Building indicator groups based on species characteristics can improve conservation planning

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Abstract
How well can indicator groups, as sets of species with well-known distributions, represent the distribution of overall biodiversity to select networks of areas for conservation? In the literature, reliable indicator groups of complementarity have proven difficult to find, with some taxon-based indicator groups resulting in no more species represented than when areas are chosen at random. We rigorously test which quantifiable characteristics of species make them better components of indicator groups of complementarity in area networks. We find that even indicator groups comprised of randomly chosen, taxonomically unrelated species perform better than randomly chosen areas, and we demonstrate the improved efficiency of protected-area networks possible when using indicator groups chosen on the basis of species’ characteristics.

INTRODUCTION
Reliable indicators of the distribution of overall biodiversity would be a boon, because conservation efforts are severely limited by time and money, and because it is not possible to survey the distributions of all organisms (Ryti, 1992; Prendergast et al., 1993; Pearson & Carroll, 1998; Williams & Gaston, 1998; Ricketts, Daily & Ehrlich, 2002). We do not consider indicators of ecosystem health (Landres, Verner & Thomas, 1988), of environmental heterogeneity (Kremen, 1992), or of how the biota might respond to stress factors (Noss, 1990), an important distinction (McGeoch, 1998). Instead, our interest is in identifying important areas for the conservation of biodiversity. As networks of areas encompassing complementary biotas represent much more biodiversity than networks chosen on the basis of richness alone (Faith & Walker, 1996; Williams et al., 1996; Howard et al., 1998; Reid, 1998), a search for indicator groups (‘indicators’ henceforth) for species richness (Prendergast et al., 1993) has shifted towards a search for groups of species whose individual distributions complement one another, and which when taken together capture much of the biodiversity of the region. Such indicator groups are sometimes called indicators of (high) complementarity.

We are interested in how well indicator groups, as sets of species with well-known distributions, represent the distribution of overall biodiversity when they are used to select networks of areas for conservation. In particular, we seek to identify which characteristics of species make them better components of indicator groups. Reliable indicators of complementarity have proven difficult to find (van Jaarsveld et al., 1998; Lund & Rahbek, 2002), with some indicators resulting in no more species being represented than when areas are chosen at random.

Some authors have suggested which species’ characteristics make them better components of indicator groups for complementarity (Table 1). To date, no one has tested these ideas rigorously. In addition to the hypotheses listed in Table 1, Howard et al. (1998) stated that successful indicators of complementarity will share ‘similar patterns of biogeography’ with the group of species to be indicated, but without defining these precisely. Andelman & Fagan (2000) reviewed many ways to characterize indicator groups, but found equivocal results for the three systems and scales that they considered. However, they restricted indicator and indicated groups to threatened species, which may have constrained their findings.

We add to this list four potential predictors of complementarity (a variety of range-sizes, measured by variance of ranges of the indicator group; mean number of ecoregions occupied by an indicator species; the variance in number of indicator presence records among ecoregions containing indicator species; mean body-size). We suspect that a successful indicator group will have species with non-overlapping ranges, so better indicator groups should tend towards small mean range-size. We know that uniformly widespread species will not be useful in an indicator group, so we also check to see if a variety
of range-sizes is important. Because range-size and body-size are related (Burness, Diamond & Flannery, 2001) but not interchangeable, we suspect that small mean body-size and a large variance in body-sizes may together be good predictors of complementarity. As an indication of the regional habitat specialization of the indicator group, we calculate the mean number of ecoregions occupied by the indicator group and the evenness of indicator species records among the ecoregions they occupy.

First we assess whether randomly chosen indicator groups can represent broader biodiversity within conservation area networks at a coarse scale within Europe. Second, we test hypotheses for quantifiable characteristics of indicator groups that make them better indicators of complementarity. We then demonstrate how using these characteristics can improve the performance of indicator groups.

MATERIAL AND METHODS

Species distribution data

Distribution data are taken from the European atlases for birds (Hagemeijer & Blair, 1997), mammals (Mitchell-Jones et al., 1999), reptiles and amphibians (Gasc et al., 1997), and the 20% of plants that have been mapped (Jalas & Suominen, 1972–94; Jalas, Suominen & Lampinen, 1996). Most eastern regions of Europe are sampled less intensively than the west (by consensus of the atlas data providers), so we do not include the European part of the former Soviet Union, but do include the Baltic countries and the Kaliningrad region. We also exclude Svalbard and the Azores, because we do not have ecoregion data available for them (see below). After excluding these regions, 2327 species of plants, 149 amphibians and reptiles, 432 birds and 184 mammals remain for analysis, distributed among 2375 50 × 50 km grid cells.

Predicting indicator success

We examine 11 factors suggested in previous studies to contribute to better indicators of complementarity, and four new ones (Table 1).

<table>
<thead>
<tr>
<th>Authors</th>
<th>Suggested predictors</th>
<th>Measure used for this analysis</th>
<th>Species in this analysis</th>
</tr>
</thead>
</table>
| Ryti, 1992 | 1. More species  
2. Proportion of plants in indicator group  
3. Proportion of narrowly distributed plants in indicator group  
4. Small range-sizes of indicator species | 1. No. of indicator species [explicitly set]  
2. Same (prop plants)  
3. Proportion of plants with ranges in the lowest 25th percentile (prop r plants)  
4. Mean range-size (mean ind range) | All |
| Andelman & Fagan, 2000 | 1. Widespread, threatened species in indicator group  
2. Large carnivores in indicator group  
3. Threatened species in indicator group | 1. Mean number of threatened species that have ranges in the 75th percentile (mean wide thr)  
2. Number of carnivorous species that have body-sizes in the top 25th percentile (mean lg carn)  
3. Proportion of threatened species in indicator group (prop thr) | Birds and mammals |
| Williams et al., 2000 | 1. Small range-sizes of indicator species  
2. Narrow endemism of indicator species  
3. Low range-overlap among indicator species | 1. Mean range-size (mean ind range)  
2. Proportion of indicator species confined to one grid cell (prop ind single recs)  
3. Mean indicator richness among grid cells with indicators (mean ind rich) | All |
| Faith & Walker, 1996; Williams et al., 2000 | High ‘ecological complementarity’ among indicator indicator species | Total ecoregions encompassed by the indicator group over mean number of ecoregions per indicator species (sum ER/mean ER) | All |
| Stork, 1994 | Variance in body-sizes of indicator group | Variance of body-sizes (var body) | Birds and mammals |
| (original) | 1. Indicator species with different range-sizes  
2. Habitat specialization of indicator species  
3. Evenness of indicators in ecoregions  
4. Small body-sizes of indicator species | 1. Variance of range-sizes (var ind range)  
2. Mean number of ecoregions occupied by an indicator species (mean ER)  
3. Among ecoregions with indicators, variance in number of indicator records (var ER)  
4. Mean body-size (mean body) | All (1–3), birds and mammals (4) |
averaged data among all available samples. The ecoregion data (DMEER), from the European Environment Agency (2000), aim to show distinct ecological regions in Europe, summarizing climatic, topographic and ‘geobotanical’ information, as well as expert opinion from WWF and several European nature-related institutions. The International Union for the Conservation of Nature (IUCN) provided threat-status data.

To compare our results with those of other authors, we needed to incorporate information that did not pertain to or was not available for all species in the database (e.g., body-size, carnivore status). Thus, for some analyses, we restricted our indicator group to those species for which we had these data: birds and mammals (Table 1).

 Trials of artificial ‘indicator groups’

We formulated scenarios consisting of an indicator group-size/network size/species group combination. There are three indicator group-sizes (10, 31 or 155 species), three network-sizes (24, 50 or 118 areas), and two species groups (any species, or only birds and mammals), for a total of 18 scenarios. With every choice of indicator group, the target group changes in composition. We do not expect this to represent a serious bias, as the size of the indicator group is always a very small proportion of the database. Even choosing 155 species for the indicator group leaves 2937 species in the target group. Then, for each scenario, we chose a group of species at random (disregarding taxonomic group) as the ‘indicator group’ and used it to choose a near-maximum-coverage network of complementary areas (Williams et al., 1996). If the specified number of areas is more than enough to capture the diversity of the indicator group, the Worldmap algorithm then chooses areas that give multiple representations of species (for details, see Williams, Burgess & Rahbek, 2000, Table 1). We repeated this process 500 times, tallying the non-indicator biodiversity captured within the network of areas, and calculating the values of the candidate predictor variables.

When choosing sets of areas, often there are several sets that could achieve the same representation of the indicator species (flexible alternative sets), though not necessarily the same representation of the target species (Williams et al., 2000; Hopkinson et al., 2001). We have no reason to suspect systematic bias in our results arising from choosing just one set, because we used a random tie-breaking rule. Therefore when there is flexibility, the set of areas obtained for each indicator group should be an unbiased, random choice.

Statistics: regression trees

We used regression tree analysis (Breiman et al., 1984) to assess the relationships between the predictors (Table 1) and the response (the number of species represented in the conservation network). Regression tree analysis is a non-parametric alternative to multivariate regression, useful for those situations when there is no a priori expectation of the form (e.g., linear) that a relationship between predictor and response might take. As the number of predictors increases, interactions among predictor variables become more difficult to model. Regression trees allow us to discern complex interactions within the set of predictors, which need not be multiplicative.

The analysis relies on recursive partitioning of the data set into groups whose elements are most similar to one another. At the start, the user has one data set (the complete set of observations). The data set is examined and divided according to the values of one of the predictor variables, resulting in two groups of observations each of which is more homogeneous (for that predictor variable) than the original complete data set. This process continues until various stopping criteria are met (e.g., subgroup-size cannot be smaller than a given number). The tree of subgroups and the decision rules that produced them is ‘overfit’, and is typically more complex than is useful to the user. It can then be pruned back to a complexity and accuracy of prediction that the user finds acceptable. We noted that pruning the trees back so that the heterogeneity within subgroups is reduced by 50% resulted in trees of relatively few nodes, while retaining predictability that was acceptable to us. This is analogous to explaining 50% of the variation in the predictor data and is the decision rule we adopted. For each of our scenarios, we produced such regression trees, and recorded how well they predicted number of species represented in the conservation network and which predictors were necessary for this prediction.

Statistical independence of indicator groups

Some species will be included in more than one indicator group when groups are chosen repeatedly at random. Choosing indicator species ‘with replacement’ within a set of 500 trials (but not within any single trial) allows many more combinations of species to be chosen. This process permits us to estimate more accurately whether groups of species with particular characteristics make indicator groups more efficient. However, the statistical dependence of such groups concerned us because it contravenes the assumptions of most statistical analyses. To address this concern we also chose indicator species without replacement within each series of trials. This necessarily reduced the number of trials we could complete (with 3092 species, if we chose indicator groups of size $n$ without replacement, then we could do only 3092/$n$ trials). Nonetheless, we ran series of trials choosing indicator groups without replacement for comparison to our original trials.

RESULTS

Can indicators work?

Table 2 shows the proportion of trials in which an indicator group (used to choose an area network) represents significantly more species than a same-size network chosen at random (simulated 2000 times, using upper 5% tail of species represented for comparison). As
the number of areas in the conservation network increases, the proportion of trials that perform significantly better than random area selections decreases.

Table 2 also shows that using larger indicator groups offsets the decrease in efficiency as the number of areas increases, so that for indicator groups composed of any species from the database, we only need 1% of those species to achieve better performance in almost all trials. If our indicator group is composed only of birds and mammals, performance is still better than random choice of areas most of the time. Results from the trials without replacement of species (Table 2, right column) support these findings, although these results rely on far fewer trials. Because these results are consistent with the trials with replacement, from this point forward we concentrate on the latter.

Are there predictors of good indicators?

The regression trees estimate the number of species represented in a conservation network, based on the characteristics of the indicator group. For each scenario, Table 3 shows the number of species represented in the best conservation network (‘Highest expected number of species represented’), and which predictors made significant contributions.

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### Table 2. Proportion of the 500 area networks chosen using trial indicator groups that represent significantly more non-indicator species than area networks chosen at random

<table>
<thead>
<tr>
<th>Indicator group size</th>
<th>Network size</th>
<th>With replacement</th>
<th>Without replacement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Birds &amp; mammals</td>
<td>Any species</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>24</td>
<td>0.03</td>
<td>0.30</td>
</tr>
<tr>
<td>31</td>
<td>24</td>
<td>0.29</td>
<td>0.99</td>
</tr>
<tr>
<td>155</td>
<td>24</td>
<td>0.98</td>
<td>1.00</td>
</tr>
<tr>
<td>10</td>
<td>50</td>
<td>0.01</td>
<td>0.09</td>
</tr>
<tr>
<td>31</td>
<td>50</td>
<td>0.12</td>
<td>0.96</td>
</tr>
<tr>
<td>155</td>
<td>50</td>
<td>0.85</td>
<td>1.00</td>
</tr>
<tr>
<td>10</td>
<td>118</td>
<td>0.01</td>
<td>0.07</td>
</tr>
<tr>
<td>31</td>
<td>118</td>
<td>0.07</td>
<td>0.85</td>
</tr>
<tr>
<td>155</td>
<td>118</td>
<td>0.67</td>
<td>1.00</td>
</tr>
</tbody>
</table>

### Discussion

Our results (Table 2) appear to show that using indicators gives little improvement over choosing areas at random when the number of areas chosen is large. This might be taken as justification for dispensing with quantitative methods and for selecting areas at random (and saving money on sampling!). A previous study (Williams et al., 2003) similarly showed that performance of random area selection approaches that of the complementarity algorithm as number of areas selected increased, but only when the performance criterion is the number of species represented at least once. However, the same study went on to show that when the performance criterion is number of representations of each species, then as area selected increases, the complementarity algorithm increasingly outperforms choosing areas at random. These multiple representations of species are important because they confer increased probability of long-term persistence.

When the number of areas chosen is small relative to the total area (the more realistic case for conservation), then the divergence between choosing areas at random and using data-directed selection is more apparent. We expect that species distribution data contain information on faunal and
Table 3. Predictors of indicator success, with prediction of best number of species represented. For a key to predictor abbreviations, see Table 1. All ‘highest expected number of species represented’ are statistically better than would be expected by chance ($P < 0.001$).

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Birds and mammals as indicators</th>
<th>Any species as indicators</th>
</tr>
</thead>
<tbody>
<tr>
<td>Indicator group-size</td>
<td>Network-size</td>
<td>Highest expected number of species represented (size of terminal branch)</td>
</tr>
<tr>
<td>10</td>
<td>24</td>
<td>1501 (25)</td>
</tr>
<tr>
<td>31</td>
<td>24</td>
<td>1600 (26)</td>
</tr>
<tr>
<td>155</td>
<td>24</td>
<td>1662 (20)</td>
</tr>
<tr>
<td>10</td>
<td>50</td>
<td>1636 (20)</td>
</tr>
<tr>
<td>31</td>
<td>50</td>
<td>1830 (24)</td>
</tr>
<tr>
<td>155</td>
<td>50</td>
<td>1872 (50)</td>
</tr>
<tr>
<td>10</td>
<td>118</td>
<td>1948 (43)</td>
</tr>
<tr>
<td>31</td>
<td>118</td>
<td>2090 (23)</td>
</tr>
<tr>
<td>155</td>
<td>118</td>
<td>2154 (50)</td>
</tr>
</tbody>
</table>

Fig. 1. Regression tree for ten species choosing 24 areas, where birds and mammals were indicators. Logical decision rules (generated from classification according to the predictor variables) govern how data are partitioned throughout the tree: true (false) outcomes on the left (right) branch. Numbers in parentheses represent the number of trials included below that point (of 500 total); all other numbers are the mean number of species represented in a conservation network at that point in the tree. The leftmost terminal node shows the species represented in a conservation network if the indicator group chosen has a var ER < 41,419 and mean ind rich < 1.8. Twenty-five of the 500 trials are represented in this terminal node, and the expected number of species in the conservation network is the average number of species represented among those 25 trials, 1501.

Fig. 2. A representative view of the improvement in performance of an indicator group, when the predictors from Table 3 are used to choose it (20 hand-picked groups, black bars). The gray bars are the trial ‘indicator groups’ constructed at random using 155 species to choose a network of 24 areas; height of the bars shows the frequency, the x-axis is the number of non-indicator species represented in the conservation network chosen using the ‘indicator group’. Leftmost on the x-axis is the upper 5% threshold of significance for choosing 24 areas at random; rightmost is the best 24-area network possible using all of the European species data. The black bars show a marked improvement in species representation than in the ‘indicator groups’.
floral differences among areas that will make indicator groups better at representing biodiversity. This idea is intuitive, but has not been assessed previously. Our results show that even randomly chosen indicator groups can perform well at representing the rest of the biodiversity of a region. Our method requires only 1% or 5% of the species to be included, and its utility is particularly apparent when all species are permitted as members of indicator groups. Of course this conclusion carries with it the implicit assumption that our knowledge of the indicator species’ distributions concerned is relatively complete.

We have shown that we can improve indicator performance even further. When we hand-picked indicator groups with particular characteristics that we found to be useful (e.g., a group with small mean range-size), we found that we can increase the number of species represented in the conservation network. For the scenario pictured in Figure 2, this improved performance represents an average of 160 more species protected in the network. However, also from Figure 2, we can see that the very best network of 24 areas (a minimum set, see Williams et al., 2000) protects 2293 species, and our hand-picked indicator groups result in fewer than 2100 species protected. With complete information on all species and distributions, performance will always be better.

Comparing our predictor variables with those of previous studies, we agree with others (Ryti, 1992; Williams et al., 2000) that small range-sizes of the indicators are predictors of good performance. In contrast, narrow endemism, measured here as species occupying one 50 km square, and low range-overlap among indicator species, were not consistent predictors of good indicator groups. We support Ryti’s (1992) assertion that more indicator species, and particularly more plant species, aid the success of an indicator group. However, contrary to Ryti’s result, we find that narrowly distributed plants are useful indicators. Our hypothesis that a range of body-sizes, as well as a tendency for small body-size, should be good predictors is supported in part by these European data. Our ecoregion-based predictors, mean ER, sum ER/mean ER, and var ER, measuring habitat specialization, ecological complementarity and evenness of indicators within ecoregions respectively, all proved very useful predictors of good indicators. We did not find any support for using widespread threatened species in an indicator group, contrasting with Andelman & Fagan (2000). We also did not find any support for using large carnivores in an indicator group, consistent with Andelman & Fagan (2000) and Linnell, Swenson & Anderson (2000). Linnell et al. showed that the large carnivores of Scandinavia thrive in human-modified habitats, and concluded that they will not necessarily indicate broader biodiversity. Sometimes we found threatened species to be good predictors, but possibly because of the correlation between threat and small range-size.

The performance of indicator species must depend on the relationship between patterns in the distribution data for the indicators and the target species to be indicated, e.g., patterns of prevalence or rarity. The algorithm only ‘sees’ and responds to a species’ presence or absence in any particular location. These distribution patterns arise in part from ‘secondary’ properties of the species, such as their ecological relationships, e.g., a body-size/range-size relationship. Most predictors in Table 1 can be classified as a ‘distributional’ predictor or an ‘ecological’ predictor. Any predictability of complementarity should be explicable by examining how a distributional predictor affects area selection, but understanding how an ecological predictor works could lead to more useful generalizations about the ecological relationships that might be expected of good indicators.

CONCLUSIONS
From these data we conclude that an indicator group formed even as a random sample from a small proportion of the species (merely 1% if we use all species) performed significantly better than would be expected by selecting areas at random. This is likely to be true in general if the indicator species distributions contain a sample of information on the general patterns of complementarity. Among the predictors based purely on the geographic distributions, an indicator group is likely to maximize success if it includes species tending to have small geographic ranges or if it encompasses a variety of range-sizes. From the predictors based on broader biological characteristics, better indicator groups are likely to include more species with small body-sizes, or species with a variety of body-sizes (these characteristics are probably associated with small ranges or a variety of range-sizes). Last, we have shown that using these predictors can indeed build a better indicator group. It may be that the success we enjoyed here varies with scale (an analysis of this issue is in preparation) or will not be realized in other areas of the world; whether our results generalize in these ways remains to be seen.

Acknowledgements
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