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INTEGRATING REPRESENTATION AND VULNERABILITY: TWO APPROACHES FOR PRIORITIZING AREAS FOR CONSERVATION

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Abstract. Reserves protect biodiversity by ameliorating the threats to the persistence of populations. Methods for efficient, systematic reserve selection have generally been designed to maximize the protection of biodiversity while minimizing the costs of reserves. These techniques have not directly addressed the factors threatening species at specific sites. By incorporating measures of site vulnerability into reserve selection procedures, conservation planners can prioritize sites based on both representing biodiversity and the immediacy of factors threatening it.

Here we develop two complementary approaches for identifying areas for conservation based on species composition and potential threats facing the species. These approaches build on two established methods of systematic reserve selection. The first approach involves mapping irreplaceability (a statistic derived from reserve selection theory that measures the potential importance of a site for protecting all species) and the degree to which the area is vulnerable to threats from three basic anthropogenic factors (the percentages of a site devoted to agriculture, to urban and suburban development, and to open mines). We classified areas with respect to both irreplaceability and the three indicators of vulnerability, producing a continuous ranking of all sites based on these factors. Our second approach was to incorporate site vulnerability into a reserve selection algorithm. This approach allowed us to locate those sets of sites that protected all species and were most likely to be threatened by human activities. These two analyses can provide regional-scale guidance for conservation in the Mid-Atlantic region of the United States, and they demonstrate two potential tools for solving complex conservation-planning problems.

Key words: anthropogenic factors; biodiversity; conservation planning; irreplaceability; optimization; reserve selection; site ranking; species composition; threats; vulnerability.

INTRODUCTION

Ecologists have estimated that between 39% and 50% of the land surface of the earth has been altered for human uses (Vitousek et al. 1997). Thus, it is not surprising that destruction and degradation of habitat are often cited as the leading threats to biodiversity (Wilcove et al. 1998). In light of the dramatic rate at which landscapes are being changed, perhaps the most effective tool for conserving biodiversity is the establishment of reserves. These areas protect biological diversity by reducing threats to the persistence of populations.

Effective conservation reserves must accurately represent biodiversity and assure its persistence. Accurate representation of biodiversity is challenging because it is possible to measure biodiversity at many levels (Allen and Starr 1982). Biodiversity encompasses genetic diversity, behavioral diversity, and the diversity of populations, species, communities, ecosystems, and biomes (Wilson 1988). Because it is not possible to account for all of these elements in even the most well-studied of geographic regions, indicators or surrogates of biodiversity are used to select reserves (Kremen 1992). By selecting areas to represent surrogates, it is assumed that many other elements of biodiversity are also represented. Although it remains unclear if specific groups of species can accurately represent biodiversity in general, there are currently no alternatives to using indicator groups at coarse spatial scales. Habitats and taxonomic groups are some of the most commonly used indicators or surrogates of biodiversity for reserve selection.

It is not enough to select areas in which the biodiversity of a region is well represented. Effective reserves protect biodiversity by increasing the probability of the persistence of populations within reserves (Rodrigues et al. 2000) or across networks of reserves (Margules et al. 1994). Persistence is influenced by a large number of factors, the most basic of which include population size and habitat quality and quantity (Soulé 1987). These simple factors are directly influenced by both reserve selection (where reserves are located) and reserve design (the shapes and sizes of reserves). One simple approach to promoting persis-

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tence has been to require multiple or ''redundant'' representation. By assuring that each species (or other conservation target) is represented at several sites, the probability of their persistence is potentially increased (Pressey et al. 1996). The proximity of, or connectivity among, selected sites may also promote persistence by increasing habitat availability to species with large ranges and enabling the recolonization of sites by individuals of metapopulations (Harrison 1994, Hess 1996). The sizes and shapes of reserves, in part, determine the amount of available habitat for many species, as well as reduce or exaggerate potentially deleterious effects of habitat edges (Harris 1988).

Most existing reserves have not been selected on the basis of representation or persistence. Most protected areas in the United States, for example, are generally at high elevations and have less fertile soils and more extreme climates; in short, they are the lands that nobody wanted (Scott et al. 2001). Such ad hoc reserve selection is unlikely to adequately protect biodiversity. A number of different systematic approaches to selecting sites that account for representation have been developed (e.g., Margules and Pressey 2000, Groves et al. 2002). Central to most of these approaches are the concepts of optimization and complementarity. Because there are almost always competing economic interests and multiple demands on potential sites for conservation, and because resources for creating reserves are limited, it is often the goal of conservation planners to minimize the costs of reserve networks while maximizing the biodiversity protected.

Efficient site selection can thus be defined as an optimization problem with the goal of protecting all conservation targets (hereafter species) with the minimum expenditure of resources (e.g., land, or costs of land). The actual selection of sites is most often done with a predefined algorithm based on the concept of complementarity (Margules et al. 1988, Csuti et al. 1997, Pressey et al. 1997). Complementarity is a measure of the degree to which a site contributes to the representation of previously unrepresented species (Pressey et al. 1993). The measure thus depends on the composition of any previously selected sites and changes as sites are added to the reserve network. A reserve selection algorithm produces a set of sites, or multiple sets of sites, that represent the maximum number of species in a given number of sites, or all species in the minimum number of sites. Many different algorithms have been tested and some have been incorporated into conservation planning tools that have been applied to select potential reserve sites in different parts of the world (Bedward et al. 1992, Ferrier et al. 2000, Groves et al. 2002).

Pressey et al. (1994) proposed an alternative to the predetermined-algorithm approach to reserve selection. Like the algorithms, this approach makes use of complementarity as a selection criterion. The approach involves mapping a continuous site attribute known as

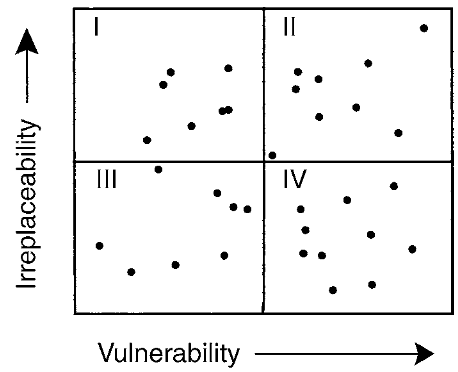

FIG. 1. Hypothetical sites plotted along two axes (adapted from Margules and Pressey [2000]). Irreplaceability is a measure of the relative contribution of a site to protecting a set of conservation targets. Sites with higher irreplaceability values can be viewed as having higher conservation value. The horizontal axis depicts the degree to which the conservation targets at a site are vulnerable to any of a number of potential threats.

irreplaceability, a measure based on complementarity (Ferrier et al. 2000), and allows planners to iteratively and interactively select sites based on these values. Irreplaceability is a measure of the importance of a site to the goal of protecting all species. Sites that are totally irreplaceable contain species that can be found at no other site. Less irreplaceable sites are not unique, and thus there are alternative sites that can be selected in their stead. The approach is more flexible than the predetermined algorithms because planners are able to interactively select reserves, using the irreplaceability values to give them a wide range of options (Margules and Pressey 2000).

Because reserves serve the purpose of removing or decreasing the threats to biodiversity, it follows that these threats should be directly addressed in the reserve selection process. In fact, a number of researchers have suggested that the effectiveness of conservation planning could be improved by prioritizing areas based both on representation and the vulnerability of sites to potential threats (Margules and Pressey 2000, Pressey and Taffs 2001). Including measures of vulnerability in the selection process allows planners to practice a form of triage (Myers 1979). Taking such an approach assumes that sites facing larger and more imminent threats should be addressed first, and that populations in less vulnerable sites will likely persist without immediate assistance, allowing those sites to be addressed later. Using this logic, conservation planners would address sites in quadrant II of Fig. 1 before addressing sites in quadrant I.

Because habitat destruction and degradation are two of the main factors threatening biodiversity (Wilcove et al. 1998, Lawler et al. 2002), some general measures of vulnerability will often be useful at scales appropriate for conservation planning. Measures incorporating human population density (Wickham et al. 2000) or projections of human population increases (Abbitt et al. 2000) have both been suggested as general measures of vulnerability. In the tropics and in many temperate forested areas, where logging and burning account for a significant portion of habitat loss, the percentage of cleared forest may be a useful indicator of site vulnerability (Pressey and Taffs 2001). In other areas where intensive agriculture predominates or the dominant trend in land conversion is from agriculture to suburban development, other more general measures of land use and landscape pattern may be good indicators of vulnerability (O'Neill et al. 1997). Despite the obvious advantages of applying our current understanding of the threats to biodiversity to the site selection process, few studies have attempted to incorporate this fundamental aspect of conservation into reserve selection methods (Abbitt et al. 2000, Reyers et al. 2001).

Here we demonstrate two approaches to integrating information about species distributions and site vulnerabilities for conservation planning. These approaches build on the two different reserve selection methods just discussed. The first approach builds on the idea of mapping a continuous measure of irreplaceability (Pressey et al. 1994). We combined a measure of site irreplaceability and the relative level of each of three indicators of vulnerability to produce maps that could be used for conservation planning. The second approach uses a reserve selection algorithm to locate sets of sites that (1) include all species, (2) include the smallest number of sites possible, and (3) maximize vulnerability across sites. Although both of these reserve selection methods are based on the concept of complementarity, the types of results they produce (maps of site ''values'' vs. one or more sets of sites) are fundamentally different and provide planners with very different types of information. For this reason, it is difficult to quantitatively compare the results of the two analyses. We present our techniques as two complementary approaches and provide some quantitative, but primarily qualitative, comparisons of the results. We applied both techniques to species occurrence data for 497 vertebrate species from five taxonomic groups and three indicators of vulnerability based on measures of land use in the Mid-Atlantic region of the eastern United States.

Methods

Data

We used a grid of 487 650-km^2 hexagonal cells (White et al. 1992) to cover an area that included the states of Delaware, Maryland, Pennsylvania, Virginia, and West Virginia. These cells served as the sites for all prioritizations and selections. Because these sites 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. Species occurrence records for 497 native vertebrate species including amphibians, birds, freshwater fish, mammals, and reptiles were compiled for each of the 487 sites (Table 1). The Natural Heritage Programs from each of the five states compiled, digitized, and performed quality control procedures on the data as directed and assisted by The Nature Conservancy (Master 1996). Occurrences were determined using literature, expert opinion, digital databases, and museum records. Experts for each of the five taxonomic groups reviewed the databases.

TABLE 1. Numbers of species and minimum sizes of reserve networks (as determined by simulated annealing) for six taxonomic groups in the Mid-Atlantic region of the United States.

Taxon	No. species	Minimum no. sites†
Fish	171	17
Birds	162	5
Mammals	67	7
Reptiles	45	6
Amphibians	52	8
All vertebrates	497	27

† The minimum number of sites necessary to include all species from each group in a reserve network.

We excluded a number of species from our analysis that were locally rare, but globally relatively common. Because rare species can have a strong influence on the outcome of reserve selection analyses, it is important to consider the reasons for including all species in the planning process (Kiester et al. 1996). We excluded any species that both occupied $<5\%$ of the sites in the region and was classified as globally relatively common from our data set. We used the lowest two sensitivity classes of a five-level global ranking system to classify species as globally common (Master 1991). This screening process eliminated 79 fish, 46 bird, 26 amphibian, 19 reptile, and 6 mammal species from a total of 673 vertebrate species.

We selected three indicators of human impact on the landscape to represent the vulnerability of a site. We chose to use the percentage of the site that had undergone urban or suburban development, the percentage committed to agriculture, and the percentage covered with open mines (e.g., strip mines and quarries). These three indicators of vulnerability were general enough to apply to many of the species in the five taxonomic groups, yet different enough to complement each other and not provide redundant information.

All three of the indicators of vulnerability were derived from National Land Characteristics Data (NLCD) generated by the Multi-Resolution Land Cover Consortium (Vogelmann et al. 2001). The NLCD classification system uses 21 categories to classify 30-m resolution Landsat Thematic Mapper imagery. We quantified the percentage of each of the 487 hexagons covered by urban and suburban development (NLCD classes: low-intensity residential, high-intensity residential, and commercial/industrial/transportation lands), agriculture (NLCD classes: pasture or hay, row crops, small grains, fallow, orchards or vineyards, and recreational grasses), and open mines (NLCD class: quarries/strip mines/gravel pits).

We considered two additional measures of vulnerability based on the density of roads and human population density in each of 487 hexagons. Because both of these measures were highly positively correlated with the NLCD-derived measure of urban and suburban development, we chose to use only one of the three. To be consistent with our other measures of potential threats from agriculture and mining, we used the NLCD-derived measure of urban and suburban development.

Mapping irreplaceability and vulnerability

We simultaneously mapped a site ranking based on species representation and site rankings based on the intensity of each of three indicators of vulnerability. To assess relative site importance based on species representation, we calculated a measure of irreplaceability for each site. We used the formulation described by Ferrier et al. (2000) in which irreplaceability is calculated for each species at each site. The following four-step process defines the calculation of irreplaceability for species *A* at site *S*. First, find all possible sets of sites (of a given size). Second, find the sets of sites from the first step that contain all species. Third, find the sets of sites from step two that contain site *S*. Fourth, find those sets of sites from step three that will no longer contain species *A*, if site *S* is removed from the set. Dividing the number of sets from step four by the number from step two produces an irreplaceability value for species *A* at site *S*. Irreplaceability values would then be calculated for all other species at site *S* and the values would be summed to produce one measure for the site. Because the calculation of irreplaceability involves finding all sets of sites that include all species, computation, particularly with large sets of sites and many species, is often infeasible in reasonable time periods. We used the conservation-planning program C-Plan that employs a statistical estimate of irreplaceability (Ferrier et al. 2000). We calculated irreplaceability for each species at a site and then summed the values to produce one value for each site. Calculated in this way, values for the irreplaceability of a site have a lower bound of zero and a theoretical upper bound of the number of species at the site. In practice, the highest irreplaceability value is much lower than this theoretical upper bound.

We calculated six different irreplaceability values for each site using six different sets of species (each of the five taxa individually and all species as one group). We mapped the values of irreplaceability against the values of each indicator of vulnerability, producing 18 maps with which site vulnerability and irreplaceability could be simultaneously assessed.

Vulnerability as a constraint in a site selection algorithm

Our second approach to integrating information about species representation and site vulnerability was based on solving the set-covering problem (Underhill 1994). The basic problem of determining the locations of the smallest number of sites that cover all conservation elements was formulated for all sites j in the universe of available sites J by Camm et al. (1996) as

$$\min \sum_{j \in J} x_j \tag{1}$$

subject to

$$x_j = (0, 1) \qquad \text{for all } j \in J \tag{2}$$

$$\sum_{j \in N_i} x_j \geq 1 \qquad \text{for all } i \in I \tag{3}$$

where x_j is a binary variable taking the value 1 or 0 depending on whether site j is included or excluded from the solution set, respectively. In addition to the simple constraint of Eq. 2, Eq. 1 is constrained by Eq. 3 such that each conservation element i of the universe of conservation elements I is included in the solution set. N_i is the set of all sites that contain the element i.

This formulation can be modified to account for differences in cost among sites (e.g., site area, monetary land value, or other measurable costs) as follows, replacing Eq. 1 with

$$\min \sum_{j \in J} c_j x_j \tag{4}$$

where c_j is the cost of selecting site j. We substituted an index of vulnerability for this cost factor. We created a simple index of vulnerability based on our three factors (development, agriculture, and open mines). We scaled each of the three factors so that their values ranged from 0 to 1 and added them together. Vulnerability at a site j is defined as

$$V_j = D_j + A_j + M_j \tag{5}$$

where D, A, and M are the scaled measures of development, agriculture, and open mines, respectively. Because we were most interested in more vulnerable sites, we scaled the index and substituted its inverse (IV_j) for c_j in Eq. 4:

$$\mathrm{IV}_j = 1 - \left[\frac{V_j}{\max(V)}\right] \tag{6}$$

$$\min \sum_{j \in J} \mathrm{IV}_j x_j. \tag{7}$$

Thus by minimizing Eq. 7, we simultaneously minimized the number of sites selected and maximized the total vulnerability across selected sites.

We used simulated annealing (Kirkpatrick et al. 1983, Possingham et al. 2000) to select the most vul-

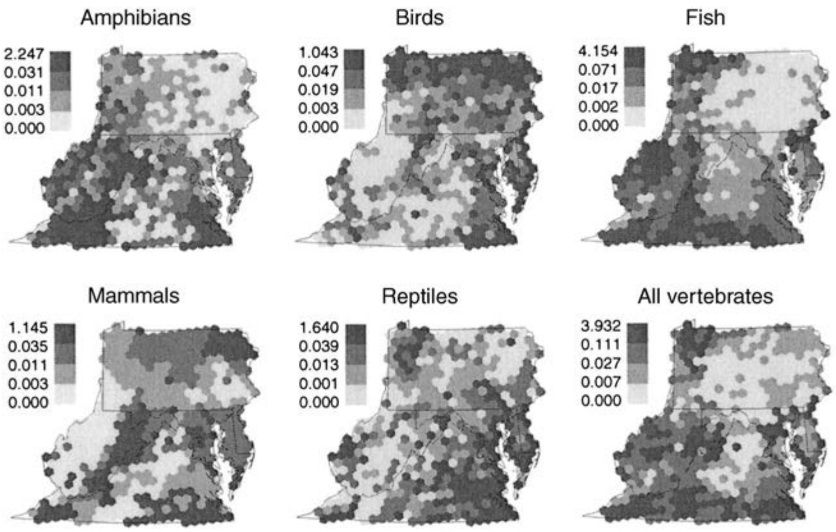

FIG. 2. A measure of summed irreplaceability for 487 sites in the Mid-Atlantic region of the United States for five taxonomic groups and for all species combined. Each shade represents a quartile of the range in irreplaceability values. The darkest hexagons represent the 25% of the sites that were most important for preserving all species.

nerable of the smallest sets of sites that included each species at least one time. Integer programming can provide the optimal solutions to reserve selection problems (Underhill 1994) and has been used to solve reserve selection problems with multiple objective equations (Rothley 1999). However, when there are large numbers of sites and species, integer programming becomes computationally difficult. Although simulated annealing does not necessarily provide the optimal solutions to such problems, it has proven to perform well in relation to other techniques and is relatively quick at finding good solutions (Csuti et al. 1997, Pressey et al. 1997).

We applied the reserve selection analysis to all species together as one group. We then compared the sites selected with this analysis to a map of irreplaceability calculated for all species and vulnerability as represented by the index composed of the three indicators of vulnerability. This allowed us to directly compare the results of the two techniques. We compared the average vulnerability of the sites selected with the reserve selection algorithm to the average vulnerability of 100 alternative solutions of the same size chosen with a basic optimization function that attempted to find the smallest number of sites that included all species but that did not attempt to maximize vulnerability across sites (i.e., Eqs. 1–3). All simulated annealing runs were done with either the reserve selection software SITES (Andelman et al. 1999) or our own code written in the C programming language.

RESULTS

Mapping irreplaceability and vulnerability

The five taxa generally showed relatively different patterns of irreplaceability across the region (Fig. 2). For example, important areas for the representation of bird diversity were concentrated in the northern portion of the region, compared to areas in the southeast and southwest for amphibians, west and south for fish, and northeast and central for mammals. However, there were a few areas, in northwestern Pennsylvania, southeast and southwestern Virginia, far western West Virginia, and along the Virginia–West Virginia border that were critical for a number of taxa. These areas were also highlighted in the simultaneous analysis of all vertebrates.

It is important to note that the distribution of irreplaceability values for any given taxon was highly positively skewed. Thus there were very few high values and a large number of low values. We chose to represent quartiles of the values on the maps because, in general, most sites included in any set covering site selection were included in the top 25% of the sites with respect to irreplaceability values. Sites in the bottom 25% were not generally included in these solution sets. Any classification of the irreplaceability values will necessarily be subjective. Because the number and location of critical areas displayed in these maps depend on the way in which the irreplaceability values were classified, these maps should only be seen as one possible representation of the data. A more practical (but less easily presented) application of these results would be to use the irreplaceability values to provide a continuous ranking of all sites.

Our three general indicators of vulnerability were also distributed differently across the region (Fig. 3). The majority of the intense urban and suburban development was concentrated in the east, stretching from Scranton, Pennsylvania south to Norfolk, Virginia. This area includes those cities as well as Philadelphia,

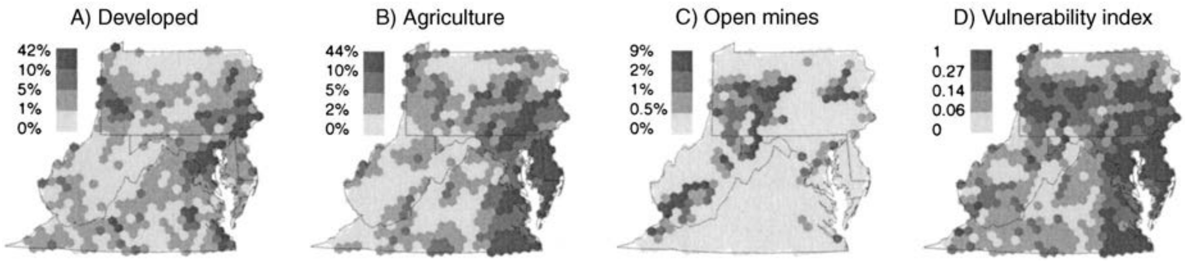

FIG. 3. Maps of general indicators of vulnerability for 487 sites in the Mid-Atlantic region of the United States. Maps represent (A) the percentage of the landscape that has undergone urban and suburban development, (B) the percentage of land in agriculture, (C) the percentage of land covered with open mines, and (D) an index composed of these three factors.

Harrisburg, Baltimore, Washington, D.C., and Richmond. Pockets of more intense development in the western part of the region were concentrated around Erie and Pittsburgh, Pennsylvania. Agriculture was even more heavily concentrated in the east. In contrast, the majority of open mines were predominantly scattered across western Pennsylvania and West Virginia. Our index of vulnerability reflected the distributions of its three component factors (Fig. 3).

We mapped the information contained in the irreplaceability values and that represented by the three measures of vulnerability to produce 18 maps of the region using a bivariate color scheme (Robinson et al. 1995; Fig. 4). These maps represent areas simultaneously ranging from low irreplaceability (white) to high irreplaceability (cyan), and from low vulnerability (white) to high vulnerability (magenta). Critical areas for species diversity that are highly vulnerable to one of the three factors (development, agriculture, and open mines), appear in dark blue on the maps. Cyan colored areas, by contrast, are those that are important for conserving species diversity, but are not highly threatened by human activities as measured by our three indicators of vulnerability.

In our example, the largest threats to critical areas from urban and suburban development tended to be in the upper Chesapeake Bay, particularly areas around Baltimore and Washington, D.C., but also areas in the vicinity of Erie, Pennsylvania and Richmond, Virginia. Amphibian, bird, and reptile diversity were likely to be more threatened by development in the southeast corner of Virginia, whereas fish and reptile diversity appeared to be more vulnerable to threats from development in an area of western Virginia in the vicinity of Roanoke. Areas of relatively intense agriculture generally coincided with critical areas for all taxa in the southeastern corner of the region, but also showed much overlap along the Delmarva Peninsula. Critical areas for each taxon overlapped with at least several sites with relatively heavy concentrations of open mines. Furthermore, our simultaneous analysis of all species showed that a small number of sites in southern West Virginia were both critical for vertebrate species diversity in general and had relatively high concentrations of mines.

Vulnerability as a constraint in a site selection algorithm

Using simulated annealing, 27 sites were required to include all 497 species. It took from five sites (for birds) to 17 sites (for freshwater fish) to cover each taxon individually (Table 1). By simultaneously minimizing the number of sites selected to cover all species and maximizing vulnerability across selected sites, we were able to identify the most vulnerable sets of sites that covered all species using the least area possible. The most vulnerable set of sites selected with the vulnerability-based algorithm (Fig. 5B) had a mean vulnerability index value of 0.24 compared to 100 alternative 27-site solutions (selected with a basic algorithm based only on complementarity) that had an average mean value of 0.19 (range 0.15, 0.23).

Comparing the two methods

The irreplaceability and the vulnerability of the most vulnerable set of sites selected by the reserve selection algorithm can be evaluated by comparing maps A and B in Fig. 5. Map A depicts the irreplaceability of sites for all vertebrates and the vulnerability of sites as an index of agriculture, open mines, and urban and suburban development. Map B shows the locations of the 27 sites selected with the vulnerability-based algorithm. All but two (93%) of the selected sites had irreplaceability values in the highest quartile. Two sites in Pennsylvania had relatively low irreplaceability values, one in the first and one in the second quartile. In contrast, only eight (30%) of the sites were in the highest quartile of vulnerability. Most of the 27 sites (15) were in the lowest two quartiles.

DISCUSSION

The rapid rate at which humans are changing the earth's surface requires that conservation-planning techniques consider both temporal and spatial aspects of reserve selection. Explicitly combining information about the representation of biodiversity and the vul-

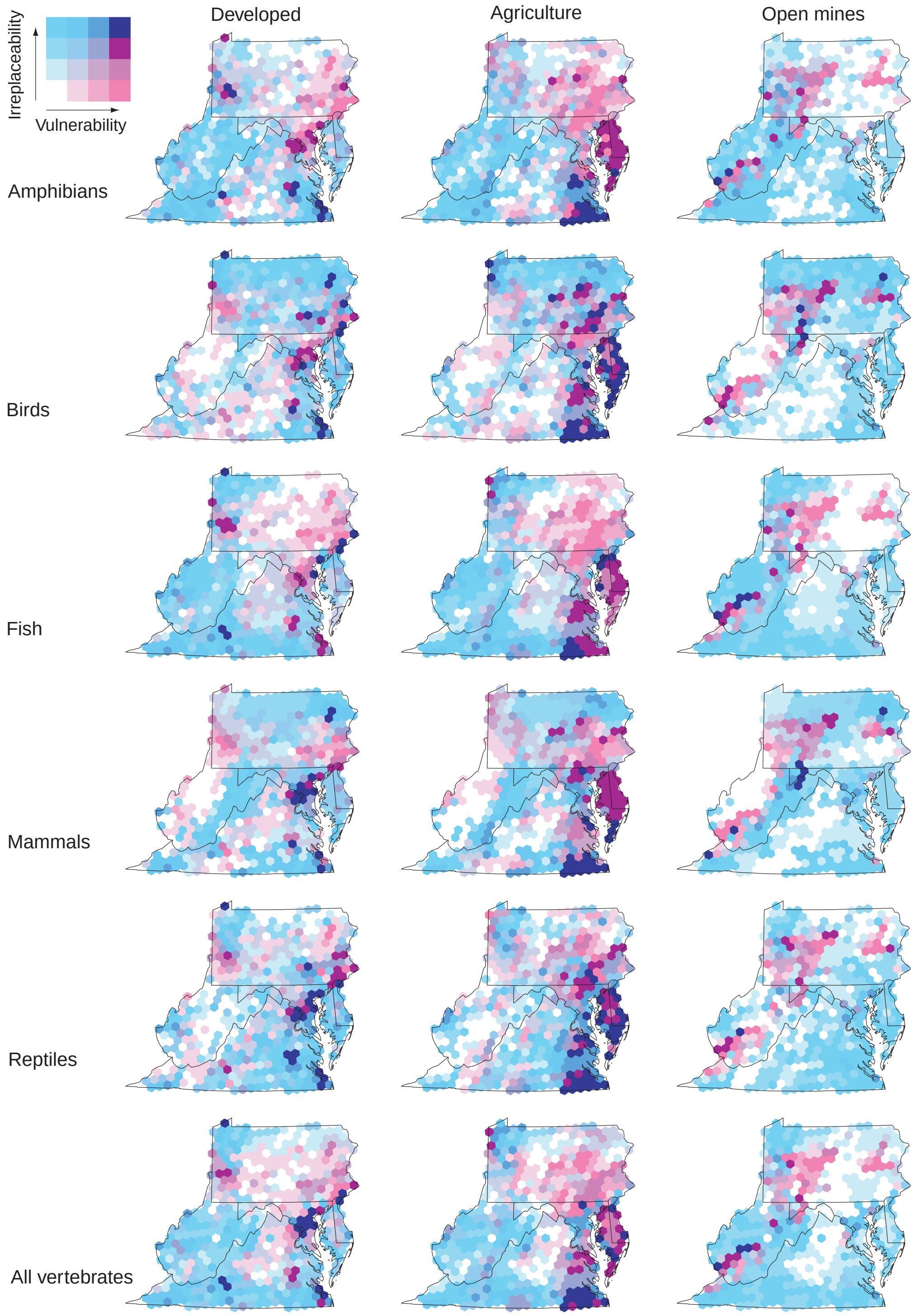

FIG. 4. Maps of irreplaceability and each of three indicators of vulnerability for each of five taxa and all vertebrate species in the Mid-Atlantic region of the United States. Irreplaceability values increase with the intensity of cyan. The vulnerability of sites to each of the three types of threats increases with the intensity of magenta. The dark blue sites are those that are both important for conserving species diversity and vulnerable to species loss, whereas the white sites are those that have both low irreplaceability values and low vulnerability values.

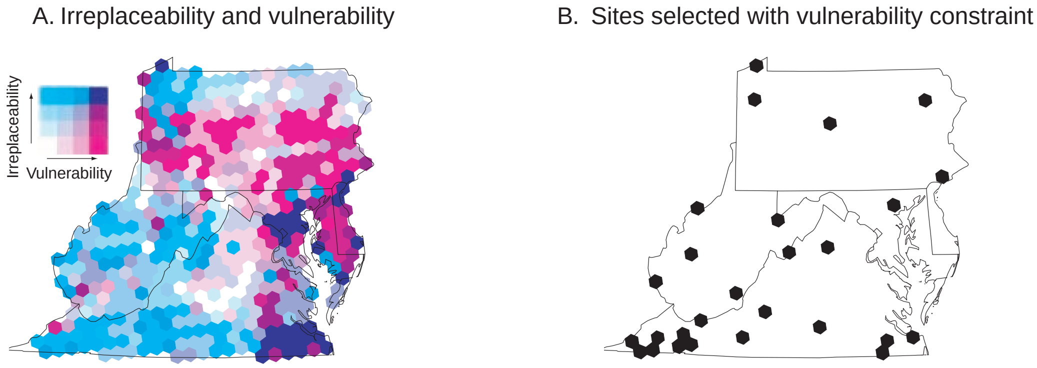

FIG. 5. Maps depicting two approaches to prioritizing areas for conservation based on species representation and site vulnerability. Map A represents both irreplaceability (a measure of conservation value for 497 vertebrate species) and vulnerability (a measure of the degree to which sites are influenced by agriculture, urban and suburban development, and open mines). Irreplaceability values increase with the intensity of cyan. The vulnerability of sites to each of the three types of threats increases with the intensity of magenta. The dark blue sites are those that are both important for conserving species diversity and vulnerable to species loss, whereas the white sites are those that have both low irreplaceability values and low vulnerability values. Map B represents a set of 27 sites that includes all 497 species and maximizes the vulnerability across sites.

nerability of sites to anthropogenic threats enables conservation planners to prioritize sites in both time and space. Using information about potential threats gives planners the ability to prioritize among sites of similar conservation value (i.e., sites facing larger threats can be slated to receive more immediate attention than those facing weaker threats). The two techniques that we have demonstrated for incorporating vulnerability into the reserve selection process enable conservation planners to address this temporal aspect of reserve selection.

The two techniques presented here may best be seen as complementary tools, each providing a different type of information. The mapping of irreplaceability and vulnerability provides more detail by creating a continuous ranking of all sites, whereas the reserve selection algorithm provides specific sets of sites that include all species. Our comparison of the results of the two techniques indicates that there is a trade-off between efficiently protecting all species in the smallest number of sites possible, and addressing the most vulnerable sites. This is evidenced by the fact that over half of the sites identifed with the reserve selection algorithm are only minimally threatened by the three anthropogenic factors (i.e., have low vulnerability). Thus it is not possible to select sets of 27 sites that include all species that are much more vulnerable than those chosen here. Furthermore, using the mapping technique to select only sites with high vulnerabilities and high irreplaceability values is not likely to provide coverage for all species.

Modifications to both techniques can, at least in part, address these trade-offs. Ferrier et al. (2000) have developed a method that allows planners to insure full coverage of all species using the mapping technique. By making the selection process iterative, one can recalculate irreplaceability after selecting each site. Thus the relative ranking of sites changes as species are included in the set of selected sites. Using this iterative selection process in conjunction with information about site vulnerability would allow for the selection of highly irreplaceable, vulnerable sites that include all species. The algorithm-based approach can also be made more flexible by modifying one of the two constraints that limit the degree to which vulnerable sites can be included in a solution set. Although there often are many solutions to reserve selection problems, the constraints placed on site selection limit the degree to which vulnerable sites can be included in a solution set. By relaxing the constraint of including all species or relaxing the objective of minimizing the number of sites selected, it is possible to select alternative sets of sites that include more vulnerable areas. We found that sets of 28, 29, and 30 sites could be selected to protect all species and include sites with higher average vulnerabilities. Thus more flexibility can be added to the site selection process, but it comes at a price of either selecting more sites or including fewer species.

One critical aspect of triage is that "lost causes" are identified and abandoned. A site, although important biologically and highly threatened by development, may require all of a planning agency's funds to protect or restore and thus eliminate the agency's ability to address other areas. Other potentially high-ranking sites might be too small, isolated, or altered to protect biodiversity. Although the mapping technique presented here could be used to screen out the most vulnerable sites, modifications would have to be made to the reserve selection algorithm to explicitly address this issue. That said, the regional scale (particularly the resolution) at which we have applied these techniques is not conducive to identifying sites that are potentially too threatened to act as viable reserves. Further analyses, conducted at a finer spatial resolution, would be necessary to determine if specific habitats were too small, altered, or isolated to support viable populations of particular species in question.

Both of the techniques that we demonstrated could be used for conservation planning in other than triage-type approaches. Some people have taken an approach in which sites with high representation and low vulnerability (sites in quadrant I of Fig. 1) are targeted as potential reserves (e.g., Davis et al. 1996). These areas are likely to be in the best condition and thus may be the best choice for ensuring species persistence if planners are limited to setting up preserves in a very small number of areas. Comparison of our two techniques indicates, however, that some combination of vulnerable and more secure sites may be necessary to include all species in a region in a relatively small number of sites.

The choice of indicators of site vulnerability will clearly influence the results of the two techniques demonstrated here. Because the analyses that we have presented are primarily intended as a demonstration of techniques, we used general measures of land cover to represent potential threats to a wide range of species. Although these indicators may be adequate at the scale of 650-km^2 sites, more appropriate measures of vulnerability could be used in future applications of these methods, particularly at finer spatial scales. Models that make spatially explicit predictions of future land costs, human demographic trends, timber harvest, or agricultural development could provide more meaningful quantifications of vulnerability (e.g., Clarke and Gaydos 1998, Parks et al. 2000). In addition, when conservation planning is applied to specific taxonomic groups of organisms, measures of vulnerability that are more closely linked to the threats faced by those species will be better indicators of vulnerability (Wilcove et al. 1998). For example, site selection procedures for freshwater fauna might use vulnerability measures that assess the degree to which hydrologic regimes have been altered, the potential for agricultural pollution, and the abundance and diversity of exotic species (Richter et al. 1997).

In addition to the choice of indicators of vulnerability, the way in which the indicators are integrated is likely to affect the results of subsequent site selections. We chose to equally weight the three vulnerability measures in the index that we created for use in our reserve selection algorithm. In instances in which the relative importance of different threats are well understood, the corresponding measures of vulnerability could easily be weighted differentially in similarly constructed indices.

The way in which the results from the two techniques outlined here are used, like the choice of measures of site vulnerability, is scale dependent. We used 487 650-km^2 hexagonal grid cells as the sites for the present analysis. This grain and extent is appropriate for conservation planning at a regional scale, but restricts the types of conservation actions likely to be undertaken. It would not necessarily be either ecologically sound or politically feasible to create reserve boundaries around the hexagonal cells identified in this study. The sites identified here could, however, be targeted for finer scale analyses to determine how best to protect target species.

In the interest of clearly demonstrating these two methods for integrating representation and vulnerability, we chose not to address several other aspects of efficient systematic reserve selection. For example, we did not address population persistence within reserves. The application of our reserve selection algorithm assumes that one site is sufficient for the protection of all species found within its boundaries. Thus it is assumed that adequate habitat and population sizes exist at the chosen site. Because larger species will require more habitat and different species will persist at different minimum population levels and be susceptible to different amounts of habitat fragmentation, this assumption is not likely to hold for all species. In demonstrating our techniques, we also chose not to consider the location of current reserves or to take into account the species that already receive the protection afforded by those reserves. In addition to assuring population persistence, considering the contribution of pre-existing reserves is a key step in the overall site selection process (Margules and Pressey 2000).

There are several established methods for indirectly addressing population persistence and for accounting for previously established reserves in reserve selection methods. Other studies have demonstrated methods for indirectly addressing persistence by incorporating redundancy (Pressey et al. 1996), connectivity (Bedward et al. 1992, Briers 2002), and environmental heterogeneity both within and across sites (Cowling et al. 1999, Rodrigues et al. 2000, Fairbanks et al. 2001) into reserve selection methods. Other studies have evaluated the role played by previously existing reserves and how these reserves affect the selection of new sites (Rodrigues et al. 1999).

The conservation planning process is extremely complex because, in part, planners must weigh ecological, economic, and cultural factors when making decisions. Thus integrating information about species representation, vulnerability, and population persistence is only one of the steps that can be made to improve techniques for conservation planning. In addition to representing species, it is becoming clear that selecting areas that protect other aspects of biodiversity (World Resources Institute 1992) as well as ecological processes (Cowling et al. 1999, Margules and Pressey 2000) will improve the ability of reserves to protect biodiversity. Furthermore, different socioeconomic constraints such as land cost or ownership (e.g., Ando et al. 1998) or natural resource use (Sala et al. 2002) can be added to site selection procedures to help planners visualize and evaluate the largest possible range of options available for meeting conservation goals. Designing methods to integrate these constraints is an important step in solving conservation-planning problems. It is by fully exploring options and making them readily accessible to planners that we are most likely to increase the probability of finding adequate solutions to such complex problems.

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