LETTERS

Global distribution and conservation of rare and threatened vertebrates

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Global conservation strategies commonly assume that different taxonomic groups show congruent geographical patterns of diversity, and that the distribution of extinction-prone species in one group can therefore act as a surrogate for vulnerable species in other groups when conservation decisions are being made[1–4]. The validity of these assumptions remains unclear, however, because previous tests have been limited in both geographical and taxonomic extent[5–12]. Here we use a database on the global distribution of 19,349 living bird, mammal and amphibian species to show that, although the distribution of overall species richness is very similar among these groups, congruence in the distribution of rare and threatened species is markedly lower. Congruence is especially low among the very rarest species. Cross-taxon congruence is also highly scale dependent, being particularly low at the finer spatial resolutions relevant to real protected areas. 'Hotspots' of rarity and threat are therefore largely non-overlapping across groups, as are areas chosen to maximize species complementarity. Overall, our results indicate that 'silver-bullet' conservation strategies alone will not deliver efficient conservation solutions. Instead, priority areas for biodiversity conservation must be based on high-resolution data from multiple taxa.

Our analyses are based on three high-resolution databases of the global distribution of birds, mammals and amphibians[13–15]. For each group, we mapped the geographical distribution of species richness for all species, rare species and threatened species (Fig. 1). These maps were based on grid cells roughly equivalent to 1° latitude by 1° longitude. For each aspect of richness, we calculated the pair-wise Pearson's correlation coefficient (r) for grid-cell richness values of the three vertebrate classes, controlling for spatial covariance when estimating the statistical significance of correlations[16] (Fig. 2a). Although all pair-wise correlations were positive and statistically significant at a global scale, the cross-taxon congruence varied markedly across the three aspects of richness. There was very high congruence with respect to total species richness ($0.79 \leq r \leq 0.90$), but congruence among rare species was lower ($0.24 \leq r \leq 0.48$), and lower still among threatened species ($0.13 \leq r \leq 0.32$). Typically, mammals and birds showed the highest global congruence, whereas mammals and amphibians showed the lowest. Caution needs to be exercised when invoking explanations for these differences, however, because amphibians have substantially smaller ranges (median range $5.6 \times 10^4\,km^2$) than mammals ($5.8 \times 10^5\,km^2$) or birds ($1.0 \times 10^6\,km^2$). The low overlap between amphibian ranges and

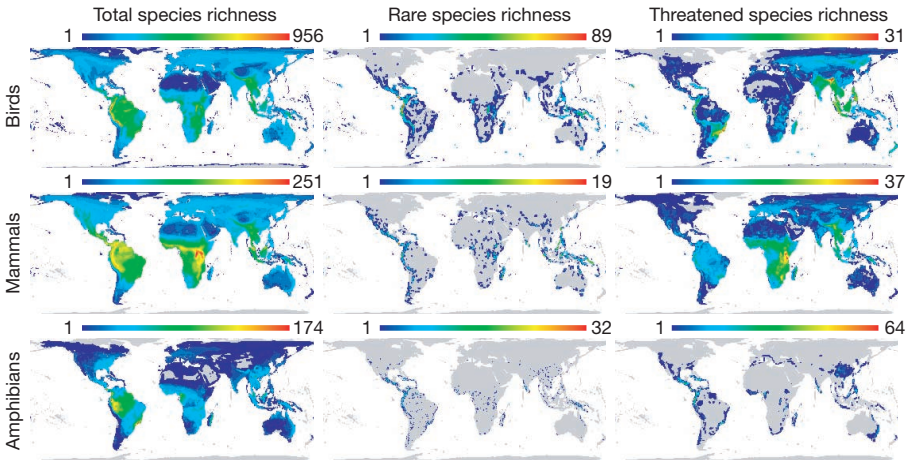

Figure 1 | Global richness maps for birds, mammals and amphibians. Global richness is shown with respect to the three different aspects of species richness used here. Colour gradients are linear with respect to species number.

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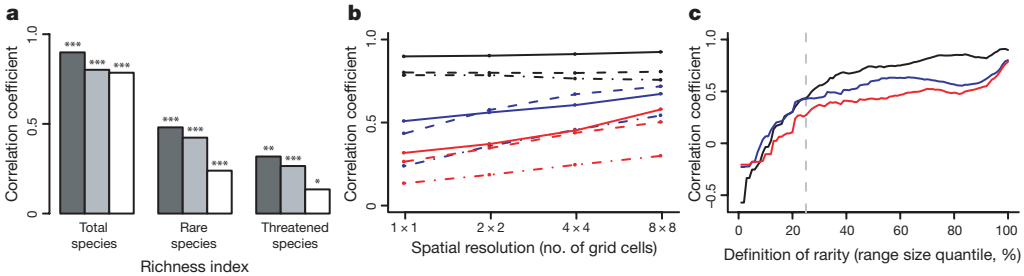

Figure 2 | Cross-taxon congruence and the effects of scale and definition of rarity on congruence. **a**, Congruence for overall species richness, rare species and threatened species between birds and mammals (dark grey bars), birds and amphibians (light grey bars) and mammals and amphibians (open bars). Asterisks indicate statistical significance controlling for spatial non-independence (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$). **b**, Effect of scale on congruence for overall species richness (black), rare species (blue) and threatened species (red). Congruence between birds and mammals (unbroken lines), birds and amphibians (dashed lines) and mammals and amphibians (dotted-dashed lines). **c**, Relationship between definition of rarity and congruence for rare species of birds and mammals (black), birds and amphibians (blue) and mammals and amphibians (red). Definition of rarity refers to the quantile of range distribution. The dashed, vertical line indicates the lower quartile of species.

those of the other two groups may, therefore, simply reflect the null expectation that small ranges are less likely to overlap with other ranges. In general, these global patterns of congruence held within biogeographic realms and biomes[17] (Supplementary Fig. 1), with congruence being particularly high in the tropics and particularly low across the Holarctic. This latter finding may reflect differences between groups in their ability to re-colonize areas after glacial retreat.

Congruence among rare and threatened species varied with the resolution of data used in the analysis[18] and increased markedly at coarser resolutions (Fig. 2b). This observation may explain differences in results between our study and those using coarser scale data[2,4,12]. An analysis using ecoregions[17], for example, reported high cross-taxon congruence for rare ('endemic') species ($0.49 < r < 0.61$)[12]. The average size of those ecoregions (median area 5.5×10^4 km^2), however, is much larger than our grid cells and is several thousand times larger than most protected areas (1.53 km^2; ref. 19 and Supplementary Fig. 2). Our results show that congruence among rare and threatened species declines rapidly as the scale approaches that more relevant to real protected areas. High congruence at the ecoregion scale does not, therefore, mean that reserves in ecoregions will also show high congruence.

Congruence among rare species also varied with the definition of rarity, and observed congruence decreased as the definition became more stringent (Fig. 2c). Indeed, across the very rarest species in each class (for example, those with the smallest 10% of ranges), all pair-wise correlations between groups were negative: the very rarest birds, mammals and amphibians inhabit different places from one another. Such patterns may explain why previous analyses have reported high congruence for rare species[2,4,12]. Although our definitions of rare species correspond to ranges of <278,250 km^2 in birds, <41,685 km^2 in mammals and <430 km^2 in amphibians, previous analyses defined rare ('endemic') species simply as those recorded as occupying single hotspots (<2,373,057 km^2; ref. 4) or ecoregions (<4,629,589 km^2; ref. 17). Our results show that such relaxed definitions of rarity lead to raised estimates of congruence.

We also tested whether geographical patterns of richness in one group act as a surrogate for those in other groups[6,7,9,11]. We tested whether richness hotspots (the richest 5% of grid cells) identified for one group overlapped with corresponding hotspots for other groups. Hotspots of total species richness showed high congruence, with 17.8% of all hotspot grid cells common across groups (Fig. 3a). Hotspots of rare or threatened species showed much lower congruence, however, with only 2.3% of rarity hotspot cells (Fig. 3b) and 0.6% of threat hotspot cells (Fig. 3c) common across groups. These patterns remained intact when we used an optimal complementarity algorithm to choose sets of grid cells that efficiently capture all species in a group (Table 1), and even when we controlled for differences in the area of the sets (Supplementary Table 1). We measured surrogacy as the proportion of species from other groups represented within sets[20].

Finally, we compared the performance of different methods of identifying priority areas with respect to their ability to capture multi-taxon diversity. For overall species richness, there were no substantial differences between sets based on single taxa and those based on multiple taxa, in terms of either area covered or species captured (Fig. 4a). For rare and threatened species, however, sets based on multiple taxa captured far more species than did single taxon sets in a similar overall area (Fig. 4b, c, and Supplementary Fig. 3). Complementarity sets based on high-resolution data on multiple taxa were also much more efficient in capturing rare and threatened species than were areas identified in previous global analyses[1,4,21], even when the complementarity sets represented each species more than once[20] (Fig. 4, and Supplementary Fig. 3). Indeed, areas identified in some previous global analyses often did not perform any better than randomly selected sets of cells of equivalent overall size, and in some cases performed worse (Fig. 4).

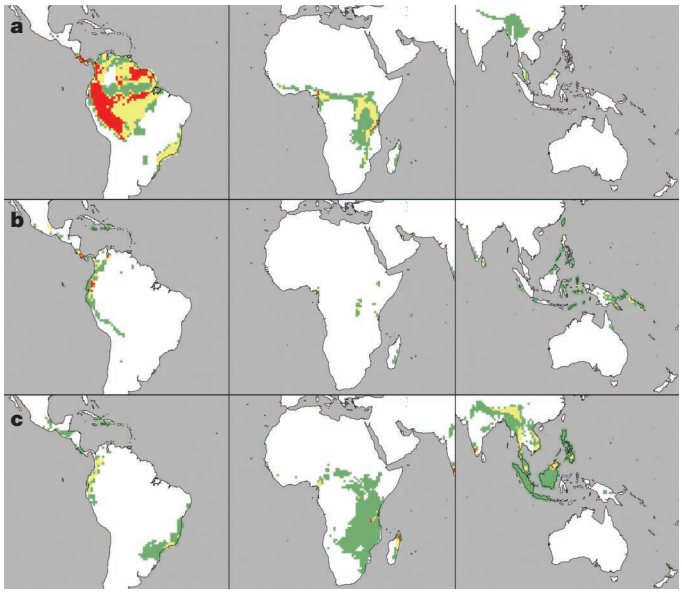

Figure 3 | Cross-taxon congruence of richness hotspots. Hotspots of total species (**a**), rare species (**b**) and threatened species (**c**) richness. Red shading shows cells that are hotspots for all three groups, yellow for two groups, and green for one group. Hotspots are the richest 5% of non-zero cells.

Our finding that cross-taxon congruence is high for total species richness, given that the richest areas are consistently associated with low latitudes and mountainous regions[13], reflects the importance of the interaction between energy and topography in predicting diversity. Caution is again needed when invoking explanations for why congruence and surrogacy are lower for rare and threatened species: such species typically have relatively small geographic ranges and thus low overlap in range might be expected. There may, however, be additional factors. For rare species, all three groups have richness peaks on the neotropical mainland, but avian rarity also peaks on oceanic island archipelagos, whereas rare mammal species are concentrated on continental shelf islands and rare amphibian species are often on continental land masses. Such differences may therefore reflect relative dispersal ability. For threatened species, low congruence may also result from differences among groups in their sensitivity to particular threatening processes. Although the main source of threat for all three groups is habitat loss, subsidiary threats differ among groups. Invasive species and overexploitation are chief secondary sources in birds[3], overexploitation is the main secondary source in mammals[3], and climate change, pollution and transmissible disease are important in amphibians[15]. Low congruence among threatened species may therefore be driven by differences in the distribution of these risks.

Could our findings that cross-taxon congruence is high for overall species richness but low for rare and threatened species be due to biases in the databases? Systematic error could result if some geographical regions, or some taxa, are relatively poorly studied; however, our key findings remain qualitatively intact even if we restrict our analyses within the best-studied areas (the Nearctic, Palearctic and Australia; Supplementary Fig. 1) or the best known groups (birds and mammals; Table 1). Bias in our estimates of overall range could also influence cross-taxon congruence because congruence should decline with decreasing range size. Our conclusions are probably conservative in this respect, however, because the extents of occurrence used tend to overestimate true ranges[22]. It is therefore unlikely that our main conclusions are artefactual: indeed, we predict that more detailed information on the geographical distribution of poorly known species will show that cross-taxon congruence and surrogacy for rare and threatened species are even lower than estimated here.

Our findings should be interpreted cautiously with respect to applied conservation. We have ignored the political and socio-economic factors that are vital in practical conservation[23,24] and have focused on species rather than ecoregions and ecosystem services[17,25]. We have also restricted our analyses to terrestrial habitats and closely related organisms. Nevertheless, we have shown that, even among terrestrial vertebrates, the extent to which rare and threatened species from one group can act as a surrogate for corresponding species in other groups is severely limited, especially at the finer scales most relevant to conservation. At such scales, we predict that low cross-taxon congruence will be a property of any set of global priority areas and that congruence is likely to be even lower among more distantly related organisms or across terrestrial and aquatic habitats. This is of concern because, although previous global analyses have explored numerous methods for identifying priority areas[25], they are fundamentally based on data from just one or two groups[1,2,4,21]. Our results suggest that designing effective protected area networks will require high-resolution data on the distribution of multiple taxa and an understanding of how these relate to ecosystems. These challenges are being tackled through projects mapping the distribution of species at a scale comparable to individual protected areas[26–28]. We anticipate, however, that 'silver-bullet' conservation strategies based on particular taxonomic groups will not be effective because locations rich in one aspect of diversity will not necessarily be rich in others.

Table 1 | Patterns of cross-taxon surrogacy across birds, mammals and amphibians

Richness index	Surrogate groups	$N_{spp.}$	N_{cells}	Target groups* (% of species represented in set) Birds	Mammals	Amphibians
Total	Birds	9,626	421	–	79.4 ± 0.3	55.5 ± 0.7
	Mammals	4,104	509	91.7 ± 0.1	–	61.1 ± 0.5
	Amphibians	5,619	831	90.9 ± 0.2	86.2 ± 0.2	–
	Birds, mammals	13,730	714	–	–	68.4 ± 0.5
	Birds, amphibians	15,245	1,028	–	89.8 ± 0.2	–
	Mammals, amphibians	9,723	1,077	95.0 ± 0.1	–	–
	All three groups	19,349	1,223	–	–	–
Rarity	Birds	2,424	380	–	43.3 ± 1.1	22.5 ± 1.3
	Mammals	1,026	432	68.3 ± 0.4	–	27.0 ± 0.7
	Amphibians	1,405	560	63.7 ± 0.5	51.6 ± 0.6	–
	Birds, mammals	3,450	656	–	–	35.7 ± 0.9
	Birds, amphibians	3,829	808	–	63.1 ± 0.6	–
	Mammals, amphibians	2,431	858	77.9 ± 0.2	–	–
	All three groups	4,855	1,033	–	—	—
Threat	Birds	1,096	282	–	51.7 ± 0.9	31.2 ± 1.4
	Mammals	1,033	357	60.7 ± 0.6	–	39.7 ± 0.9
	Amphibians	1,856	454	62.7 ± 0.4	59.7 ± 0.4	–
	Birds, mammals	2,129	518	–	–	49.2 ± 0.6
	Birds, amphibians	2,952	627	–	67.2 ± 0.5	–
	Mammals, amphibians	2,889	690	72.4 ± 0.4	–	–
	All three groups	3,985	821	–	–	–

* Values are the percentage of species in the target groups represented in complementary sets of grid cells designed to contain all members of the surrogate groups (mean ± s.d. over 100 such sets). $N_{spp.}$ is total number of species in the surrogate group. N_{cells} is number of cells in the optimal complementarity set.

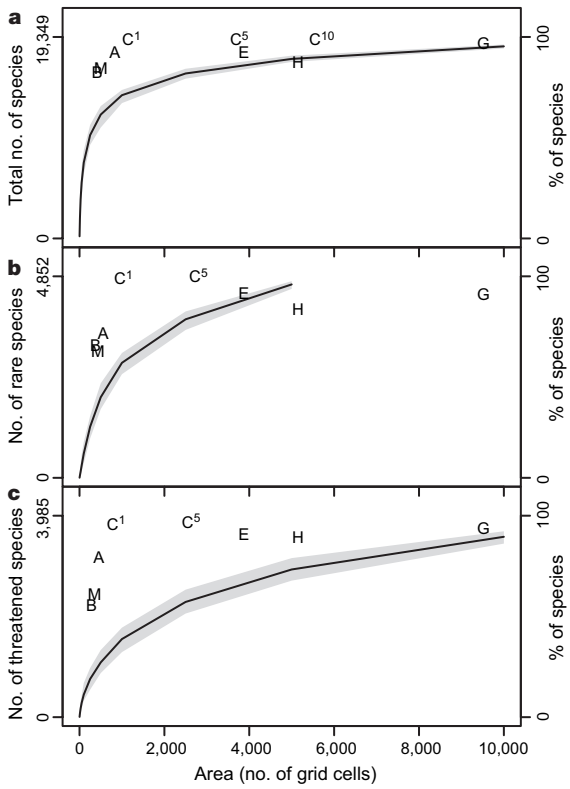

Figure 4 | Relative performance of different types of priority network. Shown is performance with respect to capturing total species (**a**), rare species (**b**) and threatened species (**c**) richness of birds, mammals and amphibians. Networks were identified by using an optimal complementarity approach based on birds alone (B), mammals alone (M), amphibians alone (A), or birds, mammals and amphibians combined (C^n, where n indicates the number of times each species is represented). Performance is also shown for biodiversity hotspots[4] (H), endemic bird areas[1] (E) and the global 200 ecoregions[21] (G), and for randomly selected sets of cells (100 replicates: median, black line; 95% confidence range, grey area).

METHODS

Databases. Analyses were based on vector range maps of 9,626 species of terrestrial birds[13], 4,104 species of terrestrial mammals[14], and 5,619 species of amphibians[27]. Range maps were projected onto a Behrmann equal-area projection and converted to a grid with resolution $96.3 \times 96.3\,km^2$ (ref. 13). Species richness was the total number of species present in each grid cell[13]. Rare species richness was the total number of rare species present, where rare species were those in the lower quartile of the range distribution of each taxonomic group[13,29]. A relative definition of rarity was used rather than an absolute one because of the large difference in absolute geographic range between the three vertebrate classes (median range: birds, $1{,}001{,}559\,km^2$; mammals, $574{,}969\,km^2$; amphibians, $55{,}642\,km^2$). No definition of rarity based on an absolute range area therefore successfully identified a consistent proportion of species in each taxonomic class. Threatened species richness was the total number of the threatened species present[13], where threatened species were those classified by The World Conservation Union (IUCN) as 'vulnerable', 'endangered' or 'critically endangered'[30]. Biogeographic realms and biomes were those identified in ref. 17. Median ranges for each group were based on grid-cell counts.

Cross-taxon congruence. Cross-taxon congruence was measured with Pearson correlation coefficients among grid cells, calculated for all pair-wise combinations of the three vertebrate classes for each of total, rare and threatened species richness. To control for spatial non-independence, statistical significance was calculated under an estimated effective sample size given the observed degree of spatial autocorrelation[16]. We adjusted sample size, rather than explicitly modelling spatial non-independence[13], because at this scale the cumulative number of pair-wise correlations required across all tests is very large and thus would be prohibitive to run with spatially explicit models.

Scale of analysis and definition of rarity. Analyses were conducted at four resolutions: 1×1 grid cell ($\sim 9{,}274\,km^2$), 2×2 grid cells ($\sim 37{,}000\,km^2$), 4×4 grid cells ($\sim 150{,}000\,km^2$) and 8×8 grid cells ($\sim 600{,}000\,km^2$). The criterion for rarity varied in stringency from rare species being those in the first percentile of the range distribution for their class (highest stringency) to rare species being those in the lower 99 percentiles of that distribution (lowest stringency).

Hotspots. Hotspots were defined as the richest 5% of grid cells[13] for each richness index, and overlap was quantified as the number of hotspot grid cells common to all three taxonomic groups as a percentage of the total number of hotspot cells[5,13]. Varying the percentage used to define hotspots[13] did not qualitatively change the pattern of overlap.

Optimal complementarity sets. We calculated the smallest number of grid cells required to represent each species in the 'surrogate' taxonomic group at least once and then identified 100 such sets of cells[20]. The surrogacy value of a group was calculated by counting the average number of species from the other 'target' groups represented in each set[7]. To control for differences in set size when comparing surrogacy, we selected the richest 250 cells (the approximate size of the smallest single-taxon set) from each set. Complementarity sets were also calculated with more than one taxon in the 'surrogate' group and by using an algorithm that attempted to represent each species in the surrogate set more than once[20]. Performance of complementarity sets was measured as the number of species that the sets contained; this value was compared with that of randomly selected sets of cells, and with areas identified in previous global analyses[1,4,21], which were rasterized to our grid. Species composition of cells was based on our databases and our definitions of rarity and threat.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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