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Assessing the mechanisms behind successful surrogates for biodiversity in conservation planning

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Abstract

Limited by the availability of data, conservation planners must use surrogates for biodiversity when selecting conservation areas. Although several methods have been proposed for selecting surrogates, no clear set of species attributes have been described that allow for the efficient *a priori* selection of surrogate groups. We used a database of 1449 species in two regions of the United States to (1) examine the consistency in the performance of simple taxonomic-based surrogates of biodiversity and (2) test five hypotheses proposed to explain surrogate performance. First, we compared the ability of sites selected to protect members of seven surrogate groups to protect non-surrogate species in the north-western United States and in the Middle-Atlantic region of the eastern United States. Then, in a separate analysis, we tested whether surrogate performance could be explained by (1) taxonomic diversity; (2) nested species distributions; (3) hotspots of biodiversity; (4) species range sizes; (5) environmental diversity. Our first analysis revealed little consistency in the performance of surrogates in the two different study regions. For example, butterflies provided protection for 76% of all other species in the north-western United States but only 56% of all other species in the eastern United States. Our second analysis revealed only weak associations between species characteristics and surrogate performance. Furthermore, these associations proved inadequate for selecting successful surrogates across study regions. Overall, our results suggest that in lieu of searching for optimal surrogate groups, research efforts will be better spent by developing alternative methods for assessing conservation value in areas where data on species distributions are limited.

Introduction

Setting aside protected areas is arguably one of the most effective ways to preserve biodiversity. Many basic methods have been proposed for selecting protected areas including systematic approaches (Margules & Pressey, 2000), dynamic approaches (Turner & Wilcove, 2006) and approaches that rely more heavily on opportunistic site selection (Knight & Cowling, 2007). However, all conservation-planning approaches require some level of knowledge about the distribution of biodiversity. Because most conservation-planning efforts are limited by both time and funding, it is generally impossible to survey more than a few components of biological diversity. Thus, conservation planners must rely on surrogates or indicators to represent biodiversity in the reserve-selection process (Kremen, 1992; Raven & Wilson, 1992; Flather *et al*., 1997). Nature reserves are often selected to protect the species of one or more taxonomic groups, different vegetation communities and/or combinations of different abiotic conditions, with the assumption that those reserves will also protect a broader array of biodiversity. The validity of this assumption depends on how well the chosen surrogate group represents biodiversity in general. Thus, selecting representative surrogate groups is an integral part of successful conservation planning (Margules & Pressey, 2000).

To be practical, surrogates must consist of species or other ecological units whose distributions are already known or are relatively easily determined. Consequently, conspicuous or easily surveyed organisms such as butterflies, birds, beetles and trees (Pearson & Cassola, 1992; Ricketts *et al*., 1999; Mac Nally & Fleishman, 2002) and remotely sensed vegetation, land cover and environmental gradients (Faith & Walker, 1996*a*; Sarkar *et al*., 2005; Trakhtenbrot & Kadmon, 2005) have been suggested as potential surrogates. Many studies have tested the ability of these and other ecological units to act as surrogates of biodiversity (Pearson & Cassola, 1992; Prendergast *et al*., 1993; Pressey *et al*., 1993; Flather *et al*., 1997; Howard, Viskanic & Davenport, 1998; Ricketts *et al*., 1999; Andelman & Fagan, 2000; Fleishman, Murphy & Brussard, 2000; Lawler *et al*., 2003; Warman *et al*., 2004).

In general, these tests of surrogates have produced diverse and often contradictory results. Because most studies differ in spatial scale, in the methods used to test surrogate groups and in the groups that are tested, it is difficult to make useful comparisons across studies. For example, studies have ranged in spatial extent from as large as the globe (Pearson & Cassola, 1992) to at least as small as 140 ha (Saetersdal *et al*., 2004). The grain, or size of the sample units, used in studies has ranged from as small as 1000 m^2 (Pharo, Beattie & Pressey, 2000) to over 100 000 km^2 (Gaston & Blackburn, 1995). The range of taxonomic groups tested as surrogates has include such diverse sets of species as liverworts, aquatic plants, non-marine mollusks, dragonflies, large moths, click beetles, butterflies, birds, amphibians, reptiles, bats, freshwater fish, mollusk shells, lichens, bryophytes, primates, woodpeckers and spiders. Finally, several methods have been used to test surrogate groups including (1) correlations of patterns of species richness (e.g. Pearson & Cassola, 1992); (2) assessments of overlap of hotspots of species richness or rarity (e.g. Prendergast *et al*., 1993); (3) complementarity-based approaches that involve selecting sets of sites to protect surrogate groups and then assessing how well those sites protect other species (e.g. Lund & Rahbek, 2002).

Many of the studies that have been conducted have led authors to conclude that some groups of species are likely to be good surrogates for biodiversity. However, because the tests of the surrogates were performed in specific places and differed so drastically with respect to scale, methods and surrogate groups, it is impossible to make any generalizations about what constitutes a good surrogate group. Furthermore, there continues to be a constant flow of studies that evaluate the performance of different surrogate groups (Schmit *et al*., 2005; Bani *et al*., 2006; Chiarucci, D'auria & Bonini, 2007; Loyola, Kubota & Lewinsohn, 2007), indicating that little consensus has been reached on how best to select surrogates. What is needed now is not another comparison of different surrogate groups in a specific region, but rather systematic investigations of the factors that are likely to influence the performance of surrogate groups (e.g. Manne & Williams, 2003). Such studies have the potential to provide an understanding of what drives surrogate performance. Without such an understanding, it is impossible to offer any guidance on which surrogates to use in different situations.

Here, we perform a systematic assessment of the factors that are likely to influence surrogate-group performance. We focus specifically on groups of species as surrogates for species richness. We refer to individual species as surrogates and groups of species as surrogate groups. Several hypotheses have been proposed to explain the performance of surrogate groups. It has been suggested that good surrogates are geographically rare (Ryti, 1992; Williams, Burgess & Rahbek, 2000; Tognelli, 2005) or endemic (Loyola *et al*., 2007), taxonomically diverse (Ricketts *et al*., 1999), exhibit relatively unnested distributions (Ryti, 1992) and occupy diversity 'hotspots' (Prendergast *et al*., 1993; Lawton *et al*., 1998). Faith & Walker (1996*a*,*b*) have provided the most compelling explanation for surrogate performance – an explanation based on environmental gradients. Surrogates work, they argue, by representing different environments. The more diverse the environments represented by the species in the group are, the more biodiversity can be protected in a set of sites selected to protect the surrogates.

Despite the multitude of potential explanations for surrogate performance, only a handful of studies have explicitly tested specific hypotheses (Araújo *et al*., 2001; Manne & Williams, 2003; Bani *et al*., 2006). Manne & Williams (2003) tested whether surrogate-group performance could be explained by 15 different characteristics of the surrogate group. Among others, these characteristics included the size of the group, the sizes of the ranges of the species in the group, the number of threatened species in the group, the mean number of ecoregions occupied by the group and the mean body size of the species in the group. Bani *et al*. (2006) tested whether inherent sensitivities to landscape patterns such as fragmentation and isolation affected surrogate performance. Finally, Araújo *et al*. (2001), in essence, tested whether environmental diversity could explain surrogate performance. From these few tests, only weak evidence for a handful of species characteristics has resulted (Manne & Williams, 2003). Manne & Williams (2003) found that surrogate-group performance was negatively correlated with the variance in surrogate richness among ecoregions, average range sizes and average surrogate richness, and positively correlated with the proportion of plants and the proportion of narrowly distributed plants in the surrogate group.

We addressed the question of what makes good species-based surrogates for biodiversity with two analyses. First, we assessed the consistency of surrogate performance by comparing the ability of seven different groups of species to act as surrogates for biodiversity in two different regions of similar size in the eastern and western United States. By controlling for scale, analytical approach and the surrogate groups tested, we performed a controlled comparison of biodiversity surrogates in different geographic regions. Second, we tested five hypotheses for explaining surrogate-group performance (Table 1). To perform these tests, we compared characteristics of the best surrogate groups in the eastern United States with those of groups selected at random. We then tested whether those characteristics we identified enabled us to select successful surrogates in the north-western United States.

Methods

Data

We used a database of the distributions of 1449 species of freshwater fish, birds, butterflies, mammals, reptiles, amphibians and freshwater mussels in two regions of the United States (Table 2). The eastern region covered 316 000 km^2 and the states of Pennsylvania, Maryland, Delaware, Virginia and West Virginia whereas the western region covered 429 000 km^2 and the states of Washington and Oregon

Table 1 Hypothesized mechanisms for explaining the performance of surrogates for biodiversity

Hypothesized mechanism	Prediction
Hotspot overlap	Better performing surrogate groups have species whose ranges overlap hotspots of diversity to a higher degree
Taxonomic diversity	Better performing surrogate groups are more taxonomically diverse
Nestedness	Better performing surrogate groups have less nested distributions
Range size	Better performing surrogates have smaller geographic ranges
Environmental diversity	Better performing surrogate groups have species with more environmentally diverse geographic ranges

Table 2 The number of species in each of seven taxonomic groups and one risk-based group in two regions of the United States

	Number of species	
Taxon	East	West
Amphibians	78	34
Birds	208	267
Butterflies	150	172
Fish	250	79
Mammals	73	142
Mussels	97	6
Reptiles	64	29
At-risk species	91	39

The eastern region consisted of the states of Pennsylvania, Delaware, Maryland, Virginia and West Virginia. The western region included the states of Washington and Oregon.

(Fig. 1). We included both terrestrial and aquatic species in our analyses because freshwater fish and mussels have the potential to perform well as surrogates for terrestrial species diversity (Lawler *et al*., 2003). Ideally, these analyses would include plant species, but we were unable to obtain accurate distribution data for plants in the two study regions. The data included all native species with confirmed or probable status in each of 487 650 km^2 hexagonal grid cells in the eastern region and 660 cells in the western region (White, Kimerling & Overton, 1992). Because these grid cells are generally too large to be considered reserves themselves, we regarded them as potential targets for finer scale analyses, leading to the establishment of reserves, restoration projects or land easements within the selected sites. The size of the cells is within the range of cell sizes used in other coarse-scale regional conservational-planning analyses (Prendergast *et al*., 1993; Ando *et al*., 1998; Abbitt, Scott & Wilcove, 2000; Dobson, Rodríguez & Roberts, 2001; Groves *et al*., 2002) and is well within the range of the sample units used in studies designed to test surrogates of biodiversity. The species data are described in more detail in Lawler *et al*. (2003).

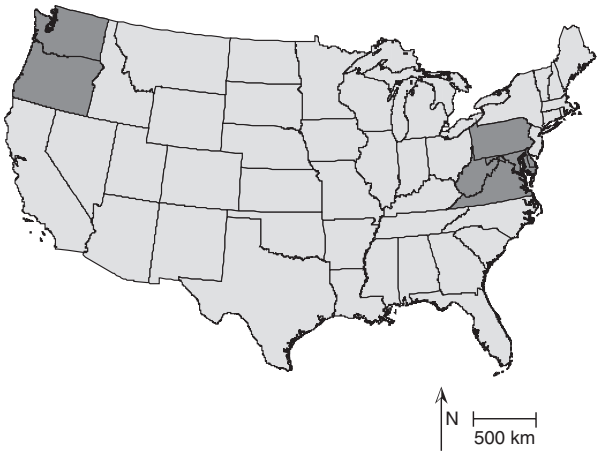

Figure 1 Study regions in the eastern and western United States.

To assess environmental diversity, we used a set of variables that represented the environments of the study region at a coarse spatial resolution for a wide variety of species. Land-cover data were derived from advanced very high-resolution radiometer satellite imagery and classified into 159 categories consistent with the Loveland level III classification (Loveland *et al*., 1991) with an extra class representing urban development (O'Connor *et al*., 1996). We obtained climate data from the Historical Climate Network (1996). Climate variables included the mean annual precipitation and mean temperatures for both July and January. The elevation correction method of Marks (1990) was used to model temperature data to 1 km resolution. The precipitation data, which had originally been modeled to 10 km resolution by Daly, Neilson & Phillips (1994), were also re-sampled to 1-km resolution with a linear model. We used the USGS Digital Elevation Models for estimates of elevation. The climate and elevation data were averaged within each hexagonal grid cell in the study. The land-cover data were represented by percentages of coverage of each of the 160 classes in each hexagon.

Comparing surrogate performance in two geographic regions

We compared the performance of birds, butterflies, amphibians, fish, mammals and at-risk species as surrogates in our two study regions. We did not include reptiles or mussels in this comparison because these groups had too few species in one of the two regions to be useful surrogate groups in themselves. We classified at-risk species in our dataset using the three most sensitive categories – critically imperiled, imperiled and vulnerable – of a global ranking system (Master, 1991; Lawler *et al*., 2003). We assessed the performance of a surrogate group by selecting eight sites (hexagonal grid cells) to protect as many of the species in the group as possible. We chose eight as the number of sites to select because it was the smallest number of sites required to represent all species of the surrogate group requiring the

least number of sites. We standardized our analyses to a set number of sites because different surrogate groups potentially require different numbers of sites to protect all of their members. We wanted to avoid drawing the simple conclusion that groups of species that require more sites for their protection are better surrogate groups. Although we do not report the results, we ran similar analyses with a modified algorithm to select sets of 4, 12 and 16 sites for each surrogate group. These analyses produced qualitatively similar results. We then tallied the number of other non-surrogate-group species found in the eight sites. The percentage of all non-surrogate species found in these sites served as our measure of surrogate performance. We selected sites using a simulated annealing algorithm. Simulated annealing is a stochastic optimization technique used to find solutions to problems with large search spaces (Kirkpatrick, Gelatt & Vecchi, 1983). The technique works by iteratively evaluating and altering potential solutions to a problem to evolve an 'optimal' solution and has been used successfully as a tool for reserve-selection analyses (Possingham, Ball & Andelman, 2000). Because it is a stochastic approach, simulated annealing often produces multiple answers to an optimization problem. We ran the algorithm to produce 100 sets of sites from which we selected the 20 sets that protected the most non-surrogate species. We then calculated mean performance for these 20 sets of sites. By performing these site-selection analyses for each of the six surrogate groups in both the eastern and western regions, we generated 12 measures of mean surrogate performance, one for each group in each region. We compared these performance measures to the mean performance of 20 sets of eight sites selected at random.

We used sets of sites chosen at random as the null model against which to compare the performance of the surrogates. We explored the possibility of using several other null models that might provide a more informative comparison. For example, with the availability of remotely sensed data, it would be reasonable to consider surrogates based on vegetation types or elevation gradients as a baseline against which to compare sets of surrogate species. We compared sets of sites selected at random to sites selected to best represent (1) the diversity of land-cover types; (2) climatic and elevation gradients; and (3) a combination of land cover, elevation and climatic diversity. Given that none of these alternative surrogates outperformed the sites selected at random, we chose to use randomly selected sites as the null model for our comparisons here.

Testing hypotheses for surrogate performance

Selecting optimal and random surrogates

To understand what factors contributed to the success of surrogate groups at representing biodiversity, we compared characteristics of some of the best performing surrogate groups with groups of species selected at random. We performed this analysis in the eastern study region only, because we wanted to hold the western region in reserve to independently test hypotheses that emerged from the eastern region. We identified the best-performing surrogate groups using a two-part optimization routine. The routine used simulated annealing in conjunction with a heuristic algorithm to select groups of 20 species that provided the most complete coverage of non-surrogate-group species. For this application of simulated annealing, our algorithm began with a randomly selected set of 20 species. The performance of these species as a surrogate group was then evaluated . Next, the set of 20 species was slightly altered with the substitution of one randomly chosen species from the remaining pool of 900 species for a randomly selected species in the group. The performance of the new group was then evaluated. The algorithm then compared the performance of the new and old groups. The group with the better performance measure was generally selected for the next iteration of the routine. However, because simulated annealing is designed to avoid local optima in favor of finding a global optimal solution, the better performing set of species was not always chosen. The probability of choosing the worse solution decreased over the course of all iterations (see Kirkpatrick *et al*., 1983). Several thousands of iterations were required to produce one set of 20 species.

For each iteration of the simulated annealing routine, we evaluated surrogate-group performance by selecting a set of sites that provided the best protection for non-surrogate species in five sites. We chose to use five sites because this was the smallest number of sites required to cover any optimally selected set of 20 species. Again, we used a standard number of sites to avoid merely concluding that surrogate groups that require more sites to protect them protect more species. We used a heuristic algorithm to select a set of sites to protect all 20 species, but only used the five sites that together covered the most surrogate species when we evaluated group performance. We computed the proportion of the 900 non-surrogate species included in these five sites. These proportions served as the performance measures that were evaluated and compared by the simulated annealing routine. Although better techniques exist for selecting the five sites that cover the largest number of a given set of species, these techniques were too computationally expensive to be used within our nested optimization framework.

The heuristic algorithm we used to select sets of sites for the 20 species was based on species rarity and comprised the following rule set: (1) select any site with unique species (any of the 20 species occurring only in one site); (2) select a site that includes the next rarest of the 20 species; (3) break ties in step 2 by selecting the site with the highest proportion of the 20 species; (4) break ties in step 3 by selecting a site at random; (5) repeat steps 2–4 until all 20 species are included (Margules, Cresswell & Nicholls, 1994). The resulting sets of sites were then checked and all redundant sites (i.e. sites that contained only species that were found at other sites in the selected set) were eliminated (Margules, Nicholls & Pressey, 1988). We then selected the five sites that included the most surrogate species. Because the algorithm involved a stochastic step, it had the potential to produce multiple sets of sites

for protecting one set of species. We used the average of 20 applications of the heuristic algorithm to evaluate the performance of surrogate groups.

Because simulated annealing is stochastic in nature, it can be used to produce many different solutions to a problem. By running our nested optimization routine 100 times, we produced 100 sets of the best performing surrogates in the eastern study region. In addition to the 100 sets of optimally selected surrogate groups, we selected 100 sets of 20 species at random. We used the same heuristic algorithm described above to evaluate the performance of each of these randomly selected groups. Thus, for all 200 groups of species (100 randomly selected and 100 optimally selected) we calculated performance as the total number of non-surrogate species included in the sets of five sites selected to cover the species in the surrogate group. Although we chose to use groups of 20 species, we ran analyses on sets of 10, 30, 40, 50, 60, 70, 80, 90 and 100 species as well. Because these results were qualitatively similar, we report only the results for the sets of 20 species. In addition to comparing the sets of sites selected to cover optimally selected surrogate groups to those selected to cover randomly selected groups, we also compared them to sets of five sites selected at random.

Comparing surrogate group characteristics

We compared the randomly selected surrogate groups to the optimally selected groups with respect to higher order taxonomic diversity, nestedness, hotspot representation, range size and environmental diversity. All of these attributes are plausible indicators of what factors make for an ideal group of surrogate species. For instance, one might argue that the ideal surrogate group should be the most diverse at the order or class level. To compare taxonomic diversity, we tallied the total number of classes, orders, families and genera represented in each randomly selected and optimally selected surrogate group. We calculated the nestedness of the distributions of each surrogate group using the measure proposed by Wright & Reeves (1992),

$$N_c = \frac{1}{2}\sum_{j=1}^{S} J_j(J_j - 1)$$

where J_j is the number of sites at which species j is present and S is the total number of species. We used the standardized version of this metric,

$$S\{N_c\} = \frac{N_c - E\{N_c\}}{\max\{N_c\} - E\{N_c\}}$$

where $\mathrm{E}\{N_c\}$ represents the expected value of N_c and $\max\{N_c\}$ is the maximum possible value of N_c. The expected value is given by

$$E\{N_c\} = \frac{1}{2S}\left(G^2 - \sum_{i=1}^{K} R_i^2\right)$$

where G is the grand total of all occurrences of all species, R_i is the species richness at site i and K is the total number of sites. The maximum value of N_c was calculated as

$$\max\{N_c\} = \sum_{i=1}^{K} (i-1)R_i$$

We assessed the degree to which surrogate groups represented hotspots of species richness by calculating the proportion of overlap between the ranges of the species in the surrogate group and hotspots of richness of all 920 species. Hotspots were defined as the grid cells that contained the top 5% of the species richness values in the region (Prendergast *et al.*, 1993). We calculated overlap as

$$O = \frac{\sum_{j=1}^{M} \frac{H \cap A_j}{H \cup A_j}}{20}$$

where H represented hotspot grid cells and A_j represented the grid cells containing species j of the 20 species in the surrogate group, M. Thus $H \cap A_j$ is the number of grid cells that were both hotspots and contained species j, and $H \cup A_j$ is the total number of grid cells that were hotspots and/or contained species j. Unlike the other four hypotheses we tested, the coincidence of surrogates and hotspots would not be useful in selecting surrogate groups. Selecting surrogates based on the presence of hotspots would require the *a priori* mapping of a much broader array of species, potentially alleviating the need for surrogates altogether. Nonetheless, because the coincidence of surrogates and hotspots has been offered as an explanation for surrogate performance, we have tested for it here.

We used the total area of the study region occupied by a species as a measure of range size. This was simply calculated as the number of cells in which the species was present times the area of a cell. Although we refer to this measure as 'range size,' it is really a measure of the local or regional distribution of a species. It is important to note that species with relatively small global geographic range sizes might be widely distributed in our study and that species with relatively large global ranges might have locally restricted distributions in our study region. We also considered using an estimate of the maximum 'diameter' of a species' range to provide an estimate of how restricted the range of a species was within the study region. However, because these two metrics were highly correlated, we chose to use only the total area to represent range size.

To describe the diversity of environments occupied by the members of the surrogate groups, we assessed the dissimilarity of the species' ranges with respect to elevation, climate and remotely sensed vegetation. Measures of dissimilarity for elevation, annual precipitation and average January and July temperatures were calculated by first computing the average values across each species' range and then calculating the mean difference among all pairs of species within the surrogate group as follows:

$$ED = \frac{\sum_{i=1}^{S-1}\sum_{m=i+1}^{S}\left(\frac{\sum_{j=1}^{A_j} E_{ij}}{A_i} - \frac{\sum_{k=1}^{A_m} E_{mk}}{A_m}\right)}{S(S-1)}$$

where E_{ij} is the value of the environmental variable in cell j of the range of species i and A_i and A_m are the number of grid cells containing species i and m, respectively. We used Bray-Curtis dissimilarity to assess the differences between the composition of vegetation represented in the ranges of each species in a surrogate group (Belbin, 1993).

Testing predictions

We tested the generality of the results of our comparisons made in the eastern United States by applying them to the study region in the western United States. We selected 20 sets each of 20, 40, 60 and 80 species from the western study region using the criteria derived from our comparison of surrogate characteristics. We then compared the performance of these sets of surrogates to 20 sets each of 20, 40, 60 and 80 randomly selected western species. We used simulated annealing to find sets of sites that maximized the number of surrogate-group species in a set number of sites for each surrogate-group size. We then calculated the number of non-surrogate-group species included in the sets of sites.

Results

Surrogate performance in two geographic regions

Using simple taxonomic surrogate groups to select areas for conservation provides protection for more species than selecting sites at random (Fig. 2). The only exception was in the case of butterflies being used as surrogates in the eastern study region. Sites selected to protect butterflies in the eastern United States provided no more protection for other species than did sites selected randomly.

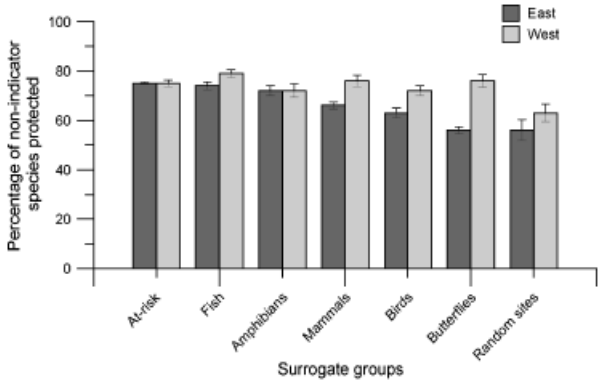

Figure 2 Comparison of the performance of five taxonomic-based and one risk-based surrogate group in two different regions of the United States. Performance was measured as the percentage of non-surrogate species included in eight sites selected to protect the surrogate group. Bar heights represent means of the results of 20 reserve-selection analyses; error bars represent standard deviations.

Some surrogate groups performed substantially better than others. In the eastern region, on average, sites selected to protect at-risk species protected 75% ($\pm$0.4% SD) of all non-surrogate-group species whereas, on average, sites selected to protect butterflies protected only 56% ($\pm$1.4% SD) of all non-surrogate-group species. In the western region, the differences in surrogate-group performance were less dramatic. The best performing group, freshwater fish, on average, provided protection for 79% ($\pm$1.6% SD) of all non-surrogate species compared with the worst performing groups, birds and amphibians, both of which provided protection for 72% ($\pm$2.0 and 2.7% SD, respectively) of all non-surrogate species. It is important to note, however, that due to the large number of species analyzed, even small percentages correspond to relatively large numbers of species.

Surrogate performance was not consistent across regions. Both mammals and butterflies were some of the better performing surrogates in the western region, each providing, on average, protection for 76% ($\pm$2.3 and 2.6% SD, respectively) of all non-surrogate species. In the eastern region, these were two of the worst performing surrogate groups, respectively, providing protection for 66% ($\pm$1.4% SD) and 56% ($\pm$1.4% SD) of non-surrogates. Amphibians were some of the worst surrogates in the west, but were the third best performing surrogates in the east. Despite these differences, there were some consistencies. Both freshwater fish and at-risk species were the two best performing surrogate groups in both regions.

What factors are associated with surrogate performance?

Optimally selected surrogate groups performed better than groups of species selected at random. On average, optimally selected groups provided protection for 92 more species than did randomly selected species (76$\pm$1% SD vs. 65$\pm$4% SD) (Fig. 3). Furthermore, sets of five sites selected

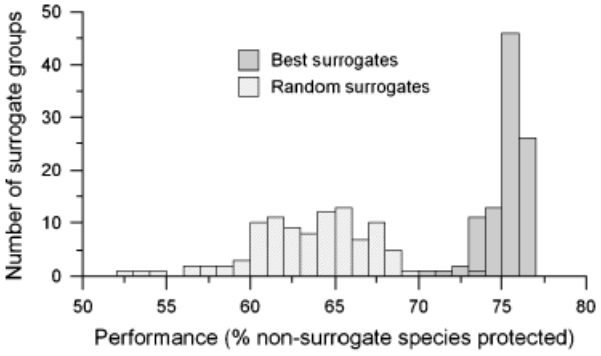

Figure 3 Histograms of the performance of randomly selected and optimally selected surrogate groups in the Middle-Atlantic region of the eastern United States. Performance was measured as the percentage of all non-surrogate-group species included in five sites optimally selected to protect the 20 species in each surrogate group.

Table 3 Comparison of characteristics of randomly selected and optimally selected surrogates for biodiversity for the selection of reserve networks of equal area

Surrogate group attribute	Best sets mean (± SD)	Random sets mean (± SD)	*t*-test (*P*)[a]
Hotspots of diversity overlap	7.0% (±0.01%)	6.2% (±0.01%)	<0.001
Taxonomic diversity			
Classes	6.3 (±0.7)	6.2 (±0.8)	0.819[b]
Orders	11.2 (±1.7)	11.1 (±1.6)	0.833
Families	15.0 (±1.9)	15.1 (±1.6)	0.717
Genera	19.2 (±0.8)	19.1 (±0.9)	0.208[b]
Nestedness	0.65 (±0.14)	0.68 (±0.11)	0.256
Mean range size (km^2)	68 000 (±24 800)	87 100 (±23 100)	<0.001
Environmental diversity			
January temperature dissimilarity (°C)	2.8 (±0.3)	2.5 (±0.4)	<0.001
July temperature dissimilarity (°C)	1.9 (±0.2)	1.8 (±0.3)	<0.001
Precipitation dissimilarity (mm)	49 (±10)	47 (±10)	0.245
Elevation dissimilarity (m)	713 (±96)	711 (±122)	0.940
Land-cover dissimilarity	0.51 (±0.05)	0.47 (±0.05)	<0.001

[a]Because surrogate groups potentially contained some of the same species, samples could not be strictly considered to be independent.
[b]Because these variables could not be transformed to meet the assumptions of a *t*-test, Kruskal–Wallis tests were preformed.

to cover both optimally selected and randomly selected species performed better than sets of five sites selected at random (on average randomly selected sites protected only 51 ± 4% SD of all species).

The best surrogates had smaller ranges and occupied more diverse environments than did randomly selected species (Table 3). Average range sizes of optimally selected species were 22% (19 100 km^2) smaller than those of randomly selected species. The differences in environmental diversity across ranges of optimally selected and randomly selected groups of species were much smaller. However, given the general homogeneity of the study region in the eastern United States, even these relatively small differences in temperature (0.1 and 0.3 °C) and environmental dissimilarity may be biologically meaningful. These small differences may be enough to result in slight variations in vegetation and hence define different habitats at relatively fine spatial scales. In contrast, the small difference in the degree to which optimally and randomly selected species were found in diversity 'hotspots' (0.8%) is not likely to be meaningful. In addition, our results indicate that good surrogate groups are neither more taxonomically diverse nor do they consist of species with ranges that are any less nested than those of species selected at random.

Testing the importance of range size and environmental diversity

We tested our conclusion that the best surrogate groups are composed of species with small ranges that together cover a diversity of environments using groups of species that fit those two criteria in the western study region. We compared the performance of groups of species (1) with small ranges; (2) with ranges that covered different environments; (3) with ranges that were both small and covered different environments; (4) selected at random. To select species based on range size alone, we randomly selected groups of species from the 100 species with the smallest ranges. To select species whose ranges covered different environments, we used Bray-Curtis dissimilarity measures based on the composition of the 160 land-cover classes represented in the ranges of each species (Belbin, 1993). We used a simulated annealing algorithm to find the species whose ranges maximized this dissimilarity measure. We selected groups of species that had both small and environmentally diverse ranges by restricting the Bray-Curtis dissimilarity-based optimization to the 100 species with the smallest ranges. To evaluate the performance of each of the surrogate groups, we selected sets of 4, 7, 8 and 10 sites to protect the groups of 20, 40, 60 and 80 species, respectively. The number of sites selected to cover each different size surrogate group was based on the smallest number of sites required to protect each of the corresponding randomly selected sets of species. Site selection was performed with a simulated annealing algorithm. In addition, we compared the performance of each of the four types of surrogate groups to the performance of corresponding numbers of sites selected at random.

At best, surrogate groups selected on the basis of species range sizes and environmental diversity performed only slightly better than groups of randomly selected surrogate species (Fig. 4). Surrogate groups selected on the basis of the diversity of environments that they occupied only outperformed randomly selected groups of species when larger surrogate groups were selected. Additional analyses, in which we controlled for the issue of geographically rare species being harder to protect, showed no difference in the performance of the surrogate species with small ranges and the groups of randomly selected species.

Discussion

Our results indicate that there is unlikely to be a simple set of principles for selecting surrogate groups based on species

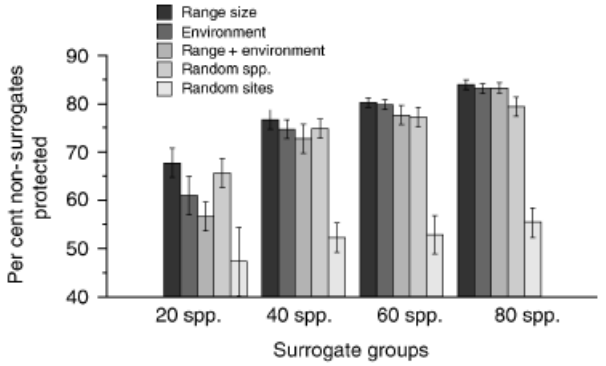

Figure 4 Performance of surrogate groups in the north-western United States consisting of 20, 40, 60 and 80 species selected using four different criteria. Surrogates were selected (1) to have small ranges; (2) to have ranges that occupied diverse environments; (3) to have small ranges that occupied diverse environments; (4) at random. Performance was measured as the percentage of non-surrogate species included in a set number of sites. The fifth bar in each of the four sets of bars represents the percentage of species included in an equal number of sites selected at random. The heights of all bars represent the means of 100 analyses; error bars represent standard deviations.

characteristics. First, even after controlling for scale, methods and the taxonomic groups tested, we found little consistency in the performance of surrogates in two different regions. Second, we found only weak evidence for two of the proposed explanations for surrogate performance. Geographically rare species and groups of species that together inhabit different environments tended to be good surrogates. However, neither of these two characteristics were particularly useful for selecting surrogate groups. Our results indicate that one of the main reasons for using rare species as surrogates may be to assure their protection, thus supporting a coarse- and fine-filter approach to conservation planning (Hunter, Jacobson & Webb, 1988; Noss, 1990; Hunter, 2005). The small but consistently superior performance of the small-range species in our dataset was due to the fact that including these species in surrogate groups meant that these difficult-to-protect species were no longer in the pool of species used to evaluate the surrogates. Beyond serving this function, we found that the geographically rare species in the north-western United States were no better surrogates than randomly selected species. Although Manne & Williams (2003) found a link between range size and surrogate performance, it is not clear how strong this relationship would have been had they controlled for this simple function that geographically rare surrogates perform.

Intuitively, one would expect that species from different environments should be better surrogates than species from more similar environments. Surrogates must work, in part, by requiring a diverse set of environments to be selected as reserves (Faith & Walker, 1996*a*,*b*). Because the breadth of niches available for organisms increases with environmental heterogeneity, we expected to see higher species richness in sets of sites representing more diverse environments. Whereas environmental heterogeneity may explain why surrogate groups work better than sites selected at random, we found only weak evidence for a link between environmental heterogeneity and the relative performance of different surrogate groups. If surrogate performance could be explained by environmental diversity, environmental diversity could be used directly as a surrogate in the reserve-selection process (Faith & Walker, 1996*b*). However, the few direct tests of environmental diversity as a surrogate for species diversity have produced mixed results (Araújo *et al*., 2001; Sarkar *et al*., 2005).

There are at least two likely explanations for why surrogate performance was not explained by environmental diversity in our analyses. First, it is possible that the spatial scale of our analyses obscured finer scale ecological relationships. One might expect a stronger relationship between surrogate performance and environmental diversity at finer spatial scales at which more detail in environmental factors will be resolved. Second, species diversity may not be closely linked to environmental diversity. Environmental diversity would fail to predict surrogate performance if species ranges are not distributed evenly across environmental space (Araújo, Densham & Humphries, 2003).

Although our analyses found no effect of taxonomic diversity on surrogate-group performance, it is possible that tests that include a broader array of taxa might produce a different result. Given that we only had seven taxonomic groups, and that randomly selected groups of species generally contained about five different taxa, our ability to detect a difference between the optimally selected groups and the random groups was lower than it would have been had our dataset contained more taxonomic groups.

Several other innovative approaches to selecting surrogate groups have been proposed. Some have suggested analyzing species responses to disturbance or landscape patterns as a way of selecting surrogates (Bani *et al*., 2006). Others have proposed statistical approaches to select sets of species that represent a wider array of species (Mac Nally & Fleishman, 2002, 2004; Fleishman *et al*., 2005). In general, these statistical approaches require determining the distributions of all species in an area before the surrogates can be selected. Thus, only if the selected surrogates are representative of biodiversity in other regions can they be successfully applied to areas that have not been thoroughly sampled. There is evidence that some statistically selected surrogates may be general enough to apply to other areas within a mountain range or even multiple mountain ranges, but most tests of this approach have been limited to one or two taxonomic groups (Mac Nally & Fleishman, 2004).

At least one promising alternative to using surrogates has been proposed (Possingham, Grantham & Rondinini, 2007). Bini *et al*. (2006) recently demonstrated a method for predicting potential distributions of yet to be discovered species. Thus, instead of trying to find groups of species that represent biodiversity, one may be able to model biodiversity and base conservation-planning decisions on the model

predictions. Modeling individual species distributions or modeling potential changes in species composition (Ferrier, 2002) may be more efficient ways to plan for biodiversity than struggling to select a set of imperfect surrogates.

We have taken an exploratory approach to determining the factors that influence surrogate performance. Although our results were robust across different sizes of surrogate groups and different sizes of reserve networks, we did not investigate the impact of the size of sites or the method chosen to evaluate surrogate performance. Both of these additional factors can affect surrogate performance and thus may affect the relationships we investigated. For example, it is possible that finer or coarser grained analyses (i.e. using smaller or larger sites) would reveal stronger associations between surrogate performance and environmental patterns based on varying strengths of the relationships between species distributions and environmental factors at different spatial scales (Mitchell, Lancia & Gerwin, 2001; Rahbek, 2005; Hess *et al*., 2006). We assessed surrogate performance by selecting sites to represent surrogates based on a combination of simulated annealing and heuristic algorithms designed to address the 'maximal covering location problem' (Church, Stoms & Davis, 1996). Analyses similar to ours that use other formulations of the reserve-selection problem and/or other selection approaches (e.g. iterative selection based on irreplaceability values, Ferrier, Pressey & Barrett, 2000) could potentially reveal stronger relationships between surrogate traits and surrogate performance. Further investigations into the effects of scale and reserve-selection approaches on the performance of surrogates for biodiversity are clearly warranted.

Conservation planning is a difficult process that must often be carried out with limited time and funding. Selecting areas to maximally protect biodiversity therefore requires tools that enable efficient use of both of these resources. We conclude that there are likely to be few shortcuts for choosing successful species-based surrogates for biodiversity. Instead of searching for surrogate groups, it may be more efficient to concentrate research efforts on further developing alternative methods for predicting or assessing conservation value when data are limited.

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