Birds as biodiversity surrogates: will supplementing birds with other taxa improve effectiveness?

Frank Wugt Larsen[1,2,3,*], Jesper Bladt[4,5], Andrew Balmford[2] and Carsten Rahbek[1]

[1]*Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen O, Denmark;* [2]*Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK;* [3]*Science and Knowledge Division, Conservation International, 2011 Crystal Drive Suite 500, Arlington, VA 22202, USA;* [4]*Department of Wildlife Ecology and Biodiversity, National Environmental Research Institute, Aarhus University, Grenaavej 14, DK-8410 Roende, Denmark; and* [5]*The Ecoinformatics and Biodiversity Group, Department of Biological Sciences, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark*

Summary

1. Most biodiversity is still unknown, and therefore, priority areas for conservation typically are identified based on the presence of surrogates, or indicator groups. Birds are commonly used as surrogates of biodiversity owing to the wide availability of relevant data and their broad popular appeal. However, some studies have found birds to perform relatively poorly as indicators. We therefore ask how the effectiveness of this approach can be improved by supplementing data on birds with information on other taxa.

2. Here, we explore two strategies using (i) species data for other taxa and (ii) genus- and family-level data for invertebrates (when available). We used three distinct species data sets for sub-Saharan Africa, Denmark and Uganda, which cover different spatial scales, biogeographic regions and taxa (vertebrates, invertebrates and plants).

3. We found that networks of priority areas identified on the basis of birds alone performed well in representing overall species diversity where birds were relatively speciose compared to the other taxa in the data sets. Adding species data for one taxon increased surrogate effectiveness better than adding genus- and family-level data. It became apparent that, while adding species data for other taxa increased overall effectiveness, predicting the best-performing additional taxon was difficult. Finally, we demonstrate that increasing overall effectiveness required supplementary data for several additional taxa.

4. *Synthesis and applications.* Good surrogates of biodiversity are necessary to help identify conservation areas that will be effective in preventing species extinctions. Birds perform fairly well as surrogates in cases where birds are relatively speciose, but overall effectiveness will be improved by adding additional data from other taxa, in particular from range-restricted species. Conservation solutions with focus on birds as biodiversity surrogate could therefore benefit from also incorporating species data from other taxa.

Key-words: biodiversity, birds, complementarity, conservation, conservation planning, indicators, surrogacy

Introduction

Despite international agreement that biodiversity loss must be halted, it is still in widespread decline (Butchart *et al.* 2010). There is an urgent need to identify and protect important sites to prevent further species extinctions. However, identification

*Correspondence author. E-mail: frankwugtlarsen@gmail.com

of key sites is challenging because most species on Earth are not formally described (a problem known as the Linnean Shortfall) and the geographical distributions of most species are poorly understood (the Wallacean shortfall) (Brown & Lomolino 1998; Lomolino 2004). Consequently, the identification of priority areas often relies on a small subset of species implicitly or explicitly assumed to be good surrogates for biodiversity as a whole. One widely adopted approach is to use

species from a single well-known taxonomic group (such as birds) as a surrogate, and assume that priority areas for this taxon are also important for other taxa (e.g. Lund & Rahbek 2002; Moore *et al.* 2003; Saetersdal *et al.* 2004; Warman *et al.* 2004; Cabeza, Arponen & Van Teeffelen 2008; Franco *et al.* 2009; see also review by Rodrigues & Brooks 2007).

Information on the distribution of birds is more commonly available than for other taxa because birds are taxonomically well known and easily surveyed. In addition, owing to the broad public appeal of birds and potential revenue of birding activities (Verissimo *et al.* 2009), general support for conservation of birds is often higher than for other taxa. In consequence, much nature conservation work is driven by a focus on bird conservation. For example, BirdLife International and its network of partners has identified nearly 11 000 Important Bird Areas (IBAs) globally (BirdLife International 2010), and within Europe, the EUs Birds Directive has focussed on the establishment of a coherent network of special protection areas for birds (EC 2009). Consequently, birds as a single taxon surrogate will drive conservation efforts in many places. Nonetheless, several studies have found birds to perform relatively poorly as biodiversity surrogates (Lund & Rahbek 2002; Moore *et al.* 2003; Williams *et al.* 2006). Given these realities, it is striking that no study to date has analysed systematically how birds can be improved as a biodiversity surrogate. It appears evident that there is clear advantage to be gained from working to improve surrogacy effectiveness by supplementing bird data with data on other taxa rather than asking which taxon performs best in isolation.

In this study, we focussed on two strategies for supplementing information on birds with data on other taxa to examine which could improve surrogacy effectiveness. First, we supplemented bird data with *species-level* data from one other taxon or several taxa. However, species-level data are not readily available or obtainable for lesser-known taxa such as many invertebrates; instead, distributional data for these taxa might only be feasible to acquire at a higher taxonomic level, i.e. genus or family level (e.g. Balmford, Lyon & Lang 2000). Therefore, we also supplemented bird information with *genus- or family-level* data for invertebrates (when available) to examine their relative ability to improve surrogacy. Data were drawn from three distinct distributional data sets for sub-Saharan Africa, Denmark and Uganda.

Materials and methods

SPECIES DISTRIBUTION DATA

Sub-Saharan Africa

This data set covered the distribution of 1084 mammals, 1789 breeding birds, 734 frogs and 467 snakes across mainland sub-Saharan Africa at a spatial resolution of 1° latitude–longitude grid cells ($n = 1922$). This represents the most complete cross-taxonomic data base so far assembled for any tropical continent and has been used for numerous research papers on macroecology and conservation (see Burgess, Fjeldså & Rahbek (1998) for mapping methodology,

but for a full description see also http://macroecology.ku.dk/resources/data_resources/african_vertebrates/).

Denmark

This data set covered the Danish distribution of 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 compiled for 10-km Universal Transverse Mercator quadrats ($n = 622$). The data set is based mostly on Danish atlas data, which in general include the majority of Danish species within each group and the entire Danish distribution of each species. The data included only species that breed in Denmark and excluded vagrant, casual and exotic species from the data set. The data set is a further development of one that has already been used for quantitative biodiversity analyses in Denmark (Lund 2002; Lund & Rahbek 2002), and the current version has previously been used by Bladt, Larsen & Rahbek (2008) and Larsen, Bladt & Rahbek (2009).

Uganda

This data set covered the distribution of 2822 species. It differs in that data are for 64 Ugandan forests sites rather than grid cells across the landscape. The data set covers 87 small mammal species, 198 large moths, 962 woody plants, 736 butterflies and 839 birds. The data were collected by inventory teams with the aim of sampling as many taxa as possible, and field time was allocated in proportion to each forest site size. This data set is more fully described in Howard *et al.* (2000) and has previously been used by Larsen, Bladt & Rahbek (2009).

SURROGATE GROUPS: COMBINING BIRDS WITH OTHER TAXA

For each data set (sub-Saharan Africa, Denmark and Uganda), we randomly divided the data set into two halves, separately for each analysis (Larsen, Bladt & Rahbek 2007). We then selected the surrogate group from one half of the species (the *surrogate set*) and used the remaining half of the species in the data set (the *test set*) to test the effectiveness of the area networks identified based on the surrogate group. This approach circumvents potential problems with interdependence between surrogate groups and the test group (see Larsen, Bladt & Rahbek 2007). See Fig. 1 for a schematic view of the analysis procedure.

We selected surrogate groups consisting of bird species combined with (i) *species-level* data for one other taxon or all taxa, e.g. for sub-Saharan Africa birds + snakes, birds + frogs, birds + mammals or birds + snakes + frogs + mammals, and (ii) *genus- and family-level* data for taxa that are particularly hard to identify to the species level in the field, i.e. all invertebrate taxa (Denmark and Uganda) or frogs and mammals (sub-Saharan Africa, because this data set does not contain invertebrates; taxonomic information above species level was not available for snakes). The specific surrogate groups are listed in Table 1.

We selected indicator groups in which the number of species differed between taxa (e.g. 806 birds + 210 snakes compared to 806 birds + 330 frogs, see Table 1, Fig. 1 and also Table S1, Supporting Information) to reflect the differences in species richness between taxa. As indicator group size, we selected a number of species proportional to the species richness of the various taxa. A random division of the full data set would on average only result in indicator sets of 50% of the species in a taxon. We arbitrarily chose 45% of
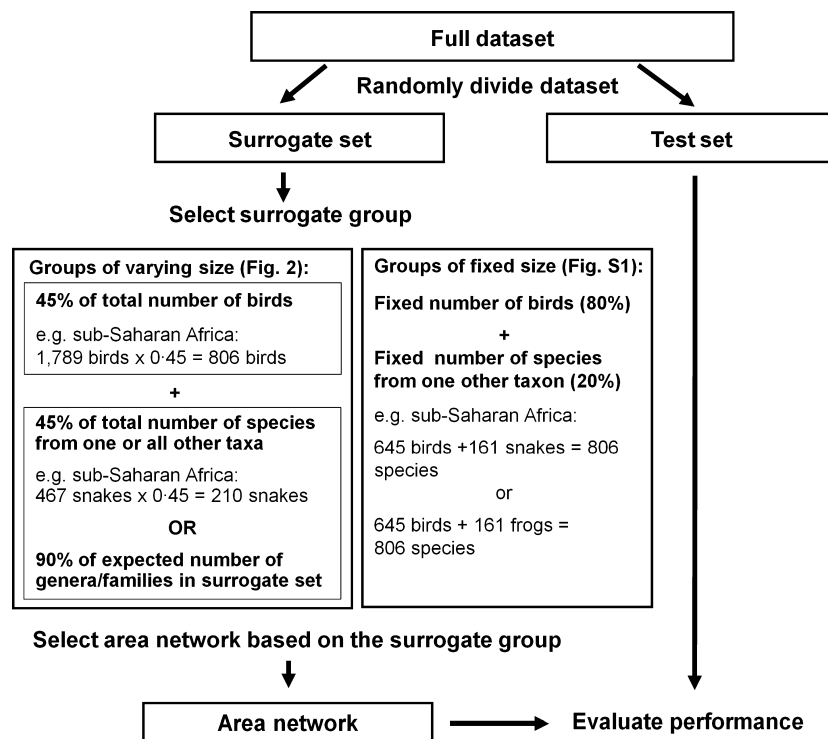
Fig. 1. A schematic view of the overall procedure for the analysis.

Table 1. The combination of taxa in the surrogate groups (column 2), the number of species in the surrogate groups (column 3) and the number of species in the surrogate groups in the analysis controlling for the effect of species number (column 4) for the three data sets

Data set	Surrogate groups	Species number (Fig. 2)	Species number (control analysis, Fig. S1, Supporting information)
Sub-Saharan Africa	Birds	806	806
	Birds + snakes	806 + 210	645 + 161
	Birds + frogs	806 + 330	645 + 161
	Birds + mammals	806 + 488	645 + 161
	Birds + frogs + snakes + mammals	806 + 1028	–
	Birds + genera (mammals + frogs)*	806 + 233	–
	Birds + families (mammals + frogs)*	806 + 52	–
Denmark	Birds	85	85
	Birds + amphibians/reptiles	85 + 9	(too few species)
	Birds + grasshoppers	85 + 12	(too few species)
	Birds + dragonflies	85 + 18	68 + 17
	Birds + orchids	85 + 18	68 + 17
	Birds + butterflies	85 + 27	68 + 17
	Birds + true bugs	85 + 28	68 + 17
	Birds + large moths	85 + 70	68 + 17
	Birds + hoverflies	85 + 113	68 + 17
	Birds + all 8 taxa	85 + 295	–
	Birds + genera (invertebrates)	85 + 173	–
	Birds + families (invertebrates)	85 + 31	–
Uganda	Birds	378	378
	Birds + small mammals	378 + 39	(too few species)
	Birds + large moths	378 + 89	302 + 76
	Birds + butterflies	378 + 331	302 + 76
	Birds + woody plants	378 + 433	302 + 76
	Birds + all four taxa	378 + 892	302 + 76
	Birds + genera (invertebrates)	378 + 156	–
	Birds + families (invertebrates)	378 + 6	–

*Taxonomic information beyond species level was not available for snakes.

the species richness as the group size as this procedure ensured that a sufficient number of species from the respective taxa would be included in the indicator set. Thus, for each taxon, we chose 45% of the total species richness in the taxon (e.g. 45% of the species richness of birds (806 spp.) supplemented with 45% of the species richness of snakes (210 spp.), see Table 1 and Fig. 1). A similar proportion of the expected number of genera and families in the indicator sets were selected. We made 500 replicates for each combination of the surrogate group (e.g. birds + frogs).

As some taxa might perform better than other taxa simply because they are more speciose (Manne & Williams 2003; Larsen, Bladt & Rahbek 2009), we performed a supplementary analysis to assess the influence of this effect. In this analysis, we kept the total number of species in the surrogate groups fixed at 806 for sub-Saharan Africa, 85 for Denmark and 378 for Uganda – equivalent to the number of bird species in the previous analysis. Birds constituted 80% of the species, while the remaining 20% came from other taxa (Table 1, Fig. 1). These group sizes 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 surrogate groups were used to select reserve networks that maximized representation of the species in the surrogate groups – maximum coverage sets (Church, Stoms & Davis 1996), i.e. the same total areas were selected for all reserve networks for each data set. We used the ILOG CPLEX software package (ILOG 2006) to select optimal area networks. We selected 5% of the total number of grid cells as reserve networks for sub-Saharan Africa and Denmark. Given that the Ugandan data set covered 64 forest sites of varying area (mean = 191 km^2, SD = 230 km^2), we selected 20% of the total area rather than a fixed number of sites (in accordance with Howard *et al.* 1998). This is partly because of difference in the sizes of the forests (with the largest forest constituting 9·2% of the total area) and partly because the inventories were conducted to support the government's plan to protect 20% of their forest estate (Howard *et al.* 1998).

SURROGATE GROUP EVALUATION

The selected area networks were evaluated in their effectiveness in representing the species in the test sets, i.e. the remaining half of the species in the data sets. We assessed the representation of all species and of rare species from the test sets. We focussed primarily on the representation of rare species 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). We defined rare species as the 25% most narrowly distributed species in their taxon (rather than the 25% most narrowly distributed species overall, which would of course be dominated by species from those taxa with smaller range sizes).

We compared the effectiveness of area networks selected using the surrogate groups with the effectiveness of area networks of similar area selected as follows:
1. Randomly (1000 times);
2. Based on surrogate groups composed of birds, but supplemented by a comparable number of species selected at random from across the other taxonomic groups in the data set (e.g. for sub-Saharan

Africa, 806 birds + 210 randomly selected species, cf. 806 birds + 210 snakes); and
3. Based on all species in the test set, to give an estimate of maximum possible representation in the given area.

The effectiveness scores for the 500 area networks based on each surrogate group exhibited a normal distribution, and we therefore performed standard analyses of variance (ANOVA) to assess the statistical significance of the differences in effectiveness between the various surrogate groups.

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

Results

Surrogate groups composed solely of birds resulted in area networks that captured around half of the rare species in all groups: 58% for sub-Saharan Africa (Fig. 2a), 49% for Denmark (Fig. 2b) and 50% for Uganda (Fig. 2c). The effectiveness was much higher when considering the representation of all the species: 86% for sub-Saharan Africa, 85% for Denmark and 81% for Uganda (see Table S2, Supporting information).

When surrogate groups of birds were supplemented with species data from other taxa, they were better at representing species than surrogate groups composed solely of birds (Fig. 2). Adding species data from all other taxa increased the representation of rare species from 58% to 67% for sub-Saharan Africa (Fig. 2a), from 50% to 66% for Denmark (Fig. 2b) and from 49% to 56% for Uganda (Fig. 2c). When birds were supplemented with species data from solely one taxon, the effectiveness did not increase as much (Fig. 2). The different taxa varied in their ability to improve the surrogate performance of bird data. For all three data sets, supplementing birds with data from speciose taxa tended to provide a higher increase in effectiveness than supplementing with species-poor taxa, although there were exceptions (Fig. 2). This trend was particularly strong for Denmark: for example, supplementing data on the 85 birds with data on grasshoppers (12 species) or amphibians/reptiles (9 species) resulted in smaller increases in effectiveness than adding data on large moths (70 species) or hoverflies (113 species) (Fig. 2b). The same overall results were found for the representation of all species (see Table S2, Supporting information).

Interestingly, only one taxon, woody plants in Uganda, was a better surrogate, alongside bird data, than a comparable number of randomly chosen species regardless of taxa, while the other taxa performed significantly worse or equal to randomly chosen species (see asterisks in Fig. 2). For sub-Saharan Africa, only frogs supplemented birds as well as a random set of species (Fig. 2a), while in Denmark this was the case for grasshoppers, dragonflies and true bugs (Fig. 2b). These patterns were corroborated in the analysis controlling for the effect of species richness in the taxa (see Fig. S1, Supporting Information), which also found frogs (sub-Saharan Africa), dragonflies (Denmark) and woody plants (Uganda) to perform relatively better than other taxa as a supplement to birds. Interestingly, in this analysis, all surrogate groups in which bird
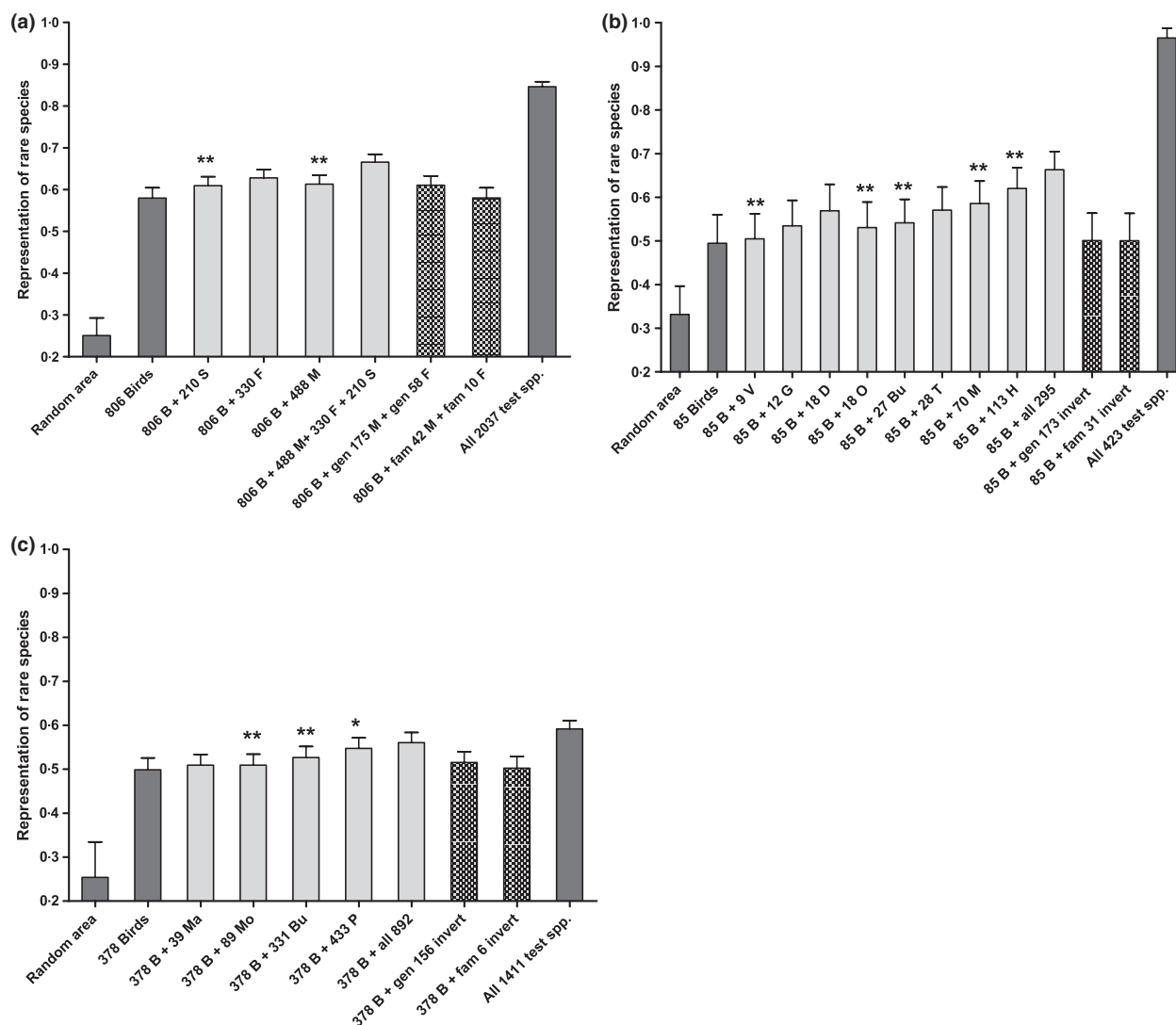
Fig. 2. The representation of rare species by area networks identified based on surrogate groups composed of birds supplemented with other taxa for (a) sub-Saharan Africa, (b) Denmark and (c) Uganda. For comparison, we show (in dark grey) the representation of rare species by area networks chosen randomly, area networks based on birds and area networks based on all species (dark grey bars). Error bars denote SD, and asterisks indicate whether statistical tests show that surrogate groups perform significantly better (*) or worse (**) than surrogate groups of birds supplemented with a comparable number of randomly chosen species ($P < 0.05$). Surrogate abbreviations are as follows: for sub-Saharan Africa (B, birds; S, snakes; F, frogs; M, mammals), for Denmark (B, birds; V, amphibians/reptiles; G, grasshoppers; D, dragonflies; O, orchids; Bu, butterflies; T, true bugs; M, large moths; H, hoverflies) and for Uganda (B, birds; Ma, mammals; Mo, large moths; Bu, butterflies; P, woody plants). Gen and fam are abbreviations for genera and families, respectively.

data were supplemented with data from another taxon performed significantly better than surrogate groups comprising just birds, even though all surrogate groups contained the same number of species (Fig. S1, Supporting information).

Supplementing data on birds with genus-level data on other groups only had a marginal influence on effectiveness (Fig. 2). For sub-Saharan Africa, adding genus-level data increased effectiveness to the same degree as using species data for mammals or snakes (Fig. 2a). In other cases, the increase in effectiveness was smaller than that achieved by adding species-level data from one other taxon. In Denmark, genus-level data for invertebrates increased effectiveness only marginally (Fig. 2b); the same was true for Uganda (Fig. 2c). For all three data sets, supplementing with family-level data

only increased effectiveness marginally (Fig. 2). The same overall results were found for the representation of all species (see Table S2, Supporting information).

As expected, all the various surrogate groups performed better than area networks selected by chance (i.e. selected using no species information) and worse than area networks identified based on all test species (i.e. the best possible solution) (Fig. 2).

Discussion

EFFECTIVENESS OF BIRDS AS SURROGATES

Previous studies have found that birds perform worse than other taxa in guiding the selection of complementary area

networks for overall biodiversity – mainly due to their relatively large distributional ranges (Lund & Rahbek 2002; Moore *et al.* 2003; Williams *et al.* 2006). Nonetheless, for all three data sets, the bird surrogate group performed fairly well and thus already provided coverage of roughly half of the rare species (and more than 80% of all species). This finding can partly be attributed to the relatively high number of bird species in the data sets compared to the other taxa in the data sets – the number of species in surrogate groups strongly affects their performance when used to select complementary reserve networks (Manne & Williams 2003; Larsen, Bladt & Rahbek 2007, 2009).

SUPPLEMENTING BIRD DATA WITH INFORMATION ON OTHER TAXA

An increase in surrogacy performance was expected when data on birds were combined with species data from other taxa – as the total number of species in the surrogate groups increased (Fig. 2). Generally, a surrogate group consisting of a larger number of species will, all other things being equal, provide better coverage of other species as it will typically occupy a wider range of habitat types (Manne & Williams 2003; Larsen, Bladt & Rahbek 2009). However, the gain in coverage by repeatedly adding *n* species to a surrogate group decreases with the size of the group. In other words, the larger the surrogate group, the larger the expected coverage of other species but the less the additional benefit of adding even more species to the surrogate group (this relationship between diminishing marginal effectiveness and increased surrogate group size is illustrated for each of the three data sets in Fig. S2, Supporting information). The increase in effectiveness achieved by supplementing bird data with species data from all other taxa might seem modest considering the large number of species added (Fig. 2). For example, adding more than 1000 species of mammals, frogs and snakes to the surrogate group of 806 birds for sub-Saharan Africa only increased the representation of rare species from 58% to 67% (Fig. 2). This is because in our data sets birds are speciose relative to the other taxa. Consequently, supplementing birds with other species had only a small effect when effectiveness was measured as simple representation of other species in an area network. However, other measures of effectiveness, e.g. multiple representations, might reveal a stronger influence of adding data on other taxa.

SPECIES-LEVEL DATA VS. GENUS- AND FAMILY-LEVEL DATA

Using genus- or family-level data is appealing because it could enable conservation planners to supplement information on birds with data for less well-known groups of organisms such as invertebrates, where species-level data are less readily available (e.g. Balmford, Lyon & Lang 2000). However, in this study, species-level data mostly outperformed genus- and family-level invertebrate data as a supplement to bird information (Fig. 2). Therefore, supplementing bird data with species data from *one* other taxon appears to be a better strategy than

adding genus- or family-level data for *several* invertebrate taxa (or vertebrate taxa, in the case of the sub-Saharan data set). The relatively poor performance of higher-taxon data can be ascribed to a combination of factors. First, important distributional information such as range-restrictedness is progressively lost with increasing taxonomic level, making distributional information at the genus-level and especially family-level less informative in guiding area network selection (Fjeldså 2000; Larsen & Rahbek 2005). Secondly, there are relatively few invertebrate genera and families in these analyses (Table 1), so adding them to the surrogate set increases its richness less than adding species-level data on other taxa.

WHICH TAXON CONSTITUTED THE BEST SUPPLEMENT TO BIRD DATA?

We found that data on species from certain taxa performed better at supplementing bird data than did others. This is partly due to differences between taxa in species richness, because those with higher species richness overall tended to perform better than less speciose taxa (Fig. 2). But regardless of species richness, certain taxa performed consistently well when compared to equivalent numbers of randomly chosen species (see asterisks in Fig. 2) or in analyses that controlled for the effect of species number (Fig. S1, Supporting information: frogs in sub-Saharan Africa; grasshoppers, dragonflies and true bugs in Denmark; and woody plants in Uganda). So, what properties make some taxa good supplementary surrogates? Distributional attributes, such as range-restrictedness, are important for the effectiveness of taxonomically diverse surrogate groups (Manne & Williams 2003; Larsen, Bladt & Rahbek 2007; Bladt, Larsen & Rahbek 2008). In this study, the best-performing taxa tended to have a relatively high proportion of species among those with a range size in the lowest quartile across all taxa (frogs in sub-Saharan Africa and grasshoppers, dragonflies and true bugs in Denmark), although there were exceptions (woody plants in Uganda) (Table S1, Supporting information). Conversely, some taxa had a high proportion of range-restricted species but performed poorly (e.g. orchids in Denmark) (Table S1, Supporting information). It might be that the factors that determine range-restrictedness in these latter groups (such as the incidence of low-nutrient soils in the case of Danish orchids – Larsen, Bladt & Rahbek 2009) are taxon-specific and do not predict distribution patterns of rare species in other groups.

Conclusions

We assessed surrogacy in terms of species representation, but this does not necessarily ensure long-term persistence of species (e.g. Araujo & Williams 2000; Rodrigues, Gregory & Gaston 2000). However, data requirements necessitated focus on the former, and ensuring representation is a first step in systematic conservation planning (Pressey *et al.* 1993). Our analysis of three distinct data sets provided insights into the use of bird data and the scope for improving their surrogacy value by adding data from other taxa. Our overall findings were consistent

for all three data sets, which cover different spatial scales, biogeographic regions and taxa. The span of spatial scales ranging from 1° grid cells (*c.* 105 km × 105 km) across a continent to national scales (10 km^2, or forest fragments; mean = 191 km^2, SD = 230 km^2) makes our findings robust.

Our study focussed on the use of surrogates for selection of reserve networks to optimize representation of overall species diversity, and our results offer some valuable practical insights. First, data on birds were good at identifying reserve networks with high absolute representation of species in other groups. This was mainly because more data were available for birds than for other taxa, so using bird data meant that relatively many species were used to guide area selection. Given the wide availability of data on them, from a pragmatic perspective, birds therefore seem to be a cost-effective start for guiding conservation planning (Gardner *et al.* 2008) – at least in areas where bird data sets are relatively more species-rich compared to those of other taxa. Secondly, there are likely to be better options than using bird data alone. For example, we found that for surrogate groups with the same number of species, those that contained species from both birds and another taxon consistently outperformed those solely composed of birds. This is supported by previous research where other taxa have been found to outperform birds as surrogates (e.g. Lund & Rahbek 2002; Moore *et al.* 2003; Williams *et al.* 2006). Thirdly, we found that adding data from one or more other taxa for reserve selection would increase coverage of rare species, but we cannot point to a specific taxon that in combination with birds would increase surrogate effectiveness considerably. Thus, the conclusion is that adding data from any single taxon has some effect (depending on the number of species) and that adding extra taxa (and species) further increases overall effectiveness. Overall, increasing the pool of species, in particular range-restricted species, used to guide priority setting would benefit surrogacy effectiveness (see also Larsen, Bladt & Rahbek 2007, 2009). Finally, adding to the species data higher-taxon information on groups that are hard to identify to species level usually increases effectiveness only marginally. Thus, the strategy of adding invertebrate data at the genus or family level rather than adding species data for one other group (e.g. of vertebrates) cannot be recommended. In conclusion, a simple strategy of adding more species from various taxa to the bird data to help guide the identification of priority sites will improve the effectiveness of site selection and ultimately increase the chances of preventing extinctions in other groups.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. The number of species, narrow ranged species, range-restricted species, and widespread species for each taxon for the three datasets.

Table S2. The representation of all species by area networks identified based on surrogate groups composed of birds supplemented with other taxa for sub-Saharan Africa, Denmark, and Uganda.

Fig. S1. The representation of rare species by area networks identified based on surrogate groups of fixed size composed of birds supplemented with species data from other taxa.

Fig. S2. The representation of rare species by area networks identified based on random sets of species.

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