LETTERS

Global hotspots of species richness are not congruent with endemism or threat

C. David L. Orme[1], Richard G. Davies[3], Malcolm Burgess[1], Felix Eigenbrod[1], Nicola Pickup[1], Valerie A. Olson[4], Andrea J. Webster[5], Tzung-Su Ding[6], Pamela C. Rasmussen[7], Robert S. Ridgely[8], Ali J. Stattersfield[9], Peter M. Bennett[4], Tim M. Blackburn[5], Kevin J. Gaston[3] & Ian P. F. Owens[1,2]

Biodiversity hotspots have a prominent role in conservation biology[1–9], but it remains controversial to what extent different types of hotspot are congruent[4,10–14]. Previous studies were unable to provide a general answer because they used a single biodiversity index, were geographically restricted, compared areas of unequal size or did not quantitatively compare hotspot types[1–10,12–22]. Here we use a new global database on the breeding distribution of all known extant bird species to test for congruence across three types of hotspot. We demonstrate that hotspots of species richness, threat and endemism do not show the same geographical distribution. Only 2.5% of hotspot areas are common to all three aspects of diversity, with over 80% of hotspots being idiosyncratic. More generally, there is a surprisingly low overall congruence of biodiversity indices, with any one index explaining less than 24% of variation in the other indices. These results suggest that, even within a single taxonomic class, different mechanisms are responsible for the origin and maintenance of different aspects of diversity. Consequently, the different types of hotspots also vary greatly in their utility as conservation tools.

We created a global database on the geographical distribution of the breeding ranges of all known extant bird species using an equal-area grid at a resolution comparable to 1° latitude × 1° longitude. We used this database to map the geographical distribution of three different aspects of avian diversity: overall species richness (Fig. 1a); threatened species richness (Fig. 1b); and endemic species richness (Fig. 1c). Overall species richness was defined as the total number of bird species recorded as breeding in each grid cell. Threatened species richness was the number of breeding bird species in each grid cell that were listed as threatened with extinction[8]. Endemic species were the 25% of species with the smallest geographical breeding ranges[19,23]. We used these three indices of diversity because they can be easily replicated, are well established in the literature[4,5,8,10] and have been assumed or predicted to show congruent patterns of spatial distribution[5–9,21,22].

The maps of avian diversity were used to identify hotspots of species richness, threat and endemism. We initially defined hotspots as the richest 2.5% of grid cells with respect to species richness, threat or endemism, respectively. We used 2.5% as our initial criterion because several previous analyses have shown that the richest 1–5% of land area can represent a substantial proportion of terrestrial species[1–10]. We found that, for all three measures of avian diversity, grid cells identified as being hotspots were aggregated in a relatively small number of biogeographic regions (Table 1, Supplementary Fig. 1). Hotspots of species richness were grouped into nine distinct biogeographic regions (Fig. 2a), whereas threat hotspots were aggregated into ten regions (Fig. 2b), and endemism hotspots were aggregated in twenty biogeographic regions (Fig. 2c).
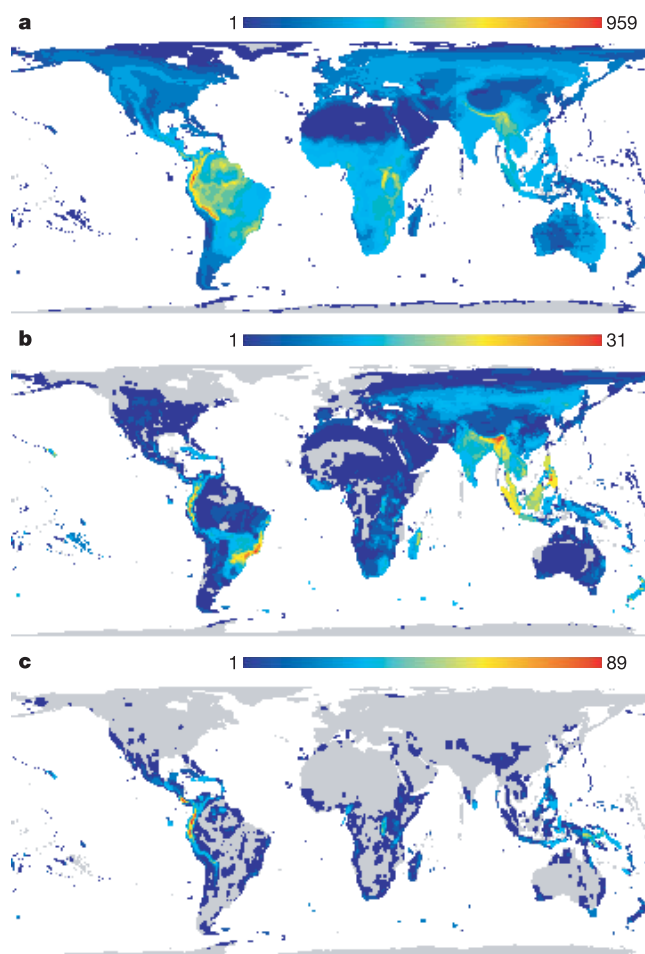

Figure 1 | Geographical distribution of three aspects of diversity. a, Total species richness. **b**, Threatened species richness. **c**, Endemic species richness. The bars above the maps show the corresponding colour scale, which is linear in terms of numbers of species.

[1]Division of Biology and [2]NERC Centre for Population Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK. [3]Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK. [4]Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK. [5]School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK. [6]School of Forestry and Resource Conservation, National Taiwan University, 1, Sec 4, Roosevelt Road, Taipei 106, Taiwan. [7]Michigan State University Museum and Department of Zoology, West Circle Drive, East Lansing, Michigan 48824-1045, USA. [8]Academy of Natural Sciences, 1,900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103, USA. [9]BirdLife International, Wellbrook Court, Girton, Girton Road, Cambridge, CB3 0NA, UK.

We tested for congruence between the three types of avian hotspot by measuring the extent of spatial overlap between hotspots[10]. In general, there was very low spatial congruence between different types of avian hotspot. Cumulatively the three sets of hotspots occupied 1,275 grid cells, of which only 2.5% (32 grid cells) were common to all types (Fig. 3a). All of these congruent hotspot grid cells were in a single biogeographic region, the Andes (Table 1). Rather than being congruent across hotspot types, 82.4% (1,051) of hotspot grid cells were idiosyncratic to individual types, with the remaining 15.1% (192) of hotspot grid cells being shared between pairs of hotspot type (Fig. 3a). One likely reason for such low congruence was that different hotspot types were associated with different aspects of large-scale topography (Table 1). For example, of the species richness hotspot regions 89% (8 out of 9 biogeographic regions) were in mountainous areas of mainland continents, whereas only 40% (4 out of 10) and 45% (9 out of 20) of threat and endemism hotspot regions, respectively, were in continental mountains. In contrast, 60% (6 out of 10) of threat and 60% (12 out of 20) of endemism hotspot regions were on large islands and/or island archipelagos, whereas none of the species richness hotspot regions were on islands. These results agree with previous analyses that have identified highlands and islands as important regions of vertebrate diversity[23,24].

To verify that low congruence between avian diversity hotspots was not an artefact of our initial hotspot definition, we recalculated the extent of overlap under a variety of hotspot criteria. This showed that, even when the definition of hotspots was greatly relaxed, the extent of overlap between the three hotspot types remained low (Fig. 3b). For example, redefining hotspots as the richest 10% of grid cells still resulted in only 4.8% (225 out of 4,664 cells) of hotspots being congruent across all three aspects of avian diversity. Low spatial overlap between different types of hotspot seems, therefore, to be a general property of global avian diversity hotspots, irrespective of the precise criterion used to define those hotspots.

Equally, the lack of congruence between different hotspot types is not an artefact of comparing only the geographical peaks of diversity, as correlations between the overall global distributions of species richness (Fig. 1a), threat (Fig. 1b) and endemism (Fig. 1c) were also surprisingly weak. Regression methods that assume that each grid cell is an independent data point are not appropriate for these data because there is strong spatial autocorrelation for all three indices of diversity (Moran's $I \geq 0.80$; $P < 0.001$ in all cases). General linear mixed models, however, can explicitly model the effects of spatial autocorrelation and were used here to explore the relationships between each pair of diversity measures. In each case, although the correlation between the two measures of diversity was statistically significant, the slope of the relationship was shallow and the proportion of variation explained was small, ranging from 7% for species endemism versus threat to approximately 22% and 24% for species richness versus threat and species richness versus endemism, respectively. These models were, therefore, consistent with our hotspot analyses and studies showing low congruence between different measures of diversity at more restricted geographical scales[4,10,12–14,17–19].
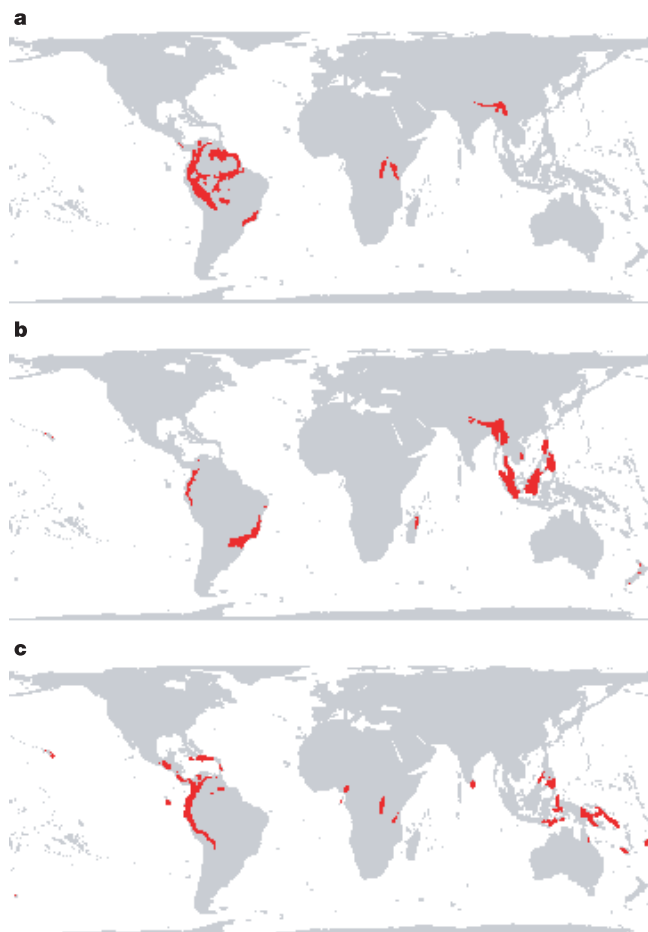

Figure 2 | Biodiversity hotspots for three aspects of diversity. a, Hotspots of species richness. **b**, Hotspots of threatened species. **c**, Hotspots of endemic species. For each measure of diversity, hotspots are defined as the richest 2.5% of grid cells. Hotspots are shown in red.
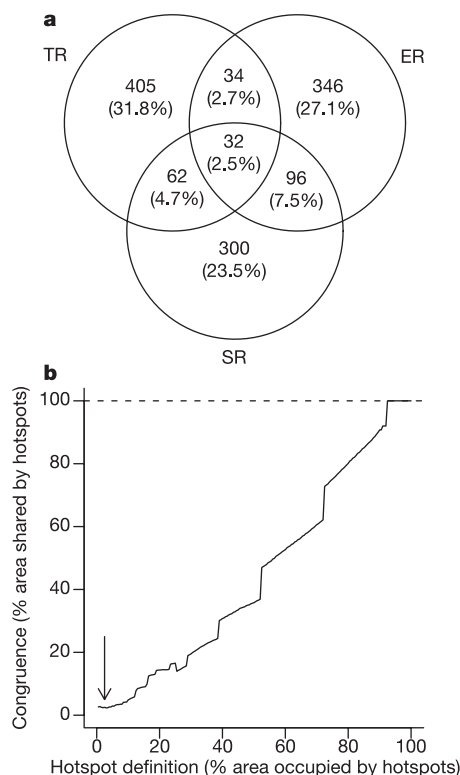

Figure 3 | Extent of congruence between hotspots. a, Venn diagram showing congruence across species richness hotspots (SR), threat richness hotspots (TR) and endemic richness hotspots (ER), where hotspots are the richest 2.5% of cells. Figures show number of cells and corresponding percentages. **b**, Relationship between the criterion used to define hotspots and congruence. Criteria are based on the percentage of land covered by hotspots. Congruence is the number of cells that are hotspots for all three diversity indices, as a percentage of the total hotspot area. Horizontal dashed line shows expectation under full congruence. Vertical arrow shows 2.5% hotspot criterion.

Table 1 | Avian hotspot regions with respect to species richness, threat and endemism

| | Type of hotspot | | | | | | | | | |
| Hotspot regions | Species-richness | | Threat | | Endemism | | Topography | | | |
	No. spp.	Area	No. spp.	Area	No. spp.	Area	CH	CL	LI	IA
Andes	2,139	178	114	39	483	164	+			
Amazon Basin	961	105	–	–	–	–		+		
Western Great Rift Valley	936	24	–	–	60	22	+			
Eastern Great Rift Valley	902	22	–	–	19	1	+			
Himalayas	878	45	52	116	–	–	+			
Guyana highlands	877	71	–	–	32	10	+			
Atlantic coastal forests	733	27	73	95	–	–	+	+		
Mato Grosso Plateau	687	15	–	–	–	–	+			
Panama & Costa Rica highlands	621	3	–	–	101	13	+			
Philippines	–	–	47	66	68	36				+
Sumatra & Peninsula Malaysia	–	–	40	110	–	–			+	+
New Zealand	–	–	34	5	16	1			+	+
Borneo	–	–	29	82	–	–			+	
Hawaii	–	–	25	2	34	7				+
Madagascar	–	–	24	11	–	–			+	
South Vietnam highlands	–	–	19	7	–	–	+			
New Guinea & Bismarck archipelago	–	–	–	–	205	89			+	+
Caribbean	–	–	–	–	96	36				+
Lesser Sundas	–	–	–	–	72	26				+
Moluccas	–	–	–	–	68	26				+
West African forests	–	–	–	–	56	12	+			+
North Central American highlands	–	–	–	–	46	18	+			
Galapagos	–	–	–	–	31	8				+
Southern Great Rift Valley	–	–	–	–	27	7	+			
Fiji	–	–	–	–	27	9				+
Sri Lanka	–	–	–	–	23	11			+	
New Caledonia	–	–	–	–	21	9			+	+
Australian wet tropics	–	–	–	–	17	3	+			
Total	4,731	490	408	533	1,447	508				
Global	9,629	19,560	1,096	19,560	2,421	19,560				
Total as % of global	49%	2.5%	37%	2.7%	59%	2.6%				
Spatial dispersion (km)		2,079		3,023		9,469				

Figures based on hotspots defined as being the richest 2.5% of terrestrial grid cells. Hotspot regions are shown in the Supplementary Figure. No. spp. represents the cumulative number of species in the hotspot cells in a region. Area represents the number of cells identified as hotspots in a hotspot region. Large-scale topographical features contained within hotspot regions: CH, continental highlands; CL, continental lowlands; LI, large islands; IA, island archipelagos. Spatial dispersion shows the median great circle distance among hotspot cells.

Our findings of lack of congruence between different types of hotspot, and weak overall correlations among different aspects of global diversity, have important implications for understanding the ecological, evolutionary and anthropogenic mechanisms that underlie the origin and maintenance of biodiversity. It seems that, even within a single taxonomic class, different mechanisms are responsible for the geographical patterns shown by different aspects of biodiversity. This is especially intriguing in the case of species richness and endemism, which have been suggested to be closely linked in terms of overall spatial pattern[15,16,20,25]. Our finding of a rather weak relationship between these indices agrees with the recent observation that patterns of avian species richness are determined by the distribution of widely distributed species, rather than restricted-range species[19]. Little is known regarding the factors determining the distribution of wide-ranging species, but a study of sub-Saharan African birds suggested important roles for energy availability[23]. Endemic species richness, on the other hand, is thought to be a product of either refugia from past extinctions or of high rates of ecological and allopatric speciation[5,23]. These observations agree with our finding that species richness hotspots are typically associated with tropical upland regions that show habitat diversity and remain forested during glacial periods, whereas endemism hotspots are more commonly on island archipelagos showing complex patterns of allopatric divergence. There have been few quantitative studies of the spatial distribution of threatened species[8], but we predict their distribution can be determined by an interaction between the biological mechanisms promoting species diversity and the anthropogenic mechanisms eroding that diversity. We therefore expect that the lack of congruence between threat hotspots and the other two types of hotspot is due to a strong influence of human impacts on the spatial distribution of threat.

Lack of congruence among hotspot types also has implications for the use of hotspots in conservation. If congruence among hotspot types were high then it may not matter which index of diversity was used to guide conservation policy, because any such index could act as an effective surrogate for other aspects of diversity. However, our finding of very low congruence among hotspots shows that such surrogacy can not be assumed. In fact, we found that the different types of hotspot varied greatly in their ability to act as surrogates for other aspects of diversity. For instance, although the species richness hotspots (Fig. 2a) contained a large proportion of all bird species (49%, 4,731 species), they contained relatively low proportions of threatened (27%, 293 threatened species) and endemic (20%, 490 endemic species) species. In contrast, threat hotspots (Fig. 2b) contained relatively high proportions of both threatened species (37%, 408 threatened species) and overall species richness (41%, 3,932 species), but only captured a small proportion of endemic species (23%, 558 endemic species). Finally, the endemism hotspots (Fig. 2c) were successful in capturing not only a high proportion of endemic species (60%, 1,447 endemic species), but also a substantial proportion of both overall species richness (58%, 5,600 species) and threatened species richness (41%, 447 threatened species). Indeed, it is striking that the endemism hotspots actually contained a greater proportion of overall species richness than did the species richness hotspots and a greater proportion of threatened species than did the threat hotspots. These patterns need to be explored in other taxa to establish their generality, but our avian analyses indicate that endemism appears to display unusual properties, being difficult to capture using alternative indices of diversity and yet itself providing an effective way of capturing those other aspects of diversity. We suggest that these unusual properties of endemism are due to the fact that endemism hotspots are significantly more widely dispersed than

the other hotspot types (Table 1; Kruskal–Wallis test: $X^2 = 525.9$; $P < 0.001$) and therefore contain a more complementary set of species[12]. This scenario provides some support for the use of endemism as a criterion for identifying hotspots[1–3,5–7,9], but more generally our results indicate the need to use multiple indices of diversity in identifying areas of high conservation priority[6,7,9].

METHODS

Mapping and hotspots. Analyses were drawn from a database of vector range maps for 9,626 extant, recognized bird species following a standard avian taxonomy[26]. Species considered extinct were excluded from the database[8]. We mapped breeding ranges as vector maps in a geographical database using a variety of published sources (see Supplementary Methods). Vector maps were converted to a grid using a Behrmann projection at a cell resolution of 96.486 km, equivalent to 1° longitude and approximately 1° latitude at the equator (1/360th of the width of the globe under a Behrmann projection using the WGS84 datum). The global grid contained 360 by 152 cells, omitting the partial cells at latitudes higher than 87.13°. Species were scored as present in a grid cell if any of the sources indicated that the breeding range fell within the cell boundaries. Threatened species were those classified as critical, endangered or vulnerable[8]. Where necessary, we converted the taxonomy used in ref. 8 back to the standard avian taxonomy[26]. Our definition of endemic species identified 2,421 species with ranges restricted to fewer than 30 grid cells. Terrestrial cells were defined as those containing any land from the Environmental Systems Research Institute (ESRI) digital chart of the world[27]. Hotspot definitions were based on the percentage of terrestrial cells covered, and where quantile values fell within a richness class we used the upper number of cells for that class. The actual percentage of cells used was therefore sometimes slightly greater than target value (see Table 1 for examples at the 2.5% level). Counts of species in hotspot regions accounted for species in multiple cells.

Statistical analysis. Moran's I values were calculated using eight neighbouring cells, with P-values estimated using 1,000 randomizations: species richness = 0.95, threatened species richness = 0.91 and endemic species richness = 0.80. Generalized linear mixed effects models[28] used Poisson errors and fitted both predictor diversity measure and land area within each cell as fixed effects. Spatial structure was modelled using exponential covariance structures; separate range parameters were included for each of eight global biogeographic realms[29]. To reduce computation running time to a few days for each model, models were fitted to a regular 50% subset of the data set. For the species richness versus endemism model we excluded the two smaller realms[29] (Antarctica and Oceania) because they prevented convergence. Estimates of the proportion of variance explained (pseudo-r^2) were computed as percentage change in total deviance of non-spatial Poisson error models. Species richness as a predictor of threat richness: slope estimate = 0.0032 (s.e. $\pm$ 0.0001; $F_{1, 9002} = 1,466.44$; $P < 0.0001$; pseudo-$r^2 = 0.218$. Species richness as a predictor of endemic species richness: slope estimate = 0.006 (s.e. $\pm$ 0.0004); $F_{1, 8699} = 190.58$; $P < 0.0001$; pseudo-$r^2 = 0.236$. Endemic species richness as a predictor of threat richness: slope estimate = 0.030 (s.e. $\pm$ 0.001); $F_{1, 9002} = 904.37$; $P < 0.0001$; pseudo-$r^2 = 0.070$. For each hotspot type, spatial dispersion was measured by first calculating for each hotspot cell the median great circle to all other hotspot cells of the same type, and then taking the median value across all hotspot cells. Median distance among endemism hotspot cells was significantly longer than corresponding distances for both species richness and threat hotspot cells (Wilcoxon tests: $P < 0.0001$ in all cases).

1. Myers, N. Threatened biotas: 'hotspots' in tropical forests. *Environmentalist* **8**, 187–208 (1988).
2. Myers, N. The biodiversity challenge: expanded hotspots analysis. *Environmentalist* **10**, 243–256 (1990).
3. Bibby, C. *et al. Putting Biodiversity on the Map: Priority Areas for Global Conservation* (ICPB, Cambridge, UK, 1992).
4. Dobson, A. P., Rodriguez, J. P., Roberts, M. W. & Wilcove, D. S. Geographic distribution of endangered species in the United States. *Science* **275**, 550–553 (1993).
5. Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. *Endemic Bird Areas of the World: Priorities for Biodiversity Conservation* (BirdLife International, Cambridge, UK, 1998).
6. Mittermeier, R. A., Myers, N., Gil, P. R. & Mittermeier, C. G. *Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions* (Cemex, Conservation International and Agrupación Sierra Madre, Monterrey, Mexico, 1999).
7. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
8. BirdLife International, *Threatened Birds of the World* (Lynx Edicions and BirdLife International, Barcelona and Cambridge, UK, 2000).
9. Mittermeier, R. A. *et al. Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions* (Cemex, Conservation International and Agrupación Sierra Madre, Monterrey, Mexico, 2005).
10. Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C. & Gibbons, D. W. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335–337 (1993).
11. Pressey, R. L., Humphries, C. J., Margules, C. R., Vane-Wright, R. I. & Williams, P. H. Beyond opportunism: key principles for systematic reserve selection. *Trends Ecol. Evol.* **8**, 124–128 (1993).
12. Williams, P. *et al.* A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conserv. Biol.* **10**, 155–174 (1996).
13. Virolainen, K. M. *et al.* Hot spots, indicator taxa, complementarity and optimal networks of taiga. *Proc. R. Soc. Lond. B* **267**, 1143–1147 (2000).
14. Bonn, A., Rodriguez, A. S. L. & Gaston, K. J. Threatened and endemic species: are they good indiators of patterns of biodiversity on a national scale? *Ecol. Lett.* **5**, 733–741 (2002).
15. Thomas, C. D. & Mallorie, H. C. Rarity, species richness and conservation: butterflies of the Atlas Mountains in Morocco. *Biol. Conserv.* **33**, 95–117 (1985).
16. Berg, A. & Tjernberg, M. Common and rare Swedish vertebrates — distribution and habitat preferences. *Biodivers. Conserv.* **5**, 101–128 (1996).
17. Howard, P. C. *et al.* Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394**, 472–475 (1998).
18. Lawton, J. H. *et al.* Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* **391**, 72–76 (1998).
19. Lennon, J. J., Koleff, P., Greenwood, J. J. D. & Gaston, K. J. Contribution of rarity and commonness to patterns of species richness. *Ecol. Lett.* **7**, 81–87 (2004).
20. Jetz, W., Rahbek, C. & Colwell, R. K. The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecol. Lett.* **7**, 1180–1191 (2004).
21. Brooks, T. *et al.* Toward a blueprint for conservation in Africa. *Bioscience* **51**, 613–624 (2001).
22. Baillie, J. E. M., Hilton-Taylor, C. & Stuart, S. N. *2004 IUCN Red List of Threatened Species: A Global Species Assessment* (IUCN, Glad, Switzerland and Cambridge, UK, 2004).
23. Jetz, W. & Rahbek, C. Geographic range size and determinants of avian species richness. *Science* **297**, 1548–1551 (2002).
24. Rahbek, C. & Graves, G. R. Multiscale assessment of patterns of avian species richness. *Proc. Natl Acad. Sci. USA* **98**, 4534–4539 (2001).
25. Gaston, K. J. & Blackburn, T. M. The spatial distribution of threatened species: macro-scales and New World birds. *Proc. R Soc. Lond. B* **263**, 235–240 (1996).
26. Sibley, C. G. & Monroe, B. L. *Distribution and Taxonomy of the Birds of the World* (Yale Univ. Press, New Haven, 1990).
27. Defense Mapping Agency (Mapping Agency, Fairfax, Virginia, USA, 1992).
28. SAS (SAS Institute, Cary, North Carolina, 2001).
29. Olson, D. M. *et al.* Terrestrial ecoregions of the worlds: a new map of life on Earth. *Bioscience* **51**, 933–938 (2001).

Author Information Reprints and permissions information is available at npg.nature.com/reprintsandpermissions. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to I.P.F.O. (i.owens@imperial.ac.uk).