The influence of spatial grain size on the suitability of the higher-taxon approach in continental priority-setting

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Abstract

The higher-taxon approach may provide a pragmatic surrogate for the rapid identification of priority areas for conservation. To date, no continent-wide study has examined the use of higher-taxon data to identify complementarity-based networks of priority areas, nor has the influence of spatial grain size been assessed. We used data obtained from 939 sub-Saharan mammals to analyse the performance of higher-taxon data for continental priority-setting and to assess the influence of spatial grain sizes in terms of the size of selection units ($1° \times 1°$, $2° \times 2°$ and $4° \times 4°$ latitudinal–longitudinal quadrates). Independent of spatial grain size, the selection of priority areas based on genus data is more effective than the random selection of these areas, while the selection of priority areas based on family data is less effective than random selection. Compared to selection based on species data, genus-based priority areas represent between 5–14% fewer species, but represent even fewer of the threatened species (6–31%) and range-restricted species (7–42%) that are normally considered most valuable for conservation. While genus-based priority areas for the $4°$ grain size represent species almost as effectively as species-based priority areas, genus-based areas perform considerably less effectively than species-based areas for the $1°$ and $2°$ grain size. Thus, our results favour the higher-taxon approach for continental priority-setting only when large grain sizes ($\geq 4°$) are used.

INTRODUCTION

Identification of priority areas for the conservation of biodiversity ultimately relies on surrogate data, since only 10–30% of the species making up our global biodiversity have been identified (May, 1988). Surrogate measures and shortcuts that have been proposed to facilitate the selection of priority areas for conservation include environmental diversity (Faith & Walker, 1996; see also Araujo *et al.*, 2001; Faith, 2003), land classes (Lombard *et al.*, 2003) as well as indicator taxa (Prendergast *et al.*, 1993). An additional short-cut used in area-selection and priority-setting is the higher-taxon approach: i.e. to use higher taxonomic level data such as genus- and family-level data to identify and prioritise areas of conservation (Gaston & Williams, 1993; Williams & Gaston, 1994; Balmford, Green & Murray, 1996*a*; Balmford, Jayasuriya & Green, 1996*b*; Balmford, Lyon & Lang, 2000).

The goal of global and continental identification of priority areas for conservation is the identification of regions of high conservation value that are significant in a global or continental context, rather than identifying areas for reserves. These coarse-scale priorities should be targets for conservation investment and detailed conservation efforts aimed at the identification of actual reserves for conservation. Clearly, the identification of priority areas for conservation should rely on surrogate data at the finest possible geographical resolution in order to provide the best possible guidance for the identification of actual reserves on the ground. However, global and continental priority-setting is limited by the lack of reliable distributional data for most groups, and priorities are currently based on a subset of taxonomic groups, such as vertebrates (Balmford *et al.*, 2001; Brooks *et al.*, 2001), birds (Stattersfield *et al.*, 1998), plants (WWF & IUCN, 1994–1997) or plants combined with habitat loss (Myers *et al.*, 2000).

Most global and continental analyses of the higher-taxon approach have focussed on the predictive value of higher-taxon richness for species richness (Gaston & Williams, 1993; Williams & Gaston, 1994; Gaston & Blackburn, 1995; Roy, Jablonski & Valentine, 1996; Grelle, 2002; La Ferla *et al.*, 2002). However, species richness *per se* remains rather ineffective in identifying an effective network of areas for conservation. A network of areas selected on the basis of species complementarity is acknowledged as a superior approach, as opposed to areas selected on the basis solely of their absolute richness or endemism (Pressey *et al.*, 1993; Mace *et al.*, 2000). Thus, an evaluation of the higher-taxon approach for priority-setting should preferably be assessed upon the predictive value of complementary higher-taxon richness for complementary species richness.

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Few studies have assessed the suitability of the higher-taxon approach for the actual selection of priority areas based on complementarity (Balmford *et al.*, 1996a,b, 2000; Fjeldså, 2000). To date, no study has examined whether the higher-taxon approach can provide a substitute for the continental identification of complementarity-based priority areas for conservation. If sufficiently reliable, the higher-taxon approach could allow the inclusion of more phylogenetically and ecologically divergent taxa in the currently vertebrate-dominated broad-scale approaches to conservation priority-setting. However, it is unclear what influence spatial scale has on the performance of the higher-taxon approach. Recent studies have shown that spatial scale in terms of area extent (Erasmus *et al.*, 1999; Rodrigues & Gaston, 2002) and grain size of selection units (Pressey *et al.*, 1999; Larsen & Rahbek, 2003; Warman *et al.*, 2004) can influence conservation priority-setting.

Here we test the higher-taxon approach for the continental identification of priority areas for conservation by assessing performance in providing species coverage by priority areas on the basis of genus- and family-level data of sub-Saharan African mammals at the 1° latitude–longitude grid-cell scale. We also test the influence of varying grain size by performing conservation analyses on the same data set compiled with a grain size of 1°, 2° and 4° latitude–longitude grid-cell scale (subsequently referred to as the 1°, 2° and 4° grain sizes). The areas of these grain sizes are equivalent to the areas of the selection units used by several continental and global conservation schemes (see Burgess *et al.*, 2002) such as endemic bird areas (Stattersfield *et al.*, 1998), biologically distinctive ecoregions (Olson *et al.*, 2001), which probably also are the only spatial scales where higher-taxon data for non-vertebrates realistically can be acquired for continents.

METHODS

Distributional data sets

We used a database on the distribution of all 939 mammalian species across mainland sub-Saharan Africa (South of 20° N) held at the Zoological Museum, University of Copenhagen (see http://www.zmuc.dk/commonweb/research/biodata.htm), which has previously been used to examine the influence of scale on conservation priority-setting (Larsen & Rahbek, 2003). The database consists of a conservative estimate of the extent of occurrence of 939 mammalian species mapped at a spatial resolution of 1° latitude–longitude grid-cell scale ($\sim 105 \times 105$ km). The mammals were classified according to the taxonomy of Wilson & Reeder (1993). Distributions of species where denoted by their presence/absence within each grid cell (a total of 1960 1° grid cells with 169 964 species-in-grid-cell data entries for the 939 mammalian species). For the larger and better-known species, the data are an estimate of distribution ranges. For smaller and lesser-known species, expected distribution ranges were interpolated by assuming a continuous distribution between confirmed records with

Table 1. Number of families, genera and species for the various orders of sub-Saharan African mammals

Order	Family	Genus	Species
Primates	4	20	67
Chiroptera	8	41	177
Insectivora	4	19	156
Macroscelidea	1	4	14
Lagomorpha	1	4	10
Rodentia	11	81	346
Carnivora	6	38	64
Pholidota	1	1	4
Tubulidentata	1	1	1
Hyracoidea	1	3	5
Proboscidea	1	1	1
Perissodactyla	2	4	7
Artiodactyla	4	36	86
Sirenia	1	1	1
Total	46	254	939

relatively uniform habitat, using available information on species' habitat associations and taking into account specialist opinions. For the least-known species, data are based on confirmed records only. For more information on mapping methodology, see Brooks *et al.* (2001). We used the species database as a template for the generation of a genus- and family-database (see Table 1).

Spatial scale

In order to assess the effect of grain size, we recompiled the 1° distributional data for the three databases (species, genus and family) at geographical resolutions of 2° and 4° latitude–longitude grid-cell scale.

Area selection methods

A highly effective selection of priority areas for conservation in terms of representing biodiversity is achieved by using the principle of complementarity: the selection of sites that complement one another in terms of biodiversity (Pressey *et al.*, 1993; Mace *et al.*, 2000). We generated near-maximum coverage sets of 5% and 20% of the total area of sub-Saharan Africa for each of the three data sets in order to represent all features (species, genus and family) as many times as possible. We selected areas using the widely used progressive rarity algorithm (Margules, Nicholls & Pressey, 1988; Williams, 1998) of the WORLDMAP software (Williams, 2000). Given the question asked and the size of the database analysed, another algorithm, e.g. a greedy algorithm, would not produce different results. Furthermore, the use of the progressive rarity algorithm is in accordance with previous complementarity analyses conducted on the same data set (Williams, Burgess & Rahbek, 2000; Balmford *et al.*, 2001; Burgess *et al.*, 2002; Larsen & Rahbek, 2003; Moore *et al.*, 2003a). The progressive rarity algorithm provides close-to-optimal solutions (Moore *et al.*, 2003b), initially selecting all grid cells with species that have single

records, then selecting grid cells that contribute with the highest incidence of unrepresented rare species, i.e. unrepresented species with the fewest grid cells records. In successive iterations of the algorithm, areas with the highest complementary richness in the rarest species are selected until the required number of areas has been obtained (see table 1 in Williams *et al.*, 2000).

Following previous priority-setting analyses on the same data set and template (see references above) as well as comparable macroecological analyses on the Sub-Saharan African faunas (Jetz & Rahbek, 2001, 2002; Jetz, Rahbek & Colwell, 2004; Jetz, Rahbek & Lichstein, 2005), coastal grid cells are not excluded since the analyses we perform are based on conservative estimates of range of occurrence. Exclusion of coastal quadrats typically eliminates much of the important biological signal as biologically rich and unique terrestrial areas are often situated along the coastline (Rahbek & Graves, 2000). In addition, the potential information loss is highly scale-dependent in terms of sample size reduction (Rahbek & Graves, 2000), which would be an unwarranted effect in our analyses.

Effectiveness of priority areas based on higher-taxon data

The effectiveness of priority areas identified on the basis of genus and family data in terms of representation of species was measured for all three grain sizes. Species representation was evaluated using two benchmarks: (1) the representation of species in priority areas based on species data, and (2) the representation of species in randomly chosen priority areas. The randomly chosen priority areas were drawn 1000 times, without replacement. Median species representation and 95% confidence intervals of the randomly selected priority areas are presented in the results. In addition, the representation of threatened and range-restricted species by the priority areas on the basis of genus- and family-level data was measured and compared with species-based and random selection of priority areas. Threatened species were defined as the 197 species categorised as critically endangered, endangered or vulnerable according to the IUCN Red List (IUCN, 2002). The range-restricted species were defined as the rare quartile species, i.e. the 25% of the species (234 out of 939 species) with the smallest ranges when measured at the 1° data set.

RESULTS

Patterns of richness and endemism

Patterns of richness for species, genus and family for the 1° grain size are highly similar, with an overall pattern of high richness around the north of Lake Victoria, the mountains of Kenya, Tanzania and Malawi, the forest–savannah ecotone north of the Congo Basin, the Cameroonian highland forest and the Guinean forests (Fig. 1). As expected, species richness is strongly correlated with genus richness ($rs = 0.98$ for all three grain sizes) and family richness ($rs = 0.85$–0.87) for all grain sizes.

In contrast to patterns of richness, patterns of endemism expressed as range-size rarity (i.e. the sum of the reciprocals of the range sizes of species, genera and families, respectively, in a grid cell) change with higher taxonomic resolution (Fig. 1). At the species level, centres of high range-size rarity are concentrated in the equatorial montane forests, such as the Guinean forests of West Africa, the forests of the Albertine Rift, Kenyan highlands and the Eastern Arc, as well as the montane forests of Ethiopia (Fig. 1). The range-size rarity pattern at the genus-level exhibits a similar pattern overall, while the pattern of family level is variable. Thus, the Guinean forests of West Africa (one of the global biodiversity hotspots according to Myers *et al.* (2000)) are no longer recognised as a centre of endemism, while western Namibia appears as such a centre (Fig. 1). For all grain sizes, species range-size rarity is strongly correlated with genus range-size rarity ($rs = 0.85$–0.91), but only modestly correlated with family range-size rarity ($r = 0.60$–0.66).

Networks of priority areas

When selecting 5% of the area of sub-Saharan Africa, the geographical location of the near-maximum coverage sets based on species-, genus- and family-level data for the 1°, 2° and 4° grain sizes reveal differences (Fig. 2). Generally, the areas selected using species data are scattered, while the selected areas are clustered when using genus-level data and especially family-level data (Fig. 2). As expected, the selected areas based on species- and genus-level data have an increasing spatial overlap (23%, 31% and 71% for the 1°, 2° and 4° grain sizes, respectively) with coarser grain size (i.e. 2°, 4°). These spatial overlaps are a conservative estimate, as flexibility in area choices is not taken into account.

Species coverage by priority areas

Genus-based priority areas represent more species than are represented following the random selection of priority areas for all grain sizes (Fig. 3). When 5% of the area of sub-Saharan Africa is selected, the genus-based priority areas represent 14%, 13% and 13% more species than random for the 1°, 2° and 4° grain sizes, respectively (Table 2). By contrast, for all grain sizes the representation of species by family-based priority areas is less effective than random selection of priority areas (Fig. 3, Table 2).

The genus-based priority areas represent 5–14% fewer species than species-based priority areas, i.e. 14%, 9% and 5% fewer species for the 1°, 2° and 4° sizes, respectively (Table 2). The difference in representation of species between genus-based and species-based priority areas is smallest for the largest grain size (4°) and largest for the smallest grain size (1°). These grain-size related differences in representation of species are more pronounced with regard to the representation of threatened and range-restricted species. Genus-based priority areas
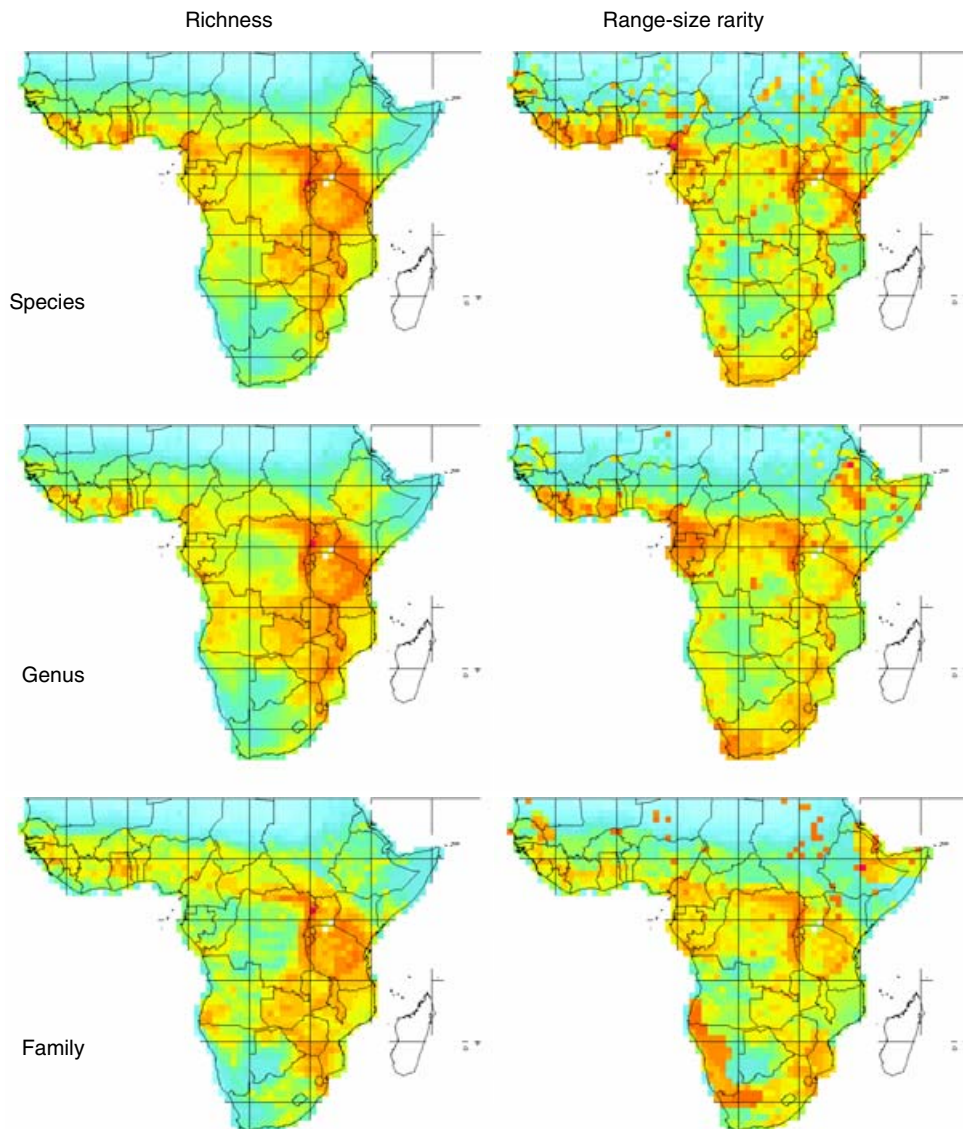
Richness   Range-size rarity

Fig. 1. Patterns for richness and endemism (based on range-size rarity scores, i.e. the sum of the reciprocals of the range sizes in each grid cell) for species-, genus- and family-level data for the 1° grain size. Range-size rarity was measured as a continuous function, i.e. each grid cell was scored according to the counts of the range-size rarity scores for taxa recorded in that grid cell. Red indicates grid cells with the highest richness and highest range-size rarity score, blue indicates the lowest richness and lowest range-size rarity score.

represent 6–31% fewer threatened species (31%, 14% and 6% for the 1°, 2° and 4° grain sizes, respectively) and 7–42% fewer range-restricted species (42%, 21% and 7% for the 1°, 2° and 4° grain sizes, respectively) than species-based priority areas (Table 2).

Family-based priority areas represent, depending on grain size, 31–38% fewer of all species, 35–55% fewer threatened species and 41–66% fewer range-restricted species compared to species-based priority areas (Table 2).

The difference in representation of species between species-based priority areas and the random selection of priority areas also varies with grain size. Species-based priority areas for the 1° grain size represent 28% more species than areas based on random selection, while this percentage drops to 22% and 18% for the 2° and 4° grain sizes, respectively (Table 2). For threatened species

the difference in representation between species-based priority areas and the random selection of priority areas as a result of varying grain size is more pronounced, i.e. 50%, 34% and 29% for the 1°, 2° and 4° grain sizes, respectively (Table 2).

DISCUSSION

Richness, endemism and complementarity

In agreement with several previous studies of global/continental scale of extent (Gaston & Williams, 1993; Williams & Gaston, 1994; Gaston & Blackburn, 1995; Roy *et al.*, 1996; Grelle, 2002; La Ferla *et al.*, 2002) we found that higher-taxon richness is a good predictor of species richness, while family level range-size rarity
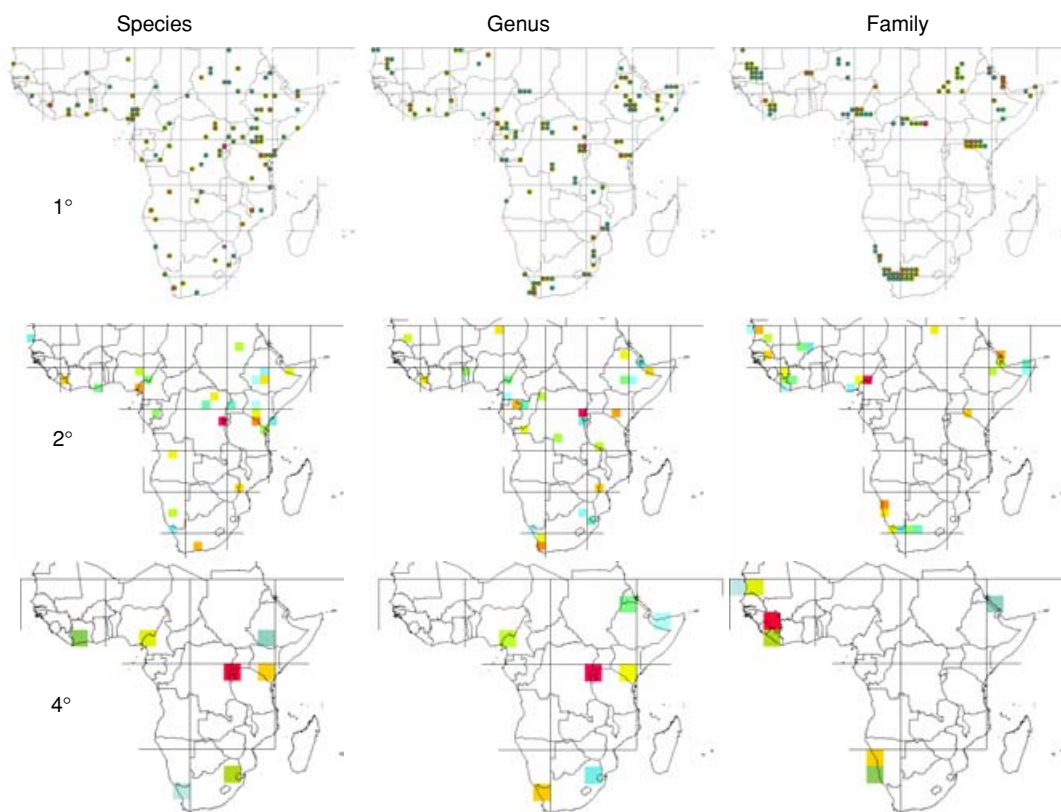
Fig. 2. Location of near-maximum coverage sets (when 5% of the area of sub-Saharan Africa is selected) for the 1°, 2° and 4° grain size identified on the basis of species-, genus- and family-level data, respectively. The colour scale indicates the number of complementary species, genera and families: the warmer the colour, the higher the number of complementary species, genera and families.

Table 2. Percentage representation of all species, threatened species and endemic species (rare quartile) by the near-maximum coverage sets (when 5% of sub-Saharan Africa is selected) for the 1°, 2° and 4° grain sizes identified based on species-, genus- and family-level data

Selection criteria	All species			Threatened species			Endemic species (rare quartile)		
	1°	2°	4°	1°	2°	4°	1°	2°	4°
Species	98	87	75	96	73	61	92	62	47
Genera	84	78	70	65	59	55	50	41	40
Family	61	56	37	41	38	18	26	17	6
Random	70	65	57	46	39	32	21	20	21

The table also presents the representation of all species and threatened species in sets selected at random (95% confidence intervals are shown).

and, to a lesser extent genus range-size rarity, are poor predictors of species range-size rarity. However, for the identification of priority areas for conservation, focus should rather be on higher-taxon analyses as predictors of complementarity richness (Balmford *et al*., 2000).

Effect of spatial grain size

Spatial patterns of co-occurrence among species depend on the spatial grain size used to compile the distribution data (Stoms, 1994; Rahbek & Graves, 2000, 2001; for a review, see Rahbek, 2005). Since conservation priorities rely on these patterns, we can expect that spatial grain size will also influence conservation priorities. However, despite the widespread use of priority-setting at varying spatial grain sizes, few studies have assessed the extent of this problem (Pressey *et al*., 1999; Larsen & Rahbek, 2003; Warman *et al*., 2004).

We found, not surprisingly, that the general effectiveness of area-selection based on species, genus and family data, as well as randomly selected priority areas decreases with larger grain sizes (Fig. 3, Table 2). The scattered, smaller, areas of the 1° scale probably represent more habitats (and thus more species) in different zoogeographical regions than would be the case in fewer, larger areas.

We also found that the grain size defining the size of selection units influences the suitability of higher-taxon data for continental priority-setting. Genus-based priority areas perform almost as well as species-based priority areas when the largest grain size (4°) is used for the analysis (Table 2). However, for the smaller grain sizes, in particular the 1° grain size, the higher-taxon approach seems less promising, as higher-taxon-based priority areas cover considerably fewer threatened and endemic species than species-based priority areas (Table 2). This is in agreement with the study by Fjeldså (2000) based on bird data compiled for ¼° grain size units in the tropical
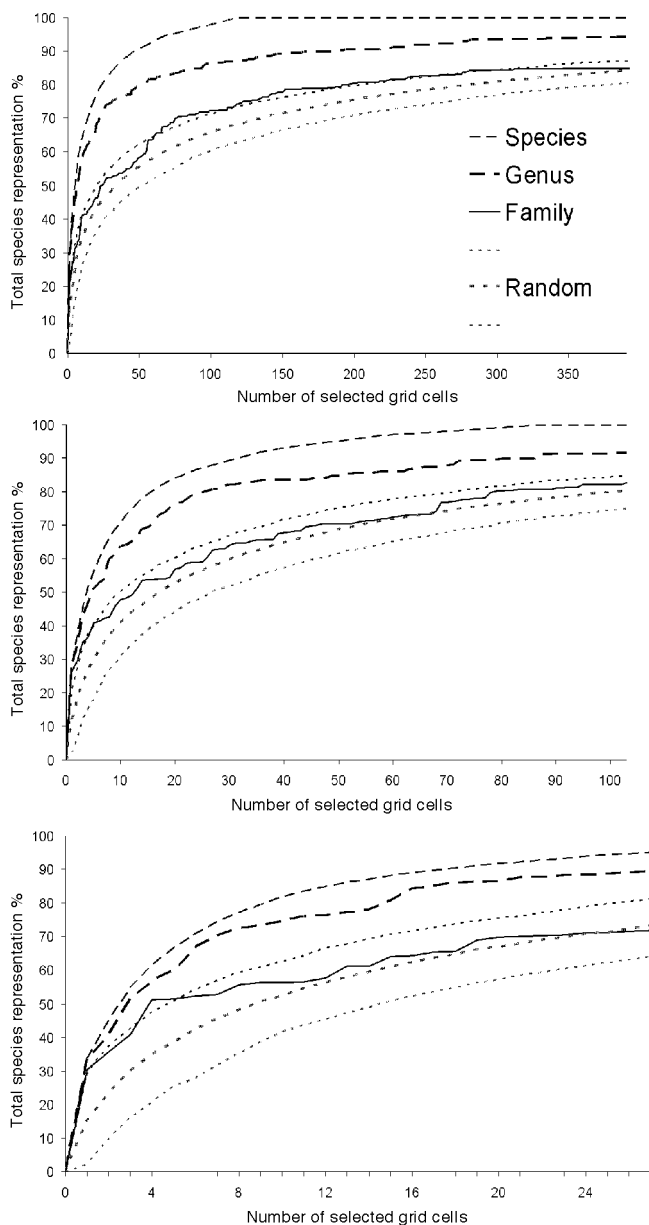
Fig. 3. Cumulative percentage representation of all 939 mammalian species in the near-maximum coverage set (when 20% of sub-Saharan Africa is selected) for the 1°, 2° and 4° grain size identified on the basis of species-, genus- and family-level data. The median representation of all species in sets selected at random is also presented. Dotted lines indicate the 95% confidence intervals of the random median.

Andes, which found that complementarity hotspots based on genus data perform poorly in representing threatened species, when compared to species-based priority areas.

One reason why higher-taxon data are less effective than species data for the smaller grain sizes (1° and 2°) is that areas important for range-restricted species may no longer be recognised with coarser taxonomic resolution. Specifically, the distributions of a genus or family consist of the distributions of the restricted-range species as well as the distributions of the other species within that genus or family. In this way, the smaller, scattered distributions of range-restricted species can be blurred at the genus-

and family-level. This trend will be most evident for the smallest grain size, i.e. the 1° quadrates ($\sim 11\,000\,\mathrm{km}^2$) since the span of range sizes is greatest at this resolution, while the trend will be expected to become less evident for large grain sizes, such as 4° quadrates (which cover 16 1° quadrates). For example, the species database for the 1° grain size contain 12 shrew species from the genus *Myosorex* with range-sizes covering 1, 1, 2, 2, 2, 2, 4, 4, 7, 14, 38 and 83 1° quadrates, respectively. When these 12 species distributions are pooled together in the genus database, the distribution of the genus *Myosorex* covers 122 1° quadrates. In the family database the genus *Myosorex* are pooled with the other genera within the family Soricidae, which gives a distribution for Soricidae of 806 1° quadrates ($\sim 41\%$ sub-Saharan Africa). The median range-sizes for the 1° data sets are 33, 352 and 1293 grid cells for species, genus and family, respectively. When using family-level data to select areas, only a few grid cells are needed to cover all families due to the large geographical coverage of families. Thus, when 5% of the area is selected, the site selection algorithm will quickly ensure one representation of all families. Hereafter, the algorithm will select areas that maximise the number of times each family is represented, which results in repeated selection of sites similar to the ones already selected. This is probably the reason why the geographical locations of the selected areas observed in Fig. 2 are clustered when using genus- and, especially, family-level data compared to when using species-level data.

Our data on sub-Saharan mammalian distributions may tend to underestimate representation of range-restricted species in our analyses, especially for the smaller grain sizes. For the least well-known mammal species, our data consist of confirmed records only, with no interpolation between confirmed records as is the case with the more well known species in the database. In fact, around 22% of the threatened species and 30% of the range-restricted species (i.e. the rare quartile) at the 1° scale only have one record in the database, i.e. their distributions only cover a single 1° quadrate. These singleton records may reflect the fact that the species' range-size is indeed very narrow, but could also reflect a limited knowledge of a somewhat more widespread species. The real range-sizes of some of the poorly known species are probably underestimated, which results in an underestimation of the true representation of the rare quartile of species by the priority areas. This factor will decrease with larger grain size.

Another spatial issue is extent of scale. Analysis at large spatial extents for higher-taxon priority-setting may be a potential problem, since numbers of species in higher-taxa can differ significantly between biogeographical regions, such as continents, in an analysis of global extent. For example, there are 310 and 292 plant families in Malesia and the Neotropics, respectively, while the number of species is 42 000 and 90 000 (Prance, 1994). Such differences will influence the predictive value of higher taxon richness for species richness at very large spatial extents. If, however, areas are selected on the basis of complementarity rather than richness, this may not pose a serious problem.

Is higher-taxon data suitable for continental priority-setting?

Several regional studies have shown that genus (and family) based site-selection can perform well in representing species (Balmford *et al.*, 1996*b*, 2000). However, since these studies did not assess random representation, no directly comparable conclusion to this study can be drawn.

Our continental analysis shows that family-level data, independently of grain size, provides very poor guidance for priority area-selection. At the 1° scale, genus-based priority areas are shown to be less effective than species-based priority areas and they fail to effectively cover the species of conservation interest. In contrast, genus-based priority areas at the 4° scale are shown to be almost as effective as species-based priority areas for continental priority-setting. Thus, the genus data seems to provide a good surrogate for species representation at large spatial grain sizes.

Unfortunately, large grain sizes are less useful than smaller grain sizes for the identification of priority areas for conservation. Large grain sizes provide less precision in priority-setting with respect to where 'action on the ground' should take place. Furthermore, the representation of species between species-based priority areas and randomly selected priority areas is highest for the 1° grain size and decreases for larger grain sizes (2° and 4°) due to sample size constraints (Fig. 3, Table 2). That is, the advantage of using a surrogate for priority-setting is smaller for the 4° grain size than for the smaller grain sizes (1° and 2°). Nevertheless, these grain sizes may realistically be the only option if higher-taxa data for more phylogenetically and ecologically divergent taxa (non-vertebrates) is to be included in continental area-based priority-setting.

In conclusion, our results do not favour the higher-taxon approach as a reliable pragmatic strategy for continent-wide priority setting at smaller spatial scales (1° and 2°) as this approach tends to overlook areas holding endemic as well as threatened species. However, genus data could be used for large grain sizes as a supplement to existing global and continental conservation schemes. We acknowledge the need for consensus for international conservation priorities, rather than building new conservation schemes (Mace *et al.*, 2000). Still, in this context, the higher-taxon conservation analyses for more divergent and ecologically different taxa could provide additional empirical evidence for the assumption that current global and continental priority areas identified on the basis of few taxa capture biodiversity more broadly.

One limitation for the conclusions regarding the use of the higher-taxon approach for continental priority setting is that they are based on rather species-poor groups, such as birds (Fjeldså, 2000) and mammals (this study). The benefits of using the higher-taxon approach are highest for the mega-diverse groups, which are the hardest to survey. Only one study, at a smaller spatial extent (United Kingdom), found that higher-taxon (genus-level) data for a mega-diverse group (macrofungi) performed well for area-selection (Balmford *et al.*, 2000) although this study did not assess random representation. The general validity of our findings at a large extent of scale, based on a rather species-poor group, compared to mega-diverse taxa such as arthropods, remains to be tested.

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