

# Indicator taxa revisited: useful for conservation planning?

Frank Wugt Larsen<sup>1,3\*</sup>, Jesper Bladt<sup>2</sup> and Carsten Rahbek<sup>1</sup>

<sup>1</sup>Center for Macroecology and Evolution, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen O, Denmark, <sup>2</sup>Institute of Biological Sciences, University of Aarhus, Ny Munkegade, building 1540, 8000 Aarhus C, Denmark, <sup>3</sup>Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK

# ABSTRACT

**Aim** Indicators for biodiversity are needed to facilitate the identification of complementary reserve networks for biodiversity conservation. One widely adopted approach is to use indicator taxa, i.e. a single taxon such as birds or butterflies, despite the ongoing debate regarding their usefulness as indicators of broader biodiversity. Here we assess several aspects, such as influence of species number, of indicator taxa for three extensive data sets to improve our insight into the effectiveness of indicator taxa.

Location Denmark, sub-Saharan Africa and Uganda.

**Methods** First, we investigate to what extent variation in species number between indicator taxa (e.g. 488 mammal spp. vs. 210 snake spp.) is causing the differences in effectiveness between indicator taxa. Second, we investigate whether indicator taxa are capable of outperforming indicator groups composed of random sets of species chosen among all taxa. Finally, we assess the correlation of specific properties such as mean range size of the indicator taxa to their effectiveness. We investigate these aspects of the effectiveness of indicator taxa through the separate analysis of three distinct distributional species data sets: sub-Saharan Africa (4,039 spp.), Denmark (847 spp.) and Uganda (2,822 spp.).

**Results** We overall found that indicator taxa comprising a greater number of species tend to perform better than indicator taxa with fewer species (e.g. 488 mammal spp. outperform 210 snake spp.), although there are some exceptions. Second, we found most indicator taxa to perform worse than indicator groups consisting of a comparable number of species selected among all taxa. Finally, the effectiveness of indicator taxa was seen to correlate poorly with selected distributional properties such as mean range size of the indicator taxa, suggesting that it is difficult to predict which taxa are efficient biodiversity indicators.

**Main conclusions** Overall, these findings might suggest that focus should simply be on increasing the number of species among all taxa as basis for priority setting, rather than striving to obtain the 'perfect' indicator taxa.

### **Keywords**

Biodiversity indicators, complementary networks, conservation planning, indicator taxa.

\*Correspondence: Frank Wugt Larsen, Center for Applied Biodiversity Science, Conservation International, 2011 Crystal Drive Suite 500, Arlington, VA 22202, USA. Tel.: +1 703 341 2754; E-mail: fwlarsen@bio.ku.dk

# INTRODUCTION

The existing reserve network is far from adequate for biodiversity conservation, and new reserves need to be added to achieve better representation of species (De Klerk *et al.*, 2004; Fjeldså *et al.*, 2004; Rodrigues *et al.*, 2004). The selection of reserve networks capable of protecting biodiversity in an effective manner

(surrogates) to characterize biodiversity as a whole because our knowledge of biodiversity is inadequate. Here, our understanding of the effectiveness of various indicators is still inadequate. It is debated what data constitute the most appropriate surrogate units to use for priority setting (Brooks *et al.*, 2004a,b; Cowling *et al.*, 2004; Pressey, 2004; Hortal & Lobo, 2006) whether it be, e.g. land classes (Lombard *et al.*, 2003), measurement of environmental diversity (Araújo *et al.*, 2004; Faith *et al.*, 2004), modelled species turnover (Ferrier & Guisan, 2006) and/or species distribution data (Brooks *et al.*, 2004a,b).

Thus, conservation planners face a difficult task in choosing biodiversity indicators for reserve selection. Taxonomically welldefined and easily monitored taxa have been used as indicators to guide the identification of important areas for biodiversity conservation (e.g. Stattersfield et al., 1998; Myers et al., 2000). Many researchers have assessed the performance of taxonomically defined indicator groups, i.e. groups composed of species from a single taxon such as birds, butterflies, etc. (hereafter referred to as indicator taxa) (e.g. Prendergast et al., 1993; Howard et al., 1998; Moritz et al., 2001; Lund & Rahbek, 2002; Moore et al., 2003; Araújo et al., 2004; Juutinen & Mönkkönen, 2004; Kati et al., 2004; Saetersdal et al., 2004; Warman et al., 2004a; Grenyer et al., 2006; Hess et al., 2006; Lamoreux et al., 2006; Williams et al., 2006) providing mixed findings. For example, birds are reported to perform both relatively well (e.g. Howard et al., 1998; Juutinen & Mönkkönen, 2004) and relatively poor (e.g. Lund & Rahbek, 2002; Moore et al., 2003; Williams et al., 2006).

These apparently contradictory findings might arise due to variation in taxonomic coverage, biogeographical realms and/or spatial scale among the different studies. For example, spatial scale in terms of grain size has been shown to influence the perception of richness patterns (Rahbek & Graves, 2001; Rahbek, 2005), area selection for conservation (Larsen & Rahbek, 2003; Warman *et al.*, 2004b) and consequently also the performance of indicators (Larsen & Rahbek, 2005; Hess *et al.*, 2006).

Furthermore, specific methodological issues concerning the evaluation of the effectiveness of indicator taxa may contribute to the lack of clarity, and addressing these issues may improve our insight into the effectiveness of various indicator taxa. First, no study evaluating the performance of indicator taxa has explicitly controlled the effect caused by the number of species in each taxon (e.g. Lawler et al., 2003; Moore et al., 2003; Kati et al., 2004; Warman et al., 2004a), although the number of species strongly influences effectiveness of indicator groups (Manne & Williams, 2003; Larsen et al., 2007). Consequently, if for example 300 birds perform better as an indicator group than 50 mammals, it might simply be caused by differences in species number between the two indicator taxa, rather than because one taxon has better indicator properties per se. Second, most indicator taxa studies relate the effectiveness of the resulting area networks to the effectiveness of area networks selected by chance (e.g. Howard et al., 1998; Lawler et al., 2003; Moore et al., 2003), but provide no comparison with area networks identified on the basis of a comparable number of randomly chosen species selected among all taxa (but see Gladstone, 2002). This is unfortunate as this information could provide further insight into the usefulness of focusing on a single taxon when using groups of species to guide conservation planning.

In this study, we evaluate the effectiveness of indicator taxa in identifying priority areas for conservation by analysing distributional species data sets from three geographical domains: sub-Saharan Africa, Denmark and Uganda. First, we investigate the effect of species number in the indicator taxa by controlling both area and the species number by using taxonomic indicator groups consisting of an equal number of species. Second, we compare the effectiveness of the indicator taxa with the effectiveness of a comparable number of species chosen randomly among all taxa. Finally, we assess the correlation of specific properties such as mean range size of the indicator taxa to their effectiveness, in order to elucidate potential explanations causing the differences in effectiveness between different indicator taxa.

# METHODS

# **Species data**

We used three data sets on species distributions.

# Sub-Saharan Africa

This data set covers the distribution of 4074 vertebrate species across mainland sub-Saharan Africa at a spatial resolution of 1° latitude-longitude grid cells (~105 × 105 km; n = 1922). The data set includes 1084 mammals, 1789 breeding birds, 734 frogs and 467 snakes. For mapping methodology see Burgess *et al.* (1998) and Brooks *et al.* (2001). Previous versions of this data set have been used in several studies (e.g. Balmford *et al.*, 2001; Burgess *et al.*, 2002; Moore *et al.*, 2003).

# Denmark

This data set covers the Danish distribution of 847 terrestrial species compiled for 10 km Universal Transverse Mercator quadrates (n = 622). The data set included 19 species of amphibians/reptiles, 189 species of birds, 252 species of hoverflies, 60 species of butterflies, 156 species of large moths, 63 species of true bugs, 26 species of grasshoppers, 41 species of dragonflies and 41 species of orchids. This data set is used by J. Bladt *et al.* (submitted), and an earlier version of the data set has been used by Lund & Rahbek (2002).

# Uganda

This data set covers the distribution of 2822 species in 64 Ugandan forest sites of varying area (mean = 191 km<sup>2</sup>, SD = 230 km<sup>2</sup>) (Howard *et al.*, 2000). The data set includes 87 small mammals, 198 large moths, 962 woody plants, 736 butterflies and 839 birds. Previous versions of the data set have been used by Howard *et al.* (1998) and Howard *et al.* (2000).

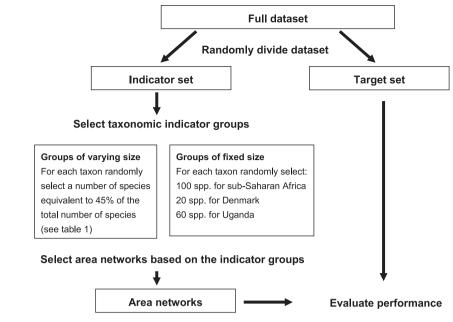


Figure 1 A schematic view of the overall procedure for the analyses.

#### Selection of taxonomic indicator groups

Indicator groups are often evaluated for their effectiveness in representing all of the species that are not included in the indicator group, i.e. nonindicator species (e.g. Lund & Rahbek, 2002; Lawler *et al.*, 2003; Moore *et al.*, 2003; Warman *et al.*, 2004a), and as a result the target group varies with each indicator group. This test approach could substantially influence the conclusions regarding indicator properties as good indicator properties may be a function of the target group, not the indicator group (see Larsen *et al.*, 2007; J. Bladt *et al.* submitted). Therefore, we implemented a test approach whereby the data sets were randomly divided into an indicator set from which the indicator group was drawn, and a target set, which constituted the target group (Larsen *et al.*, 2007; J. Bladt *et al.* submitted).

The overall procedure for the analysis was as follows (see also Fig. 1). From the indicator set, we randomly selected a certain number of species from one distinct taxon such as birds as the taxonomic indicator group. Each taxonomic indicator group was subsequently used to select an area network, which was assessed for its effectiveness in representing all the species in the target set at least one time. This procedure was repeated 500 times for each taxon to ensure representative samples of both possible taxonomic indicator groups as well as area networks. For each repetition, the species in the full data set was randomly divided into the indicator set and the target set, i.e. 500 unique random divisions for each taxonomic indicator group (e.g. 100 mammal spp.).

To account for the effect of species number, we selected indicator groups with both a varying and fixed number of species between the different taxa (See Table 1). Firstly, we selected indicator groups in which the number of species differed between taxa (e.g. 210 snakes spp., 330 frog spp.) to reflect the differences in species richness between taxa. As the indicator group size, we selected a number of species proportional to the species richness of the various taxa. For each taxon we arbitrarily chose 45% of the total species richness in the taxon as the indicator group size (e.g. 45% of the species richness of snakes (467 spp.) gives an indicator group size of 210 spp., see Table 1). This procedure of selecting 45% of the species richness as the group size ensures that sufficient species from the respective taxa would be included in the indicator set (a random division of the full data set would on average only result in indicator sets 50% of the species in a taxon). Thus, this variation in the number of species among the indicator groups for different taxa is similar to most other indicator taxa studies (e.g. Howard et al., 1998; Lund & Rahbek, 2002; Lawler et al., 2003; Moore et al., 2003). Secondly, we also selected taxonomic indicator groups containing an equal number of species between taxa. We chose 100 spp. from each taxon for sub-Saharan Africa, 20 spp. from each taxon for Denmark, and 60 spp. from each taxon for Uganda. These numbers reflect a trade off between the inclusion of as many taxa as possible in the analysis, and the attainment of reasonably large group sizes. As a consequence, reptiles/amphibians and grasshoppers in the Danish data set, and small mammals in the Ugandan data set contained too few species to permit their inclusion in this analysis (see Table 1).

#### Area network selection

The taxonomic indicator groups were subsequently used to select reserve networks that maximized representation of the species in the indicator groups (maximal covering sets (Church *et al.*, 1996)), i.e. the selection of areas that complement one another in terms of species representation (Vane-Wright *et al.*, 1991). The area selection was optimized using the C-PLEX integer linear programming software for resource optimization (ILOG, 2006). The data sets for sub-Saharan Africa and Denmark were compiled for grid cells (1° latitudinal-longitudinal and 10 km grid cells, respectively) covering the entire continent/country, and for these data sets we selected 5% of the total number of grid cells as

Data set	Taxa	Number of species	Indicator group size (varying)	Indicator group size (fixed)
Sub-Saharan	Snakes	467	210	100
Africa	Frogs	734	330	100
	Mammals	1084	488	100
	Birds	1789	805	100
Denmark	Reptiles/amphibians	19	9	None
	Grasshoppers	26	12	None
	Orchids	41	18	20
	Dragonflies	41	18	20
	Butterflies	60	27	20
	True bugs	63	28	20
	Large moths	156	70	20
	Birds	189	85	20
	Hoverflies	252	113	20
Uganda	Small mammals	87	39	None
	Large moths	198	89	60
	Butterflies	736	331	60
	Birds	839	378	60
	Woody plants	962	433	60

 Table 1 The number of species in the taxonomic indicator groups of varying and fixed group size.

reserve networks (mid scenario in Larsen *et al.*, 2007). As the Ugandan data set covered 64 forest sites of varying area, we selected 20% of the total area rather than selecting a fixed number of sites (following Howard *et al.*, 1998).

# Taxonomic indicator group evaluation

The selected area networks were evaluated for their effectiveness in representing both all the species and the restricted-range species in the target sets (i.e. the remaining half of the species in the data sets). We focused primarily on the representation of restrictedrange species, defined as the lower quartile of the range distribution of each taxonomic group, because species with limited geographical range sizes are more prone to extinction and are consequently of greater conservation interest (e.g. Purvis *et al.*, 2000). This relative, rather than absolute, definition of restricted-range species ensures that the pool of restricted-range species is composed of species from all taxa rather than exclusively from the taxa with relatively smaller geographical range sizes.

To evaluate the performance of the taxonomic indicator groups, we compared their effectiveness with:

Area networks selected randomly (1000 times), which gives an estimate of the effectiveness of area networks selected by chance.
 Area networks selected on the basis of indicator groups comprising a comparable number of species randomly chosen (500 times) among all taxa.

**3** Area networks selected on the basis of all species in the target set, which gives a measure of the maximal representation possible in networks of the given area.

**Table 2** Spearman correlation coefficients for the effectiveness in representing restricted range species and various indicator group properties for the taxonomic indicator groups of 100 species for sub-Saharan Africa ( $n = 2000^*$ ), 20 species for Denmark (n = 3500), and 60 species for Uganda (n = 2000). Asterisks indicate statistical significance (\* $P \le 0.05$ ).

Indicator group properties	Africa	Denmark	Uganda
No. of restricted-range spp.	0.52*	-0.04*	0.03
No. of very restricted-range spp.	0.42*	-0.11*	0.11*
No. of widespread spp.	$-0.48^{*}$	$-0.18^{*}$	$-0.14^{*}$
Mean range size of spp.	-0.38*	-0.11*	-0.18*
Range overlap	-0.39*	-0.08*	-0.10*

\**n* = 2000 is the sum of 500 indicator groups of 100 mammal spp., 100 bird spp., 100 frog spp. and 100 snake spp., respectively.

We carried out standard ANOVA to determine the level of statistical significance of the differences in effectiveness between all the different indicator groups.

# Influence of indicator group properties

In an attempt to explain differences in effectiveness between taxa, we measured the following properties of each indicator group from the taxonomic indicator groups of equal size:

**1** number of restricted-range species (i.e. the 25% of the species with smallest distributions)

**2** number of very restricted-range species (i.e. species occurring in less than 6 cells)

**3** number of widespread species (i.e. the 25% of species with the largest distribution amongst all taxa)

4 mean range size of the species, and

5 range overlap between the species (measured as the mean indicator richness among grid cells with indicators (Manne & Williams, 2003).

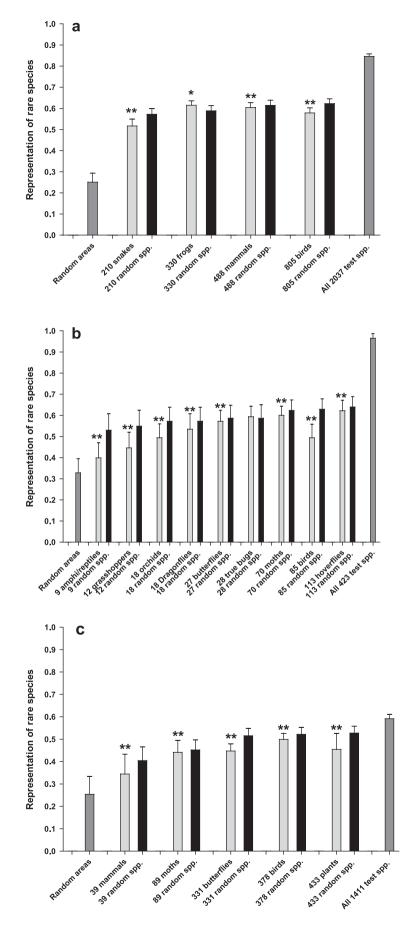
For the 500 indicator groups from each indicator group setting (i.e. 100 sub-Saharan African mammals) we calculated Spearman rank correlation coefficients between effectiveness in representing species and indicator group properties for sub-Saharan Africa, Denmark and Uganda (Table 2).

The procedures for the selection and evaluation of indicator groups were implemented in Java using the Java 2 Platform (Enterprise Edition Technology, version 1.4, Sun Microsystems, USA).

# RESULTS

# Taxonomic indicator groups with varying numbers of species

When the number of species in the indicator groups varied between taxa, the effectiveness of the selected area networks in representing species tended to perform better for taxa with more species (Fig. 2, see Fig. 1. in Appendix S1 in Supplementary Material for representation of all species), although there were



**Figure 2** The representation of restricted-range species in the target set (i.e. half of the species) by area networks identified based on taxonomic indicator groups of varying size for (a) sub-Saharan Africa (b) Denmark and (c) Uganda. For comparative purposes, the representation of species is shown for area networks selected (1) randomly (2) based on the same number of randomly chosen species among all taxa, and (3) based on all species in the target set. Error bars denote standard deviations, and asterisks indicate taxa that perform significantly better (\*) or worse (\*\*) than the respective multitaxa random set of species ( $P \le 0.05$ ).

exceptions. For Denmark, taxa with a higher number of species performed significantly better in representing all species, including rare species, than taxa with fewer species – moths and birds are exceptions to this pattern (Fig. 2b). For Uganda, speciose taxa performed significantly better in representing all species, except plants (see Appendix S1), whereas both plants and butterflies constitute exceptions when the representation of rare species was considered (Fig. 2c). For sub-Saharan African, taxa with a higher number of species performed significantly better in representing all species, except birds (see Appendix S1), but not when the representation of rare species was considered (Fig. 2a).

Most of the taxonomic indicator groups (composed of randomly chosen species within the taxon) performed poorly compared to indicator groups consisting of a comparable number of species chosen randomly among all taxa (Fig. 2). Of the 18 taxonomic indicator groups, 16 groups performed significantly worse than multitaxa random sets of species, and only one group performed significantly better (Fig. 2). Similar results were obtained for the representation of all species (see Appendix S1). The multitaxa random sets of species consistently increase in effectiveness correlating with increasing species number.

All taxonomic indicator groups were more effective than area networks selected by chance, and less effective than area networks based on all species in the target group (i.e. best possible solution; Fig. 2).

# Taxonomic indicator groups with an equal number of species

Differences in effectiveness between the various indicator taxa are still apparent when keeping the number of species in the indicator groups constant (Fig. 3). Here we found that 8 of 15 taxonomic indicator groups performed significantly worse in representing restricted-range species than multitaxa random sets of species (Fig. 3). Only two taxonomic groups, frogs of sub-Saharan Africa and birds of Uganda, performed significantly better (Fig. 3).

All of the taxonomic indicator groups were more effective in representing restricted-range species than randomly selected area networks, and less effective than area networks based on all species in the target groups (Fig. 3).

### Indicator group properties and effectiveness

The selected properties of the taxonomic indicator groups exhibited a limited degree of correlation with the effectiveness of the indicator groups in representing restricted-range species (Table 2). For sub-Saharan Africa, the effectiveness in representing restricted-range species was positively correlated with the number of restricted-range species ( $r_s = 0.52$ ) and very restricted-range species ( $r_s = 0.42$ ) in the taxonomic indicator groups, and negatively correlated with the number of widespread species ( $r_s = -0.48$ ), the range overlap ( $r_s = -0.39$ ) and mean range size of the species in the indicator groups ( $r_s = -0.38$ ) (Table 2). For Denmark and Uganda, the correlations were overall very weak ( $r_s < 0.18$ ) (Table 2).

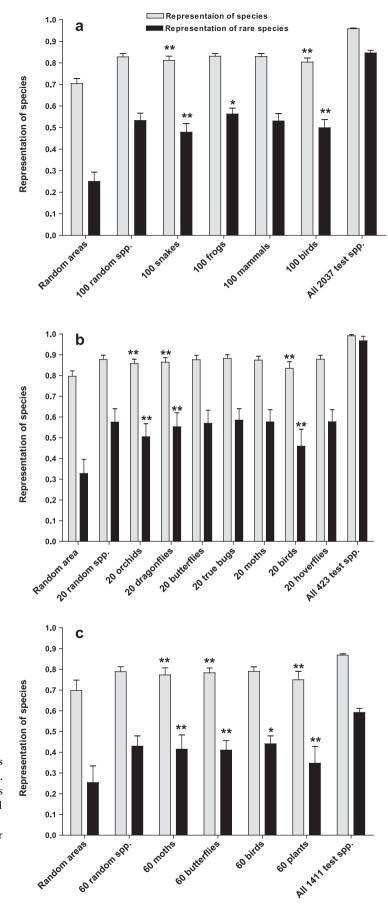
# DISCUSSION

## Species number matter

Our findings suggest that some of the taxa previously highlighted in the scientific literature as good biodiversity indicators might be so merely because they have outperformed other taxa because of the taxonomic group being more speciose than other groups, rather than because the taxa have good indicator properties per se. Most studies assessed the indicator effectiveness in terms of the representation of other taxa by the area network chosen, based on the indicator taxon (e.g. Lund & Rahbek, 2002; Moore et al., 2003; Kati et al., 2004; Warman et al., 2004a). Several studies used the indicator taxa to select minimum sets (e.g. Kati et al., 2004) where differences in effectiveness between taxa could merely reflect differences in size of the selected network of reserves (e.g. groups with many species may result in larger minimum sets), rather than in differences in indicator properties per se. In this study we assessed whether taxa with greater numbers of species tend to outperform indicator taxa with smaller numbers of species when the size of the selected network of reserves is controlled for (Fig. 2). Ultimately, the performance of indicator groups will depend on the patterns of complementarity between biota (e.g. Williams et al., 2006), i.e. the relationship between the distributional pattern of the indicator species and the distributional pattern of the species to be indicated. Therefore, all other factors being equal, the mere addition of unique distributional information for a species, i.e. more species, will provide a better representative sample of overall biodiversity, and therewith better indicator properties. Therefore, the number of species in indicator groups chosen randomly among all species also strongly influences the effectiveness of indicator groups (Manne & Williams, 2003; Larsen et al., 2007). Our results suggest that the number of species to some extent also influences the relative performance among indicator taxa, although there are exceptions to this pattern. Thus, it appears as the influence of species number on indicator taxa performance is complicated by characteristics of the specific taxa. For example, will widespread species contribute with little or no guidance in area selection because of their large geographical distributions (e.g. Gaston & Rodrigues, 2003; Larsen et al., 2007). Thus, the number of limited-distribution species in the indicator taxa is probably more important in determining the effectiveness than the actual number of species, including widespread species. Consequently, if species-rich taxa contain many widespread species, the taxa may perform worse than expected from the relatively high species richness. For example, this might explain why birds for sub-Saharan Africa (Fig. 2a) and Denmark (Fig. 2b) performed relatively poorly, despite their large numbers of species (see also Lund & Rahbek, 2002; Moore et al., 2003).

# What makes some taxa better than others?

Although species number appears to influence effectiveness between indicator taxa to some extent, differences in effectiveness between taxa are still apparent when controlling for species number (Fig. 3). Is it possible, on the basis of our findings, to



restricted-range species in the target set (i.e. half of the species) by area networks identified based on taxonomic indicator groups consisting of an equal number of species for (a) sub-Saharan Africa (b) Denmark, and (c) Uganda. For comparative purposes, the representation of species is shown for area networks selected (1) randomly (2) based on the same number of randomly chosen species among

Figure 3 The representation of all species and

all taxa, and (3) based on all species in the target set. Error bars denote standard deviations, and asterisks indicate taxa that perform significantly better (\*) or worse (\*\*) than the respective multitaxa random set of species ( $P \le 0.05$ ).

explain why some taxa perform better than others? A few studies have previously assessed factors influencing indicator group effectiveness, and found that factors such as smaller range size tend to improve the effectiveness of indicator groups (Manne & Williams, 2003; Larsen et al., 2007; J. Bladt et al. submitted). However, these studies assessed randomly chosen indicator groups, which were not restricted to species from a single taxon. In this study, using indicator groups of species from a single taxon, we assessed the influence of a number of these factors, such as small range size, that are capable of influencing the effectiveness of taxonomically diverse indicator groups (Manne & Williams, 2003; Larsen et al., 2007), but these appear to be limited in their ability to explain the effectiveness of the indicator taxa (Table 2). The correlation of the measured indicator properties to the effectiveness of the indicator taxa was generally weak and varied (sometimes contradictory) between the taxonomic indicator groups for Denmark and Uganda, but showed some correlation for sub-Saharan Africa (Table 2). It is difficult to explain why only the sub-Saharan African data set shows some pattern, but it might be because of the greater spatial extent of the African template, which increases the overall heterogeneity within the domain compared to the smaller template of Denmark and Uganda. Nevertheless, no general patterns are evident from our results, suggesting that it is difficult to predict what taxa would be most suitable to use as indicator group to guide conservation planning.

For both taxonomic indicator group scenarios (Figs 2 and 3), the taxonomic indicator groups generally performed more effectively than areas selected by chance, supporting the results from several previous studies (e.g. Howard et al., 1998; Lund & Rahbek, 2002; Lawler et al., 2003; Moore et al., 2003). However, indicator taxa occasionally perform worse than expected by chance (e.g. Araújo et al., 2004). Another important finding of this study is that multitaxa random sets of species generally perform more effectively than most taxonomic indicator groups. This observation was valid for both taxonomic indicator groups of variable size (Fig. 2) as well as for those based on an equal number of species (Fig. 3). These results suggests that focus on a single taxon as indicator may result in reserve networks that are less effective in capturing other species than when multiple taxa are used as indicators. This finding is particularly significant because it is often preferable to select a single taxon as indicator for pragmatic reasons such as data availability and local taxonomic expertise.

### Implications

Our analysis evaluates the effectiveness of indicator taxa in representing species diversity (as our measure of biodiversity), and thus does not incorporate other factors important for the persistence of biodiversity, such as the viability of populations, threatening processes, etc. However, this is the result of limited state of knowledge on the majority of the species in our three extensive data sets, and other factors could potentially be included if data were to become available. Notwithstanding this caveat, our study based on analysis on three separate data sets revealed that (1) indicator taxa with a greater number of species to some extent perform better than indicator taxa consisting of fewer species; (2) most indicator taxa are outperformed by random sets of a comparable number of species selected among all taxa; and (3) it is difficult to predict which taxa have the potential to be efficient indicators of biodiversity. Overall, these findings suggest that increasing the number of species (excluding widespread species) from various taxa may be more relevant for the efficient management of conservation planning than the attainment of the 'right' indicator taxa.

Finally, it should be remembered that efficient conservation planning will require that the 'implementation crisis' of conservation planning can be overcome (Knight *et al.*, 2006). Thus, although science-based knowledge on the ability of indicators (surrogates) to characterize biodiversity is still needed, it is urgently important also to address the research impediment on solving the 'implementation crisis' in conservation planning (Knight *et al.*, 2006).

### ACKNOWLEDGEMENTS

We thank the Natural History Museum of Denmark for providing access to the sub-Saharan African data, and L. A. Hansen for his extensive assistance with respect to these data. We thank the many people who kindly provided the sub-Saharan African data and supported the development of the data bases (listed in Burgess et al., 2002). We thank A. H. Petersen for help with the Danish data, and following persons for providing data: K. Fog (reptiles and amphibians), M. Grell and the Danish Ornithological Society (birds), S. Tolsgaard (true bugs), S. Kaaber (moths), M. Stolze (butterflies), M. Holmen (dragon flies) and E. Torp and R. Bygebjerg (hoverflies). We thank the following persons for updating data: J. F. Rasmussen (dragonflies), P. S. Nielsen (butterflies), O. F. Nielsen (grasshoppers), and A. Tøttrup (birds). We thank the people who collected the Uganda data (see Howard et al., 2000). We thank A. Balmford for valuable discussions of the results, and A. Rodrigues & J. Hortal for valuable comments on the manuscript. J.B. and F.W.L. both acknowledge the International Ph.D. School of Biodiversity Sciences (ISOBIS) for financial support. F.W.L. acknowledges a grant from the Danish Research Council (272-07-0411). J.B. acknowledges the Department of Wildlife Ecology and Biodiversity, National Environmental Research Institute of Denmark for financial support. C.R. acknowledge support by the Danish National Science Foundation grant J. no. 21-03-0221.

# REFERENCES

- Araújo, M.B., Densham, P.J. & Williams, P.H. (2004) Representing species in reserves from patterns of assemblage diversity. *Journal* of *Biogeography*, **31**, 1037–1050.
- Balmford, A., Moore, J.L., Brooks, T., Burgess, N., Hansen, L.A., Williams, P. & Rahbek, C. (2001) Conservation conflicts across Africa. *Science*, **291**, 2616–2619.
- Brooks, T., Balmford, A., Burgess, N., Fjeldsa, J., Hansen, L.A., Moore, J., Rahbek, C. & Williams, P. (2001) Toward a blueprint for conservation in Africa. *Bioscience*, **51**, 613–624.

Brooks, T., da Fonseca, G.A.B. & Rodrigues, A.S.L. (2004a) Protected areas and species. *Conservation Biology*, 18, 616–618.

Brooks, T., da Fonseca, G.A.B. & Rodrigues, A.S.L. (2004b) Species, data and conservation planning. *Conservation Biology*, **18**, 1682–1688.

Burgess, N., Fjeldså, J. & Rahbek, C. (1998) Mapping the distributions of Afrotropical vertebrate groups. Species, 30, 16–17.

Burgess, N.D., Rahbek, C., Larsen, F.W., Williams, P. & Balmford, A. (2002) How much of the vertebrate diversity of sub-Saharan Africa is catered for by recent conservation proposals? *Biological Conservation*, **107**, 327–339.

Church, R.L., Stoms, D.M. & Davis, F.W. (1996) Reserve selection as a maximal covering location problem. *Biological Conservation*, **76**, 105–112.

Cowling, R.M., Knight, A.T., Faith, D.P., Ferrier, S., Lombard, A.T., Driver, A., Rouget, M., Maze, K. & Desmet, P.G. (2004) Nature conservation requires more than a passion for species. *Conservation Biology*, **18**, 1674–1676.

De Klerk, H.M., Fjeldsa, J., Blyth, S. & Burgess, N.D. (2004) Gaps in the protected area network for threatened Afrotropical birds. *Biological Conservation*, **117**, 529–537.

Faith, D.P., Ferrier, S. & Walker, P.A. (2004) The ED strategy: how species-level surrogates indicate general biodiversity patterns through an 'environmental diversity' perspective. *Journal of Biogeography*, **31**, 1207–1217.

Ferrier, S. & Guisan, A. (2006) Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, **43**, 393–404.

Fjeldså, J., Burgess, N.D., Blyth, S. & De Klerk, H.M. (2004) Where are the major gaps in the reserve network for Africa's mammals? *Oryx*, **38**, 17–25.

Gaston, K.J. & Rodrigues, A.S.L. (2003) Reserve selection in regions with poor biological data. *Conservation Biology*, 17, 188–195.

Gladstone, W. (2002) The potential value of indicator groups in the selection of marine reserves. *Biological Conservation*, **104**, 211–220.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature*, 444, 93–96.

Hess, G.R., Bartel, R.A., Leidner, A.K., Rosenfeld, M.K., Rubino, M.J., Snider, S.B. & Ricketts, T.H. (2006) Effectiveness of biodiversity indicators varies with extent, grain and region. *Biological Conservation*, **132**, 448–457.

Hortal, J. & Lobo, J.M. (2006) Towards a synecological framework for systematic conservation planning. *Biodiversity Informatics*, 3, 16–45.

Howard, P.C., Davenport, T.R.B., Kigenyi, F.W., Viskanic, P., Baltzer, M.C., Dickinson, C.J., Lwanga, J., Matthews, R.A. & Mupada, E. (2000) Protected area planning in the tropics: Uganda's national system of forest nature reserves. *Conservation Biology*, 14, 858–875.

Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A. &  Balmford, A. (1998) Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature*, **394**, 472–475.
 ILOG (2006) *CPLEX 10.0*. ILOG, Gentilly, France.

Juutinen, A. & Mönkkönen, M. (2004) Testing alternative indicators for biodiversity conservation in old-growth boreal forests: ecology and economics. *Ecological Economics*, **50**, 35–48.

Kati, V., Devillers, P., Dufrene, M., Legakis, A., Vokou, D. & Lebrun, P. (2004) Testing the value of six taxonomic groups as biodiversity indicators at a local scale. *Conservation Biology*, 18, 667–675.

Knight, A.T., Cowling, R.M. & Campbell, B.M. (2006) Planning for implementation: an operational model for implementing conservation action. *Conservation Biology*, **20**, 549–561.

Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W. & Shugart, H.H. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature*, **440**, 212–214.

Larsen, F.W. & Rahbek, C. (2003) Influence of scale on conservation priority setting – a test on African mammals. *Biodiversity and Conservation*, **12**, 599–614.

Larsen, F.W. & Rahbek, C. (2005) The influence of spatial grain size on the suitability of the higher-taxon approach in continental priority-setting. *Animal Conservation*, **8**, 389–396.

Larsen, F.W., Bladt, J. & Rahbek, C. (2007) Improving the performance of indicator groups for the identification of important areas for species conservation. *Conservation Biology*, 21, 731–740.

Lawler, J.J., White, D., Sifneos, J.C. & Master, L.L. (2003) Rare species and the use of indicator groups for conservation planning. *Conservation Biology*, **17**, 875–882.

Lombard, A.T., Cowling, R.M., Pressey, R.L. & Rebelo, A.G. (2003) Effectiveness of land classes as surrogates for species in conservation planning for the Cape Floristic Region. *Biological Conservation*, **112**, 45–62.

Lund, M.P. & Rahbek, C. (2002) Cross-taxon congruence in complementarity and conservation of temperate biodiversity. *Animal Conservation*, 5, 163–171.

Manne, L.L. & Williams, P.H. (2003) Building indicator groups based on species characteristics can improve conservation planning. *Animal Conservation*, **6**, 291–297.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Moore, J.L., Balmford, A., Brooks, T., Burgess, N.D., Hansen, L.A., Rahbek, C. & Williams, P.H. (2003) Performance of Sub-Saharan vertebrates as indicator groups for identifying priority areas for conservation. *Conservation Biology*, **17**, 207–218.

Moritz, C., Richardson, K.S., Ferrier, S., Monteith, G.B., Stanisic, J., Williams, S.E. & Whiffin, T. (2001) Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings* of the Royal Society B: Biological Sciences, 268, 1875–1881.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C.& Gibbons, D.W. (1993) Rare species, the coincidence of

diversity hotspots and conservation strategies. *Nature*, **365**, 335–337.

- Pressey, R.L. (2004) Conservation planning and biodiversity: assembling the best data for the job. *Conservation Biology*, **18**, 1677–1681.
- Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of* the Royal Society B: Biological Sciences, 267, 1947–1952.
- Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224– 239.
- Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA*, **98**, 4534–4539.
- Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J. & Yan, X. (2004) Effectiveness of the global protected area network in representing species diversity. *Nature*, 428, 640–643.
- Saetersdal, M., Gjerde, I., Blom, H.H., Ihlen, P.G., Myrseth, E.W., Pommeresche, R., Skartveit, J., Solhoy, T. & Aas, O. (2004) Vascular plants as a surrogate species group in complementary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. *Biological Conservation*, **115**, 21–31.
- Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. (1998) Endemic bird areas of the world: priorities for biodiversity conservation. BirdLife, Cambridge, UK.
- Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect? Systematics and the agony of choice. *Biological Conservation*, **55**, 235–254.
- Warman, L.D., Forsyth, D.M., Sinclair, A.R.E., Freemark, K., Moore, H.D., Barrett, T.W., Pressey, R.L. & White, D. (2004a)

Species distributions, surrogacy, and important conservation regions in Canada. *Ecology Letters*, **7**, 374–379.

- Warman, L.D., Sinclair, A.R.E., Scudder, G.G.E., Klinkenberg, B.
  & Pressey, R.L. (2004b) Sensitivity of systematic reserve selection to decisions about scale, biological data, and targets: case study from Southern British Columbia. *Conservation Biology*, 18, 655–666.
- Williams, P., Faith, D., Manne, L., Sechrest, W. & Preston, C. (2006) Complementarity analysis: mapping the performance of surrogates for biodiversity. *Biological Conservation*, **128**, 253–264.
- Wilson, K.A., McBride, M.F., Bode, M. & Possingham, H.P. (2006) Prioritizing global conservation efforts. *Nature*, 440, 337–340.

Editor: Mathieu Rouget

# SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Figure S1** The representation of all species in the target sets (i.e. half of the species) by area networks identified based on taxonomic indicator groups of varying size for (a) sub-Saharan Africa (b) Denmark and (c) Uganda.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/ j.1472-4642.2008.00507.x (This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.