
Rare Species and the Use of Indicator Groups for Conservation Planning

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Abstract: *Indicators of biodiversity have been proposed as a potential tool for selecting areas for conservation when information about species distributions is scarce. Although tests of the concept have produced varied results, sites selected to address indicator groups can include a high proportion of other species. We tested the hypothesis that species at risk of extinction are not likely to be included in sites selected to protect indicator groups. Using a reserve-selection approach, we compared the ability of seven indicator groups—freshwater fish, birds, mammals, freshwater mussels, reptiles, amphibians, and at-risk species of those six taxa—to provide protection for other species in general and at-risk species in particular in the Middle Atlantic region of the United States. Although sites selected with single taxonomic indicator groups provided protection for between 61% and 82% of all other species, no taxonomic group provided protection for more than 58% of all other at-risk species. The failure to cover at-risk species is likely linked to their rarity. By examining the relationship between a species' probability of coverage by each indicator group and the extent of its geographic range within the study area, we found that species with more restricted ranges were less likely to be protected than more widespread species. Furthermore, we found that although sites selected with indicator groups composed primarily of terrestrial species (birds and mammals) included relatively high percentages of those species (82–85%) they included smaller percentages of strictly aquatic species (27–55%). Finally, of both importance and possible utility, we found that at-risk species themselves performed well as an indicator group, covering an average of 84% of all other species.*

Especies Raras y el Uso de Grupos Indicadores para la Planeación de la Conservación

Resumen: *Los indicadores de la biodiversidad han sido propuestos como una herramienta potencial en la selección de áreas para conservación cuando la información sobre la distribución de algunas especies es escasa. A pesar de que algunas evaluaciones de este concepto han producido resultados variados, los sitios seleccionados para evaluar grupos indicadores pueden incluir una alta proporción de otras especies. Evaluamos la hipótesis de que las especies en riesgo de extinción probablemente no se incluyan en sitios seleccionados para proteger grupos indicadores. Usando la metodología de selección de reserva, comparamos la capacidad de siete grupos indicadores (peces de agua dulce, aves, mamíferos, almejas de agua dulce, reptiles, anfibios y especies en riesgo de estos seis taxones) para proveer protección a otras especies en general y especies en riesgo, en particular, en la región del Atlántico Medio de los Estados Unidos. A pesar de que los sitios con un solo grupo indicador proporcionaron protección para el 61% al 82% de todas las otras especies, ningún grupo taxonómico proporcionó protección para más del 58% de todas las otras especies en riesgo. La incapacidad de proteger especies en riesgo posiblemente se vincule con su rareza. Al examinar la relación entre la probabilidad de cobertura de una especie para cada grupo indicador y la extensión de su rango geográfico dentro del área de estudio, encontramos que las especies con rangos más restringidos tenían menor probabilidad de ser protegidas que las especies de distribución más amplia. Además, encontramos que, a pesar de que los sitios seleccionados con grupos indicadores compuestos principalmente por especies*

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terrestres (aves y mamíferos) incluyeron porcentajes relativamente altos de estas especies (82%–85%), éstos incluyeron porcentajes más bajos de especies estrictamente acuáticas (27%–55%). Finalmente, de importancia y posible utilidad, encontramos que las especies en riesgo, por sí mismas, funcionaron bien como grupo indicador, abarcando, en promedio, el 84% de todas las otras especies.

Introduction

Conservation planning must often be conducted in the absence of even the most basic information about species distributions. Indicators of biodiversity have been proposed as one possible tool for addressing this problem (Kremen 1992; Raven & Wilson 1992; Flather et al. 1997). In the context of selecting areas for conservation, the indicator concept is based on the assumption that areas selected to address members of an indicator group also capture a broad range of other organisms or conservation targets. Potential indicator groups that have received attention include well-known taxa, species of conservation concern, and landscape features or vegetation types (Prendergast et al. 1993; Wessels et al. 1999). Tests of the performance of these indicator groups have yielded mixed results (Howard et al. 1998; Ricketts et al. 1999; Andelman & Fagan 2000).

Sites selected to include members of an indicator group have the potential to cover a large percentage of organisms outside the group if the distributions of the members of the group are representative of a larger set of organisms. Simple tests of taxonomic indicators have often failed to show a strong coincidence of cross-taxon patterns of species richness and hotspots of richness or rarity hotspots (Prendergast et al. 1993; Dobson et al. 1997). Furthermore, the congruence of cross-taxon patterns of diversity and rarity tend to vary across scales and in different areas (Flather et al. 1997). Despite this lack of coincidence, taxonomic indicators perform well when tested with the concept of complementarity, which is the idea that areas selected to cover all species of an indicator group often include a high proportion of other species as well (Howard et al. 1998). Again, however, the results of similar tests have varied depending on the composition of the indicator group and the scale of the study (Flather et al. 1997).

In the absence of cross-taxon patterns in species distributions, the success of a taxonomic indicator group derives, in part, from its ability to effectively sample a wide range of environmental conditions (Kremen 1992; Margules et al. 1994; Faith & Walker 1996). Thus, indicator groups work by increasing the probability of including any given nonindicator species by sampling distinct regions of the environmental space. Species with different distributions will likely be differentially covered by this sampling. In general, widely distributed species are more likely to be covered by sites selected to cover an

indicator group. Unless there is a strong congruence of cross-taxon patterns of the distributions of species at risk of extinction, these species should be poorly covered by indicators. To date, such congruence has not been demonstrated (Lombard 1995; Dobson et al. 1997; Kerr 1997). Because rare species are often those most likely to be lost if they are not protected, it is crucial that we understand the degree to which they are included in selected sites if indicator groups are to be used as a conservation tool.

We investigated the ability of indicator groups to provide coverage for at-risk species. We used seven different indicator groups composed of, respectively, freshwater fish, birds, mammals, freshwater mussels, reptiles, amphibians, and at-risk species from those six taxa. First, we examined the ability of indicator groups to provide protection for all species and more specifically for species at risk of extinction. We conducted these analyses by selecting sites that included all members of an indicator group. We then tallied the number of species and at-risk species that were included in those sets of selected sites. To investigate potential explanations of indicator performance, we examined cross-taxon distribution patterns of at-risk species and the relationship between the geographic range of species and their likelihood of protection by different indicator groups.

Methods

The study encompassed an area of the eastern United States including the states of Delaware, Maryland, Pennsylvania, West Virginia, and Virginia. We used a hexagonal grid with 487 cells of approximately 650 km² each to delineate the sites from which all selections were made (White et al. 1992). Species-occurrence records for 772 species from six taxonomic groups were compiled for the 487 sites (Table 1). The research, compilation, digitization, and quality control of the species-occurrence data were carried out by the Natural Heritage programs in each state as directed and assisted by staff of The Nature Conservancy (Master 1996). The data included all native species with confirmed or probable status in each 650-km² hexagon. Status was derived from the literature, museum records, experts, and digital databases. Only species known to be native to a site were included in the site's species-occurrence list. The database was re-

Table 1. The number of species, species at risk of extinction, and sites required to cover all species of each of seven indicator groups used for reserve selection in the Middle Atlantic region of the United States.

<i>Indicator group</i>	<i>Number of species</i>	<i>Number of at-risk species</i>	<i>Number of sites required to include all species</i>
Freshwater fish	251	37	26
Birds	208	3	17
Freshwater mussels	96	37	14
Amphibians	78	6	14
Mammals	76	4	10
Reptiles	63	4	12
At-risk species	91	91	24

viewed by selected groups of experts for each of the six taxonomic groups.

We defined at-risk species using the three most sensitive classes—critically imperiled, imperiled, and vulnerable—of a five-class global ranking system (Master 1991). The database contained 91 at-risk species, the majority of which were freshwater fish and mussels (Table 1).

We used two approaches to test the performance of indicator groups. First, we selected the smallest sets of sites that included each species in the indicator group at least one time; this is full-set coverage, known as the “set coverage location problem” (Underhill 1994). This approach allowed us to evaluate the best possible performance of each group. Second, we selected sets of 10 sites each that included the maximum possible number of species in each indicator group; this is partial-set coverage, known as the “maximal covering location problem” (Church et al. 1996). This approach provided a more consistent basis for comparing the performance of the different indicator groups by standardizing the number of sites used. We chose to use 10 sites for our standard comparison because this was the smallest number of sites required by any one indicator group for complete coverage of all species in the group. For comparison, we also selected sets of 10 sites at random and sets of 10 sites to protect all species from all six taxa (a simple null model and the ideal set of sites, respectively).

We selected sets of sites with a simulated annealing algorithm (Kirkpatrick et al. 1983; Possingham et al. 2000). Simulated annealing is a stochastic optimization technique that derives its name from the annealing of metals and glass. Simulated annealing works by iteratively perturbing and testing potential solutions to a given problem. Improvements over previous solutions are always accepted, but poorer solutions are accepted with some probability that diminishes over the course of the iterations. By occasionally accepting worse solutions, simulated annealing attempts to avoid finding “local” optima and increases the probability of finding the global optimum. Simulated annealing is one of many techniques

that have been used to solve reserve-selection problems (Csuti et al. 1997; Pressey et al. 1997). Although it does not guarantee the optimal solution that would be provided by an integer-programming approach, simulated annealing is relatively efficient and performs well in comparison to other selection techniques (Cocks & Baird 1989; Csuti et al. 1997).

There are often multiple sets of sites that provide solutions to the types of reserve-selection problems we addressed; therefore, we used simulated annealing to select 100 sets of sites for each indicator group, for both the full-set and partial-set analyses. Each set of sites in a group of 100 was composed of the smallest number of sites that included all species (full-set analysis) or protected the maximum number of species in 10 sites (partial-set analyses). For example, the best solutions obtained through simulated annealing used 26 sites to protect all freshwater fish species. Thus, all 100 sets of sites selected for fish in the full-set analysis were composed of 26 sites. For the partial-set analysis, the best solutions of 10 sites obtained through simulated annealing for fish covered 228 (91%) of the 251 fish species. Because simulated annealing often produces suboptimal answers as well, we ran the algorithm enough times to produce 100 of the best solutions. From the sets of 100 sites, we then analyzed only those solutions that were unique, the number of which varied by indicator group. In the full-set analysis, for example, we found 100 unique sets of sites that covered all fish, but only 35 unique sets of sites that covered all mussels.

We compared the means of the number of nonindicator species protected by each set of unique solutions across indicator groups for both full-set and partial-set analyses using analysis of variance with Tukey-Kramer tests for unplanned comparisons. Although the sets of sites used in these analyses were unique, the fact that solution sets for a given indicator group often contained very similar groups of sites means that they were not independent samples. Thus the results of the Tukey-Kramer tests should be viewed conservatively. In addition to these analyses, we report the means and standard deviations of the percentage of species covered by each indicator group.

To investigate the congruence in cross-taxon distribution patterns of at-risk species, we first mapped the occurrences of the at-risk species of each taxon. We used pair-wise comparisons made with a modified Cramér von Mises test (Syrjala 1996) to test for differences in the spatial distributions of at-risk species counts for the different taxa. We then calculated the number of different taxa represented by at least one at-risk species in each site.

We examined the relationship between the geographic range of a species and the protection afforded it by indicator groups by using the sets of sites selected to protect each indicator group in our full-set analyses. For each species in the data set, we compared the propor-

tion of the study area over which the species occurred and the proportion of sets of sites in which that species was protected.

Results

Sites selected for full coverage of indicator taxa included, on average, between $61 \pm 3\%$ and $82 \pm 1\%$ of all other species (Fig. 1a). The number of sites required for full coverage ranged from 10 for mammals to 26 for fish (Table 1). The sets of 10 sites from our partial-set analyses included fewer species but in general showed similar patterns of relative indicator performance (Fig. 1b). Although all indicator groups provided better coverage for other species than did sets of randomly selected sites ($p < 0.05$), the performance of mammals and birds as indicators were only slightly better than the performance of randomly selected sites. Sites selected to cover

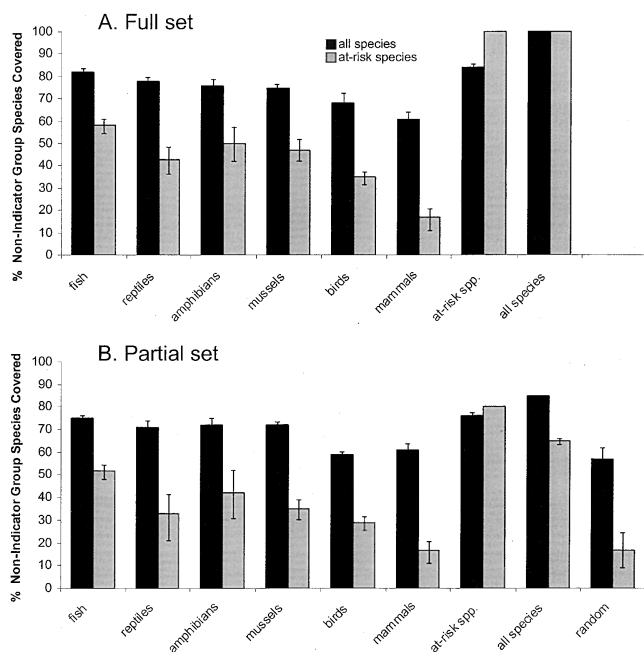


Figure 1. The percentage of all nonindicator group species and all nonindicator at-risk species included in (a) sets of sites selected to cover all members of indicator groups and (b) sets of 10 sites selected to maximize the number of indicator group species covered. Each set of bars represents the mean percentage of species included in multiple unique sets of sites selected for each indicator group. The numbers of unique sets of sites for the full-set analyses were 100 for fish, amphibians, birds, and reptiles; 99 for mammals; 98 for at-risk species; and 35 for mussels. The number of unique sets compared in the 10-site analysis are listed in Table 2. Error bars represent \pm SD.

mammals and birds included a high percentage of the species in those groups ($82 \pm 2\%$ and $85 \pm 2\%$), but they included relatively few strictly aquatic species (fish and mussels) ($27 \pm 5\%$ to $55 \pm 2\%$) (Table 2). Conversely, sites selected to cover fish and mussels included a relatively large proportion of each of the six taxa ($62 \pm 2\%$ to $83 \pm 1\%$).

Although indicator groups protected a relatively large percentage of all other species, they protected rather low percentages of at-risk species (Fig. 1). Even when full coverage of the indicator groups was required, the best-performing indicator, fish, only included $58 \pm 3\%$ of all other at-risk species. Mammals provided the worst coverage of at-risk species, $17 \pm 5\%$. Despite this overall poor performance, some indicator groups provided better protection for the at-risk species of certain taxa than for those of others (Table 2). For example, sets of 10 sites selected to protect birds included an average of $80 \pm 10\%$ of the four reptile species, amphibians provided protection for $74\% \pm 18\%$ of the four mammal species, and mussels protected $67\% \pm 0\%$ of the three bird species. Although the indicator groups generally did not provide protection for most at-risk species, we found that at-risk species used as an indicator group outperformed each of the taxonomic groups (Fig. 1, Table 2).

With the exception of fish and mussels, the six taxa showed rather disparate distributions of at-risk species (Fig. 2a–2f). All 15 pairs of taxa had different spatial distributions of at-risk species ($p < 0.003$). Of the 487 sites, 180 (37%) contained at least one at-risk species from one of the six taxa, 101 (21%) had at-risk species from two taxa, 27 (6%) from three taxa, and 3 (<1%) from four taxa (Fig. 2g). No sites contained at-risk species from more than four of the six taxa.

Individual at-risk species occurred in <1% to 17% of the sites in the study region ($\bar{x} = 2 \pm 3\%$). The proportion of sites occupied by a species was positively related to the probability of inclusion in sites selected to cover indicator groups (Fig. 3). In general, species occurring in at least 20% of the sites in the study region were always included in selected sets of sites, but the probability of inclusion was variable for species that occupied <20% of the sites in the region. This potential threshold appeared to be lower (between 10% and 20% of the study region) for fish and bird indicators and higher (from 25% to 50% of the study region) for the other four taxa.

Discussion

Our results indicate that sites selected with taxonomic indicator groups can include a large percentage of other species (Fig. 1). Although other researchers have reached similar conclusions, many have found that indicator groups fail to outperform randomly selected sites or that

Table 2. Percentage of species in each of six taxa included in sites selected to protect each of nine indicator or target groups.

Indicator or target group (n) ^b	Percentage of species covered (% of at-risk species covered) ^a					
	fish	reptiles	amphibians	mussels	birds	mammals
Fish (4)	91 (88)	65 (25)	62 (21)	73 (63)	83 (33)	81 (31)
Reptiles (100)	65 (33)	97 (100)	69 (9)	52 (38)	85 (0)	79 (57)
Amphibians (100)	72 (42)	71 (42)	95 (77)	53 (63)	76 (36)	81 (74)
Mussels (68)	73 (41)	62 (2)	62 (3)	96 (94)	74 (67)	79 (38)
Birds (95)	55 (27)	73 (80)	62 (10)	39 (50)	97 (95)	85 (54)
Mammals (99)	49 (14)	76 (57)	72 (24)	27 (11)	82 (53)	100 (100)
At-risk species (50)	74 (84)	72 (80)	74 (34)	74 (84)	81 (100)	82 (62)
All species (2)	85 (88)	81 (50)	81 (42)	78 (65)	91 (33)	87 (50)
Randomly selected sites (100)	48 (18)	59 (20)	54 (7)	27 (36)	74 (9)	77 (32)

^aPercentage of species in each of six taxa included in sets of 10 sites selected to cover members of each of seven indicator groups, sites selected to cover all species, and randomly selected sites. The mean percentage of species included by multiple unique sets of sites is reported. Standard deviations ranged from <1% to 6% for all species (with the exception of mussels by reptiles, amphibians, and randomly selected sites [SD = 11%–13%]) and 0% to 23% for at-risk species.

^bNumber of unique sets of 10 sites used to calculate the mean percentage of species and at-risk species protected by each indicator or target group.

successful indicator groups require the selection of large areas of land (Lomolino 1994; Howard et al. 1998; Andelman & Fagan 2000). Contrary to these findings, several of our indicator groups performed better than sites selected at random and required the selection of relatively small percentages (2–5%) of the study region. Despite these relatively optimistic results, our study highlights a critical shortcoming of many indicator groups. Unless the distributions of the rare species in an indicator group closely correspond to the distribution of other rare species, these species are not likely to be included in sites selected with indicator groups.

There are several important criteria to consider when selecting groups of species to be used as indicators of biodiversity (Pearson & Cassola 1992; Pearson 1994). First, the distributions of species in the groups should be well-known or easily determined. Unfortunately, the best-monitored and best-described species have not always performed well as indicators (Lawton et al. 1998; Ricketts et al. 1999). Likewise we found that birds and mammals, the two best-known taxa worldwide (Tuxill 1998), were poor indicators of other species in general and of at-risk species in particular (Fig. 1). The failure of both birds and mammals as indicator groups in our study was driven in large part by their inability to protect aquatic species (Table 2). Not surprisingly, these results indicate that conservation-planning efforts based solely on terrestrial indicators may inadequately address the needs of aquatic species.

A second criterion for indicator-group selection pertains to both the diversity of areas inhabited by the group as a whole and the specificity of the habitats occupied by each species in the group. A good indicator group is likely to have many species and species with relatively distinct ranges covering many different environments (Ryti 1992; Pearson 1994; Faith & Walker 1996). The best taxonomic indicator in our study—

fish—fit these criteria well. The range of indicator groups we tested, however, was limited by the availability of data in our study region. It is possible that groups of other species, such as insects, that generally respond to more fine-grained differences in habitat would perform better as indicator groups. Furthermore, indicator groups composed of species from diverse taxonomic groups might be expected to perform well as indicators if species in those groups respond differently to environmental gradients (Pearson 1994; Ricketts et al. 1999). In support of this prediction, we found that at-risk species, a taxonomically diverse group in our study, was the best-performing indicator group overall.

Researchers testing indicators of biodiversity have often come to rather different conclusions (e.g., Prendergast et al. 1993; Howard et al. 1998; van Jaarsveld et al. 1998). The variation in the results of these and other studies is driven in part by the differences in the indicator groups tested, the scales of the analyses, the methods used to test the indicators, and the areas in which the studies were conducted. For example, the differences between the results of our analyses and those of Andelman and Fagan (2000) result largely from the different ways in which indicator performance was evaluated in the two studies. Andelman and Fagan (2000) demonstrated the relatively poor performance of small groups of at-risk species when they were used to select sites for other at-risk species. They found that few groups performed better than sites selected at random, and those that did required the selection of large percentages of the study areas. We evaluated the performance of at-risk species as a whole on all other (not-at-risk) species and came to the conclusion that they performed well as an indicator group. The difference in the results can be explained largely by the different groups of species used to measure indicator performance (other at-risk species vs. other species in general). In concor-

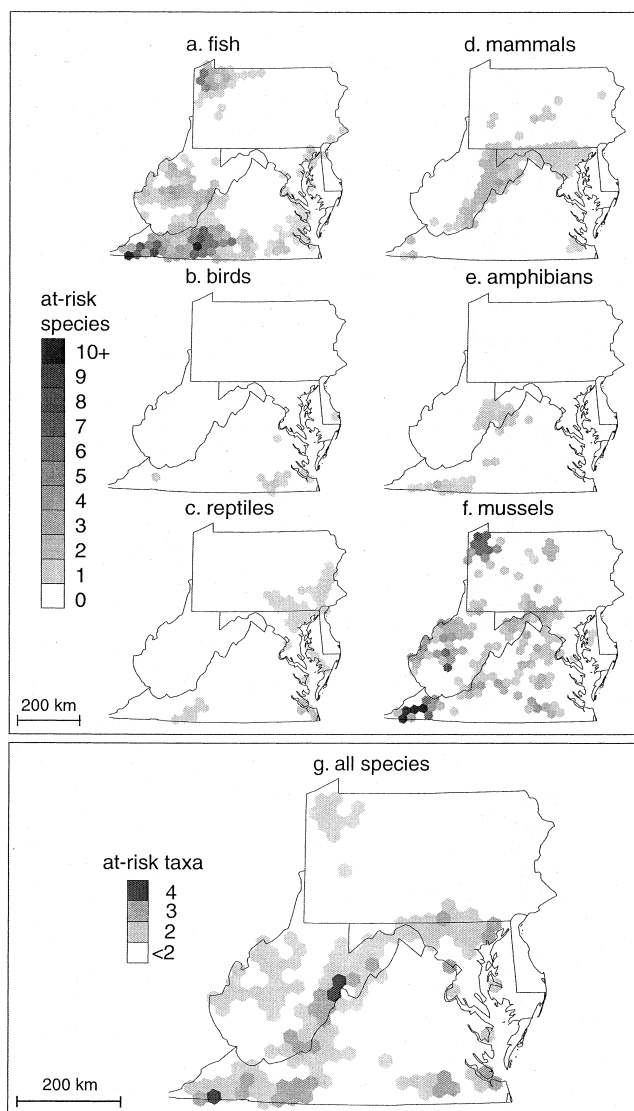


Figure 2. Distributions of at-risk species for six animal taxa: (a–f) the number of at-risk species recorded in each of 487 hexagonal sample units in the Middle Atlantic region of the United States and (g) the number of taxa with at least one at-risk species occurring in each hexagon.

dance with Andelman and Fagan (2000), we would predict the failure of subsets of the at-risk species in our study to protect other at-risk species as a result of the lack of congruence in distributions of at-risk species in the Middle Atlantic region (Fig. 2).

Several additional issues should be considered when evaluating indicator performance. Indicators are likely to perform differently in different areas, based on regional patterns of species distributions (Ryti 1992; Ricketts et al. 1999). Thus, the ranking of the performance of the indicator taxa in our study are likely to hold else-

where only if similar relationships between the patterns of species distributions exist.

The scale of analysis is also likely to affect the conclusions drawn about indicator performance. Conservation planners generally use smaller sites than those in our study. Because at-risk species usually have relatively small ranges and occur in restricted habitats, using large sites is likely to artificially increase the ranges of rare species relative to those of more common species. Thus, although our estimates of the performance of both taxonomic indicators with at-risk species and of at-risk species indicators with all species may be higher than one would expect at finer scales, the latter is likely to be affected to a lesser degree. Therefore, if our analyses had been conducted using smaller sites, we would probably have concluded that indicator taxa provided even less coverage for rare species.

Although the at-risk species in our study performed relatively well as an indicator group, their use in other regions of the world is likely to be more problematic given the inherent difficulty in obtaining information about their distributions. In many temperate areas where the distributions of rare species are best known, larger groups of these species from diverse taxonomic groups may serve as successful indicators of more general patterns of species diversity. Unfortunately, where indicators are most needed, as in much of the tropics, the existence, much less the distribution, of many rare species remains unknown (Groombridge 1992).

Conservation planning is a complex process that must often be carried out with limited and heterogeneous knowledge. Although indicator groups may provide a useful tool with which to deal with these difficulties, they are not always likely to be successful. Our results show that conservation areas selected with terrestrial indicator taxa may provide poor coverage for many aquatic species. In addition, if information on the distributions of at-risk species is not explicitly incorporated into the site-selection process, these species are not likely to be included in conservation areas selected on the basis of indicator taxa. Such a failure to protect at-risk species is likely to result in an accelerated loss of biodiversity (Terborgh & Winter 1980). Our results also suggest, however, that in those areas where data on distributions of at-risk species are available, these species are good candidate indicators for selecting sites to preserve species diversity.

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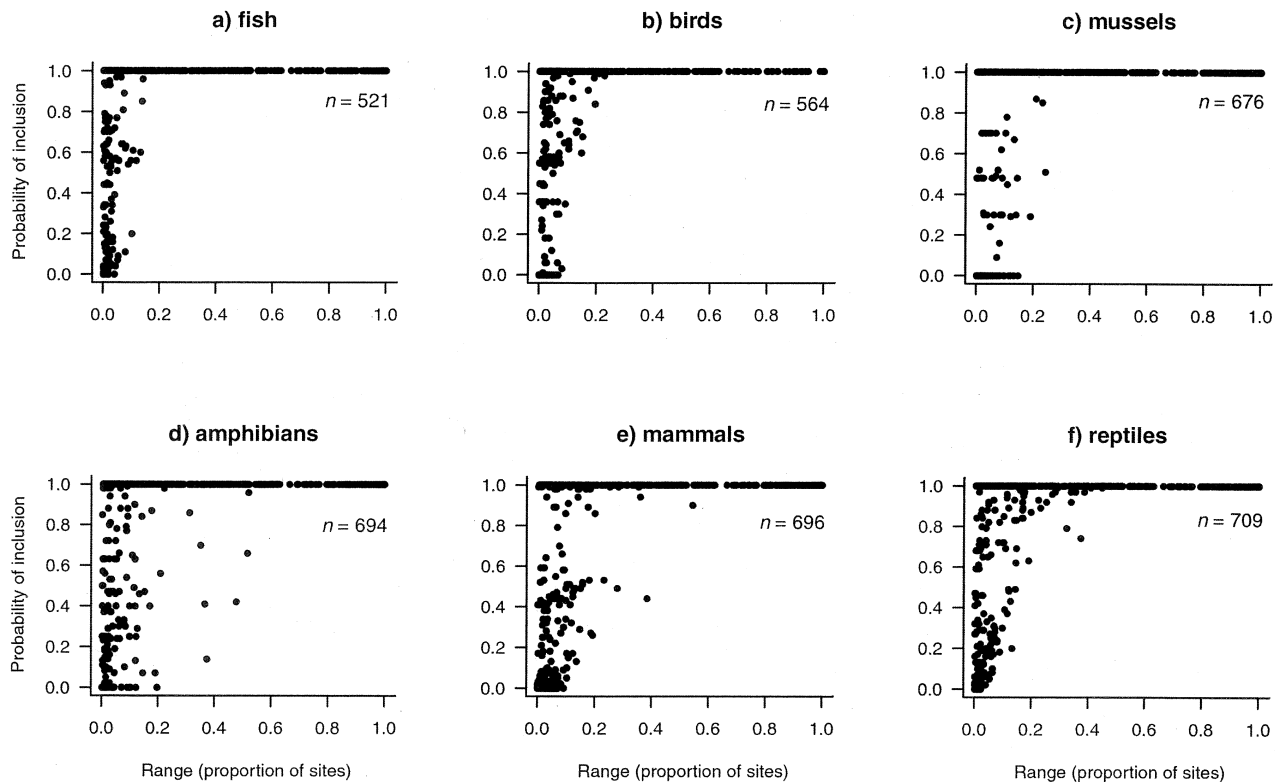


Figure 3. (a–f) The relationship between the probability of inclusion in a set of sites selected to cover each of six indicator groups and the extent of a species' range within the study area. Each point represents one species. Because nonindicator species were used in each analysis, the number of species (n) is different for each indicator group. The probability of inclusion is represented by the proportion of sets of sites, selected to cover all members of each of the six taxonomic indicator groups, that contained the species.

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