

Global patterns of terrestrial vertebrate diversity and conservation

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Identifying priority areas for biodiversity is essential for directing conservation resources. Fundamentally, we must know where individual species live, which ones are vulnerable, where human actions threaten them, and their levels of protection. As conservation knowledge and threats change, we must reevaluate priorities. We mapped priority areas for vertebrates using newly updated data on >21,000 species of mammals, amphibians, and birds. For each taxon, we identified centers of richness for all species, small-ranged species, and threatened species listed with the International Union for the Conservation of Nature. Importantly, all analyses were at a spatial grain of 10 × 10 km, 100 times finer than previous assessments. This fine scale is a significant methodological improvement, because it brings mapping to scales comparable with regional decisions on where to place protected areas. We also mapped recent species discoveries, because they suggest where as-yet-unknown species might be living. To assess the protection of the priority areas, we calculated the percentage of priority areas within protected areas using the latest data from the World Database of Protected Areas, providing a snapshot of how well the planet's protected area system encompasses vertebrate biodiversity. Although the priority areas do have more protection than the global average, the level of protection still is insufficient given the importance of these areas for preventing vertebrate extinctions. We also found substantial differences between our identified vertebrate priorities and the leading map of global conservation priorities, the biodiversity hotspots. Our findings suggest a need to reassess the global allocation of conservation resources to reflect today's improved knowledge of biodiversity and conservation.

endemism | species distributions | conservation planning | biogeography

Defining priority areas for conservation is a major goal of conservation science, one that advances steadily as better data and methodologies become available. Fundamentally, we must know where individual species live, which ones are vulnerable, where human actions threaten them, and the level of protection devoted to them. As conservation knowledge and threats change, it is essential that we reevaluate global priorities. Furthermore, practical conservation actions often unfold on a smaller geographical scale than these global considerations, requiring us to translate actions from broad, global strategies to local tactics.

We know that the broad distribution of the planet's biological diversity follows basic “laws,” that is, general patterns that apply widely and across taxonomic groups (1). One law is that the numbers of local species—henceforth, “richness”—are uneven. Some places have thousands of times more species than do others. A second and important law is that species with small geographical ranges also have uneven distributions, but these distributions often differ markedly from that of species overall. These patterns are purely biogeographical, although their extension to conservation is obvious. Small range size generally is the strongest predictor of a species' risk of extinction (2, 3). The surprising result of Myers' work (4–6) is that, malevolently, habitat destruction is particularly extensive in the places where small-ranged species concentrate. That is, there are “hotspots.” Certainly, there are some concentrations of small-ranged species

where few are threatened. Conversely, there are areas extensively converted to human uses that cause local, but not global, jeopardy to the species living there. Identification of the former is essential because their inadequate habitat protection may soon turn these concentrations into hotspots as well. Finally, although there are broad similarities across taxonomic groups in these patterns, there also are differences among taxa, often making simplistic taxonomic surrogacy approaches ineffective. These facts affect fundamentally where and how society should be directing conservation resources.

In this assessment of global conservation priorities, we use the latest global data for three well-known terrestrial vertebrate taxa (mammals, birds, and amphibians) to identify priority areas for conservation using the numbers of all species, numbers of threatened species, and numbers of small-ranged species. Each of these familiar metrics poses separate questions that sometimes are conflated. Then, to evaluate the allocation of protection efforts toward these priority regions, we measure the number of species in these three categories within a protected area using the latest available data. We also extend all prior work in this domain and compare the priority areas we identify for vertebrates with those of the most widely recognized map of global conservation priority, the biodiversity hotspots (4–6). We perform this assessment on a much finer scale than previous assessments and briefly relate our results to local, tactical issues of biodiversity protection.

There have been previous global assessments of vertebrate diversity, although each has limitations and caveats. All have used relatively coarse spatial grains, typically about 10,000 km². This scale is much coarser than typically used in areas of conservation such as protected areas (Table 1). Although many previous efforts did make comparisons across taxa (7–12), only two looked at protection efforts (8, 9).

Significance

Identifying priority areas for biodiversity is essential for directing conservation resources. We mapped global priority areas using the latest data on mammals, amphibians, and birds at a scale 100 times finer than previous assessments. Priority areas have a higher—but still insufficient—rate of protection than the global average. We identify several important areas currently ignored by biodiversity hotspots, the current leading priority map. As the window of opportunity for expanding the global protected area network begins to close, identifying priorities at a scale practical for local action ensures our findings will help protect biodiversity most effectively.

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Table 1. Key studies evaluating global vertebrate diversity patterns and priority areas for conservation

Study (reference no.)	Resolution	Taxa	Species richness measures
Stuart et al., 2004 (13)	10,000 km ²	Amphibians	Threatened
Brooks et al., 2004 (7)	One-half of a degree of latitude	Mammals, amphibians, birds	All, threatened
Rodrigues et al., 2004a, 2004b (8, 9)	One-fourth to one-half of a degree of latitude	Mammals, amphibians, threatened birds, turtles	All, threatened, ranges <50,000 km ²
Orme et al., 2005, 2006 (14, 15)	10,000 km ²	Birds (breeding ranges only)	All, threatened, 25% smallest ranges
Grenyer et al., 2006 (10)	10,000 km ²	Mammals, amphibians, birds	All, threatened, 25% smallest ranges
Lamoreux et al., 2006 (11)	Ecoregions	Mammals, amphibians, birds, reptiles	All, scaled endemism
Ceballos & Ehrlich, 2006 (17)	10,000 km ²	Mammals	All, threatened, ranges <0.25 million km ²
Schipper et al., 2008 (18)	22,300 km ²	Mammals	All, phylogenetic diversity, 25% smallest ranges
Present study	100 km ²	Mammals, amphibians, birds	All, threatened, small ranges, recent discoveries

Among the first of the modern global studies was the Global Amphibian Assessment (13), which also was a significant step forward in providing open access to species-distribution databases. Although large global datasets did exist previously, they typically were difficult to access or required direct permission from the researchers possessing them. Several studies associated with the 2003 World Parks Congress soon followed, providing multitaxa views of vertebrate diversity patterns and their protection (7–9). Orme and colleagues (14, 15) then presented a pair of studies on bird diversity, looking at congruency between richness patterns of threatened species, richness of small-ranged species, and species richness overall. They also established what would become a general pattern for viewing the data using three maps: one of overall species richness, one of threatened species, and one of small-ranged species. In 2006, Grenyer et al. (10) similarly assessed the three well-known vertebrate taxa (mammals, birds, and amphibians). In that same year, Lamoreux et al. (11) looked at vertebrates, including reptiles for the first time, but did so at the coarser spatial grain of ecoregions. Expanding upon their earlier work (16), Ceballos and Ehrlich (17) then focused in detail on mammals. Two years later the results of the Global Mammal Assessment (18) appeared, providing the most comprehensive assessment yet for mammals.

We build on these earlier findings in several important ways. We analyze the latest biodiversity data and do so at a grain more relevant for conservation. Previous studies generally analyzed data using grid cells of approximately 1° latitude/longitude (~100 × 100 km). This scale degrades the raw data and obscures crucial patterns of diversity in regions of rapid species turnover, such as mountains, that also tend to have the greatest levels of endemism. For example, a cell in a 100 × 100 km grid in the Colombian Andes could include multiple mountain ranges, obscuring the fact that each mountain range has sets of species different from each other range and from the intervening valleys. Moreover, the distribution of protected areas is likely to be nonrandom within that complex topography. Here, we produce more finely resolved maps of global biodiversity and conservation priorities than previously available. We then ask the following questions.

First, we ask which areas contain the most species and which areas contain the greatest number of small-ranged species. Even if the importance of mapping species for conservation is obvious, these questions are, by design, purely biogeographical. Our second purely biogeographical question asks how concentrated are the species distributions. That is, what fraction of all species or small-ranged species can we encompass within some specified area?

With these patterns in hand, our third question asks where threatened species are located. For our fourth topic, we compare our findings with the best-known scheme for conservation priority, the Myers biodiversity hotspots (4). Myers et al. designated

a region as a hotspot if it had >1,500 endemic plant species and <30% remaining natural land cover. In their work, Myers et al. were considering a different taxon—plants—and assessed threat indirectly, using habitat loss, rather than mapping out threatened species directly. However, they did include data on vertebrates in their tables.

Fifth, we evaluate the level of protection for the identified priority areas, providing a global snapshot of how well the planet-wide system of protected areas encompasses vertebrate biodiversity.

Finally, we explore how recent discoveries of species might alter our results by suggesting areas where as-yet-unknown species might be living.

Importantly, many of the priority locations we identify are substantially different from earlier findings. This point is crucial, because identifying specific land parcels within broad geographic regions is vital for guiding conservation actions. We attribute the differences to two main factors. First is the improved availability of digital species-range maps, largely through the Global Amphibian (13) and Mammal Assessments (18), as well as from efforts led by NatureServe and BirdLife International (19, 20) and the work of countless individual volunteers. The second factor is the finer spatial grain of analysis. Quite simply, analyzing the data using a 1° of latitude grain as in previous studies renders the most vital patterns invisible. In the past it may have been a necessity to use such a crude lens for looking at the world, but no longer. To inform conservation best, we should strive to look at the world through a lens more relevant to the scale of conservation actions.

Results

Where Are Species Found? Taxa are similar in where their areas of greatest diversity are located (Fig. 1 *Top Row*). For birds and mammals, these areas are nearly identical: The moist forests of the Amazon, Brazilian Atlantic Forest, Congo, Eastern Arc in Africa, and the Southeast Asian mainland and islands house the greatest numbers of bird and mammal species. The pattern for amphibians is similar, but amphibians have exceptional diversity in the Neotropics.

Small-ranged species are even more specific in their localities. Small-ranged birds and mammals both have concentrations in the Andes, Madagascar, Southeast Asian islands, and other scattered localities (Fig. 1 *Bottom Row*). Amphibians are exceptional in that so many have such small ranges that relatively few places have large concentrations.

The three parts of Fig. 1 allow comparisons among groups (all, threatened, and small-ranged species) and among the three taxa. In Fig. 2, we simplify these comparisons by mapping the globally richest 5% of the land area for each combination. When combining such centers of diversity for multiple taxa, as in Fig. 2 and

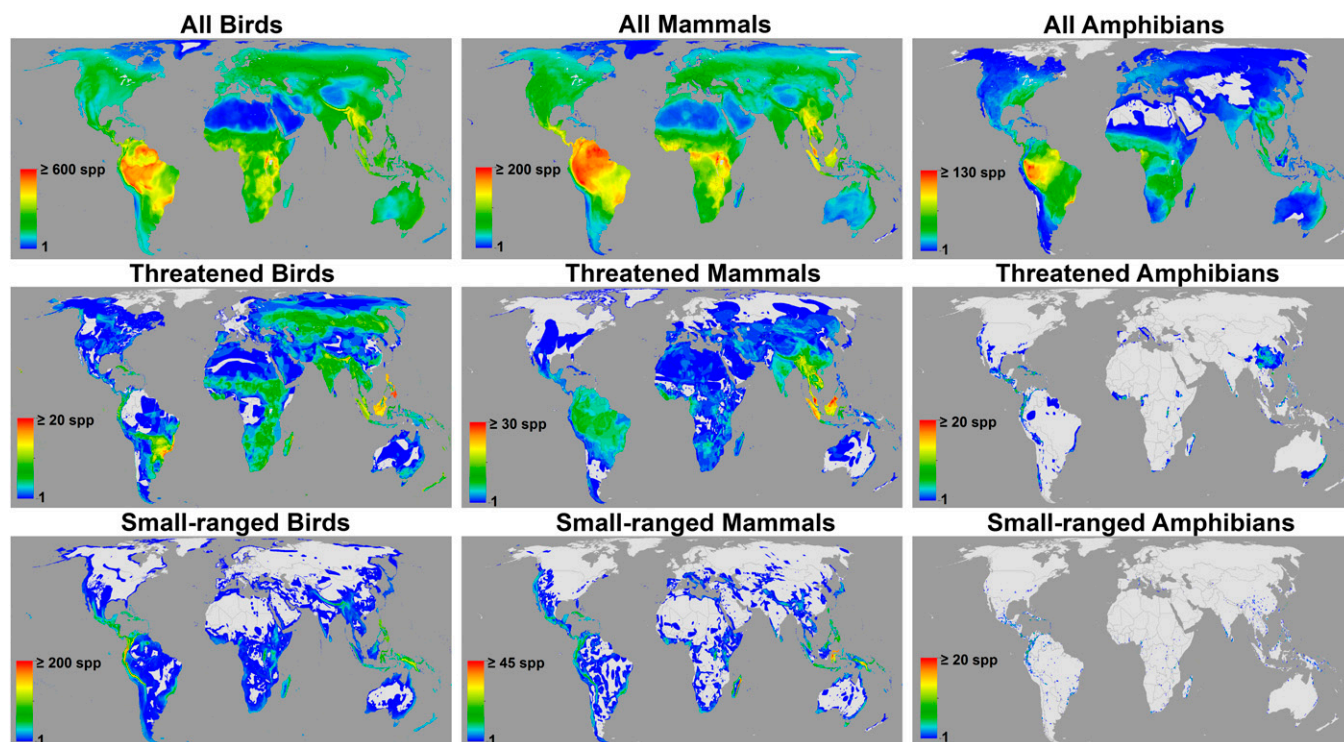


Fig. 1. Global maps of species richness for different categories of species. The top row shows the richness of all species in the taxon. For birds, we used breeding ranges only. The middle row shows the richness of threatened species (vulnerable, endangered, or critically endangered in the IUCN Red List). The bottom row shows the richness of species whose geographic ranges are smaller than the median range size for that taxon. Maps use a 10×10 km grid and the Eckert IV equal-area projection.

Table 2, the total area exceeds 5% of the planet's land area because the centers of diversity for different taxa do not completely overlap. Also, centers of diversity between groups do not overlap. For example, the centers of diversity for small-ranged species are largely nonoverlapping with those for species richness overall (Fig. 2 *A* and *C*). This lack of congruence is a widely observed law: Large-ranged species drive patterns of overall richness, obscuring diversity patterns that may be more important for conservation (1, 21).

How Concentrated Are Species Distributions? The Amazon, southeastern Brazil, and parts of central Africa dominate as centers of total diversity, defined as the top 5% richest cells on the planet for each taxon (Fig. 2*A*). Collectively, these areas cover 7.2% of the global land area but include ~50% of all species, with similar percentages for the richness centers of individual taxa (Table 2). By including a species, we mean that all or a portion of a species' range overlaps the region.

Amphibians are the most geographically concentrated taxon, with a mere 2.2% of the world's area (2.97 million km²) containing the entire known ranges of 50% of the world's amphibians (Fig. 1 *Bottom Row, Right* and *Tables S1* and *S2*). Those areas also contain a portion of the ranges for 46.6% of the remaining amphibians, for 96.6% of all amphibian species.

Combined, the centers of diversity for small-ranged vertebrates cover 8.2% of the world's land area, slightly more than the centers for species overall, but include an astounding 93% of all vertebrate species. This concentration has an inordinate importance for conservation planning, because it means that nearly all vertebrate species conceivably might be protected in less than 10% of the world's land area, assuming the area is chosen correctly.

As a comparison, the 25 Myers hotspots cover ~12.5% of the land area and include ~78% of the vertebrate species considered here (Table 2). This area is significantly larger than the area

identified using small-ranged vertebrates and captures substantially fewer species (Table 2). However, as Myers realized when creating the hotspots concept, the hotspots include many more species than are captured using simple species richness to guide priorities (Table 2). Notice that habitat loss is included in the definition of hotspots; habitat loss is likely one of the reasons that hotspots cover more area but harbor fewer species. Some places with small-ranged species do not yet face severe habitat loss, but those places are few. The often-quoted number for the area covered by hotspots (e.g., <2% of the planet's area) refers to the estimated amount of habitat remaining within the hotspot regions, not to the original extent of the habitat.

Where Are Species Threatened? The centers of small-ranged species diversity also differ substantially from those for currently threatened species (Fig. 1 *Middle Row*). Thus the localities of species at future risk of extinction may differ from those of species currently considered at risk. For example, the island of New Guinea has many small-ranged birds, mammals, and amphibians, but relatively few of these species presently are threatened. For mammals, the islands of Sulawesi and Madagascar also appear to hold a disproportionate number of small-ranged species relative to the number of species presently considered threatened.

Richness patterns for threatened species also differ dramatically from those for richness overall (Fig. 1 *Top Row*). Moreover, the patterns differ substantially among taxa. Threatened birds concentrate in the Andes, southeast Brazil, and Southeast Asian islands (Fig. 1 *Middle Row, Left*), whereas threatened mammals are concentrated on the Southeast Asian mainland and islands (Fig. 1 *Middle Row, Center*). Threatened amphibians are globally scattered, but, because of their generally small ranges, they occupy in total a tiny fraction of the global land area (Fig. 1 *Middle Row, Right*).

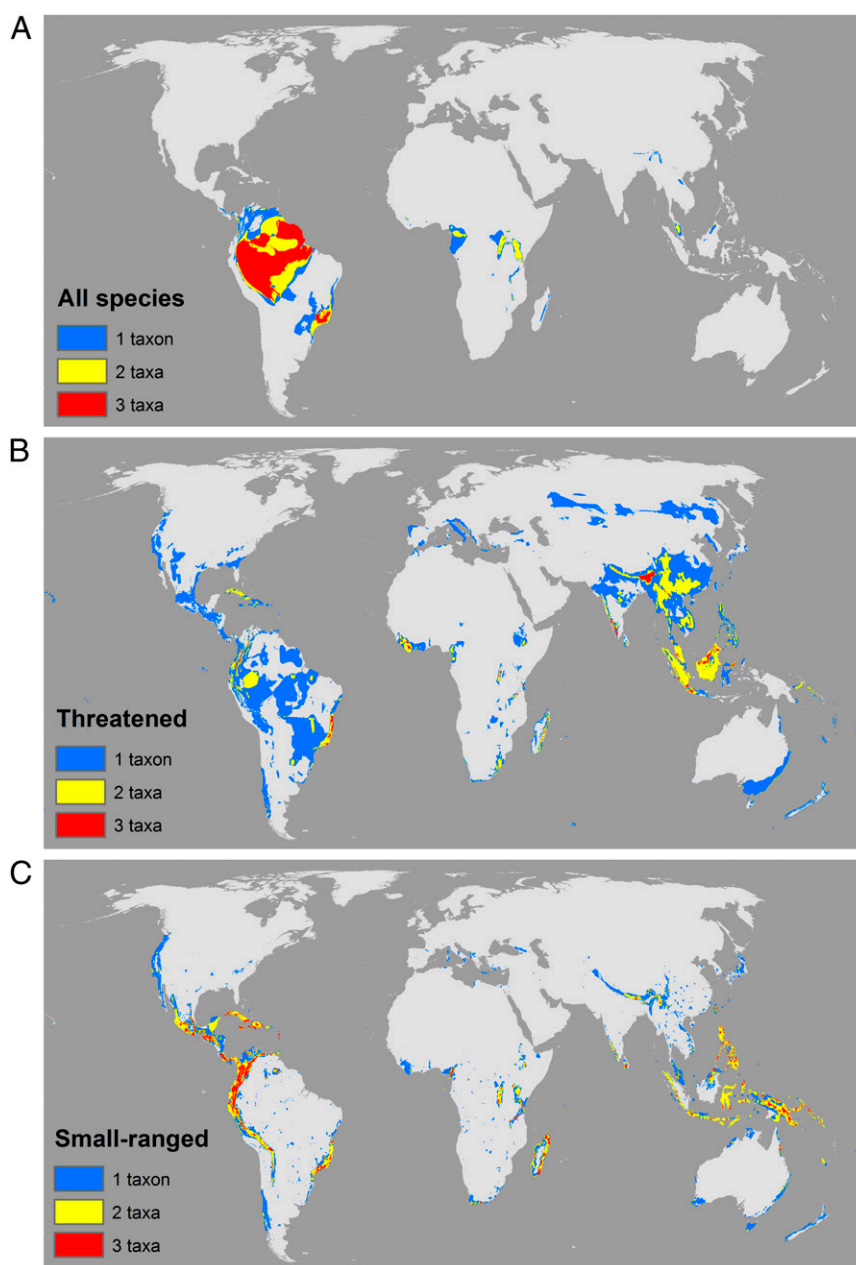


Fig. 2. Overlap of global species richness centers. Richness centers include cells that are among the globally richest 5% for at least one of the taxa. (A) All species, (B) IUCN listed threatened species, (C) Small-ranged species.

How Similar Are Vertebrate Priorities to Plant-Based Hotspots? How do these findings compare with other schemes for prioritizing the planet for conservation? The best-known scheme is the biodiversity hotspots of Myers, originally delineated in the late 1980s before global digital databases of species ranges were available (4–6). We found substantial disagreement in the locations of the Myers hotspots and our priority areas defined using small-ranged vertebrates. In Fig. 3, bright green indicates an overlap between the two priority schemes, and thus agreement. Dark green indicates an area that is a Myers hotspot but that is not ranked as a priority using small-ranged vertebrates. That is, Myers designated the area as a priority based on plant endemism and habitat loss, but we do not categorize it as such when using small-ranged vertebrates. Also shown in Fig. 3 are the additional hotspots (blue) proposed by Mittermeier and colleagues (22). Although these identifications are not as widely accepted as Myers' original find-

ings, they do overlap with centers of small-ranged diversity in some instances (yellow).

The red areas in Fig. 3 are the most critical result. They are priority areas for small-ranged vertebrates that coincide with no biodiversity hotspot. They are the areas missing from global priority designations.

Differences in scale account for part of the differences between Myers' hotspots and our priority areas. The hotspots as currently mapped are delineated using the Olson ecoregions (23), limiting their potential for fine-scale prioritizing. For a fairer comparison, we redid our vertebrate-based map using the ecoregions as our spatial units. We selected those ecoregions with high concentrations of small-ranged vertebrates while trying to minimize the total area (Fig. 4). That set of ecoregions still has less total area and many more vertebrate species than does the set of hotspot ecoregions (Table 2). Nonetheless, the set of chosen ecoregions still substantially underperforms the direct identification of areas

Table 2. Geographic area of the multitaxa richness centers and the numbers of species occurring in them

Richness center type	Area* (%)	No. bird species (%)	No. mammal species (%)	No. amphibian species (%)	Total species (%)
≥5% all species	9,740 (7.2)	5,355 (53.4)	2,334 (44.3)	3,080 (49.8)	10,769 (50.1)
≥5% small-ranged	11,090 (8.2)	9,226 (92.0)	4,702 (89.2)	6,065 (98.0)	19,993 (93.0)
≥5% threatened	23,566 (17.5)	9,221 (91.9)	4,536 (86.1)	5,630 (91.0)	19,387 (90.2)
Combined	31,367 (23.3)	9,599 (95.7)	4,920 (93.4)	6,130 (99.1)	20,649 (96.1)
Myers hotspots	16,756 (12.5)	8,268 (82.4)	3,851 (73.1)	4,583 (74.1)	16,702 (77.7)
Selected ecoregions	13,843 (10.3)	8,922 (88.9)	4,097 (77.7)	5,210 (84.2)	18,229 (84.8)
Global area/species	134,468	10,033	5,270	6,188	21,491

Numbers in parentheses are the percentage of the global land area or percentage of the total species in the taxon occurring in the richness centers. For example, 98% of amphibian species occur in the small-ranged species richness centers.

*1,000 km².

using species ranges. Essentially, the restriction imposed by using ecoregion-scale planning units forces us to choose more area for fewer species.

What Fraction of Priority Regions Do Protected Areas Encompass?

Although a small fraction of the world's area contains most of its vertebrates, and an even smaller fraction contains the species of conservation concern, most of that area is unprotected. Only a third of the diversity centers for total species richness have any protection, and only 11% has strict protection (Table 3). Encouragingly, multitaxa richness centers do have higher protection rates than richness centers for only a single taxon (Table 3). The situation for the centers of diversity for small-ranged and threatened species is more worrisome. Less than 20% of either has protection, and substantially less has strict protection, with only 10.2% of the centers of diversity for small-ranged species and 7.1% of the centers for threatened species having strict protection (Table 3).

Where Are As-Yet-Unknown Species Likely to Live? Finally, because scientists still are describing new vertebrate species (24), we should consider the potential implications of the still-missing species (25). We looked at the locations where species have been discovered since 1950, assuming that discoveries likely will continue in these areas. Discoveries occurred mainly, but not exclusively, in the tropics and mostly the Neotropics (Fig. 5). There have been relatively few birds discovered (297 or 3% of the global total) compared with mammals (914 or 17% of the global total). In contrast, taxonomists have discovered more than half of all known amphibian species in the past half-century (3,418 or 55% of the global total). Nearly a thousand amphibian species do not even enter our maps, because they still await published descriptions or are known so poorly that a formal range map has yet to be produced for the global database.

Bird discoveries concentrate in the Amazon and a few parts of the Andes, along with scattered localities around the world. However, it is likely that too few birds await discovery to have much influence on our current priority maps. Mammal discoveries have been more numerous and have an overwhelming concentration in the Amazon and Andes. Continuing discoveries in these regions likely will reinforce already identified priority areas in the Andes for small-ranged species. Amphibians are the most active source of discoveries, with many of those discoveries being in the western Amazon, northern Andes, and Brazilian Atlantic Forest. Continued discoveries in these areas would reinforce the patterns of priorities that we observe.

Discussion

The most efficient conservation targeting from a space-for-species perspective would rely on small-ranged species. Their centers of diversity cover 93% of vertebrate species in just 8% of the world's land area. Moreover, a substantial fraction of vertebrates is endemic to these priority areas. We can protect those species nowhere else. This situation is most evident for amphibians, of which 54% are endemic to the priority areas, but it is also significant for mammals (16% endemic) and birds (11% endemic). The broad conclusion is clear. These areas should be high priorities for conservation, and for a substantial number of species they are the only possibilities for survival.

As discussed below, we identify five main implications of our findings:

- Priority areas for different vertebrate taxa largely do not overlap.
- Protection levels for priority areas are greater than the global average but still are insufficient.

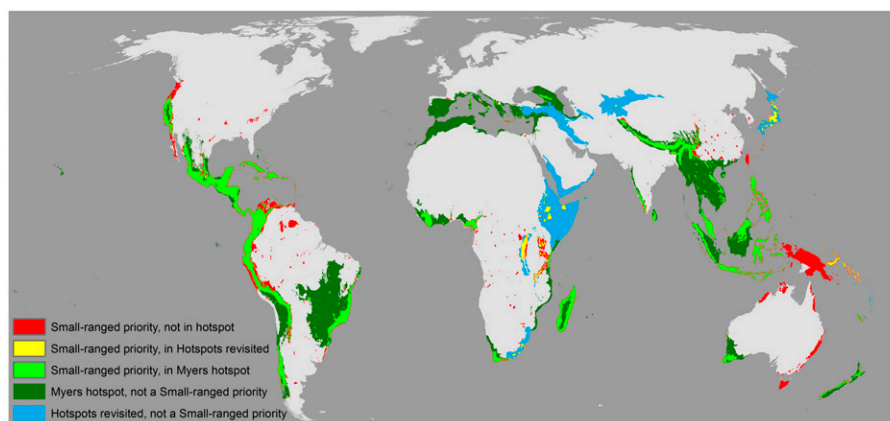


Fig. 3. Comparison of diversity centers for small-ranged vertebrates with the 25 original Myers biodiversity hotspots (4) and the 34 hotspots from Hotspots Revisited (22).

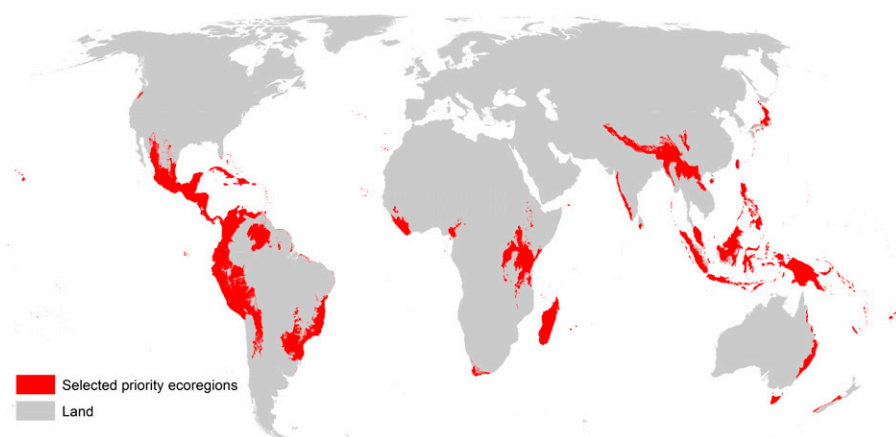


Fig. 4. Selected priority ecoregions based on small-bodied vertebrates.

- iii) Priority areas for vertebrates differ from the plant-based Myers biodiversity hotspots.
- iv) The spatial grain of analysis matters.
- v) When setting local-scale priorities, first refine the species range maps for remaining habitat.

Priority Areas for Different Vertebrate Taxa Largely Do Not Overlap.

Although the priority areas for small-bodied species of multiple taxa often do overlap, about half (52%) of the priorities are based on a single vertebrate taxon. This means that protecting the areas that are most important for one taxon may not ensure protection of others. In other words, the critical places for amphibians do not necessarily coincide with those for birds or mammals, and vice versa. That is not to say that these would not be valuable for all three taxa, but only that they may not be the most valuable areas.

Moreover, the terrestrial vertebrates examined cover only a small fraction of the planet's total species, most of which are plants, invertebrates, or fungi (24). In a necessarily coarse-scale comparison of plants with vertebrates, Kier et al. (26) found that global patterns of plant and vertebrate diversity do correlate, but those correlations vary substantially by vertebrate taxa. Similarly, in comparing ant and vertebrate diversity, Jenkins et al. (27) found global patterns for ants that were very different from those for some vertebrate taxa (e.g., amphibians), particularly for the

small-bodied taxa. Going forward, we are hopeful that advances in the mapping of fine-scale patterns of plant (28) and insect (29) diversity will enable more comprehensive assessments of diversity patterns and conservation priorities.

Protection Levels for Priority Areas Are Greater than the Global Average but Still Are Insufficient.

There are reasons for optimism. The percentage of these priority areas that is within protected areas (19%) is greater than the global average of 13% (30). The same pattern is true for the percentage within strictly protected areas, with a 10% rate versus the 6% global average. (The terms "protected" and "strictly protected" are defined in *Methods*.) Despite the known biases in the location of protected areas (31), their locations do bias toward the best areas for preventing vertebrate extinctions. Nevertheless, we still consider the level of protection of the priority areas to be inadequate given their high biodiversity value. A stronger focus on the concentrations of small-bodied species would have an inordinate impact in preventing vertebrate extinctions, especially given the large-scale evidence that protected areas benefit habitat protection worldwide (32–34).

Priority Areas for Vertebrates Differ from the Plant-Based Myers Biodiversity Hotspots.

When comparing our explicitly vertebrate-based map of priorities with what is perhaps the most widely known map of global conservation priorities, the biodiversity hotspots, we found substantial differences in these two priority

Table 3. Protection levels of the richness centers

Diversity center	Total area	Unprotected area (%)	Total protected area (%)	IUCN I-VI (%)	IUCN I-IV (%)	Other (%)
All species						
One taxon	2,951	2,305 (78.1)	645 (21.9)	382 (12.9)	217 (7.4)	263 (8.9)
Two taxa	2,891	1,557 (53.9)	1,334 (46.1)	906 (31.3)	496 (17.2)	428 (14.8)
Three taxa	3,898	2,567 (65.9)	1,331 (34.1)	793 (20.3)	359 (9.2)	539 (13.8)
Total	9,740	6,429 (66.0)	3,310 (34.0)	2,081 (21.4)	1,072 (11.0)	1,230 (12.6)
Small-bodied species						
One taxon	5,776	4,641 (80.3)	1,134 (19.6)	927 (16.0)	606 (10.5)	207 (3.6)
Two taxa	3,933	3,246 (82.5)	688 (17.5)	526 (13.4)	344 (8.7)	162 (4.1)
Three taxa	1,381	1,073 (77.7)	308 (22.3)	256 (18.5)	179 (13.0)	52 (3.8)
Total	11,090	8,960 (80.8)	2,130 (19.2)	1,709 (15.4)	1,129 (10.2)	421 (3.8)
Threatened species						
One taxon	18,384	15,140 (82.4)	3,244 (17.6)	2,335 (12.7)	1,319 (7.2)	909 (4.9)
Two taxa	4,720	3,978 (84.3)	743 (15.7)	556 (11.8)	300 (6.4)	187 (4.0)
Three taxa	462	374 (81.0)	88 (19.0)	71 (15.4)	60 (13.0)	17 (3.7)
Total	23,566	19,492 (82.7)	4,075 (17.3)	2,962 (12.6)	1,679 (7.1)	1,113 (4.7)

Values are thousands of square kilometers. Numbers in parentheses indicate the percentage of the richness center having that category of protection (or unprotected). The category "Other" includes protected areas with no IUCN category and indigenous people territories.

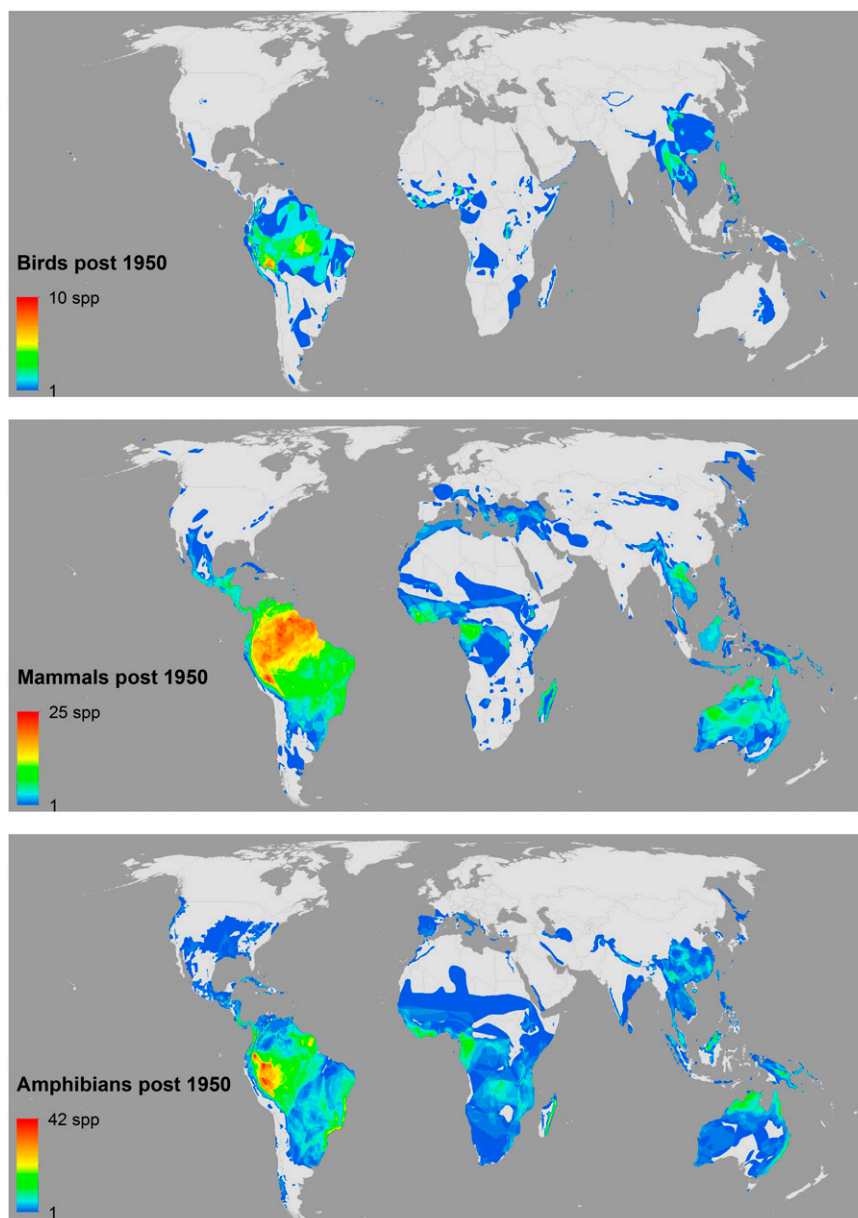


Fig. 5. Species discoveries since 1950. Maps show only species having range maps.

schemes in addition to the use of vertebrates vs. plants. For instance, the hotspots explicitly consider habitat loss, albeit not in a repeatable way. (There are no actual maps showing habitat remaining in most hotspots.) Also, the hotspots use a much coarser scale of analysis, the ecoregions. However, even when we used ecoregions in defining vertebrate priorities, our results differed substantially from the hotspots.

The Spatial Grain of Analysis Matters. The importance of the grain at which the data are analyzed merits attention. Conservation decisions typically take place at scales finer than those used for most previous global analyses, which have tended to be on the order of 100×100 km. Such a coarse scale unnecessarily blurs the data, most importantly the data on where species occur. Although we recognize that the boundaries of range maps are not always precise, they generally are more precise than 100 km, especially for the small-ranged species most critical for conservation planning. If they were not, one could not use the maps to find the

species in the field, nor could one visualize the patterns of endemism in mountains (e.g., which parts of the Andes harbor the most endemics). Generalizing the data to a grain of 100×100 km destroys vital information. We emphasize using an appropriate grain, not to pretend that the data are better than they are but to avoid throwing away valuable information. One cannot improve the data simply by blurring them. The inaccuracies still would be there, hidden behind the veil of one-degree grid cells.

When Setting Local-Scale Priorities, First Refine the Species Range Maps for Remaining Habitat. Finally, there are remaining practical issues. Although most of the identified priority areas lack protection, it is true that some areas no longer have habitat to protect. For instance, much of the Brazilian Atlantic Forest is a high priority by almost any measure, but it is heavily deforested (35), and thus many species likely have been eliminated from much of the biome. The overall approach of using species range maps poses inherent limits to solving this problem. Such maps

describe the general area where one can find a species but do not necessarily mean the species is present in all parts of the area (36). Moreover, even in areas where the species does occur, its abundance will vary across the range. The consequence is that even when range maps overlap a protected area, not all of those overlapping species will occur there. Although this limitation is real, range maps currently are still the best data available for assessing very large areas for large numbers of taxa.

Upon choosing a priority area, we recommend using a finer-scale tactical approach to guide specific conservation actions within the area. One should construct and use maps of remaining suitable habitat for the locally occurring species. For instance, one can refine the broad range maps using forest cover or species' elevation ranges to reduce their errors of commission, which are widely seen as their main drawback (37). We have done such modeling for smaller regions, where data were sufficient and the task was tractable (1, 38–40). Such a task is very challenging at a global scale and is especially so for the species of most conservation concern, because they often are rare and difficult to study, making them poor candidates for fine-scale distribution modeling. It seems unlikely that the needed data will become available in the near future for all of the taxa in our study, although others are making progress in this direction (41).

In summary, we identify special places in the world that are critical for preventing vertebrate extinctions. These areas differ in important ways from the biodiversity hotspots previously identified using plants. This analysis suggests a need for reconsidering the allocation of conservation resources globally to achieve maximum impact with limited conservation resources. The priority areas we identify tend to have more protection than the world in general, although the level of protection is still insufficient. To guide local conservation planning, we recommend that within the identified priority areas there be further tactical assessments to direct local conservation actions. Although this more detailed approach tends to be impractical in a global analysis, it is practical, and indeed vital, for effective local action.

Methods

For birds, we used data on breeding ranges from BirdLife International (20). For mammals and amphibians, we used range maps from the International Union for the Conservation of Nature (IUCN) (42), which now distributes updated data from the Global Mammal and Global Amphibian Assessments. We did not include marine mammals, even though some (e.g., seals) may

spend time at shorelines. When the original range data were split into subspecies, we merged the subspecies into a single species range map. Threatened species were those considered vulnerable, endangered, or critically endangered in the IUCN Red List (42). Because we are interested in planning for conservation of extant species, we did not include species considered Extinct or Extinct in the Wild.

For the 25 Myers hotspots (4), we selected the most closely matching areas from the publicly available Geographic Information System (GIS) layer of the 34 Conservation International hotspots from Hotspots Revisited (22) (available at www.conservation.org). The modern GIS hotspot boundaries are matched to World Wildlife Fund ecoregion boundaries (23) and thus differ slightly from those originally designated by Myers. To our knowledge, there is no publicly available GIS layer of the original hotspots.

For protected areas, we used the most recent version available of the World Database of Protected Areas (WDPA) (43). We excluded from our analyses all areas designated only by international conventions (i.e., not nationally gazetted) and all protected areas with a status other than "designated" (i.e., Not Reported, Proposed). For protected areas represented only as points in the database, we created a circular buffer around the point equal to the reported size of the protected area. All protected areas in the WDPA either are classified as one of the six IUCN Protected Area Management Categories (IUCN, 1994) or lack an IUCN category altogether. We categorized protected areas into three groups for analysis: (i) all protected areas, (ii) all IUCN categories, and (iii) strictly protected IUCN categories (I–IV). When there were overlaps in protected areas, we classified the area as the highest IUCN category occurring in that location. We considered areas not designated with an IUCN category to be the lowest protection level (i.e., below IUCN category VI).

To choose the vertebrate-based priority ecoregions, we selected ecoregions that overlapped areas with high concentrations of small-ranged vertebrates. The decision on what constituted a high concentration differed by taxa because they have varying numbers of total species and levels of variation in local diversity. We also included some lower-diversity ecoregions if they were exceptionally small in total geographic area (e.g., island ecoregions). Such ecoregions add species while adding relatively little total area.

All analyses were for terrestrial areas only and used a spatial resolution of 10 × 10 km and an equal area projection. We considered a species occurring anywhere within a grid cell to be present in that cell. To identify the centers of species richness, we included the richest cells for a set of species until a minimum of 5% of the global land area was included, excluding Antarctica. The exception was the small-ranged amphibians, because 2.2% of the land area includes the full distributions of all small-ranged amphibians (Tables S1 and S2). Analyses used ArcGIS 10.1 (ESRI).

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