14.7%) |
| Threatened species | | | | | | |
| Mammals ($n = 1,063$) | 22,902 | 149 (14.0%) | 314 (29.6%) | 191.8 (18.0%) | 218.2 (20.5%) | 151.6 (14.3%) |
| Birds ($n = 1,171$) | 4,015 | 232 (19.8%) | 437 (37.3%) | 349.7 (29.9%) | 409.6 (35.0%) | 275.4 (23.5%) |
| Turtles ($n = 119$) | 167,611 | 12 (10.1%) | 32 (26.9%) | 15.9 (13.3%) | 17.3 (14.6%) | 15.5 (13.1%) |
| Amphibians ($n = 1,543$) | 896 | 411 (26.6%) | 767 (49.7%) | 604.5 (39.2%) | 740.0 (48.0%) | 423.3 (27.4%) |
| All species analysed ($n = 11,633$) | 38,229 | 1,424 (12.2%) | 2,847 (24.5%) | 1,902.3 (16.4%) | 2,286.2 (19.7%) | 1,330.3 (11.4%) |

The total numbers of species and their respective median range size are given for comparative purposes. Values in parentheses are the percentage of all species/threatened species analysed within a given taxon. PAs, protected areas.

skewed towards particular ecosystems, often those that are less economically valuable, leaving others inadequately protected[12]. At the global scale, however, the degree to which biodiversity is represented within the existing network of protected areas is unknown.

In this analysis, we considered a species to be a 'covered species' if any protected area overlapped any extent of its mapped distribution, and otherwise to be a 'gap species'. Overall, 1,424 gap species (12% of all species analysed) were identified (Table 1). Protected areas may not retain all of their species if they are too small to maintain viable populations[13] or if they are used extractively[14]. Of the covered species, 1,423 were not represented in any protected area larger than 1,000 ha and in stricter conservation classifications (The World Conservation Union (IUCN) categories I–IV[15]). Threatened and restricted-range species are those of most conservation concern[16–18]. Sets of species with smaller median range sizes tend to have a higher proportion of gap species (Table 1). Hence, amphibians are the least represented taxon and, within any given taxon, threatened species (which tend to have smaller ranges) have proportionally higher numbers of gap species than do all species considered together. Overall, 20% of all threatened species analysed were identified as gap species.

The number of covered species is an overestimate, mainly because of two unrealistic assumptions. First, all protected areas are considered to be adequate for protecting every species, whereas in reality even those classified in IUCN categories I–IV vary substantially in the degree of effectiveness and enforcement[19]. Second, it assumes that species can be protected equally effectively in any part of their range, regardless of habitat suitability, and by the protection of any fraction of that range, regardless of viability constraints. In practice, simple presence within a protected area is insufficient to ensure the long-term persistence of many species, particularly those with demanding habitat or area requirements[13], and does not consider threats such as global climate change[20].

As species are only considered to be gap species if they are not touched by any protected area, concentrations of gap species in a

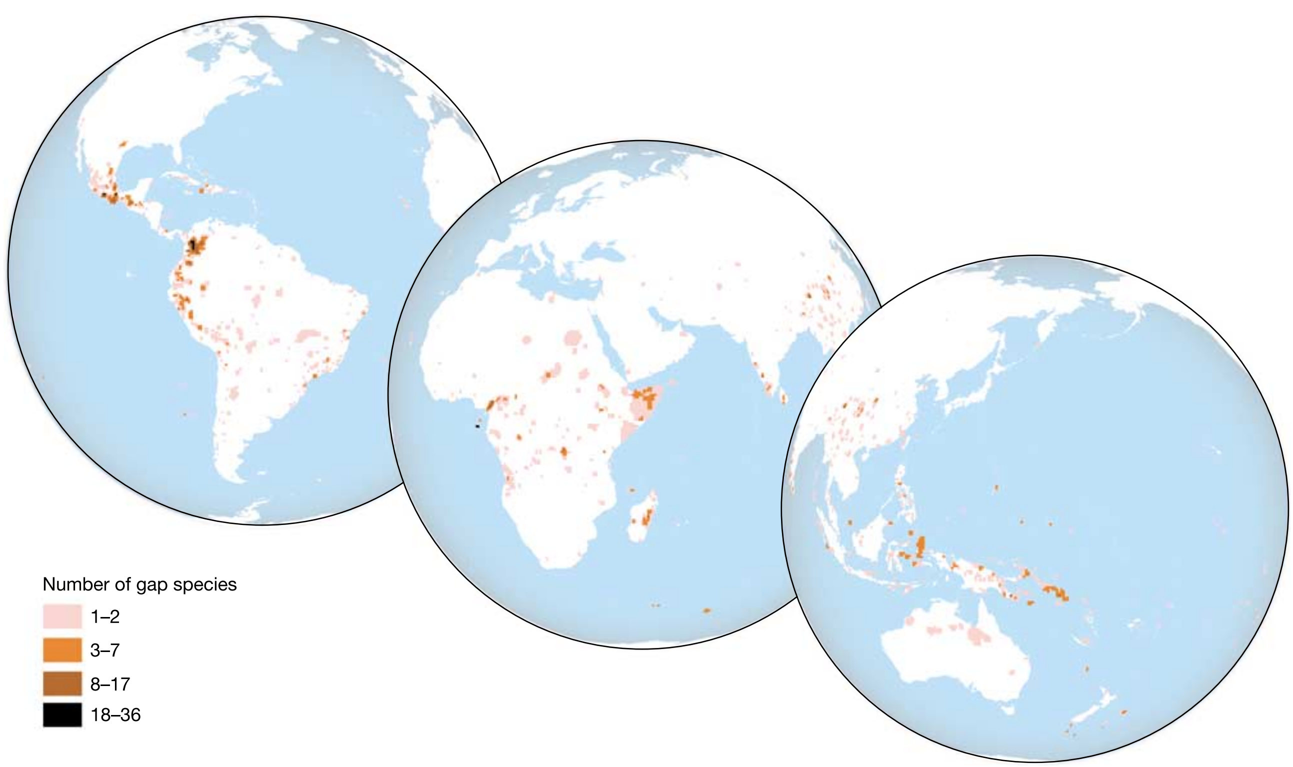


**Figure 1** Density map of gap species per half-degree cell, created by overlaying the ranges of all species not covered by any protected area.

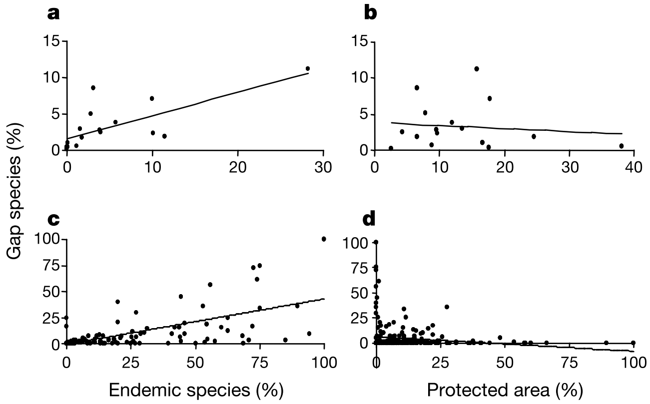


**Figure 2** Percentage of gap species in relation to endemism levels and percentage of area protected across biomes and countries. **a**–**d**, Relationships between: percentage of species in each biome that are endemic and percentage that are gap species (**a**) ($n = 16$, $r = 0.72$, $P < 0.005$); percentage of each biome's protected area and percentage of gap species (**b**) ($P > 0.5$); percentage of species in each country that are endemic and percentage that are gap species (**c**) ($n = 247$, $r = 0.69$, $P < 0.001$); percentage of each country's protected area and percentage of gap species (**d**) ($n = 247$, $r = 0.15$, $P < 0.05$).

given region may be explained by sparse protected area coverage and/or by a concentration of narrowly distributed species. The global distribution of gap species (Fig. 1) is influenced more strongly by the latter. Indeed, within a given biome[21], the percentage of species that are gaps is highly significantly correlated with the level of endemism, independent of the percentage of area protected (Fig. 2a, b). Across countries, the percentage of gap species decreases with percentage of area protected, but is more strongly correlated with levels of national endemism (Fig. 2c, d). Consequently, although in some regions the absence of protected areas allows for relatively widespread gap species (notably in Somalia), the map of gap species mainly reflects the presence of narrowly distributed species (Fig. 1). The regions highlighted include many widely recognized centres of endemism[16,22], such as Yunnan province and the mountains surrounding the Sichuan basin in southern China, the Western Ghats of India, Sri Lanka, the islands of Southeast Asia and Melanesia, the Pacific islands, Madagascar, the Cameroon highlands, Mesoamerica, the tropical Andes, the Caribbean, and the Atlantic Forest of South America. Most of these are montane or insular regions in the tropics.

These results have implications for global conservation planning strategies, as they clearly demonstrate that the percentage of area already protected in a given country or biome is a very poor indicator of additional conservation needs. Contrary to frequent recommendations[1,23], current protection levels should not be used as a significant criterion to guide priorities for allocation of future conservation investments. Indeed, the regions with greatest need for expansion of the global protected area network are not necessarily those with a lower percentage of their area protected; rather, they typically are those with higher levels of endemism[24]. Conversely, uniform targets based on percentage of area protected (except for 100%) cannot be used as a ceiling to distinguish between regions sufficiently protected and those that need additional protection[4–5].

Global conservation strategies based on the recommendation that 10% (or other similar targets) of each country or biome be protected will not be effective because they are blind to the fact that biodiversity is not evenly distributed across the planet[25]; by the same token, neither should protected areas be. Indeed, a network with the same total area as the existing one but evenly distributed across the world would perform less adequately than the current network in representing species of mammals, amphibians, turtles and threatened birds (Table 1). The better performance of the current network indicates uneven distribution of protected areas relative to biodiversity pattern. Indeed, the current network is significantly (albeit not overwhelmingly) biased towards sites with higher richness of all species, restricted-range species and threatened species. This may be the legacy of decisions to locate some protected areas in better sites, and/or be symptomatic of higher levels of biodiversity loss outside protected areas[19]. Nonetheless, the current global network could still perform better in terms of species coverage. For example, a network biased towards the tropics (to match their higher level of endemism) would have fewer gap species than the current network, and far fewer gap species than a random unbiased network (Table 1).

Our results demonstrate that if the conservation goal is species representation, then the expansion of the global network of protected areas must account for biodiversity patterns, rather than rely on general percentage-based targets that are formed largely by political and feasibility considerations[4–5]. Given the increasing threats to biodiversity, such expansion should be made strategically by focusing on those regions that would contribute most to the global system and prioritizing, within those, the regions where the urgency for conservation action is greatest[22]. Conservation strategies must also address the complexity of natural ecosystems, including genetic and phylogenetic diversity, and ecological and evolutionary processes[26].

The existing protected area network provides an invaluable service in shielding habitat from destructive use and hence in reducing biodiversity loss[19]. However, our global gap analysis clearly demonstrates that the global protected area network is still far from complete, even for terrestrial vertebrates, the best known and most popular of all species groups[27]. Of the species considered, at least 12% are not represented in any protected area, despite the extremely strict assumptions applied for identifying gap species. It is likely that other taxa with high levels of endemism, such as plants and insects, are even less well represented, given the tendency for sets of species with smaller range sizes to have higher proportions of gap species.

Protected areas are not the only tactic available to conservation planners, but they are highly cost effective in protecting biodiversity[28]. Advances in data availability and in the science of conservation planning enable us to act strategically in the face of increasing human pressure. Clearly, the task ahead is as urgent as it is challenging, as much biodiversity remains to be protected. □

## Methods

### Data

Data on the global distribution of protected areas were obtained from the 2003 World Database on Protected Areas[29]. Distribution maps were obtained for 11,633 species of terrestrial vertebrates: 4,735 terrestrial mammals, compiled by the IUCN Global Mammal Assessment; 1,171 globally threatened birds[17]; 273 freshwater turtles and tortoises[30]; and 5,454 amphibians, compiled by the IUCN Global Amphibian Assessment. These species data also include assessments of conservation status, with 1,063 mammals, 1,171 birds, 119 turtles and 1,543 amphibians having been listed as globally threatened by the IUCN Red List[17–18]. See Supplementary Information for more details.

### Randomly distributed networks

Two null models were created to simulate a network of protected areas with similar characteristics to the existing one, but evenly spread around the world: Model I (equal area sites), 69,794 circles, of the same size as the mean area of a protected site, and 11,119 points were randomly spread around the world's land surface (excluding Antarctica); Model II (variable area sites), 69,794 circles, with the same distribution of sizes as the current protected area network, and 11,119 points were randomly spread around the world's land surface (excluding Antarctica).

Of all species that are restricted to either the tropical or the non-tropical regions (that is, excluding species that span both), 75.8% are found in the tropics; however, only 45.8% of the global protected area network is in the tropics. Therefore, we considered a third model in which the percentage of the global protected area in the tropics was increased to match its level of endemism: Model III (tropical bias), 69,794 circles, of the same size as the mean area of a protected site, and 11,119 points were distributed such that 75.8% of each occurred in the topics, having random distributions within tropical and non-tropical areas.

Sixty replicates were obtained for each of these randomly distributed networks. These were then overlaid with species distributional data to analyse the number of gap species in each case. See Supplementary Information for the confidence intervals for each of the models.

### Richness of protected and unprotected cells

The richness of each quarter-degree cell touching land (outside Antarctica) was calculated for all species, restricted-range species[16] (occupying $\leq$50,000 km$^2$) and threatened species. Cells touching protected areas were considered 'protected'. Protected cells are significantly ($P < 0.001$) biased towards higher richness of all, restricted-range and threatened species. See Supplementary Information for a comparison of frequency distributions.

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# Spatial structure often inhibits the evolution of cooperation in the snowdrift game

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**Understanding the emergence of cooperation is a fundamental problem in evolutionary biology[1]. Evolutionary game theory[2,3] has become a powerful framework with which to investigate this problem. Two simple games have attracted most attention in theoretical and experimental studies: the Prisoner's Dilemma[4] and the snowdrift game (also known as the hawk–dove or chicken game)[5]. In the Prisoner's Dilemma, the non-cooperative state is evolutionarily stable, which has inspired numerous investigations of suitable extensions that enable cooperative behaviour to persist. In particular, on the basis of spatial extensions of the Prisoner's Dilemma, it is widely accepted that spatial structure promotes the evolution of cooperation[6–8]. Here we show that no such general predictions can be made for the effects of spatial structure in the snowdrift game. In unstructured snowdrift games, intermediate levels of cooperation persist. Unexpectedly, spatial structure reduces the proportion of cooperators for a wide range of parameters. In particular, spatial structure eliminates cooperation if the cost-to-benefit ratio of cooperation is high. Our results caution against the common belief that spatial structure is necessarily beneficial for cooperative behaviour.**

The Prisoner's Dilemma illustrates that cooperating individuals are prone to exploitation, and that natural selection should favour cheaters. In this game, two players simultaneously decide whether to cooperate or defect. Cooperation results in a benefit $b$ to the recipient but incurs a cost $c$ to the donor ($b > c > 0$). Mutual cooperation thus pays a net benefit of $R = b - c$, whereas mutual defection results in payoff $P = 0$ for both players. With unilateral cooperation, defection yields the highest payoff, $T = b$, at the expense of the cooperator bearing the cost $S = -c$. It follows that it is best to defect regardless of the co-player's decision. Thus, defection is the evolutionarily stable strategy, even though all individuals would be better off if they all cooperated. This outcome is a simple consequence of the ranking of the four payoff values: $T > R > P > S$. Despite this seemingly convincing argument, many natural species show altruism, with individuals bearing costs to the benefit of others: vampire bats share blood[9], alarm calls warn from predators[10], monkeys groom each other[11], and fish inspect predators preferably in pairs[12].

In field and experimental studies it is often difficult to assess the fitness payoffs for different behavioural patterns, and even the proper ranking of the payoffs is challenging[13,14]. This has led to a considerable gap between theory and experimental evidence, and to an increasing discomfort with the Prisoner's Dilemma as the only model to discuss cooperative behaviour[15,16]. The snowdrift game is a viable and biologically interesting alternative. It differs from the Prisoner's Dilemma in that the payoffs $P$ and $S$ have a reverse order: $T > R > S > P$. This changes the situation fundamentally and leads to persistence of cooperation.

To illustrate the snowdrift game, imagine two drivers that are caught in a blizzard and trapped on either side of a snowdrift. They can either get out and start shovelling (cooperate) or remain in the car (defect). If both cooperate, they have the benefit $b$ of getting home while sharing the labour $c$. Thus, $R = b - c/2$. If both defect, they do not get anywhere and $P = 0$. If only one shovels, however, they both get home but the defector avoids the labour cost and gets

# Supplementary information to "*Effectiveness of the global protected area network in representing species diversity*"

*** Notes on data and methods, and extended acknowledgements ***

## 1 Data sources

### 1.1 Protected areas

Data on the global distribution of protected areas were obtained from the recently released World Database on Protected Areas[1]. This is a freely available database compiled by a consortium of organizations including BirdLife International, Conservation International, Fauna & Flora International, The Nature Conservancy, United Nations Environmental Programme – World Conservation Monitoring Centre, the World Resources Institute, the Wildlife Conservation Society, and the World Wildlife Fund.

Protected areas in the WDPA are recorded either as polygons (58,514 records) and/or as points (106,215 records, of which 73,863 have no corresponding polygon information). Both types of data were provided as ArcView shapefiles[2], with associated tables of attributes. Data for each protected area include a unique site code, protected area name, country, geographical coordinates, designation (e.g., Nature Reserve, National Park), IUCN categories, and status (e.g., Designated, Proposed, Degazetted). Additionally, the WDPA includes data on protected areas with international status (e.g., UNESCO Man and the Biosphere Reserves, World Heritage Sites, Ramsar Wetlands), but this information was included in this analysis only when the area was also designated at a national level.

For purposes of the global gap analysis, the following records were eliminated from the WDPA: a) Point records with both *Lat* and *Lon* as zero, that is, those with no information on the exact geographical location of an area; and b) records that do not seem to correspond to established protected areas, including those with *Areaname* recorded as "Area Not Protected", or *Status* recorded as "Degazeted", "Proposed", "Recommended", "In Preparation" or "Unset".

For the remaining records, we kept the maximum level of geographic data provided by the WDPA. Point records with no information on area were kept in a separate point shapefile. Point records with associated area were converted into circular shapes of the same area (centered on the coordinates provided for the point) and merged with the polygon records into a common polygon shapefile.

The resulting polygon layer contains records of areas that overlap spatially (e.g., core areas of Biosphere Reserves on top of the wider reserves). To avoid having the total protected area of the planet overestimated by these overlaps, we merged all protected areas into one single layer. For the purposes of this analysis, a single 'protected site' is then either an individual protected area or a set of contiguous/overlapping protected areas.

The network of protected areas as defined above is constituted of 69,794 polygons (protected sites) occupying in total about 16,002,000 $km^2$ (11.9% of the land area outside Antarctica), and of 11,119 points for which no area was associated. Antarctica represents a highly unusual situation, as the vast region south of $60^o$ South latitude can be considered a protected area on its own (protected though the 1959 Antarctic Treaty and its Environmental Protected Protocol), yet it holds virtually none of the species considered in the global gap analysis. We followed the WDPA 2003[1] and the 2003 UN List of Protected Areas[3] in excluding it from the network of protected areas.

### 1.2 Mammals

Distribution maps for all mammal species were compiled, as part of the IUCN Global Mammal Assessment, by W. Sechrest (*unpublished*), L. Boitani (for large mammals of Africa[4]; *unpublished* for rodents of Africa), M. Tognelli (for rodents of South America[5]), and G. Ceballos (for bats of Central America[5]). Although all of these maps are currently undergoing formal review, draft maps were available for this global gap analysis.

The taxonomic classification of all species used in this analysis followed the second edition of *Mammal Species of the World*[6], with modifications from draft chapters of the third edition made to incorporate the latest taxonomic information wherever possible (Reeder & Wilson, *unpublished*). Spatial data were compiled from primary and secondary literature (e.g., taxonomic accounts, regional atlas projects, Mammalian Species Accounts), museum records, and other scientific reports and documents. Over 1,700 sources were consulted for information on species distributions. Preference was given to more recent sources, as well as sources that have comprehensive information for an entire species' range.

Data on the extent of occurrence of mammal species were composed of polygons corresponding to different levels of certainty about species' presence, to differences between historical and current ranges, and to native or introduced ranges. For this analysis, only polygons where the species was both reported as *native* and with presence coded as *extant* or *possibly present* were used, thus excluding historical and introduced ranges. Marine mammals were also excluded from the analysis (i.e., Cetacea, Sirenia, and marine species in the Order Carnivora). In total, 4,735 species were analysed corresponding to 94% of all mammals. According to the 2003 IUCN Red List[7] these include 174 Critically Endangered species, 314 Endangered, and 575 Vulnerable species, although a perfect match between the IUCN assessment and the distribution maps was not possible due to minor differences in the taxonomic classification. The majority of these species were assessed in 1996[8] using version 2.3 of the IUCN criteria[9] (now supplanted by version 3.1[10]).

When complete, the data and results of the Global Mammal Assessment will all be freely available through the IUCN Red List web site (www.redlist.org).

### 1.3 Globally threatened birds

The data on the world's globally threatened bird species were compiled by the BirdLife International partnership[11], and reviewed by hundreds of experts. These data include assessments of threat for each species, following the IUCN Red List criteria (version 3.1[10]) and range maps.

Where possible, these range maps were based on locality records that included sightings and specimen records (ideally recent sightings, although, for some species, old records are the only records). A species' *known range* was derived from these records, using additional habitat and topographical information to aid range definition. For some species, a *projected range* was added to the known range to reflect areas between well-spaced localities of suitable habitat, and areas close to known localities that are likely to hold the species. Known and projected ranges have been combined to give an estimate of *extent of occurrence* for each threatened species[12]. For some species, possible and historical ranges were also mapped, but these were not included in this analysis. Twelve species were excluded because their ranges (if still extant) are not sufficiently known to be mapped. Each polygon included within a species' extent of occurrence has been coded according to the season of occurrence of the species: *breeding*, *non-breeding*, or *resident*. For marine species (those with a mainly oceanic non-breeding range) only breeding range was considered. For two species only non-breeding range is known.

The taxonomic classification used followed BirdLife International[11]. Of the 1,171 globally threatened birds included in this analysis (11% of all birds), 170 are Critically Endangered, 320 are Endangered, and 681 are considered Vulnerable species. The three species classified as Extinct in the Wild were excluded from the analysis. In order to match the available distribution maps, we retained for each species the threat categories as published in the 2000 assessment[11], even though a more recent threat assessment is available[7].

### 1.4 Tortoises and freshwater turtles

Data on species of tortoises and freshwater turtles were mainly obtained from the EMYSystem World Turtle Database 2003[13] as point data (~ 26,000 records) corresponding to museum specimens and literature citations. These points were converted into polygons and preliminarily reviewed by K. Buhlmann and T. Akre. This information will form the basis of a formal IUCN Global Turtle Assessment.

In total 273 species were analysed (a little more than 3% of all reptiles). According to the 2003 IUCN Red List[7] these include 21 Critically Endangered species, 42 Endangered, and 56 Vulnerable species. However, a perfect match between the IUCN assessment and the distribution maps was not possible due to minor differences in the taxonomic classification. The majority of these species were assessed in 1996[8] using version 2.3 of the IUCN criteria[9] but more than 80 Asian species were re-assessed in 1999 using the 3.1 version[10].

When complete, the data and results of the Global Turtle Assessment will all be freely available through the IUCN Red List web site (www.redlist.org).

### 1.5 Amphibians

With the exception of North America (see below), amphibian maps were developed by the on-going IUCN Global Amphibian Assessment[14]. Distribution maps were created for all species in two stages. First, an expert on amphibians in each of 33 designated regions collected data on all species in the region. Each of these experts was responsible for collating information on species taxonomy, geographic range (including a preliminary distribution map), population status, habitat preferences, trade status, and major threats and conservation measures that are currently in place or that are needed. Each regional expert also provided a preliminary assessment of threat for each species according to the IUCN Red List categories[10]. Second, all of the data collected in this initial stage are being reviewed (most have already been so) either through expert workshops (particularly for the more species-rich regions), or by correspondence.

The global gap analysis used the most recent data available including reviewed maps of species distributions for South America, Mesoamerica, Madagascar, South-east Asia, South Asia, New Zealand, New Guinea, Russia and the Confederation of Independent States. Distribution maps have also been reviewed for three quarters of African species, most of the species in Japan and some of the species in Australia. Data are still being reviewed for the Caribbean, West Asia, Europe, and for the remaining species of Africa, Japan and Australia. Overall, about 80% of all amphibian species have had their distribution maps formally reviewed. For many of the unreviewed species, such as those from Europe and West Asia, the data are derived from reliable published sources.

NatureServe provided the distribution maps for species in US and Canada. The main source for these maps was a database on county of occurrence developed by M. Lanoo at Ball State University[15]. These maps fed into the Global Amphibian Assessment as part of the process for the Red List assessment of North American species.

The taxonomic classification used follows Frost[16], with modifications where deemed necessary by the experts involved in the Global Amphibian Assessment. After excluding 24 extinct species, 5,454 amphibians were included in this global gap analysis (i.e., all living amphibians). Based on the currently available assessment of threat for each species (unreviewed for the regions mentioned above), this included 341 Critically Endangered, 550 Endangered, and 652 Vulnerable species.

When complete, the data and results of the Global Amphibian Assessment will all be freely available through the IUCN Red List web site (www.redlist.org), AmphibiaWeb (www.amphibiaweb.org), and the American Museum of Natural History Amphibian Species of the World web site[16] (http://research.amnh.org/herpetology/amphibia/index.html).

## 2 Data limitations

The global gap analysis is based on the comparison between maps of protected areas and maps of species distributions. Although these are the best datasets of its kind ever compiled at the global scale, they have limitations that introduce errors to the results of the analysis. Hence, two types of error are possible:

- *Omission error*s, which occur when a given species is considered a gap species when, in fact, it is covered, and

- *Commission errors*, which occur when a given species is considered covered by one or more protected areas when, in fact, it is a gap species.

For conservation purposes, it is more important to minimize commission errors than omission errors, because ignoring a species that is genuinely not represented in protected areas may have high conservation costs. Unfortunately, the current data are much more prone to commission errors.

Here, we discuss the limitations in the protected area and species data more likely to be sources of errors in the global gap analysis, to provide a better understanding of the results and implications of this study. These limitations are not exclusive to the data used in this analysis – in fact they are prevalent amongst published studies at the macroecological scale[17-20].

### 2.1 Limitations in the protected area data

#### *2.1.1 Missing records*

Even though the WDPA is the most complete record of the world network of protected areas, it does not include all existing protected areas. The database is incomplete in part because there are gaps in information about existing protected areas, and in part because the global network is dynamic and changing. These missing records will cause omission errors.

#### *2.1.2 Incorrect records*

The results of the global gap analysis will be sensitive to records that include incorrect information about protected areas. Inaccuracies in the location of protected area boundaries or changes in status of an area (e.g. from “Proposed” to

" Designated" or from "Designated" to "Degazetted") may result in either commission or omission errors in the analysis.

### *2.1.3 Protected areas with point data only*

Nearly half of the records used in this analysis were point data (52,694 records). For 41,575 of these, some data on area were available, and these were represented as circles centered in the respective latitude and longitude coordinates. The remaining 11,229 were represented as points. Point representations can lead to omission errors, while protected areas represented as circles can lead to both omission and commission errors. In most cases, the magnitude of errors will be much higher when using point data only. However, point records are heavily biased toward the representation of smaller protected areas, reducing the predicted magnitude of errors created by these data.

### *2.1.4 Uneven global coverage*

The quantity and quality of data in the WPDA are unevenly distributed across countries, which will result in discrepancies in the results of the global gap analysis.

### *2.1.5 Lack of data on management effectiveness of protected areas*

One of the major limitations of the WDPA data for the purposes of the global gap analysis is the scarcity of information regarding the management effectiveness of each protected area, i.e., the degree to which a protected area is likely to succeed in preserving the biodiversity values it contains. Without this information, any evaluation of the coverage of the global network of protected areas is necessarily an approximation in which the number of species represented is a gross overestimate of the number of species effectively protected. IUCN management categories I to VI[21] provide some information on the level of management of individual protected areas, but for a large number of protected areas this information is not available. Additionally, not all countries have systematically applied IUCN categories; and among those that have, the classification has not been applied consistently. Furthermore, categories I-VI are more likely to reflect the legal status of a reserve (intended level of management) than its real management effectiveness.

The WDPA will change continuously as the global network itself changes and better regional data become available. Given the limitations described above, it is difficult to assess whether the published[22] figure that 11.5% of the planet's land area is protected is an underestimate or an overestimate of the true global coverage. On the one hand, there are certainly many records missing from the WDPA, particularly in relation to less traditional protected areas (e.g., private reserves) and areas classified at the sub-national level (e.g., state reserves). On the other hand, it is not possible at present to estimate the fraction of records in the WDPA which correspond to areas without any real protection.

## 2.2 Limitations in the biological data

### *2.2.1 Narrow taxonomic scope*

The global gap analysis included only those taxonomic groups for which it was possible to obtain compiled maps of global coverage in digital format: mammals, amphibians, freshwater turtles and tortoises, and globally threatened birds. No attempt was made to collect species distribution maps for other taxa.

These species are analysed here as conservation targets on their own right. While other taxa would certainly benefit from the conservation of regions highlighted by the results of the global gap analysis[23], no assumption is made that a network of protected areas adequate for the representation of mammals, amphibians, and threatened birds is sufficient for other taxonomic groups. Indeed, previous studies have demonstrated that vertebrate species are not likely to be adequate surrogates for other groups, particularly those with more species and high levels of endemism, such as plants and invertebrates[24].

### *2.2.2 Missing species and incomplete species maps*

Even though the taxa considered in the global gap analysis correspond to the best-known fraction of the world's biodiversity, many vertebrate species are still being described[25]. Even where distribution maps are available, many are incomplete in the sense that they do not include areas where a species is actually present but has never yet been recorded. Poorly known species and poorly known regions are most likely to be affected by these kinds of limitations of biological data.

### 2.2.3 *Species ranges mapped as extent of occurrence*

For the majority of species, mapped ranges are gross overestimates of locations where species truly occur, as they generally correspond to *extent of occurrence* range maps, rather than *area of occupancy*[12]. Most of these ranges were obtained as "envelopes" including original records (point data) and through extrapolation (using, for example, habitat information) from original records. They are likely to include relatively extensive areas from which the species is absent. These overestimates of species locations are a substantial source of commission errors in this analysis, as species may be listed as present in protected areas that overlap their mapped extent of occurrence but where they do not occur (see below).

### 2.2.4 *Uneven global coverage*

As with the protected area data described above, the quality and quantity of biological data is unevenly distributed across the world. Well-known regions are less likely to have missing species, and maps of individual species from these regions will tend to show greater accuracy and levels of detail, even approaching the area of occupancy in a few cases.

### 2.2.5 *Lack of data on species viability across the range*

Even those portions of the range where the species is truly present are not all equivalent, and so it is relevant in which of those portions protected areas are located. Hence, the current presence of a species in a protected area is not a guarantee of its future persistence, even on a time scale of a few years or decades[26-27]. Consequently, the complete list of species reported from a given protected area is likely to be a considerable overestimate of those species whose long-term persistence can actually be effectively ensured by the protected area.

## 3 Test of data limitations: omission and commission errors in threatened amphibians of Mesoamerica

In addition to species range maps, the Global Amphibian Assessment collected, including information on conservation measures currently in place for each species, such as presence in or absence from protected areas. These data provide an opportunity to evaluate the accuracy of the results obtained by the global gap analysis, based on information provided by regional experts with ground knowledge on both the species and the protected areas.

The 280 threatened species of amphibians of the Mesoamerican region (from Mexico to Panama) were analysed as a preliminary case study. A comparison of the lists of species considered covered by the global gap analysis with those reported as covered in the Global Amphibian Assessment[14] (Figure 1), found: 71% match (species reported by both assessments as either covered or gaps), 9% omission error (species reported as gaps by the global gap analysis but as covered by the Global Amphibian Assessment), and 19% commission error (species reported as covered by the global gap analysis but as gaps by the Global Amphibian Assessment).

Hence, overall, the global gap analysis underestimated the number of gap species: 38%, as compared to 48% reported by the Global Amphibian Assessment. Furthermore, for about 10% of the covered species, the experts reported that presence in protected areas is no guarantee of the species' persistence, due to habitat degradation or because the species has not been recorded in the protected areas recently despite searches.

For the majority of the species, it was possible to determine the most likely source of the omission and commission errors (Figure 1, Table I). As predicted, most errors are due to the spatial representation of species' ranges as extent of occurrence, which overestimate the species' true area of occupancy and result in commission errors.

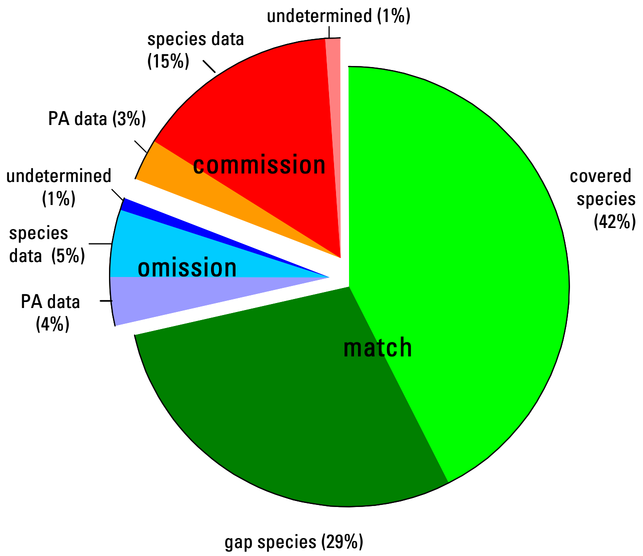


**Figure 1. Sources of omission and commission errors obtained by comparing the lists of species considered covered by the global gap analysis with those reported as covered in the Global Amphibian Assessment.**

**Table I. Likely sources of omission and commission errors.**

| Error type | Error source | % | Explanation |
|---|---|---|---|
| omission errors | protected areas data | 4% | - protected area(s) not mapped<br>- protected area(s) mapped in the wrong place<br>- protected area(s) represented as points<br>- protected area(s) represented as circles |
| | species' distribution data | 5% | - incomplete species' range maps |
| commission errors | protected areas data | 3% | - protected area(s) mapped in the wrong place<br>- protected area(s) represented as circles |
| | species' distribution data | 15% | - species' range maps include unoccupied areas |

The spatial implications of these commission and omission errors were evaluated by comparing maps of density of gap species found, respectively, by the global gap analysis and by the Global Amphibian Assessment (Figure 2, top and bottom panels, respectively). The overall pattern is similar, indicating that the regions highlighted by the global gap analysis correspond to true gaps in the protected area network. However, the results using data from the Global Amphibian Assessment produced a wider gap area, increased the species density in the previously existing peaks and highlighted a new area (in Panama) concentrating gaps species. This reinforces the prediction that the global gap analysis underestimates the magnitude of the gaps in coverage by the global network of protected areas.

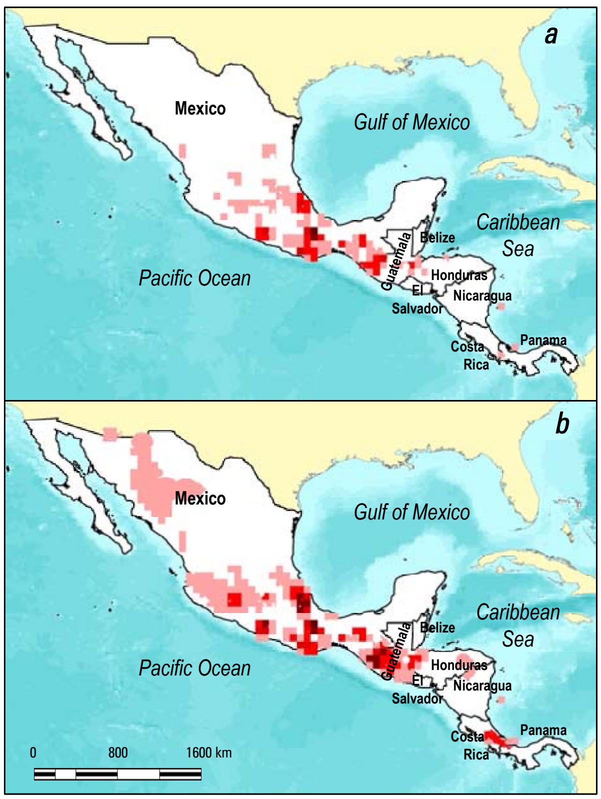


**Figure 2. Distribution of gap species found by the global gap analysis (a) and by the Global Amphibian Assessment (b). Darker shades of red correspond to higher species density.**

## 4 Note on targets based on percentage of area protected

This global gap analysis demonstrates the inadequacy of general targets based on a uniform percentage of area protected. However, percentage-based targets are useful when scaled to reflect the conservation requirements for each biodiversity component, by integrating information on aspects such as persistence, vulnerability and rarity (see reference 28 for a review).

Uniform targets are deeply ingrained in the conservation strategies of national governments and international conservation organizations. These include:

- The IUCN recommendation at the 1992 World Parks Congress (Caracas, Venezuela) that protected areas should cover a minimum of 10 per cent of each biome by 2000[29].

- The *Forests for Life* Campaign launched by WWF (www.panda.org/forests4life/), which had an initial target "to establish an ecologically representative network of protected areas, covering at least 10% of the world's forest area by the year 2000" (the target has subsequently been changed to "Protect a global network of protected areas which are well-resourced, well-managed and representative of all the world's threatened and most biologically significant forest regions by 2010"). This campaign was joined by IUCN, and gained further momentum with the creation of the WWF/World Bank Alliance. The flagship project of this Alliance is the *Amazon Region Protected Areas Program* (ARPA), anchored in the 1998 commitment by Brazilian President Fernando H. Cardoso to set aside at least 10 percent of Brazil's forests as conservation areas.

- The *Endangered Seas* Programme by WWF (www.panda.org/endangeredseas/), which is campaigning for at least 10% of marine areas to be under some form of protection by 2012.

- The Yaoundé Summit Declaration, signed on March 1999 by Cameroon, Central African Republic, Chad, the Popular Republic of Congo, Equatorial Guinea and Gabon, which commits these countries to conserving a minimum of 10% of the nation's forests in protected areas[30].

- The Protected Area Strategy released in 1993 by the Government of British Columbia, Canada, which had a goal "to designate and manage, by the year 2000, a system of protected areas which protected a diversity of natural, cultural heritage and recreational values encompassing a full 12% of the province's land base" (http://www.cd.gov.ab.ca/preserving/parks/fppc/bc_eng.pdf).

- Target 4 of the *Global Strategy for Plant Conservation*[31], which reads "At least 10 per cent of each of the world's ecological regions effectively conserved [by 2010]". The Strategy is supported by a wide range of organisations and institutions – governments, intergovernmental organizations, universities, research institutes, nongovernmental organizations and their networks, and the private sector. In particular, the Strategy was approved by the sixth Conference of the Parties to the Convention on Biological Diversity (COP6).

These targets have certainly played important roles in galvanising governments, the public opinion, and the private sector to conservation action. However, while they are generally intended to be a floor to conservation efforts (e.g., '*at least* 10%') there is a danger that they become *de facto* ceilings[32]. For example, the 12% target set by the Government of British Columbia gave critical impulse to a doubling of the total protected area in the province, achieved in 2001. However, there is growing concern by the non-governmental and scientific communities that the 12% figure has become a cap inhibiting the designation of additional protected areas by the Government[33].

When used to establish priorities for action amongst different regions or biomes, uniform targets may lead to the wrong conclusion that some of these are already 'finished', even though they may be the ones where protection is still most urgently needed. For example, the Global Strategy for Plant Conservation and corresponding COP6 decision use the 10% target to support the statement that "*in general, forests and mountain areas are well represented in protected areas, while natural grasslands (such as prairies) and coastal and estuarine ecosystems, including mangroves, are poorly represented*"[31]. Yet, this global gap analysis found that tropical montane forests are precisely the ecosystems most in need of additional protected area coverage.

## 5 Notes on methods

### 5.1 Confidence intervals for species coverage in networks of randomly distributed protected areas

**Table II. Numbers of gap species in randomly selected protected areas, according to each of the models analysed. Numbers of all species and of gap species for all protected areas in the current network are provided for comparative purposes. Values in parentheses are percentages of all species/threatened species analysed within a given taxon.**

| Taxon | | Current network | Model I (equal area sites) | | Model II (variable area sites) | | Model III (tropical bias) | |
|---|---|---|---|---|---|---|---|---|
| | | | Mean | 95% C.I. | Mean | 95% C.I. | Mean | 95% C.I. |
| All species | Mammals (*n* = 4,735) | 258 (5.5%) | 297.7 (6.3%) | [294.2, 301.3] | 342.3 (7.2%) | [338.6, 346.1] | 226.6 (4.8%) | [223.9, 229.4] |
| All species | Turtles (*n* = 273) | 21 (7.7%) | 24.6 (9.0%) | [24.0, 25.2] | 26.5 (9.7%) | [26.0, 27.0] | 23.8% (8.7) | [23.2, 24.4] |
| All species | Amphibians (*n* = 5,454) | 913 (16.7%) | 1230.2 (22.6%) | [1215.3,1245.1] | 1507.8 (27.7%) | [1489.5, 1526.1] | 804.2 (14.7%) | [796.9, 811.6] |
| Threatened species | Mammals (*n* = 1,063) | 149 (14.0%) | 191.8 (18.0%) | [187.8, 195.8] | 218.2 (20.5%) | [215.7, 220.7] | 151.6 (14.3%) | [149.7, 153.7] |
| Threatened species | Birds (*n* = 1,171) | 232 (19.8%) | 349.7 (29.9%) | [346.5, 352.9] | 409.6 (35.0%) | [405.5, 413.6] | 275.4 (23.5%) | [272.5, 278.6] |
| Threatened species | Turtles (*n* = 119) | 12 (10.1%) | 15.9 (13.3%) | [15.4, 16.3] | 17.3 (14.6%) | [17.0,17.7] | 15.5 (13.1%) | [15.1, 16.1] |
| Threatened species | Amphibians (*n* = 1,543) | 411 (26.6%) | 604.5 (39.2%) | [598.7, 610.3] | 740.0 (48.0%) | [729.1, 750.9] | 423.3 (27.4%) | [410.6, 435.9] |
| All species analysed (*n* = 11,633) | | 1,424 (12.2%) | 1,904.4 (16.4%) | [1886.2, 1918.3] | 2,256.9 (19.4%) | [2263.3, 2309.2] | 1,330.1 (11.4%) | [1321.5, 1340.0] |

## 5.2 Comparison between protected and unprotected sites in terms of richness of all species, threatened species, and restricted-range species

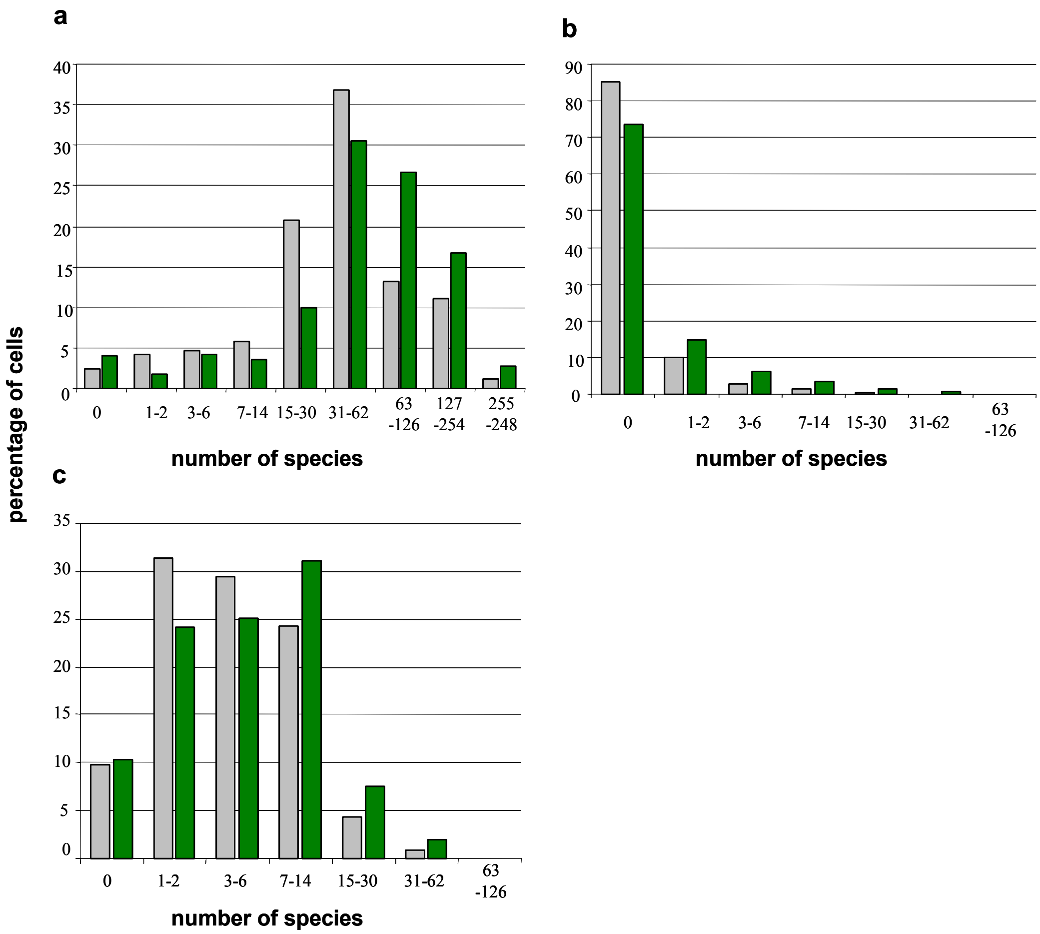


**Figure 3. Frequency distribution of the percentage of half-degree protected (green) and unprotected (grey) cells which fall in each class of species richness, for: a) all species; b) restricted range species; and c) threatened species.**

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