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How much of the vertebrate diversity of sub-Saharan Africa is catered for by recent conservation proposals?

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Abstract

A database documenting the distribution of birds, mammals, amphibians and snakes across 1° latitude and longitude squares of mainland sub-Saharan Africa provides an opportunity to quantify how many of these vertebrates are potentially catered for by recent large-scale conservation proposals. Sets of priority areas proposed by BirdLife International, the World Wildlife Fund (USA), the World Conservation Union and the World Wide Fund for Nature, Conservation International, and the World Resources Institute contain between 45 and 93% of 3752 species of birds, mammals, snakes and amphibians breeding in this area. Gaps in the coverage of vertebrates were found in all large-scale proposals, and these are mapped. Most of the conservation proposals perform better than random selection of similar sized areas of Africa, with the proposals focused on species performing more efficiently than schemes based on large areas of intact habitat or process-related criteria. Four of the schemes approach the performance of a complementarity-based algorithm that aims to maximise the number of species captured within a given area of land, and which has been widely advocated as a tool for conservation planning. The reasons for this are discussed and the relevance of the results for conservation planning at coarse and fine scales are explained.

Keywords: Vertebrates; Africa; Conservation; Biodiversity

1. Introduction

Growing international concern over the scale of the ongoing extinction of species and the scarcity of resources available to prevent it from occurring (Pimm et al., 1995) has resulted in a spate of programmes aimed at identifying those areas where conservation efforts could result in the maximum number of species being conserved. While some approaches have focused on countries as units for analysis (Mittermeier and Werner, 1988; WCMC, 1992; Caldecott et al., 1996; Mittermeier et al., 1997), attention in recent years has shifted to large ecological rather than political units of land. Here we confine our attention to these ecologically based units and investigate how well they capture species' distributions.

Myers (1988, 1990) was the first to present a set of global priority areas by identifying 18 highly threatened 'Hotspots' containing 20% of the world's plant species in only 0.5% of the land area. For Africa the work of Myers built on an existing tradition of identifying centres of plant endemism (e.g. White, 1983; Brenan, 1978). Following this, BirdLife International used data on birds to identify 221 Endemic Bird Areas worldwide (ICBP, 1992); between them these areas contain the entire breeding ranges of 20% of the world's bird species with ranges $<50{,}000$ km^2 in only 2% of the global land surface. For Africa the analyses of BirdLife also built upon previous studies of bird richness and endemism patterns (e.g. Crowe and Crowe, 1982; Crowe, 1990). The World Wide Fund for Nature with the World Conservation Union, Conservation International, the World Wildlife Fund (USA), and the World Resources Institute have all developed additional global prioritisation schemes in the past few years. The World

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Wide Fund for Nature and the World Conservation Union (WWF and IUCN, 1994–1997) used expert analyses of plant distribution to identify 234 "first order" Centres of Plant Diversity. Conservation International focused on plants as well in developing Myers' pioneering analysis to identify 24 Hotspots, where ca. 46% of the world's plant species are found (Mittermeier et al., 1998, 1999; Myers et al., 2000).

As a complement to the Hotspots approach, Conservation International have identified three Major Tropical Wilderness Areas, which are both species-rich and retain $>75\%$ of their original vegetation cover (Mittermeier et al., 1998). World Wildlife Fund (USA) used information from all biological groups to produce a Global 200 list of Ecoregions, selected to represent both species and biological phenomena within each of the world's major habitat types (Olson and Dinerstein, 1998). For Africa, further analyses of endemism and species richness values of all Ecoregions has led to the identification of the most biologically distinctive Ecoregions (Underwood et al., 1999; WWF, unpublished data). Finally, World Resources Institute has identified 24 Frontier Forests—forest areas which are largely pristine and where natural processes are thought to be continuing largely unchecked by human intervention (Bryant et al., 1997).

Part of the rationale behind most of these prioritisation approaches is that the priority areas identified should permit the conservation of a high proportion of the world's species, even for those areas identified using one taxon group. Indeed, for several systems—the Endemic Bird Areas, the Centres of Plant Diversity, and the most biologically distinctive Ecoregions—representation of species has been the overwhelming concern behind area selection. Other schemes give greater weight to broader concerns, such as the importance of maintaining large-scale biological phenomena (e.g. Olson and Dinerstein, 1998), or of selecting areas according to how threatened they are (Mittermeier et al., 1998). For example, concerns about key ecological phenomena, such as major migrations of large mammals, have been incorporated in the selection of the Global 200 Ecoregions (Olson and Dinerstein, 1998; WWF, unpublished data). Likewise, both Conservation International's Major Tropical Wilderness Areas and World Resource Institute's Frontier Forests have been chosen as areas where natural vegetation is sufficiently extensive and human settlement sufficiently sparse that major biological processes continue with relatively little human interference (Bryant et al., 1997; Mittermeier et al., 1998).

At the other end of the threat spectrum, the need to target areas under the greatest human pressure is reflected in Conservation International's Hotspot system (Mittermeier et al., 1998; 1999), where, to be selected, ecosystems must have already lost $>70\%$ of their original vegetation. None of the published schemes has used phylogenetic approaches to establishing conservation priorities across the region, which might provide additional insights on areas of relictualisation or recent speciation. Fjeldså (1994), Fjeldså and Lovett (1997) and Linder (1995) have made a start in this direction for birds and plants, and if phylogenetic data were available for other taxonomic groups across Africa, then this would provide a useful methodology for assessing potential of conservation proposals to conserve evolutionary history.

Given that there are now several global priority systems in place, it is timely to assess how well they might succeed in achieving the concerns of conservationists. We use sub-Saharan Africa (the Afrotropical Realm) as our test area. For this geographical area we attempt to measure the success of the priority systems at addressing a common concern of conservation biologists—the representation within conservation proposals of as many species as possible within a practically manageable total area.

For each priority system, we perform three identical tests to assess their performance at capturing species distributions. First, we identify the number of species included in each of the given schemes. Second, we determine those areas richest in species not represented in the proposed priority schemes. Third, we compare species capture by these different schemes against both random and systematic selection of land areas of comparable size in sub-Saharan Africa. The systematic approach to area selection addresses variation in both the biological richness and the biological distinctiveness (or complementarity) of different candidate areas (see Williams, 1998 for detailed explanation).

2. Methods

2.1. Conservation priorities investigated

We studied seven sets of conservation areas, running from those with a particular species conservation focus, through to those with a focus on the conservation of extensive areas of spatially contiguous habitat free from human disturbance.

BirdLife's Endemic Bird Areas—regions with at least two bird species with global breeding ranges of $<50{,}000$ km^2; there are 22 Endemic Bird Areas in our study area (for details see Stattersfield et al., 1998). It has been argued that birds with restricted ranges are a good surrogate for overall biodiversity (ICBP, 1992; Balmford and Long, 1995; Brooks et al. 2001a).

World Wildlife Fund–USA's most Biologically Distinctive Ecoregions—the top 20 out of 80 ecoregions listed by Olson and Dinerstein (1998) across sub-Saharan Africa. The most biologically distinctive ecoregions are determined from endemism and species richness values for birds, mammals, amphibians, reptiles, plants and invertebrates (Underwood et al., 1999; Olson et al., 2001).

World Wide Fund for Nature and World Conservation Union's Centres of Plant Diversity—those sites, characterised by high plant species richness and/or endemism, that are most important for the conservation of plant diversity (WWF and IUCN, 1994–1997). There are 82 such sites in our study area, of which 29 are "first order" sites which are used in the present analyses.

Conservation International's Hotspots—these are areas of the world where at least 0.5% of the global total of plant species (minimum of 1500 species) is strictly endemic, and where <30% of the natural habitat remains (Mittermeier et al., 1999). Hotspots contain many endemic vertebrates in addition to their endemic plants (Mittermeier et al., 1999; Myers et al., 2000). There are four such areas in our study region.

World Wildlife Fund–USA's Ecoregions of Global Importance for 'Biological Phenomena'—the Biological Phenomena Ecoregions are those assessed to be globally important for their rare habitats, large areas of undisturbed habitat, major migrations of large mammals or birds, or high concentrations of endemic families or genera. The latest assessment indicates that 17 of these ecoregions are found in our study area (WWF, unpublished).

Conservation International's Major Tropical Wilderness Areas—areas of high-biodiversity tropical ecosystems where >75% of the habitat remains (Mittermeier et al., 1998); there is one major tropical wilderness area, the Greater Congo Basin, in sub-Saharan Africa.

World Resource Institute's Frontier Forests—largely undisturbed forests considered big enough to maintain all of their biodiversity in viable populations, and whose structure and composition are determined largely by natural events (Bryant et al., 1997). There are 24 Frontier Forests in sub-Saharan Africa. Unlike the other systems examined, Frontier Forests deal with just a single habitat; they have been included here for comparison only.

It is important to note that none of the schemes envisage protection of the entire land areas that they identify. Rather, they are regarded as foci for detailed conservation planning at the landscape scale and on-the-ground conservation action at the scale of sites.

2.2. Data compilation and data issues

We used a database mapping the distribution, among 1° latitude–longitude grid cells (ca. 105 km along each side), of 1755 bird species, 942 mammal species, 433 snake species, and 622 amphibian species breeding in sub-Saharan Africa. Sources for the distribution data included 1115 primary publications and unpublished reports, and consultation with 74 taxon specialists (for full source list, see http://www.zmuc.dk/commonweb/research/biodata.htm). The species' distribution data were computerised within WORLDMAP (Williams, 1999) onto a grid of 1962 1° grid cells covering mainland sub-Saharan Africa. The mapping has been conducted over 6 years at the Zoological Museum, University of Copenhagen, Denmark as has been previously described (Burgess et al., 2000; Williams et al., 2000; Brooks et al., 2001b). The database is updated regularly and the version we used for these analyses dates from July 2001.

2.2.1. Mammals

For mammals, our taxonomy follows Wilson and Reeder (1993), modified according to recent species descriptions and taxonomic opinions. For the Galagonideae we follow Kingdon (1997), based on the work of S. Bearder and others. Our mammals database comprises maps of the distribution of 942 species across sub-Saharan Africa. For the larger mammal species, most records in 1° grids were mapped as unconfirmed range data using standard references for the area (Dorst and Dandelot, 1970; Haltenorth and Diller, 1977; Skinner and Smithers, 1990; Kingdon 1997). For as many species as possible these unconfirmed records were checked against other sources, including the IUCN-SSC action plans and unpublished museum data, to add 'confirmed' records to the map database. For the smaller species we compiled records into 1° grids using the literature (hundreds of references), with both 'confirmed' and extrapolated unconfirmed range data comprising the map for the best known species, and only the 'confirmed' records comprising the maps for the poorest known species.

2.2.2. Birds

For birds, our taxonomy follows Sibley and Monroe (1990, 1993), which is the most recent and comprehensive treatment of the world's avifauna. For this analysis, we excluded all species found only on islands off the coast of Africa, marine species, and all Palaearctic/Afrotropical migrant birds. Our birds database comprises maps of the distribution of 1755 species across sub-Saharan Africa. We initially compiled distribution maps for these species as unconfirmed records in 1° grids, by using the published volumes of the "The Birds of Africa" (Brown et al., 1982; Urban et al., 1986, 1997; Fry et al., 1988; Keith et al., 1992). These base maps were then checked, refined and completed for unmapped species using published bird distribution Atlases for Africa (Hall and Moreau, 1962, 1970; Snow, 1978; Jensen and Kirkeby, 1980; Irwin, 1981; Benson et al., 1971;

Louette, 1981; Nikolaus, 1987; Lewis and Pomeroy, 1989; Gatter, 1997; Harrison et al., 1997a, b; Stattersfield et al., 1998; Ash and Miskell, 1998; Parker, 1999), many papers (see earlier URL), and the restricted range birds database of BirdLife International. This updating process allowed records in 1° grids to be mapped as confirmed in all countries and regions of Africa where there is a published bird Atlas, or where detailed papers on bird localities exist. Hence most of the maps used here contain confirmed records from the available publications and unconfirmed range map data from other sources. For the rarest species only the confirmed records are used in the maps.

2.2.3. Snakes

For snakes, our species list was based on Welch (1982), with the addition of newly described species and recent taxonomic re-interpretations by Dr. Jens B. Rasmussen of the Zoological Museum in Copenhagen and Dr. D. Broadley of Zimbabwe. Our snakes database comprises maps of the distribution of 433 species across sub-Saharan Africa. Base maps of unconfirmed records in 1° grids were produced using books on poisonous snakes (Sprawls and Branch, 1996) and covering the southern Africa region (Branch, 1998). Dr. Jens B. Rasmussen of the Zoological Museum of the University of Copenhagen compiled confirmed records in 1° grids for these species and all others across sub-Saharan Africa from an extensive review of the literature, visits to museums, and discussions with colleagues. For the better known species he was also able to extrapolate a range map of unconfirmed records from the confirmed specimen records, but for the rarest and poorest known species the map used comprises on the confirmed records based on specimens. The maps used therefore comprise mainly confirmed locality data from biological specimens, generalised into range maps where this was regarded as permissible according to the distributional, taxonomic and ecological knowledge of the species.

2.2.4. Amphibians

For amphibians, our taxonomy follows Frost (1975) and Duellman (1983). We updated this list where necessary using recently published papers and prevailing taxonomic opinions, especially those of Dr. John Poynton, Dr. Alan Channing and Dr. Arne Schiøtz. Our amphibians database comprises maps of the distribution of 622 species across sub-Saharan Africa. Data for the majority of the maps comprise confirmed records in 1° grids from specimens identified by expert taxonomists and provided to us from their own databases, or from specimen records extracted from published scientific papers. For some of the better known species these confirmed records have also been extrapolated across 1° grids as a range map of unconfirmed records.

2.3. Species representation and mapping gaps

We investigated species representation within the different priority systems by overlaying a grid covering these areas onto our database and assessing how many species of each group were contained in all wholly or partly overlapped cells. Because the grid squares assessed covered a greater area of land than was proposed in the original schemes, this approach will overestimate species coverage by any given scheme. We mapped gaps in the coverage of African vertebrates in the various conservation schemes, by summing richness in each grid cell for those species that were not contained in the one-degree cells wholly or partly covered by the mapped priority areas. Again it should be noted that this would be an underestimate of the real species gaps in each system, because some of the species recorded in a partly overlapped cell are probably absent from the priority area itself.

2.4. Performance of the different schemes

We were also interested to assess how well the proposals captured species when compared with some mathematical procedures applied to our database. We first conducted this exercise analysing our data at the scale of 1° grids. We used WORLDMAP (Williams, 1999) to identify networks of cells chosen using a complementarity-based procedure, which has been widely advocated for selecting conservation areas (Muruki et al., 1997; Williams, 1998; Margules and Pressey, 2000). The simple greedy algorithm we used is based on Margules et al. (1988), updated to include redundancy checking (Williams et al., 2000). The programme first selects all areas with taxa that are equally or more restricted than the representation goal (i.e. for a goal of representing each species at least once, it begins by selecting all areas that have unique records for endemic species: which thus are irreplaceable). Areas continue to be chosen to represent the rarest as yet unrepresented species until either the target number of areas are chosen (near-maximum coverage set) or all species are represented (near-minimum set). Once the set of cells has been selected, the areas are re-ordered using complementary richness (Williams, 1999). As with the proposed large-scale schemes themselves, cells selected by this process are not suggested as conservation areas per se, but rather as areas within which conservation planners need to consider if the species of conservation concern are already adequately protected, and, if not, what needs to be done.

Although plotting species capture by the various priority systems and capture by randomly and systematically chosen 1° grids enables comparison of all schemes on a single graph, it is of limited utility because the schemes differ widely in the size of the areas they are selecting. Because of this, we next re-ran the same systematic area selection procedure, this time after aggregating the Copenhagen database to 2°×2°, 4°×4° and 8°×8° grids. We also used WORLDMAP to randomly pick sets of 1°×1°, 2°×2°, 4°×4° and 8°×8° grids to calculate the median representation of species (and 95% confidence limits about that median) across 1000 such sets of each size. We then plotted the performance of each priority system against the species accumulation curves derived from complementary and random selection of those grid cells that most closely approximated the median grain size of the system concerned (Table 1).

3. Results

3.1. Species representation

The priority schemes proposed by different organisations varied widely in how fully they represent species in the four vertebrate groups examined (Table 1). Species representation was most nearly complete within the Endemic Bird Areas (90.7% of all species, and >85% of species in each group), and the Biologically Distinctive Ecoregions (90.2% overall, and >80% of each group). Other systems covered fewer species, with Frontier Forests and Major Tropical Wilderness Areas both representing less than half of all the species in the Afrotropical region. Some obvious reasons for the differences in species representation between schemes are discussed later.

One problem with interpreting how efficiently the different systems represent species' distributions was the huge difference in area that they covered (Table 1). While the Biologically Distinctive Ecoregions and the Endemic Bird Areas included similar numbers of species the former covered around double the area of the latter.

3.2. Mapping gaps

Maps highlighting gaps in species coverage further illustrate some differences between the different priority schemes (Fig. 1). All three of the priority schemes based on species (Fig. 1a–c) tended to omit species typical of the Sahel and southern Sahara, because these rarely occur in the areas characterised by high species richness or narrow endemism targeted by these systems. In addition, Endemic Bird Areas missed a species-rich region in the south east of the Democratic Republic of Congo and in Namibia (see also Crowe and Brooke, 1993), the most biologically distinctive Ecoregions missed species typical of Kenya's mountains, the Angola Scarp and south eastern Africa, and the Centres of Plant Diversity did not adequately cover the Angola Scarp, Albertine Rift or Eastern Arc Mountains.

The pattern of gaps varied more between the systems developed to incorporate broader concerns, such as threat or areas of intact habitat with little human disturbance. Hotspots (Fig. 1d) missed species in Ethiopia and the Horn of Africa, the Albertine Rift and Kenyan Highlands, the Angola Scarp, southeastern Democratic Republic of Congo and scattered mountains in Malawi and Zimbabwe. Not surprisingly, the Biological Phenomena Ecoregions, Major Tropical Wilderness Area system and the Frontier Forests (Fig. 1e–g), which largely focus on wilderness habitats with relatively intact animal assemblages, missed species from the centres of narrow endemism identified in the first three schemes.

3.3. Performance of the different schemes at 1° resolution

When the number of species represented by each priority system was plotted against its total area and compared with systematic selection of 1° cells, all the

Table 1

Percentage and numbers (in parentheses) of Afrotropical bird, mammal, snake and amphibian species captured in large priority areas proposed by WWF and IUCN (Centres of Plant Diversity, CPD), BirdLife International (Endemic Bird Areas, EBA), World Wildlife Fund-US (Biological Distinctive Ecoregions, BDE), Conservation International (Hotspots), WWF-US (Biological Phenomena Ecoregions, BPE), Conservation International (Major Tropical Wilderness Areas, MTWA), and World Resources Institute (Frontier Forests)

Schemes	Total area (1°×1° units)	Number of proposed areas in schemes	Median area of component areas in schemes (as 1°×1° units)	Grid units used for analyses	Birds (1755)	Mammals (942)	Snakes (433)	Amphibians (622)	Combined (3752)
WWF and IUCN: CPD	160	29	2	1°×1°	90.2 (1584)	78.45 (739)	73.2 (317)	76.0 (473)	82.9 (3110)
BirdLife: EBAs	306	22	10.5	4°×4°	95.8 (1682)	86.9 (819)	86.4 (374)	85.5 (532)	90.7 (3404)
WWF-US: BDE	474	20	16	4°×4°	94.7 (1663)	85.6 (807)	86.6 (375)	87.3 (543)	90.3 (3387)
CI : Hotspots	230	4	34	4°×4°	76.4 (1341)	67.3 (634)	62.7 (272)	61.4 (382)	70.0 (2628)
WWF-US: BPE	310	17	14	4°×4°	80.2 (1408)	65.1 (614)	64.6 (280)	56.4 (351)	70.8 (2653)
CI: MTWA	189	1	189	8°×8°	51.9 (911)	42.7 (403)	39.0 (169)	33.6 (209)	45.0 (1689)
WRI: Frontier Forests	84	24	3	2°×2°	51.4 (902)	43.7 (412)	35.1 (152)	35.5(221)	44.9 (1688)

The number of 1 degree cells wholly or partially overlapped by the different schemes is the measure of total area covered by each scheme. Results are presented with those schemes that were specifically designed with species representation goals first, through to those schemes that sought to represent wilderness values last.

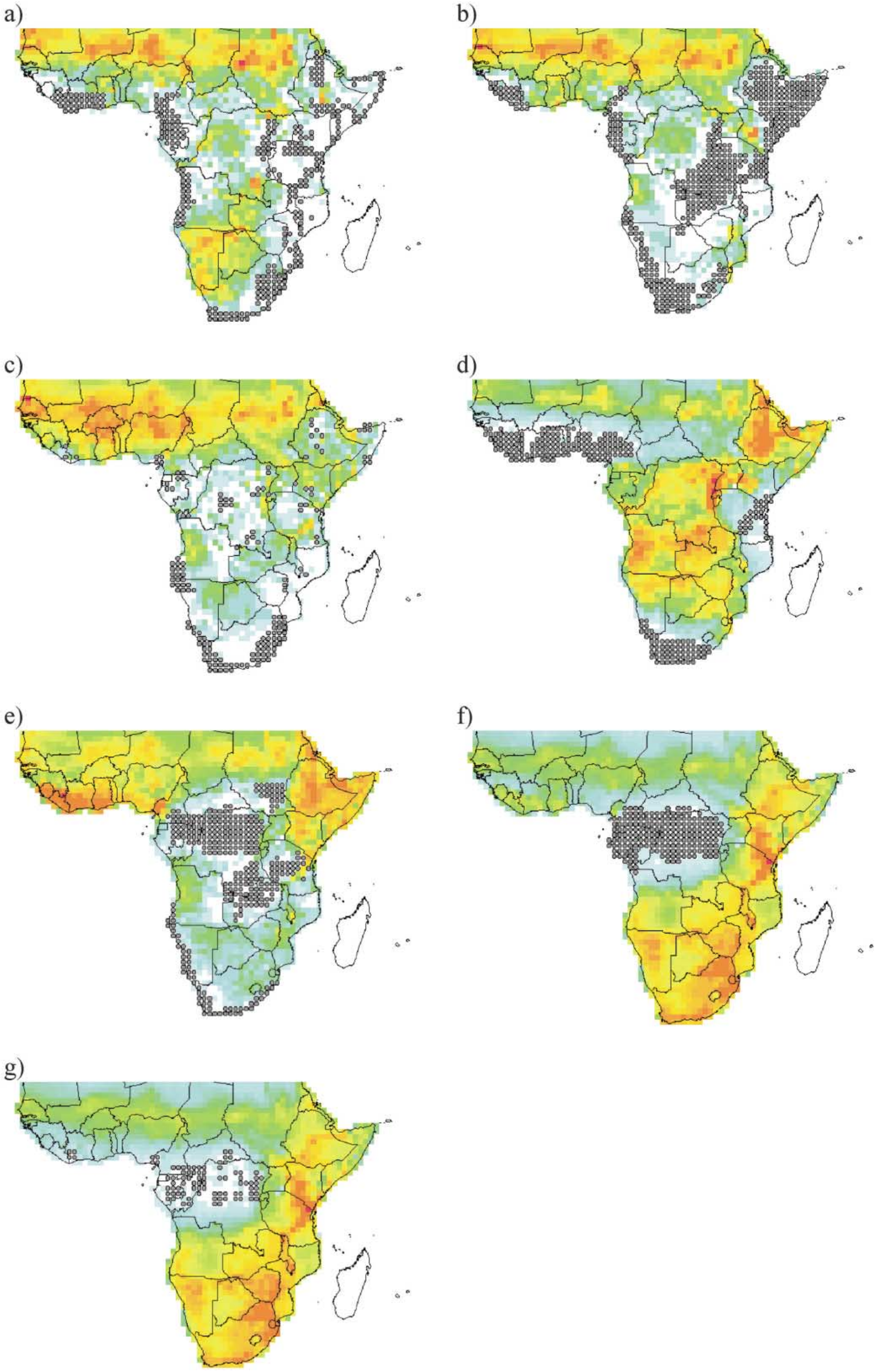

Fig. 1. Pattern of species richness for the combined vertebrate groups that is not covered by the different conservation schemes. Endemic Bird Areas (a), Biologically Distinctive Ecoregions (b), Centres of Plant Diversity (c), Hotspots (d), Ecoregions of Global Importance for Biological Phenomena (e), Major Tropical Wilderness Areas (f), and Frontier Forests (g). Cells covered wholly or partly by a priority system are shown in Grey. The species richness not covered by these schemes is plotted according to the following colour scale: Red is the maximum score, corresponding to 22 species in (a), 28 species in (b), 39 species in (c), 134 species in (d), 123 species in (e), 327 species in (f) and 355 species in (g). Blue is the minimum score, representing one species in all maps. Colours between red and blue represent intermediate values of species richness between the two extremes stated, with each map containing 33 colour bands divided according to an equal frequency distribution (Williams, 1999). Areas in white contain zero species.

systems examined covered fewer species than did a scattered network of 1° cells of the same total area (Fig. 2). All points lay well below the species-accumulation curve for the complementarity-based algorithm. This means that none of the schemes provides a set of conservation areas which is as effective at covering the distributions of all African vertebrates as that which can be generated using the complementarity algorithm. Priority areas at the 1° scale have been more fully explored in Brooks et al. (2001b).

3.4. Performance of the different schemes at varying scales

The performance of the simple greedy algorithm changed markedly with the size of the grid cells used for analysis (Fig. 3). Complementarity methods required progressively more area to represent all recorded species as the size of the units of analysis increase from 1°×1° to 2°×2°, 4°×4° and finally to 8°×8° grids. Because scale affects efficiency so much and the different conservation proposals for Africa vary widely in the size of the areas they analyse, their performance is best evaluated against other approaches using units of approximately the same grain size.

Comparing the species captured by the different schemes with species captured when similar-sized areas are selected from the database, either systematically or randomly, reveals considerable variation in performance (Fig. 4). Species-based schemes are often nearly as efficient, for their total size, as complementarity algorithm-based selections of similarly sized grid cells. The fact that the schemes that aim to capture species as their primary goal achieve this aim well is encouraging. Many of the schemes have used only one taxon group (e.g. birds or plants) to develop their sets of priority areas, and our tests are based on all the species in four vertebrate groups, further indicating the value of the species-based schemes.

Looking in more detail at the 1°×1° plot (Fig. 4a), the Centres of Plant Diversity perform better than the random selection of 1° cells. It is also worth noting that as their median area is two 1° cells (Table 1), the relative performance of Centres of Plant Diversity for their grain size is somewhat underestimated by comparing them with selection of 1°×1° cells. Moving on to the 2°×2° plot (Fig. 4b), the Frontier Forests, chosen to represent forest wilderness areas, do not perform very well, mainly because they are all tropical forest areas within same bioregion (Guineo-Congolian forest) of Africa. On the 4°×4° plot (Fig. 4c), the Endemic Bird Areas perform remarkably well, with their species capture in terms of their area only slightly worse than that achieved by the complementarity-based algorithm. The Biologically Distinctive Ecoregions are somewhat less efficient, because the method selects the most distinctive ecoregion within major biomes, and some of these biomes (e.g. savanna-woodlands) have a largely homogeneous biota. Hotspots are less efficient, although this is partly because their median grain size is three times greater (Table 1). The Biological Phenomena Ecoregions (4°×4° plot—Fig. 4c) and Major Tropical Wilderness Areas (8°×8° plot—Fig 4d) both performed poorly in this test, largely because they have been chosen not for species representation but to capture evolutionary and ecological phenomena (migrations, intact functioning habitats, etc), or large areas of intact habitat with low human populations.

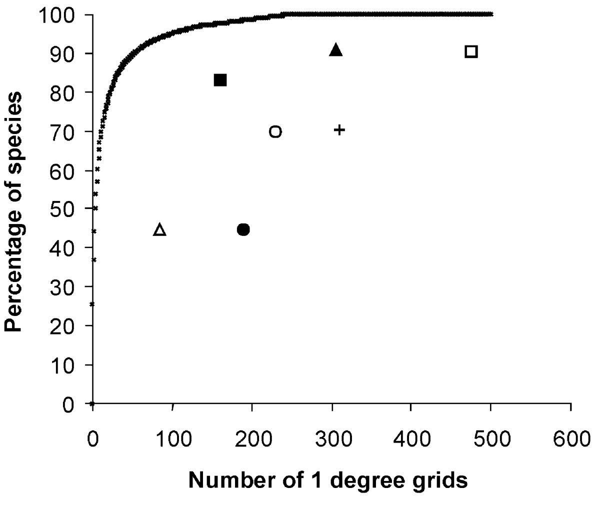

Fig. 2. Percentage capture of the 3752 species on mainland sub-Saharan Africa by different conservation schemes against a species accumulation curve generated by running a greedy complementarity algorithm (Margules et al., 1988, updated to include redundancy checking, see Williams et al., 2000) on the vertebrate database at the 1°×1° grid cell unit scale. From left to right—open triangle = Frontier Forests, closed square = Centres of Plant Diversity, closed circle = Major Tropical Wilderness Area, open circle = Hotspots, closed triangle = Endemic Bird Areas, cross = Biological Phenomena Ecoregions, open square = Biologically Distinctive Ecoregions.

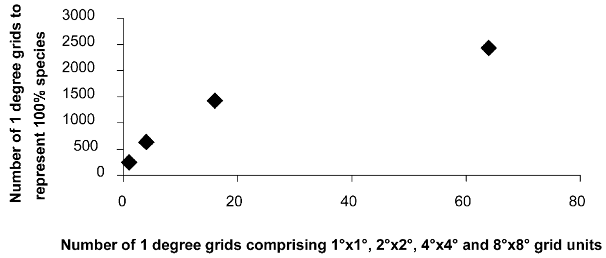

Fig. 3. Total area required to achieve 100% coverage of the 3752 species in the database if a greedy complementarity algorithm is used to capture species diversity from the database using grid cell units in four different size classes, 1°×1° (= one 1° grid), 2°×2° (= four 1° grids), 4°×4° (= 16 1° grids) and 8°×8° (= 64 1° grids). Scales are in 1° grid squares as the area of each grid varies according to latitude (although each is ca 10,000 km^2 in area).

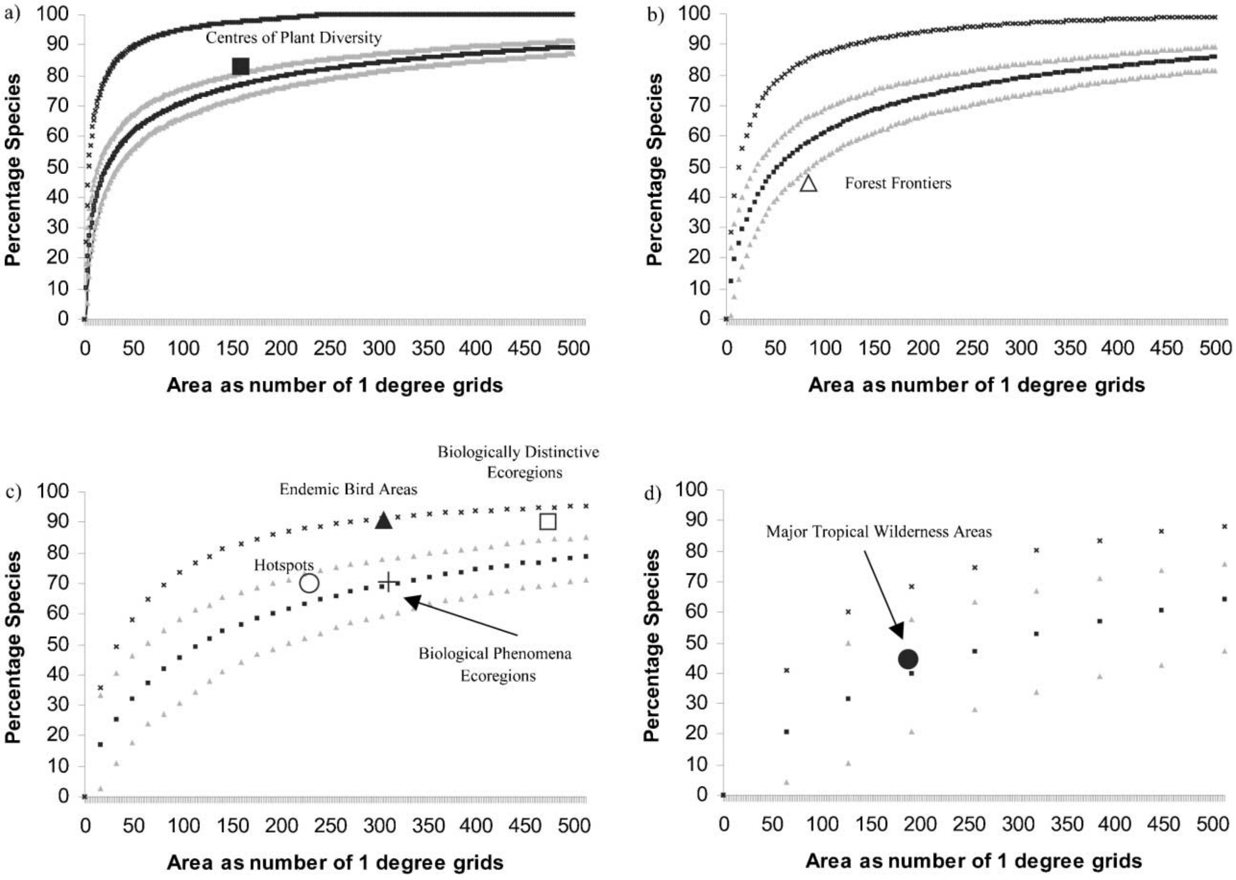

Fig. 4. Percentage capture of the 3752 species on mainland sub-Saharan Africa when using random draws and the complementarity-based algorithm on grid cells of different area, compared to the percentage of species captured by the different conservation schemes when plotted at the most appropriate scale. In all plots the species accumulation curve above in black is derived from a greedy complementarity algorithm; the species accumulation curve below in black is derived by running 1000 random iterations for each step and taking the median value of the species captured; and the positive and negative 2.5% confidence limits to the random species accumulation curve are in grey above and below the random line. (a) Plot based on 1°×1° grids. The percentage species captured by Centres of Plant Diversity is marked as a closed square. (b) Plot based on 2°×2° grids. The percentage species captured by Frontier Forests is marked as an open triangle. (c) Plot based on 4°×4° grids. The percentage species captured by Biologically Distinctive Ecoregions is marked with an open square, for Endemic Bird Areas by a closed triangle, by Biological Phenomena Ecoregions as a cross, and by Hotspots as an open circle. (d) Plot based on 8°×8° grids. The percentage species captured by Major Tropical Wilderness Areas is marked with a closed circle.

4. Discussion

These are the most comprehensive data assembled for the study area, but inevitably have limitations. Because mapping of species distributions in Africa is incomplete, some of the mapped species distributions are likely to be different to their actual distributions. For those species that are hunted for meat (many of the larger ground-dwelling mammals and primates) or for body parts (e.g. elephant and the two species of rhinoceros) the mapped range is larger than the current range (Channell and Lomolino, 2000). However, these species form a small proportion ($<5\%$) of the total number of species considered here. For species that are poorly known (and often rare) our maps contain the few known, or sometimes the only record. In these cases the distribution maps often show a smaller range than is real. Collection effort is also a concern. The intensity of collection effort varies widely across Africa, so some species may be patchily recorded even though they are actually quite widespread (Nelson et al., 1990). These problems cannot easily be solved and hence we have performed our tests on what we believe is the best available, although not perfect, dataset.

Our results reveal wide variation in how well the different priority schemes put forward for Africa cover vertebrate species. Looked at in absolute terms, all schemes are less efficient, given their total size, than are sets of 1° grid cells selected using a complementarity-based algorithm (Fig. 2). However, our results also illustrate that the efficiency of species representation is extremely sensitive to the grain size of the candidate areas (Fig. 3). The complementarity-driven algorithm shows that the total area required to represent all vertebrate species once is roughly 10 times greater using 8°×8° cells than using 1° cells. Scale in turn explains much of the apparent inefficiency (in absolute terms; Fig. 2) of larger-grained schemes such as Hotspots. When the schemes are instead evaluated against similarly-sized grid cells, those developed using species-based criteria perform generally well. On the other hand, those targeting intact habitats or ecological process concerns are consistently less efficient in terms of species capture (see Fig. 4).

We have performed only some of a series of possible tests and even for species our tests are only related to the presence or absence of species in an area, not to their long-term persistence. We encourage investigation of the potential success of the schemes against a variety of other test criteria. For example, recent attempts have started to develop methods to address the concerns of conservation biologists about the maintenance of large-scale biological processes (Nicholls, 1998; Williams, 1998; Williams and Araújo, 2000). We believe that an assessment of the different values of these schemes will allow further refinements, and will also assist in developing consensus around a common set of large-scale priority areas which can serve as foci for gaining support from the world's politicians and conservation funding agencies (Mace et al., 2000).

4.1. Species-based schemes

When compared with systematic and random selection of grid cells of roughly similar size, the species-based priority-schemes—Centres of Plant Diversity, the Endemic Bird Areas, and the Biologically Distinctive Ecoregions—all perform well, capturing nearly as many vertebrate species for their combined area as the complementarity-based algorithm. Hotspots appear to perform less well, which could reflect their relatively large size (cf. the 4°×4° grids they are compared with) and the fact that they were designed to reflect concerns about threatening processes as well as species distributions. Overall, the strong performance of the species-based schemes is encouraging news for conservation planning, especially as three of the schemes were developed using species data on only a single taxon (rather than the four vertebrate groups used to measure their performance), and for the Centres of Plant Diversity, this group was plants. This indicates that, at this scale, priority areas selected using one taxonomic group can cater efficiently for many other groups as well (also see Moore et al., in press). By concentrating on places of high endemism, these systems comprise areas that are generally highly complementary to one another, even for those groups that were not used in their formulation.

One important caveat to this conclusion is that, despite their relative efficiency (in the percentage of species captured for their combined area), the species-based schemes evaluated here all have limited effectiveness (Rodriguez et al., 2000), that is, they all fail to capture some species. The size of the gaps again varies, from 8.3 to 30.0% of Africa's vertebrates, with the distribution of the missing species reflecting the concerns of each prioritisation scheme. The need to identify where such gaps are located, and ensure that their conservation is not neglected, highlights the value of databases that attempt to provide comprehensive distribution data for an ecologically and taxonomically broad sweep of organisms.

Another caveat is that all of the schemes performed less well than using a complementarity algorithm to select networks of 1° grid cells scattered across Africa. The set of priority areas at the 1° scale presented in Brooks et al. (2001b) would represent a more efficient set of conservation proposals, if the aim was to maximise the number of species represented in the minimum number of grid cells. Marginal gains in efficiency over the results of Brooks et al. (2001b) might also be possible if instead of using a 'greedy' complementarity algorithm, a fully optimal mathematical solution were employed instead (Rodriguez et al., 2000).

4.2. Biological process-based schemes

All priority systems that are based on areas of intact habitat or ecological or evolutionary phenomena—Frontier Forests, Major Tropical Wilderness Areas, and Biological Phenomena Ecoregions—were far less efficient and generally less effective than the other schemes at representing Africa's vertebrate species, even taking their grain size into account. This is not necessarily surprising, as none of these schemes were designed with species capture in mind. It could thus be argued that a fairer test of the performance of any system would be to assess how efficiently it achieves its stated target. But in this case, quantitative evaluation would be hard, because as yet we have very few tools at our disposal to assess how well a set of priority areas might maintain functioning biological processes (for some interesting first steps, see Nicholls, 1998; Williams, 1998; Cowling et al., 1999a, b; Rodrigues et al., 1999; Cowling and Heijnis, in press). We also need much better data concerning the maintenance of large scale biological processes, for example, migrations. Even information on the population status of the largest African mammals is scarce (see Cumming et al., 1990; Said et al., 1995; East, 1999), and data on the scale of remaining large mammal migrations are largely anecdotal. In the meantime, we suggest that some comparison across priority systems, measured by a common metric, is needed. Given that conserving as many species as possible within a cost- and size-limited set of priority areas is a legitimate and important concern, we believe that assessing the capture of species does yield useful conservation insights.

4.3. Implications for conservation goals

The consistent divergence, in terms of efficient species capture, between species-oriented systems and those designed around broader biological concerns, has ramifications for how we think about conservation goals. It might be believed that priority sets designed to be capable of conserving broad-scale processes would, de facto, serve to conserve species efficiently as well. Our results, which echo finer scale findings from South Africa by Cowling et al. (1999a, b), suggest otherwise. Hence, the debate over the merits of focusing on species versus those of focusing on habitats and maintenance of biological processes has important practical implications. If the focus is largely on processes it is likely that many species will go unconserved. At present, we cannot assess whether the reverse is true, although we expect it will be (WWF, unpublished). A focus solely on the conservation of narrowly endemic species will likely not conserve key large-scale ecological and evolutionary processes very effectively, nor will it protect the remaining areas of intact habitats with few people (the wildernesses).

The idea that conserving endemic species and maintaining biological processes will often necessitate different approaches to conservation is borne out by recent work on where reserves are located. Much of Africa's endemism is concentrated in areas where there are high numbers of people undertaking settled farming activities, where habitat patches and protected areas are small, and where there is little remaining space for new reserves (Lombard, 1995; Balmford et al., 2001a, b; Harcourt et al., 2001). On the other hand, priority schemes based around biological processes and wilderness areas tend to locate large ecosystems that contain wide-ranging species and that are not very suitable for either human habitation or settled agriculture (e.g. Congo rainforest, miombo woodland); much of Africa's existing reserve system is located in these regions. The former areas present one kind of conservation challenge—that of maintaining small patches of habitat and in some cases restoring others in order to prevent extensive extinction of endemics. The latter areas present a rather different conservation challenge—that of maintaining large areas of habitat within which large-scale ecological and evolutionary processes can persist.

A second practical message that emerges from these results is the importance of scale in conservation planning. While large-scale prioritisation systems of the sort analysed here are of undoubted significance in drawing global attention to exceptionally important regions within which further conservation action is needed, our results underline the benefits of subsequent finer scale prioritisation (for discussion, see Mace et al., 2000; da Fonseca et al., 2000). Provided the units assessed for detailed land-use planning are still large enough to retain viable populations of the species they contain, focusing down will greatly increase the efficiency of conservation measures within large-scale priority areas (Pressey and Logan, 1998). However, caution should also be taken in generalizing species-maintenance processes found at larger spatial scales down to finer scales (Rahbek and Graves, 2000), and vice-versa for extrapolating speciation processes found at finer spatial scales to larger scales (Rahbek and Graves, 2001).

In conclusion, we think that the species/biological process and wilderness areas debate highlighted by this paper is critical, and cannot be ignored (see Mace et al., 2000). If we are to resolve it satisfactorily, we need to be clearer about how we value ecological and evolutionary processes and the existence of wilderness areas. We need new methods and better data for quantifying how fully a particular area meets such concerns, which we can then put to use, both in systematic site selection, and in the more comprehensive evaluation of the performance of different priority systems. This will allow us to combine approaches to conservation planning based on considerations of both existing species pattern and underlying biological process. Having achieved that we may be able to produce a common set of maps of conservation priorities across whole continental areas that will address the concerns of many conservation planners. This will in turn allow the conservation movement to speak more effectively to donors and decision-makers about what we collectively agree needs safeguarding into the future. This is an important goal and one that we believe is possible if we all work together. In this way we strongly endorse recent sentiments that debate over which scheme is best somewhat misses the point. They are all valuable. In combination, and if clearly explained, they have the potential to become substantially more effective.

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