Improving the Performance of Indicator Groups for the Identification of Important Areas for Species Conservation

FRANK WUGT LARSEN,*‡ JESPER BLADT,† AND CARSTEN RAHBEK*

*Center for Macroecology, Institute of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen O, Denmark
†Jesper Bladt, Department of Systematic Botany, Institute of Biological Sciences, University of Aarhus, Ny Munkegade, Building 1540, 8000 Aarhus C, Denmark

Abstract: *Indicator groups may be important tools with which to guide the selection of networks of areas for conservation. Nevertheless, the literature provides little guidance as to what makes some groups of species more suitable than others to guide area selection. Using distributional data on all sub-Saharan birds and mammals, we assessed factors that influence the effectiveness of indicator groups. We assessed the influence of threatened, endemic, range-restricted, widespread, and large-bodied species by systematically varying their number in indicator groups. We also assessed the influence of taxonomic diversity by systematically varying the number of distinct genera and families within the indicator groups. We selected area networks based on the indicator groups and tested their ability to represent a set of species, which, in terms of species composition, is independent of the indicator group. Increasing the proportion of threatened, endemic, and range-restricted species in the indicator groups improved effectiveness of the selected area networks; in particular it improved the effectiveness in representing* other *threatened and range-restricted species. In contrast increasing the proportion of widespread and large-bodied species decreased effectiveness. Changes in the number of genera and families only marginally affected the performance of indicator groups. Our results reveal that a focus on species of special conservation concern, which are legitimate conservation targets in their own right, also improves the effectiveness of indicator groups, in particular in representing other species of conservation concern.*

Keywords: complementary networks, conservation planning, indicator taxa, sub-Saharan mammals and birds

Mejoramiento del Desempeño de Grupos Indicadores para la Identificación de Áreas Importantes para la Conservación de Especies

Resumen: *Los grupos indicadores pueden ser herramientas importantes para guiar la selección de redes de áreas para conservación. Sin embargo, la literatura proporciona escasas guías sobre lo que hace que algunos grupos de especies sean más adecuados que otros para guiar la selección de áreas. Utilizando datos de la distribución de todas las aves y mamíferos sub Saharianos, evaluamos factores que influyen en la efectividad de los grupos indicadores. Evaluamos la presencia de especies amenazadas, endémicas, de distribución restringida, de distribución amplia y de cuerpo grande mediante la variación sistemática de su número en grupos indicadores. También evaluamos la influencia de la diversidad taxonómica mediante la variación sistemática del número de géneros y familias distintas dentro de los grupos indicadores. Seleccionamos redes de áreas con base en los grupos indicadores y probamos su habilidad para representar un conjunto de especies, el cual, en términos de la composición de especies, es independiente del grupo indicador. El incremento de la proporción de especies amenazadas, endémicas y de distribución restringida en los grupos indicadores mejoró la efectividad de las redes de áreas seleccionadas; particularmente, mejoró la efectividad en la representación*

‡*email fwlarsen@bi.ku.dk*
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de otras *especies amenazadas y de distribución restringida. En contraste, el incremento de la proporción de especies de amplia distribución y de cuerpo grande disminuyó la efectividad. Cambios en el número de géneros y familias solo afectaron el funcionamiento de los grupos indicadores marginalmente. Nuestros resultados revelan que el enfoque en especies de particular interés para la conservación, que son objetivos de conservación legítimos por derecho propio, también mejora la efectividad de los grupos indicadores, particularmente en la representación de otras especies de interés para la conservación.*

Palabras Clave: aves y mamíferos sub Saharianos, planeación de la conservación, redes complementarias, taxa indicadores

Introduction

An increased awareness of the magnitude of global biodiversity loss resulted in an international commitment at the 2002 Johannesburg World Summit on Sustainable Development to achieve, by 2010, a significant reduction in the current rate of biodiversity loss (UNEP 2002). Because the in situ conservation of viable populations in natural ecosystems constitutes a cornerstone in the effort to fulfill the 2010 goal, areas important for the maintenance of biodiversity need to be identified and added to the existing global network of protected areas because the current reserve network is inadequate (Rodrigues et al. 2004). At larger (e.g., continental) scales, the aim of priority setting is to identify regions valuable for conservation, rather than to identify actual reserves. Once identified these coarse-scale priorities should then be targets for more concerted conservation efforts leading to the identification of the most valuable areas at a local scale to manage for biodiversity.

Because our knowledge of biodiversity is still rather limited, several indicators for the identification of important areas for biodiversity conservation have been proposed, including data on higher taxa (e.g., Gaston & Williams 1993; Balmford et al. 1996; Larsen & Rahbek 2005), species indicator groups (e.g., Prendergast et al. 1993; Andelman & Fagan 2000; Williams et al. 2000), and various broad-scale biodiversity correlates, such as environmental diversity (Faith & Walker 1996; Faith 2003) and land classes (Lombard et al. 2003). The underlying assumption is that areas identified based on these indicators are important for overall biodiversity conservation. Species data are considered an important component in successful priority setting when it comes to selecting areas for preservation of species (Brooks et al. 2004). In that framework conservationists need to examine whether some groups of species are useful in guiding the selection of a network of areas in which individual areas complement one another in terms of species representation (Pressey et al. 1993; Howard et al. 1998). Many researchers have assessed the performance of indicator groups as conservation surrogates for overall biodiversity (e.g., Howard et al. 1998; Andelman & Fagan 2000; Lawler et al. 2003; Moore et al. 2003*a*), albeit with varying conclusions. Some of these disparities may arise due to differences in spatial scale (spatial extent and grain size), biogeographic region, and methods used to measure the effectiveness of indicator performance.

When testing indicator performance, certain methodological issues should be considered. First, the common approach is to select indicator groups from the full data set and evaluate their effectiveness in representing the remaining species of the data set, which then constitute the target group (i.e., the species that should be represented by the indicator groups) (e.g., Lawler et al. 2003; Warman et al. 2004; Tognelli 2005). Consequently, the species composition of the target groups depends on the species composition of the indicator groups. Accordingly, the species composition of the target group varies between each indicator group, which may make it difficult to disentangle, whether the effectiveness of the indicator group is attributable mainly to the target group rather than the indicator group. For example, range-restricted and threatened species, in particular, have been identified as useful indicators (Lawler et al. 2003; Warman et al. 2004; Tognelli 2005). Nevertheless, the promising indicator performance of range-restricted and threatened species could be attributable to the fact that the target groups are relatively easier to represent because the difficult species to represent (i.e., threatened and endemic species) have been eliminated from the target groups because they constitute the indicator group. Thus, range-restricted and threatened species may not be more effective than other species in representing a fixed target group of species, including *other* range-restricted and threatened species.

Second, most researchers have assessed indicator groups that were based on all the species belonging to a taxon (e.g., butterflies, birds, or mammals) (Prendergast et al. 1993; Lund & Rahbek 2002; Moore et al. 2003*a*) or falling within various species attributes (e.g., flagship, umbrella, or endemic species) (Andelman & Fagan 2000; Williams et al. 2000; Tognelli 2005). Because these approaches have failed to identify consistently good indicators, it seems fitting to shift focus toward a systematic assessment of factors influencing the effectiveness of indicator groups (Manne & Williams 2003), especially in terms of how the inclusion or exclusion of different types of species affects indicator group performance.

We attempted to identify factors that influence the effectiveness of indicator groups for the selection of area networks based on data for sub-Saharan birds and mammals. We tested the effectiveness of randomly chosen indicator groups for which we systematically varied the number of threatened, endemic, range-restricted, widespread, and large-bodied species and the number of distinct genera and families (as a measure of taxonomic diversity). To make the species composition of the target group independent of the species composition of the indicator group, we performed analyses on a divided data set in which indicator groups were selected from one half of the species data set, with the remaining half of the species constituting the target group.

Methods

Species Distribution Data

Analyses were performed on databases covering the distribution of 949 mammalian species and 1922 avian species across mainland sub-Saharan Africa, south of 20° N. These databases were based on an estimate of the extent of occurrence and were mapped at a spatial resolution of 1° latitude–longitude grid-cell scale, approximately corresponding to 105 × 105 km grid cells. The classification of species follows Wilson and Reeder (1993) for mammals and Sibley and Monroe (1990, 1993) for birds. Distributions of species were defined by their presence or absence within each grid cell. For the larger and better-known species, the data comprised an estimate of recent distributions. For smaller and lesser-known species, expected distributions were interpolated following the assumption of a continuous distribution between confirmed records with relatively uniform habitat based on available information on species' habitat associations. We consulted with taxon specialist to check interpolation. For the least-known species, we used data based only on confirmed records. For more information on mapping methodology, see Burgess et al. (1998) and Brooks et al. (2001).

Indicator Group Characteristics

We examined how changing the proportion of particular types of species in indicator groups influences performance of the indicator. Species from these groups either receive high conservation attention (endemics, range-restricted, and threatened species) or are commonly available for priority setting (widespread and large-bodied species) and are thus of practical relevance for the real-world selection of species for indicator groups. We examined threatened, endemic, range-restricted, widespread, and large-bodied species.

Threatened species ($n = 286$) included mammals and birds in the vulnerable, endangered, and critically endangered World Conservation Union (IUCN) categories (IUCN 2004). Because threatened species already receive the most conservation attention, it is important to know how the inclusion or exclusion of these species in indicator groups influences the effectiveness of selected area networks.

Endemic species ($n = 315$) were defined as those having a geographical distribution of no more than five 1° × 1° cells (approx. 50,000 km^2) (following BirdLife International's definition of a restricted-range bird species [Stattersfield et al. 1998]). Species with a small geographical range size are more prone to extinction (Purvis et al. 2000). Range-restricted species ($n = 718$) comprised the 25% of bird ($n = 481$) and mammal species ($n = 237$) with the smallest geographic distribution.

Widespread species ($n = 718$) were defined as the 25% of bird ($n = 481$) and mammal species ($n = 237$) with the largest geographic distribution. Species from this category are typically well described, and data are readily available. Thus, widespread species often constitute a proportionately large share of the species data available for priority setting.

Large-bodied species ($n = 625$) were defined for larger mammals as species belonging to the orders Primates, Carnivora, Proboscidea, Perissodactyla, Artiodactyla, Sirenia, and Tubulidentata and for larger birds as species belonging to the orders Struthionidae, Craciformes, Upupiformes, Bucerotiformes, Trogoniformes, Cuculiformes, Musophagiformes, Strigiformes, Columbiformes, Gruiformes, Falconides, and Ciconiides. Together, these orders include 625 species. As is the case with widespread species, large-bodied species are generally well described, and data are usually readily available. Some overlap in species can be expected to exist between these groups (e.g., 66% of the threatened species are also included in the group of range-restricted species).

Finally, we examined the performance of indicator groups varying in taxonomic diversity, measured as the number of genera (out of 689) and families (out of 119), to determine the influence of varying taxonomic diversity on indicator performance.

Selection and Test of Indicator Groups

We tested the effectiveness of the different indicator groups on nine area-selection scenarios that consisted of combinations of three indicator group sizes (50, 150, and 300 species) and three network sizes (1%, 5%, and 10% of the total area of sub-Saharan Africa). We randomly divided the total species pool of 2871 species into two halves, drawing the indicator group from one half, while the other half constituted the target group. From

Table 1. Numbers of threatened, endemic, range-restricted, widespread, and large-bodied species in the indicator groups of 50, 150, and 300 species used in the selection of networks of areas for conservation.*

		Variation in indicator group characteristics			
Number of species in indicator group	*indicator group characteristics*	*no species*	*number of species expected by chance*	*addition of species at two levels*	
50	threatened spp.	0	5	20	35
	endemic spp.	0	5	20	35
	range-restricted spp.	0	13	28	43
	widespread spp.	0	13	28	43
	large spp.	0	11	26	41
150	threatened spp.	0	15	65	115
	endemic spp.	0	16	66	116
	range-restricted spp.	0	38	88	138
	widespread spp.	0	38	88	138
	large spp.	0	33	83	133
300	threatened spp.	0	30	80	130
	endemic spp.	0	33	83	133
	range-restricted spp.	0	75	125	175
	widespread spp.	0	75	125	175
	large spp.	0	65	115	180

**For example, we selected 500 indicator groups consisting of 50 species that contained 0, 5, 20, and 35 threatened species, respectively.*

the indicator species pool we randomly selected sets of species as our indicator groups and systematically varied the proportion of threatened, endemic, range-restricted, widespread, and large-bodied species within each set. For each of the five groups of species (here exemplified with threatened species), we generated indicator groups containing: (1) no threatened species, (2) the number of threatened species expected by chance (for an indicator group of the given size), and (3) an additional number of threatened species (Table 1). For example, in the 150-species scenario we selected randomly chosen species indicator groups containing no threatened species, 15 threatened species (randomized species groups of 150 species included on average 15 threatened species), 65 threatened species (+50 species), and 115 threatened species (+100 species). For the 50-species scenario we added 15 and 30 species, whereas for the 300-species scenario we added 50 and 100 species as in the 150-species scenario (because the indicator species pool did not contain a sufficient number of threatened species, i.e., on average half of 286, to add a higher number).

In addition, we randomly selected indicator groups with decreased or increased numbers of distinct genera and families. Thus, indicator groups were generated based on the number of distinct genera and families expected by chance (for an indicator group of the given size) and on the number of distinct genera and families decreased or increased by 50% compared with the number expected by chance. Thus, for the 150-species scenario, we randomly selected species indicator groups that contained species from 58 distinct genera (the number of genera decreased by 50%), 116 distinct genera (randomized species groups of 150 species contained on average species from 116 distinct genera), and with all 150 species coming from distinct genera (the number of genera increased by 50% if possible). The genera and families were selected at random with the probability of selection proportional to the number of species within each genus or family. In cases where the randomly selected genera or families did not contain sufficient species to fill the indicator group, we rejected the set of genera or families and selected a new random set.

The procedures were repeated 500 times for each indicator group set (e.g., 150 species that contain 115 threatened species). Some species were inevitably included in more than one indicator group, which potentially compromised the independence of the indicator groups. Nevertheless, because the species could be combined in an almost infinite number of different groups, this resampling was not expected to create any bias within the results.

We used the indicator groups to select networks of priority areas based on complementary species richness (Pressey et al. 1993; Mace et al. 2000). We generated near-maximum coverage sets (Church et al. 1996) in order to represent the species in the indicator groups as often as possible. Areas were selected with the widely used progressive rarity algorithm (Margules et al. 1988; Williams 1998), which provides close-to-optimal solutions (Moore et al. 2003*b*) by initially selecting all grid cells with species that have single 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. The algorithm was implemented with a random tie-breaking role (see Table 1 in Williams et al.(2000) for exact algorithm outline).

We assessed the effectiveness of each area network in representing the species (all species, threatened species, and rare-quartile species, i.e., the 25% of the species with the smallest distribution) in the target group (Howard et al. 1998; Moore et al. 2003*a*; Warman et al. 2004), which here constituted half of the species in the data set. As our performance benchmark we compared with three other scenarios: (1) the effectiveness of the area networks chosen at random (1000 times), which gives an estimate of the expected effectiveness by selecting the given area without any information on species' distributions; (2) the effectiveness of the area networks selected based on random sets of the same number of species (500 times), which gives insight into whether the indicator groups perform better than what would be expected from using any species data; and (3) the effectiveness of the area networks selected on the basis of all species in the target group, which gives an estimate of the maximal representation possible within the given area. All methods were implemented in Java with the Java 2 Platform (Enterprise Edition Technology, version 1.4, Sun Microsystems, Santa Clara, California).

Results

For all nine area-selection scenarios, comprising all combinations of indicator group and area network sizes, area networks identified based on randomly selected indicator groups proved more effective in representing species than area networks identified on the basis of random area selection (Fig. 1). In addition, species representation and increased indicator group sizes (50, 150, and 300 species) were positively correlated, as were species representation and increased network size (1%, 5%, and 10% area). Because the species representation results from all nine scenarios showed comparable trends, we restricted subsequent analyses on the effectiveness of species representation to one of the nine scenarios: indicator group size of 150 species and an area network size of 5% of sub-Saharan Africa.

Changing the number of threatened, endemic, range-restricted, widespread, and large-bodied species in the randomly chosen indicator groups led to either an increase or a decrease in the overall effectiveness with which the group represented species compared with the randomly selected indicator group (Fig. 2). Increasing the number of threatened, endemic, and range-restricted species in the indicator group with 50 and 100, respectively, increased ($p < 0.05$) the effectiveness of species representation (between 0.6–1.9%), especially for an increasing number of endemic and range-restricted species, whereas omitting these species in the indicator groups decreased effectiveness ($p < 0.05$). In contrast increasing the proportion of widespread and large-bodied species decreased ($p < 0.05$) the effectiveness of species representation (between 0.8–7.2%), whereas omitting these species increased effectiveness ($p < 0.05$) (Fig. 2a). Nonetheless, area networks for all indicator groups, with the exception of the group with the largest number (138) of widespread species, performed better ($p < 0.05$) than would be the case with random selection of areas. When considering the representation of threatened and rare-quartile species, there were more-substantial increases in effectiveness when we increased the proportion of threatened, endemic, and range-restricted species (Fig. 2b) (e.g., effectiveness increased by 3.9–10.9% for threatened

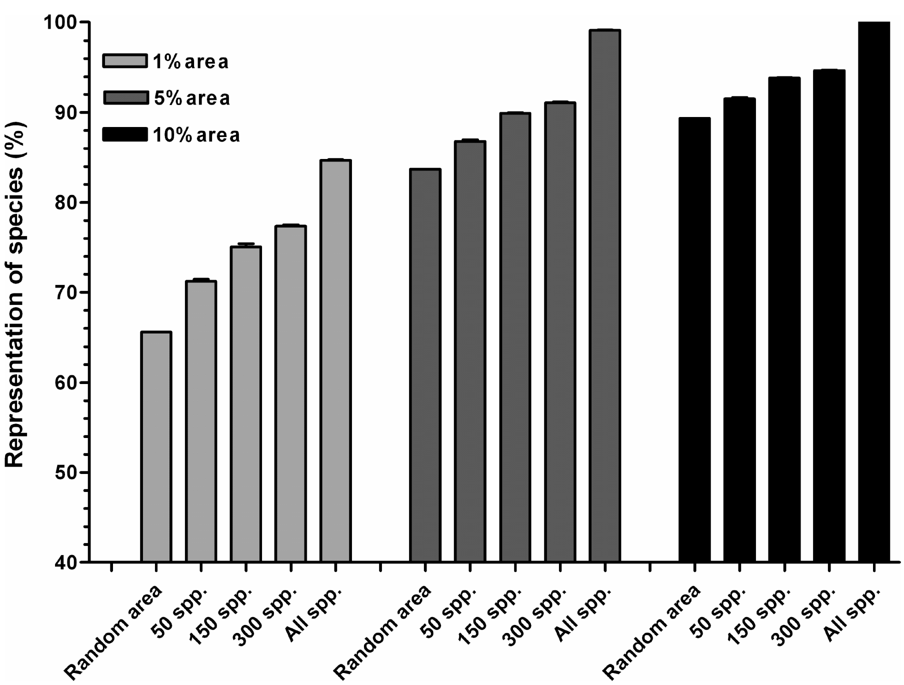

Figure 1. Representation of species in the target group (i.e., half the species data) for randomly chosen indicator groups (500 times) for each of the nine indicator-group-size/network-size scenarios. Species representations based on randomly chosen area networks (upper 2.5%) and area networks based on all species are shown as evaluation benchmarks. Error bars denote 95% confidence intervals about the mean.

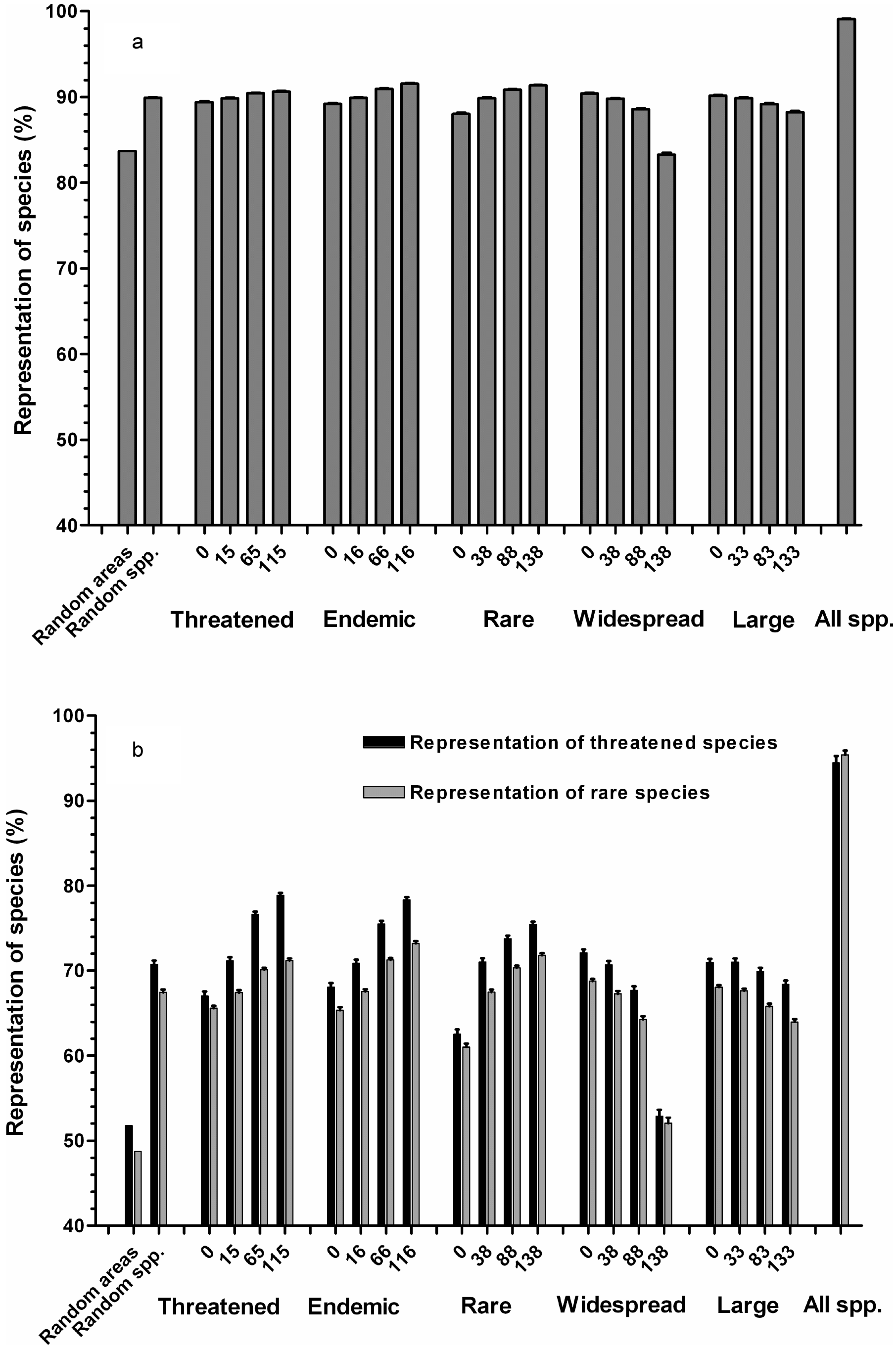

Figure 2. Representation of (a) all species and (b) threatened and rare-quartile species (i.e., 25% of the species with the smallest distributions) in the target group (i.e., half of the species data) for randomly chosen species indicator groups with varying numbers of threatened, endemic, range-restricted, widespread, and large-bodied species. The four bars for each of the five species groups show from left to right (exemplified with threatened species) indicator groups with no threatened species, the number of threatened species expected by chance, the addition of 50 threatened species, and the addition of 100 threatened species (see Table 1). Species representation by area networks based on random selection (upper 2.5%), fully random sets of species, and all species are shown as evaluation benchmarks. Error bars denote 95% confidence intervals about the mean. The results are derived from the species group of 150 species and 5% area.

species and by 4.0–8.4% for rare species, respectively). Increasing the proportion of widespread and large-bodied species decreased the effectiveness: 1.6–25.2% for threatened species and 2.6–22.7% for rare species, respectively.

Changing the number of distinct genera and families represented in the indicator groups had only a marginal, although statistically significant ($p < 0.05$), effect on overall effectiveness (Fig. 3). Increasing the number of distinct genera and families resulted in a slight decrease in the effectiveness of the indicator groups, whereas decreasing the number of distinct genera and families slightly increased the effectiveness. We observed a similar tendency when the representation of threatened and rare-quartile species was considered (data not shown). All indicator groups were considerably more effective in representing species than was the case following the random selection of areas.

Discussion

In agreement with previous studies (Bonn et al. 2002; Manne & Williams 2003), we found that networks of areas identified on the basis of random sets of species data

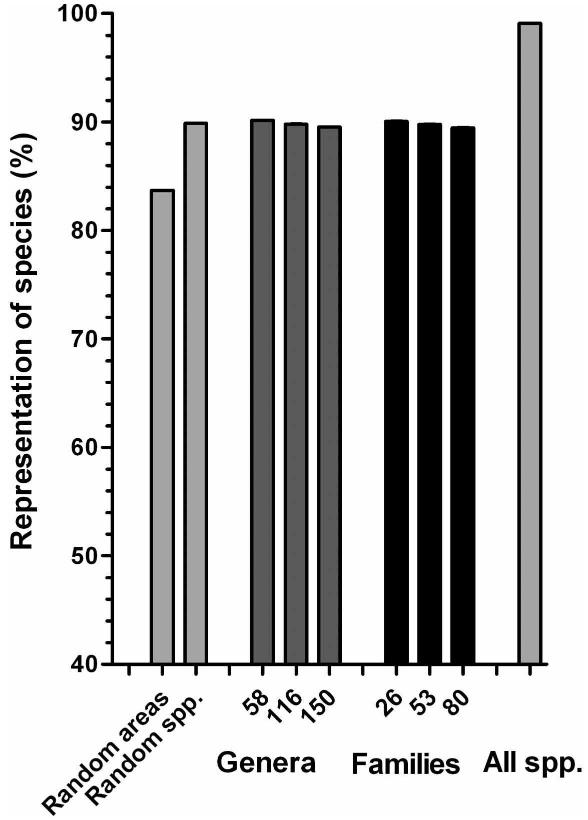

Figure 3. Representation of species in the target group (i.e., half of the species data) by randomly chosen species groups with varying degrees of taxonomic diversity. The three bars for each of the two measures of taxonomic diversity show (from left to right) the representation by randomly chosen indicator groups with 50% fewer distinct genera/families, the number of distinct genera/families as expected in random sets, and 50% more distinct genera/families. Species representations by area networks based on random selection (upper 2.5%), fully random sets of species, and all species are shown as evaluation benchmarks. Error bars denote 95% confidence intervals about the mean. The results are derived from the species group of 150 species and 5% area.

represented species considerably better than networks of areas identified on the basis of random area selection. Thus, it makes a difference whether indicator performance is evaluated against the effectiveness of area networks identified on the basis of random area selection or of random sets of species. Accordingly, Bonn et al. (2002) found that area networks identified based on the indicator groups (threatened and endemic species) better represent overall species richness than random area selection, whereas the indicator groups perform no better than a randomly chosen set of species. Similarly, Tognelli (2005) found that in general all indicator groups perform better than random area selection, whereas a single indicator group outperforms random sets of species. Many indicator studies evaluated only indicator-group performance with random area selection as a benchmark (e.g., Lund & Rahbek 2002; Lawler et al. 2003; Moore et al. 2003*a*; Warman et al. 2004). Consequently, some of the suggested indicator groups from these studies may be less effective in representing species than a random set of species; only further tests of suggested indicator groups against random sets of species (rather than solely random area selection) can reveal their effectiveness.

Rare and threatened species, in particular, have been identified as useful indicators (Lawler et al., 2003; Warman et al., 2004; Tognelli 2005). Nevertheless, these studies appraised indicator performance on target groups that comprise the remaining species in the data set (i.e., nonindicator species). We found that considerably increasing the number of threatened, endemic, and range-restricted species in an indicator group increased the effectiveness of species representation compared with the use of random sets of species. Furthermore, our results demonstrate that these species in particular appear to perform better as indicators for the representation of *other* range-restricted and threatened species. It is promising that these species, which are legitimate conservation targets in their own right, are also good indicators for other species of conservation concern. In contrast to our findings with threatened, endemic, and range-restricted species, increasing the number of large-bodied and widespread species (for which data are often commonly available for priority setting) in the indicator groups decreased effectiveness. This finding is supported by the results from other studies (e.g., Andelman & Fagan 2000; Williams et al. 2000; Moritz et al. 2001) and indicates that species with large distributions (which are often also large-bodied species; i.e., typical flagship species) perform poorly as indicator species. What may explain these observed patterns? The occurrence of range-restricted species are geographically scattered in many different parts of sub-Saharan Africa (Jetz et al. 2004). Thus, increasing the number of range-restricted species in the indicator groups probably results in more scattered reserves because the species in the indicator groups have relatively less overlap in their range sizes. In fact the range overlap, defined as the mean indicator richness among grid cells with indicators (sensu Manne & Williams 2003), was smaller ($p < 0.05$) for indicator groups with more threatened, endemic, and range-restricted species compared with randomly chosen groups. For example, randomly chosen indicator groups of 150 species had an average range overlap of 19.6 (SD = 2.1, $n = 500$), whereas considerably smaller range overlaps were found for indicator groups of 150 species with 115 threatened species (mean = 8.1, SD = 2.1, $n = 500$), 116 endemic species (mean = 5.4, SD = 1.3, $n = 500$), and 138 rare-quartile species (mean = 3.3, SD = 0.6, n = 500), respectively.

Consequently, the networks of areas likely provide a wide coverage of different habitats because the selected areas are found in various biogeographical provinces. This would likely increase the representation of species. This explanation is in accordance with the recommendation that the best set of indicator taxa will cover a turnover for a large part of environmental space (Faith & Walker 1996; Faith et al. 2004). Furthermore, not only are the occurrence of range-restricted species geographically scattered, they also tend to be clustered in the areas where they occur. That is, certain areas, often called centers of endemism, have a larger number of such species than would be expected by chance alone (Jetz et al. 2004). This co-occurrence of range-restricted species may explain the finding of increased representation of other range-restricted species when the proportion of range-restricted species in the indicator group is increased. A similar co-occurrence of range-restricted species occurs at national scales (e.g., Williams et al. 1996), which may support the generality of our findings to other regions and scales.

For a fixed indicator group size, reducing the number of widespread species, which is uninformative for area selection, will improve effectiveness simply because the number of species in the indicator group influences effectiveness (Manne & Williams 2003 and this study). Thus, reducing the proportion of uninformative widespread species will improve effectiveness as if the indicator group size were increased (because the number of informative species increases). Omitting widespread species does improve effectiveness compared with randomly chosen groups (Fig. 2), which can be ascribed to the effect of decreasing the proportion of uninformative species. Thus, an apparent explanation for the improved effectiveness caused by increasing the number of range-restricted species could simply be that it results in a decrease in the number of uninformative widespread species. Nevertheless, increasing the number of range-restricted species resulted in a greater improvement in effectiveness than omitting widespread species (Fig. 2). Consequently, increasing the number of range-restricted species improved effectiveness further than what could be attributed to the decreased number of widespread species.

Taxonomic diversity in the indicator group did not influence the effectiveness of indicator groups in any significant way. In fact we observed a slight decrease in performance when the number of distinct genera and families in the indicator groups was increased. A possible explanation for this slight decrease may be that an increase in the number of different genera or families in an indicator group resulted in a selection of species from genera and families with relatively fewer species. Species from species-poor genera and families tended to have relatively wider distributions. For example, the species belonging to genera with two or fewer species have an average range size of 392 grid cells (SD = 452, n = 522), whereas the species within genera with three or more species had an average range size of 224 grid cells (SD = 321, n = 2349).

It would have been illuminating to compare the robustness of our findings with assessment criteria that take persistence into account to a higher degree (e.g., by setting different representation targets for the various species depending on their area requirements or incorporating threat). Nevertheless, because of the high number of species we considered and a generally poor understanding of the requirements for the majority of the species, we only assessed the effectiveness of the indicators in representing the target species as many times as possible within a given area.

Furthermore, because our study was restricted to terrestrial vertebrates the results may not be similar for nonterrestrial and nonvertebrate taxa or at other spatial scales. Nonetheless, the analyses are based on an extensive data set of almost 2900 species on a continent-wide scale and reveal some insights into factors that influence the effectiveness of indicator groups. Randomly selected indicator groups performed considerably better than random area selection. Thus, it is tempting to suggest that the methodical selection of indicator groups may be replaced with a random sample of the species as indicator group. Indeed, an optimal data set derived from a random representative subset of species may be effective for the selection of area networks. Nevertheless, the data available for priority setting will seldom constitute a representative sample because data are biased toward specific species groups, especially groups with high public interest (e.g., birds and butterflies). Thus, the more well-known and widespread species will probably be overrepresented. Moreover, in the context of practical conservation, a more relevant approach probably would be to use all available species data for priority setting, rather than restricting the selection to a subset of the available species. Nevertheless, not all species data within a region will be of sufficient quality to be included in a complementarity-based selection of area networks because such an analysis requires a complete knowledge of the species' distribution, which is particularly important for the most range-restricted species because they have a large influence on area selection (Rodrigues & Gaston 2002).

Thus, the implementation of our approach will necessitate the preparation of species data of suitable quality and possibly the allocation of additional resources for the acquisition of new data for species that are either of special conservation concern or believed to be good indicators. Our results give an indication of the groups of species that should be included in the existing pool of available species data of sufficient quality for priority setting. Although we expect that a representative sample of species (unbiased toward species with well-known distributions) will perform fairly well, the inclusion of data on threatened, endemic (defined as very small range), and other range-restricted species is highly recommended. Finally, our results show that if well-known species (large bodied and widespread) make up a large share of the species data set, it is particularly important to include more threatened, endemic, and range-restricted species in the indicator groups. Because species-distribution data are scarce and environmental data are widely available (Turner et al. 2003), the best strategy in many cases probably will be to make the best possible use of both types of data. One strategy for this is the environmental diversity framework that combines environmental and available species data to reflect compositional turnover (Faith & Walker 1996; Ferrier 2002; Faith et al. 2004).

Our results show that careful selection of indicator species can improve the effectiveness of indicator groups, particularly for species of special conservation concern. Although indicator groups should not be perceived as the ultimate tool for biodiversity conservation, they still constitute an important resource for conservation in a world facing rapid biodiversity loss, scant resources for conservation, and limited knowledge of biodiversity.

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