

Cross-taxon congruence in complementarity and conservation of temperate biodiversity

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Abstract

Identification of reliable surrogate indicator taxa and effective shortcuts for the preservation of overall biodiversity is a major challenge. Encouragingly, complementarity-derived priority sets of focal taxa were found highly effective in representing non-target taxa in a study from Ugandan forests. It has been proposed cross-taxon congruence in complementarity is less distinct in temperate regions than in the tropics, because temperate regions have fewer species, and hence focal taxa may be less effective as they are less diverse. To test this, we used all available atlas data (10 × 10 km scale) in Denmark (butterflies, birds, amphibians, reptiles, large moths, bats and click beetles, $n = 434$ species), and looked at whether conservation priority areas based on one taxonomic group represent species richness of other groups in a highly fragmented landscape. We apply a new approach (based on G -statistics) that enables statistical evaluation of cross-taxon congruence in complementarity-derived priority sets. We found indications that the same taxa represented other groups effectively and exhibited cross-taxon congruence in complementarity-derived priority sets. Birds performed significantly, but relatively poorly, butterflies somewhat better and bats relatively well in representing species richness of other groups. Large moths performed best and may be an overlooked predictor of diversity in other animal taxa.

INTRODUCTION

Conservation biology faces a fundamental problem: the vast majority of biodiversity is not known (May, 1988). The number of distinct eukaryotic species alive on earth lies in the 5–15 million range, of which roughly only 1.5 million are known to science (May, 1999). Still, conservation biology is concerned with preserving overall diversity of species and must, accordingly, attempt to secure the continued existence of species, unknown as well as known.

In accordance with Article 6 of the Convention on Biological Diversity (Glowka *et al.*, 1994), every nation must outline strategies to manage regional and local biodiversity. Within the last 20 years certain guidelines have emerged on how to manage known biodiversity. Acknowledging that resources are limited, as many natural features (e.g., species) as possible should be represented as many times as possible within a minimum set of sites (Margules, Nicholls & Pressey, 1988; Pressey *et al.*, 1993) or within the most inexpensive set of sites (Faith & Walker, 1996b; Ando *et al.*, 1998). Identification of alternatives to sets of priority areas is

very important in order to bring flexibility into the prioritization process (Pressey *et al.*, 1993) as other interests of land-use have to be considered. The most efficient and flexible way to decide which set of areas constitutes the most complete representation of species for a given region is using iterative site-selection algorithms based on complementarity as well as richness (Kirkpatrick, 1983; Pressey & Nicholls, 1989; Vane-Wright, Humphries & Williams, 1991; Pressey, Possingham & Margules, 1996; Reyers, van Jaarsveld & Krüger, 2000).

The reliability of sets of priority areas for known taxa to act as surrogates for the preservation of overall biodiversity should be assessed (Gaston, 1996). At scales relevant to practical conservation, the existence of cross-taxon congruence patterns in distribution would offer a shortcut. The indicator value of a focal taxon can be determined using other known taxa as target groups. In this way indirect evidence of indicator effectiveness is provided.

At continental scales, distribution patterns do correspond across taxa (Pearson & Cassola, 1992; Curnutt *et al.*, 1994; Balmford & Long, 1995; Pearson & Carroll, 1999). However, the spatial resolution of data at the scales in question is too coarse for practical conservation planning (Prendergast, Quinn & Lawton, 1999). At finer scales, congruence patterns are ambiguous (Gaston,

1996; Reid, 1998). General patterns of cross-taxon congruence in species richness or endemism have not been established (Prendergast *et al.*, 1993; Lombard, 1995; Oliver & Beattie, 1996; Flather *et al.*, 1997; Prendergast & Eversham, 1997; Lawton *et al.*, 1998; Williams & Gaston, 1998), nor have patterns between complementary sets of priority areas for different taxonomic groups (Sætersdal, Line & Birks, 1993; Dobson *et al.*, 1997; van Jaarsveld *et al.*, 1998). Congruent patterns are dependent on scale and level of landscape fragmentation (Prendergast *et al.*, 1993; Curnutt *et al.*, 1994) and vary according to the taxa examined and measures of diversity compared (Balmford & Long, 1995; Flather *et al.*, 1997).

A different way to examine small-scale cross-taxon congruence may be to test the extent to which the priority areas of one taxon represent species richness in other taxa (Williams, 1993, 1998; Balmford, 1998). Recently, a study from Ugandan forests found indications that priority areas of single taxa represent species richness in other groups as effectively as using information on all taxa (Howard *et al.*, 1998). These results were not caused by cross-taxon congruence in species richness, but were rather a reflection of cross-taxon congruence in complementarity. Uganda consists of several distinct biogeographical zones and it was suggested that all zones should be sampled in order to represent all species within the focal taxon. Thereby, species richness in other groups similarly adapted to a heterogeneous biogeography were effectively represented. This is encouraging from a conservation-planning perspective in Uganda and countries with similar biogeography. However, Balmford (1998) suggests that patterns of cross-taxon congruence in complementarity may be less distinct in temperate regions where focal taxa will be less effective as they are less diverse (Ryti, 1992) or contain far fewer species than the number of candidate sites. Additionally, high levels of landscape and habitat degradation and fragmentation may disrupt the underlying 'natural' distribution of species.

If correct, conservation planning in the highly industrialized, agricultural, densely populated countries may be complicated. The dilemma of tropical countries with limited resources and lack of data and knowledge is also very real in the industrialized countries, although at another scale. Not much land is left for management of biodiversity, which demands high-resolution information on which to base priority-decisions. Even in Denmark, a densely populated country (123 people/km²) with a historically long tradition of national faunistic inventories, knowledge of the distribution of most of the country's *estimated* 30,000 species (Stoltze & Pihl, 1998) is lacking at the required scale of management, i.e., single land-lots.

Priorities, management and monitoring of overall temperate biodiversity may thus also rely on shortcuts as in the tropics. As decisions are made for the implementation of the national obligations following the Convention on Biological Diversity, it is important to evaluate the potential of various suggested shortcut

approaches. Cross-taxon congruence in complementarity remains one of the most promising (Balmford, 1998). In this study, we test whether conservation priority areas based on one taxon represent species richness in other groups in a temperate region. Denmark is biogeographically homogeneous, but has a highly fragmented and thoroughly regulated landscape. Further, we test if patterns of representativeness match patterns of cross-taxon congruence in complementarity-derived priority sets.

METHODS

We used all Danish atlas data that were compiled at a UTM grid with area standardized to the spatial scale of 10 km × 10 km (Fig. 1(a)–(f)). Atlas survey data were available for bats (Baagøe, 2001), amphibians/reptiles (Fog, 1993), click beetles (Martin, 1989), butterflies (Stoltze, 1994), large moths (Kaaber, 1982) and birds (Grell, 1998). Uneven sampling size and effect of area influence statistics derived from analyses dealing with species richness and species distribution. To ensure standardization of sampling sizes, we only considered the 124 grid cells with data for all surveyed groups (Fig. 1(g)). The 124 grid cells contained 434 species. The species were distributed as follows: 14 species of bats (Chiroptera), 18 species of amphibians/reptiles (Amphibia/Reptilia), 23 species of click beetles (Coleoptera: Elateridae), 57 species of butterflies (Lepidoptera: Hesperioidea, Papilionoidea), 155 species of large moths (Lepidoptera: species within Hepialoidea, Cossioidea, Zygaenoidea, Tineoidea, Yponomatoidea, Bombycoidea, Geometroidea, Sphingoidea, Notodontidae, Noctuoidea) and 167 species of breeding birds (Aves). Click beetles are associated with old, decaying wood, and are in the present study the taxon with the narrowest habitat requirements. This does not, however, influence the general results of our analysis reported here, as the overall pattern remains the same when tests are carried out on the total data set (i.e., including grid cells with no records for one or more groups).

The Danish surveys are among the most detailed worldwide, relative to the fine scale at which they are carried out. The three surveys with the poorest geographical coverage (bats, click beetles and large moths) were mainly carried out by professionals and the richness maps reflect the actual overall distributions of the taxa in Denmark. Differences in sampling effort within and between surveys are judged to be relatively small and the analyzed data most likely represent one of the least sampling-biased compilations of atlas data ever used for scientific analyses.

The Danish landscape is highly influenced by man: 62% is cultivated, 12% is afforested (< 1% is natural forests), 12% is built-up areas and infrastructure, and 14% is natural and semi-natural habitats (lakes, heathland, bogs, dunes, etc.) (Utzon-Frank *et al.*, 1999). An average grid cell contains a mosaic of smaller biotopes within a matrix of arable land.

A rarity-based heuristic algorithm is used to select priority sets of complementary areas, using WORLDMAP

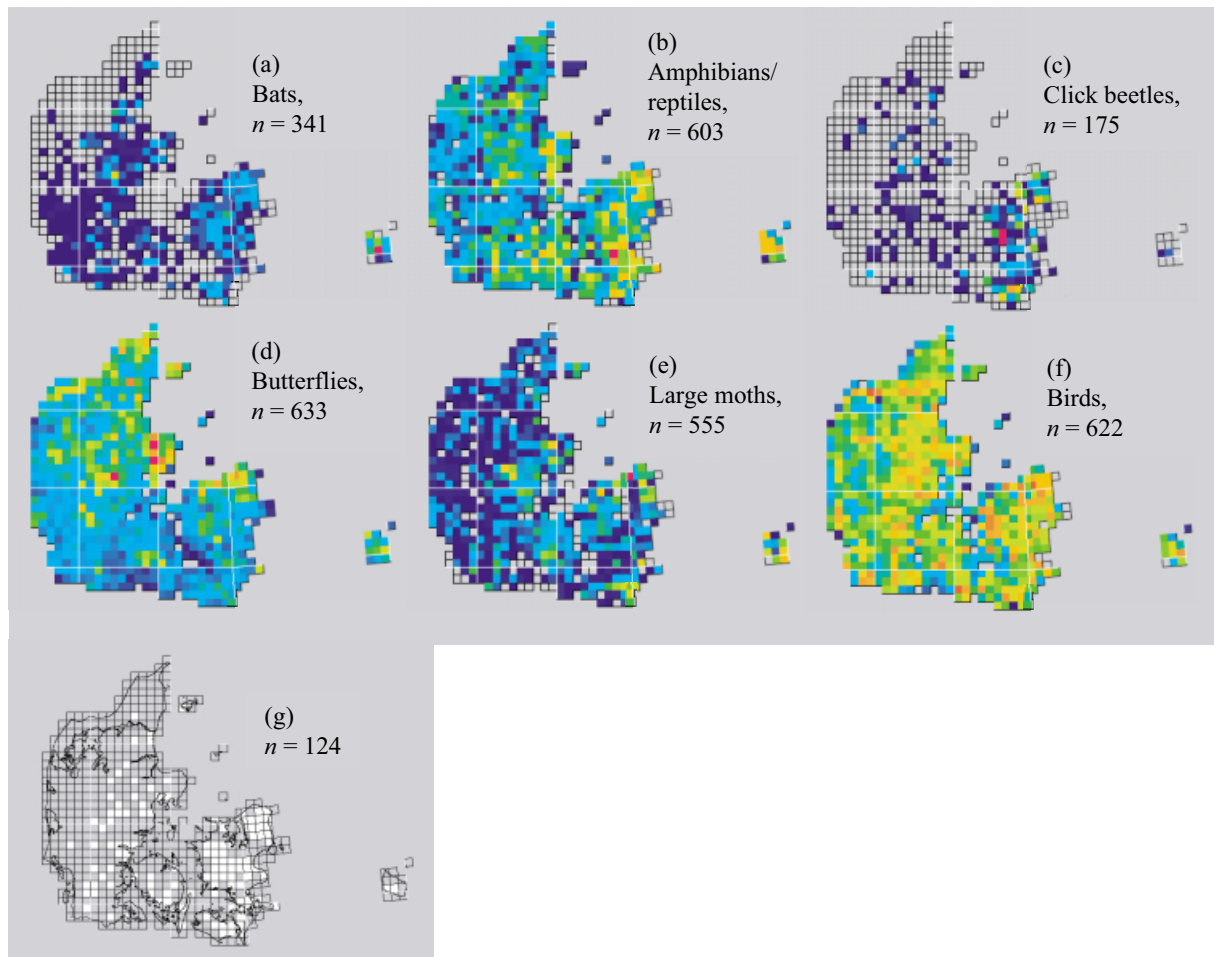


Fig. 1. Species-richness patterns and coverage of the six analyzed Danish atlas surveys (a)–(f). Colour gradients refer to increasing species-richness scores from dark blue (minimum) to red (maximum). White squares indicate the 124 grid cells surveyed for all taxa (g). Map of Denmark modified from template made by P. Williams and D. Vane-Wright in 1993 at the Wissenschaftskolleg zu Berlin.

software (Williams, 1999). Rarity is defined as each species' inverse range-size (Usher, 1986; Williams *et al.*, 1996). Rarity-based algorithms assign high priority to areas that contain species with narrow distributions. They are slightly more effective than other heuristic algorithms when the priority sets are to represent all species (Kershaw, Williams & Mace, 1994; Csuti *et al.*, 1997) and produce results very close to optimal (Csuti *et al.*, 1997). The selection procedure employed here first selects all grid cells with species that have single records. The following grid cells to be selected are the ones contributing with most as yet unrepresented rare species, i.e., unrepresented species with the fewest grid cell records. In successive iterations of the algorithm, areas with the highest complementary richness in the rarest species are selected until the required number of areas has been obtained (see Williams, Burgess & Rahbek, 2000, Table 1 for more details).

We performed 'near-maximum-coverage analysis' (Williams, 1998; similar in principle to the 'maximal covering location problem' of Church, Stoms & Davis, 1996) to examine how effective conservation priority areas based on one taxon represent species in other

groups. For each taxon, a set of 31 areas (i.e., 25% of the 124 cells with data for all groups) were selected to give best possible representation for that taxon, giving six sets in all. Subsequently, the grid cell selection sequence for each taxon was rerun on data for the other five groups (excluding the focal taxon) and cumulative species numbers were recorded. Additionally, a priority set was selected using data on all taxa to illustrate near-maximum effectiveness of area selection when all species are known. Random area selection (1000 simulations without replacement) was performed to assess minimum effectiveness. For a focal taxon to be regarded as a reliable indicator, we require that its performance in representing other taxa must be better than that delimited by the upper 95% confidence limit achieved by random area selection.

We tested for cross-taxon congruence in three different ways:

(1) As we used a rarity-based algorithm to select priority sets, the occurrence of the rare species determines which grid cells make up the priority set. If rare species of the focal taxon co-occur with high species numbers in other taxa, success in representing species richness in

other groups may be related to the particular algorithm. Using Spearman's rank correlation we tested if the sum of inverse range-size rarity of species in the focal taxon was congruent with species richness in the other taxa ($n = 124$).

(2) To test cross-taxon congruence in complementarity we used the same method as Howard *et al.* (1998), examining complementarity between grid cells compared pairwise. We calculated complementarity scores according to Colwell & Coddington (1994: 112): the sum of unique species occurring in one or the other of two grid cells is divided by the combined total of species in the same two grid cells, and multiplied by 100. Complementarity scores between a random grid cell and each of the remaining 123 cells are calculated for each taxon. Subsequently, scores for corresponding grid cells are compared across taxa, and congruence is tested using Spearman's rank correlation coefficients. This was repeated for 31 random cells (a quarter of the total number of cells) in order to compare grid cells only once in each of the 31 sets, and at the same time to consider each grid cell more than once in the overall analysis. Finally, based on these 31 sets, one common correlation coefficient (Zar, 1984) was calculated for each cross-taxon comparison. Correlation coefficients were calculated in this way to avoid pseudoreplication.

(3) Another way to evaluate cross-taxon congruence is to examine correspondence between priority sets of complementary areas selected by different taxa (i.e., cross-taxon congruence in complementarity-derived priority sets). Such correspondence has previously been searched for, but not established (Sætersdal *et al.*, 1993; Dobson *et al.*, 1997; van Jaarsveld *et al.*, 1998). However, these studies did not compare the results with a random test, which would provide additional information on the degree of correspondence that was found. We propose a way to do so (see the recent paper by Moritz *et al.* [2001] for a different random approach from ours). Near-maximum-coverage analysis was performed on each of the focal taxa to form six priority sets, selecting a quarter of the total number of grid cells in each set. Accordingly, a 1:3 ratio of repeated priority areas would be expected when priority sets are compared pairwise across taxa (the relation between priority areas selected by taxon X and by taxon Y and between priority areas selected by taxon X and not by taxon Y is one to three). We used G -statistics, replicated goodness of fit (Sokal & Rohlf, 1995), which apart from testing the overall concordance with the expected ratio also provides information on the uniformity of individual ratios in replicated tests. First, we test individual ratios: i.e., whether the focal taxon represents a uniform or a varying number of priority areas of the other taxa ($G_{Heterogeneity}$). Significant G_H -values will indicate that the focal taxon varies in representing priority areas of other taxa, and may be unfit as indicator of a broader range of taxa. Second, the individual ratios for each focal taxon are summed and treated as one ratio (G_{Pooled}) to test if the overall ratio is different from the expected ($H_0 = 1:3$). This test corresponds with a chi-square test, but indi-

vidual chi-square values are not completely additive. If the number of shared priority areas is homogeneous and H_0 is rejected and the deviation from the expected is caused by a higher number of shared areas, we will conclude that taxa exhibit cross-taxon congruence in priority sets.

Further, we test for thresholds in congruent relationships using the sum of G_H and G_P , G_{Total} , which considers heterogeneity of data and any deviation from the expected ratio at the same time. Three levels are tested to see if the number of areas included in near-maximum-coverage analyses influences congruence of priority sets. The three levels are: $n = 31$ grid cells (the quarter of the total number of grid cells), $n = 21$ grid cells (all species can be represented within 21 grid cells) and $n = 12$ grid cells (10% of the grid cells referring to an arbitrarily set conservation goal [discussed in Soulé & Sanjayan, 1998]).

RESULTS

Priority sets of four taxa are significantly more effective in representing total species richness than sets selected at random (Fig. 2). Butterflies are better than random from the second grid cell selected, bats from the fourth grid cell, and large moths from the seventh grid cell selected. Noticeably, birds are only slightly better than random selection from the tenth grid cell. Two taxa, amphibians/reptiles and click beetles, are not reliable as focal taxa, as they do not represent significantly more species than would random area selection. Using data from all groups is more effective than using any single group at all times. All species within the 124 grid cells can be represented in just 21 selected grid cells. All species in the focal taxa are represented at the third cell for bats and amphibians/reptiles, at the fifth cell for click beetles, at the sixth cell for butterflies, at the eighth cell for large moths, and at the eleventh cell for birds.

We found significant relationships between range-size rarity and richness in 20 of 30 possible combinations of taxa (adjusted for error rate $P < 0.05$ or less), but significant correlation coefficients were very low ($0.23 < r_s < 0.34$). All taxa exhibited non-significant relationships of cross-taxon congruence in complementarity when grid cells were compared pairwise, except for two taxa: amphibians/reptiles and birds ($r_{sw} = 0.31$, adjusted for error rate $P < 0.05$).

Four taxa exhibited cross-taxon congruence in complementarity-derived priority sets when tested with G -statistics (Table 1), interestingly the same taxa that were effective in representing total species richness: butterflies, bats, large moths and birds. Going more into detail, all data sets were considered homogeneous as all individual G_H -values are non-significant. Looking at values of G_P , we found that when $n = 31$ areas, the priority sets of birds, butterflies, bats and large moths did reject the H_0 -hypothesis, suggesting cross-taxon congruence in priority sets. When $n = 21$ areas, the priority set of birds was no longer able to reject the H_0 -hypothesis; when $n = 12$ areas, none of the priority

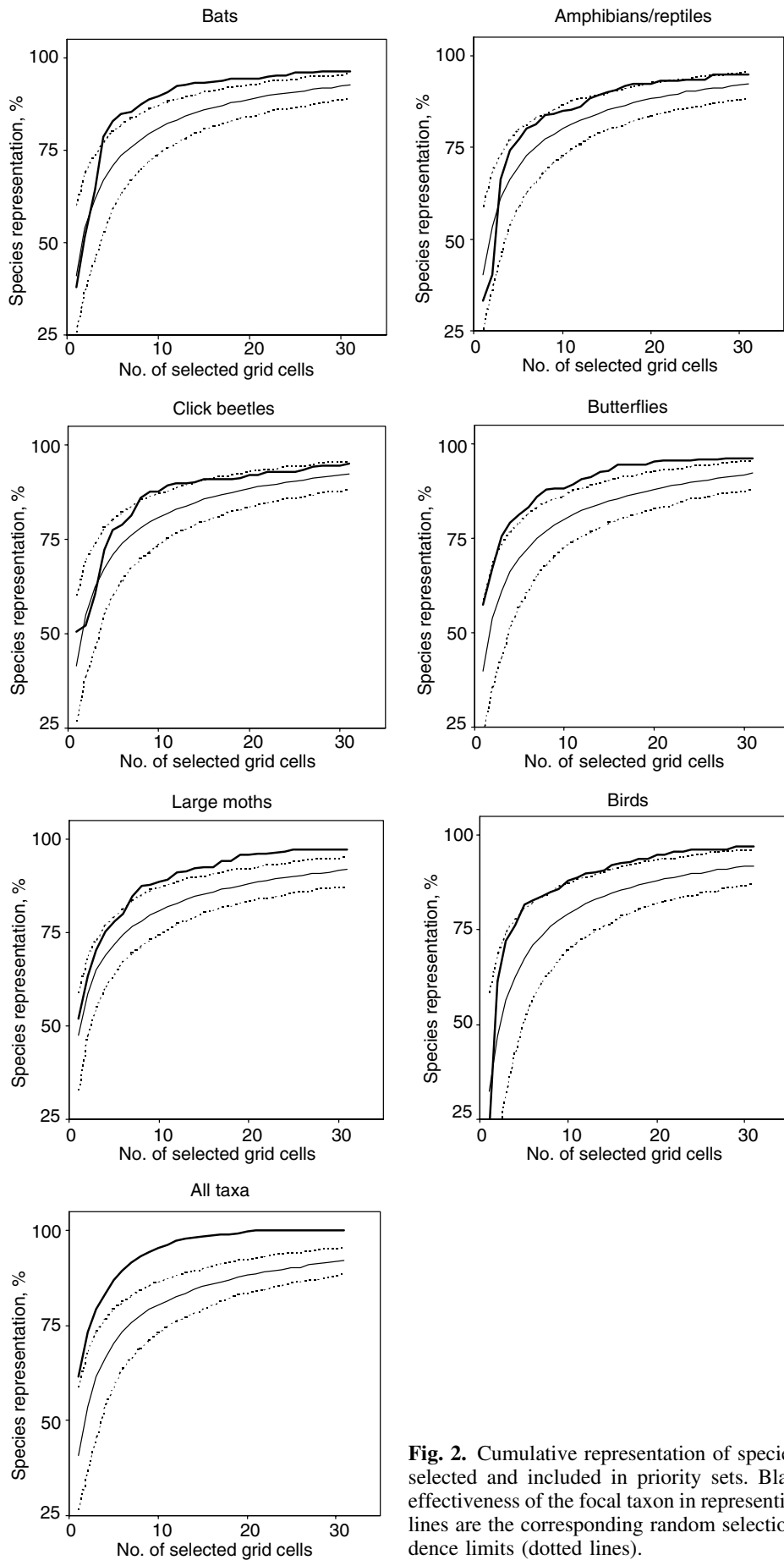


Fig. 2. Cumulative representation of species as grid cells are selected and included in priority sets. Black solid lines are effectiveness of the focal taxon in representing other taxa; grey lines are the corresponding random selection with 95% confidence limits (dotted lines).

sets was able to reject the H_0 -hypothesis. Considering values of G_T , only bats and large moths rejected the H_0 -hypothesis at $n = 31$, and only butterflies and large moths rejected the H_0 -hypothesis at $n = 21$. Large moths and bats performed well, as these taxa represented uniformly high numbers of priority areas of the other taxa (Tables 1 and 2). Butterflies performed well at $n = 21$, exhibiting a significant G_T -value (11.69) in spite of a relatively small G_P -value (4.50). This was caused by a relatively high, but non-significant, G_H -value ($G_T - G_P = G_H$), revealing some heterogeneity in the butterfly data. The heterogeneity originates in butterflies having many priority areas in common with large moths (12 areas) while having no more than expected with bats (five areas) and birds (five areas) (Table 2). No taxa rejected the H_0 -hypothesis at $n = 12$.

DISCUSSION

We found indications that some taxa do exhibit cross-taxon congruence in distribution patterns and can be used as surrogates of biodiversity in other groups. The best match is found when representativeness and congruence in complementarity-derived priority sets are compared. The same taxa (bats, butterflies, large moths and birds) differ significantly from random (Fig. 2, Tables 1 and 2). Bats and large moths appear as the most robust taxa in selecting grid cells also included in priority sets of other taxa. Butterflies appear fairly robust, but as revealed by the G -statistics, butterflies are effective indicators of large moths and less reliable when it comes to the other taxa. Accordingly, butterflies may not be able to represent a taxonomically broader range of biodiversity. Birds are the least robust taxon. The latter is surprising as birds are usually argued as effective predictors of diversity in other groups (ICBP, 1992), and do represent high species numbers when comparing data

Table 1. Cross-taxon congruence in complementarity-derived priority sets. Values are results of replicated tests of goodness of fit (31 grid cells = 25% of cells in analyses; 21 grid cells = all species can be represented in 21 cells; 12 grid cells = 10% of cells in analyses). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.

	$n = 31$ grid cells	$n = 21$ grid cells	$n = 12$ grid cells
Pooled G			
Bats	12.86 ***	7.57 **	0.09 NS
Amphibians/ reptiles	2.81 NS	2.20 NS	3.57 NS
Click beetles	2.24 NS	0.15 NS	2.43 NS
Butterflies	5.66 *	4.50 *	0.37 NS
Large moths	16.78 ***	12.79 ***	0.77 NS
Birds	5.66 *	0.38 NS	2.43 NS
Total G			
Bats	13.80 **	9.87 NS	2.08 NS
Amphibians/ reptiles	5.03 NS	4.20 NS	5.41 NS
Click beetles	3.93 NS	3.65 NS	5.82 NS
Butterflies	10.06 NS	11.69 *	1.87 NS
Large moths	19.67 **	16.99 **	2.91 NS
Birds	7.84 NS	2.47 NS	4.92 NS

Table 2. Number of grid cells in priority sets also selected by other taxa. Numbers in bold = the expected ratio (1:3, i.e., 8:23, 5:16 and 3:9 at $n = 31$, 21 and 12 grid cells, respectively). Notice that at $n = 31$ and 21 three quarters of the sets have more cells than expected in common and only in one case fewer, while at $n = 12$ only a quarter have more cells in common and half the sets have fewer than expected.

	Amphibians /reptiles	Click beetles	Butter- flies	Large moths	Birds
$n = 31$ grid cells					
Bats	13	10	11	14	13
Amphibians/ reptiles	-	8	9	9	9
Click beetles	-	-	8	12	9
Butterflies	-	-	-	15	9
Large moths	-	-	-	-	12
$n = 21$ grid cells					
Bats	9	5	8	9	8
Amphibians/ reptiles	-	5	6	7	6
Click beetles	-	-	5	9	4
Butterflies	-	-	-	12	5
Large moths	-	-	-	-	6
$n = 12$ grid cells					
Bats	3	2	3	5	3
Amphibians/ reptiles	-	1	2	2	1
Click beetles	-	-	2	4	1
Butterflies	-	-	-	4	2
Large moths	-	-	-	-	3

on species-richness hotspots (Prendergast *et al.*, 1993; Lombard, 1995). Strong cross-taxon congruence patterns between range-size rarity and richness were not found ($0.23 < r_s < 0.34$). Area selection based on range-size rarity alone would not represent species effectively (see also Prendergast *et al.*, 1993; Williams *et al.*, 1996). Likewise cross-taxon congruence in complementarity between pairwise-compared grid cells was not established as only two taxa exhibited weak congruence (birds and amphibians/reptiles). Thus, an underlying pattern of congruence in complementarity of species distributions is not detected at the scale of 10×10 km of this study.

When evaluating the effectiveness of one taxon as a surrogate to represent another group of species in area selection, the issue of flexibility in area choice is commonly ignored; basically because the total number of alternatively fully flexible sets when considering near-maximum coverage problems is often far too large to assess exhaustively (see Williams *et al.*, 2000). However, a recent study by Hopkinson *et al.* (2001) indicates that significantly higher levels of overlap are found between pairs of minimum sets for different taxonomic groups when all fully flexible alternatives are considered than when one arbitrarily chosen priority set for each taxon are compared, as is the case in this study. That is, the current test could be viewed as a conservative evaluation of cross-taxon congruence.

Differences in sampling effort may inflate the coincidence of different taxa, if the same areas are more thoroughly sampled across taxa (i.e., grid cells containing nature reserves or close to cities). However, this is unlikely to be the case here, given the independence and different background among the various atlas surveys as

well as the general high level of standardization within surveys. A more likely cause of high coincidence of different taxa is that the fragmentation of the Danish landscape artificially (though the effect is real) restricts the occurrence of many species in some taxa (but less so in others, e.g., birds) to the seminatural and natural areas that are left. We possibly find higher congruence of species occurrence than would be found in a hypothetical, non-fragmented, biogeographically homogeneous, region of the same size as Denmark.

The present study investigated representativeness of total species richness in other taxa. However, a focal taxon could represent total species richness effectively and still miss species-poor taxa. It may be more appropriate to weigh taxa rather than species richness equally. When calculating mean % representation of all taxa in the Danish data set, we found that each of the six taxa represented the other taxa more effectively than mean random selection. The general pattern was as reported above: bats, butterflies, large moths and birds represent other taxa more effectively than amphibians/reptiles and click beetles. However, none of the taxa was more effective than the mean upper 95% confidence limit (except for all taxa at once). Furthermore, the 95% confidence intervals used here were calculated as the means of the confidence intervals for the representation of each of the taxa separately. These confidence intervals will probably be overestimates of the true confidence intervals, and so we refrain from interpreting these results further.

Contrary to expectations (Ryti, 1992; Balmford, 1998), the most species-rich group (birds) is not the most efficient in representing species richness in other groups. Further, the taxon poorest in species (bats) is an effective focal taxon, both at representing species richness in other groups and at selecting grid cells of high priority for other groups. Birds as a group comply with two key qualities considered important when the effectiveness of a focal taxon is evaluated: high species richness, as mentioned above, and a wide range of habitats spanned (Ryti, 1992; Faith & Walker, 1996a). A third key quality recently described by Williams *et al.* (2000) is that the more effective indicator group had low overlap in species distribution. Birds have wide ranges compared to other species, and this is probably why the bird group is not as effective as generally believed. Bats have less overlap among themselves in the Danish data compared to birds, not because of low overlap in habitat but rather because of fragmented and isolated pieces of woodland (woods or old trees are the primary habitat of bats as it is for most Danish species) and perhaps because of less thorough sampling than that of birds, the most intensively sampled taxa of all.

An important but as yet unattended issue that calls for further investigation has arisen from this study: how many complementary areas should a priority set include before it can be considered effective in preserving taxa other than the focal? Congruence between priority sets breaks down and disappears, as the number of areas in the priority sets is lowered (Tables 1 and 2). In this study, below approximately 20% of the data set patterns of

cross-taxon congruence in complementarity are statistically non-detectable. Accordingly, cross-taxon congruence in priority sets would not be an effective method to preserve all-over biodiversity at, e.g., an arbitrarily set conservation goal of 10%. This should be taken into consideration if cross-taxon relationships based on priority sets are to be used in practical conservation.

Specific comparisons of test results with those of other studies are not straightforward as all of our comparative analyses among taxa are conducted on fixed number of grid cells, i.e., equal sample sizes. This approach is in contrast to that of most previous studies of cross-taxon congruence (e.g., Prendergast *et al.*, 1993; Lombard, 1995; Dobson *et al.*, 1997; van Jaarsveld *et al.*, 1998; Reyers *et al.*, 2000) that have used unequal numbers of sampling units despite the fact that differing sample sizes can significantly influence derived statistics in comparative analyses of species richness and distribution (see, e.g., Colwell & Coddington, 1994). We will advocate our approach of standardization to equal sample sizes, although it could appear to come at the cost of losing information by the exclusion of grid cells that are surveyed for some but not all taxa (Fig. 1). Further, using our approach, the problem of false negatives has to be considered carefully, but this problem is inherent in most cross-taxon studies. However, taxa with full coverage are typically vertebrates rather than the less well-known invertebrate taxa which constitute > 95% of all animal diversity (May, 1999). Thus, reducing sample size to the level set by the less well-known taxa can actually be regarded as securing a more balanced, less vertebrate-biased information. Also, the challenge of predicting species distributions seems more likely to succeed if species share basic environmental conditions.

The study most comparable to our temperate study in overall analytical approach is Howard *et al.* (1998) from tropical Uganda, as they had all areas sampled for all taxa. The Ugandan study found cross-taxon congruence in complementarity for pairwise-compared areas in contrast to the lack of complementarity between pairwise-compared grid cells in our study. This indicates that this measure provides little information *per se* about the relative ability of different taxonomic groups to act as effective indicators. However, a main issue warrants some caution before drawing any firm conclusions: in the present study each grid cell supports a highly fragmented landscape. The 10 × 10 km grid is a coarse resolution with respect to Danish biotope size. Howard *et al.* (1998) exclusively sampled one spectrum of habitats (forests), but of varying sizes of areas. We speculate that homogeneity of habitat between sampled sites will accumulate less 'noise' from species associated with different habitats; distinct patterns of species distributions between cells in the Danish data may be smoothed by presence of many habitats within the same grid cell. Cross-taxon congruence in complementarity may arise because of heterogeneity of biogeography in Uganda, as hypothesized by Howard *et al.* (1998), but a limited range of habitats may be a precondition if the pattern is to be re-established in other regions.

When designing national and regional strategies for biodiversity prioritization, the best approach is to use quantitative, quality data from the same region and define appropriate focal taxa from these data (Ryti, 1992; see also McGeoch, 1998). If this is not possible owing to lack of time or funding, choice of focal taxa should be based on analyses made in regions of similar biogeography and land-use intensity. Indicator relationships cannot be assumed (Williams, 1998). The identification of guidelines on how to preserve overall biodiversity is far from accomplished, but where highly fragmented, temperate regions are concerned, our study indicates that cross-taxon congruence between complementarity-derived priority sets does exist. We propose that a combination of representativeness and *G*-statistics should be employed in future assessments of effectiveness of focal taxa. The ability to represent species richness in other groups will identify effective focal taxa and *G*-statistics analysis will provide additional information on correspondence between priority sets.

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