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30. We thank C. D. Putnam, A. M. Bilwes, J. Skinner, and R. M. Sweet for help with data collection, NSLS and SSRL for use of data collection facilities, and J. R. Winkler and H. B. Gray for access to Beckman Institute resources. We also thank C. Mol, T. Macke, A. M. Bilwes, C. D. Putnam, M. Marietta, and B. S. S. Masters for helpful discussions. Supported by NIH grant HL58883 and a Helen Hay Whitney Fellowship to B.R.C. D.J.S. is an Established Investigator of the American Heart Association. The Protein Data Base codes are 1nod for H₄B-ARG, 2nod for H₄B-H₂O, and 3nod for H₄B-SCIT.

16 December 1997; accepted 11 February 1998

Species Distributions, Land Values, and Efficient Conservation

Amy Ando, Jeffrey Camm, Stephen Polasky, Andrew Solow*

Efforts at species conservation in the United States have tended to be opportunistic and uncoordinated. Recently, however, ecologists and economists have begun to develop more systematic approaches. Here, the problem of efficiently allocating scarce conservation resources in the selection of sites for biological reserves is addressed. With the use of county-level data on land prices and the incidence of endangered species, it is shown that accounting for heterogeneity in land prices results in a substantial increase in efficiency in terms of either the cost of achieving a fixed coverage of species or the coverage attained from a fixed budget.

The establishment of biological reserves in which development activity is prohibited or otherwise regulated is a common tool for species conservation. By making use of county-level data on the distribution of endangered species within the United States, Dobson *et al.* showed that a large number of endangered species are contained within a relatively small number of counties and concluded that "[i]f conservation efforts and funds can be expanded in a few key areas, it should be possible to conserve endangered species with great efficiency" (1, p. 553). This implicit equation of efficiency with the number of counties needed to achieve a given coverage of endangered species is reasonable when land prices are homogeneous. However, a better definition of efficiency takes account of differences in land prices between counties. Counties targeted in (1) included some of the highest priced land in the United States. Land purchases within these counties could quickly exhaust limited resources and lead to a lower total cov-

erage than if the same resources were expended elsewhere. Even if land is protected by conservation easements or other regulations, rather than by outright purchase, protecting land in these counties may come at high opportunity costs.

Here, we study the effect of heterogeneous land prices on the efficient selection of reserve sites. We considered two versions of the reserve site selection problem (2). Under the first version, known as the set coverage problem (SCP), the objective is to minimize a loss function such as the number or cost of reserve sites subject to the constraint that all species are covered. Under the second version, called the maximal coverage problem (MCP), the objective is to maximize coverage subject to the constraint that the loss not exceed a specified amount.

Both the SCP and the MCP are examples of integer programming problems (3). Effective methods for solving them have been developed, and off-the-shelf optimization software has progressed to the point where it can be used effectively on large versions of the SCP and MCP (4). These methods have been applied to reserve site selection (5), and we applied them here.

We used county-level data on the estimated distribution of endangered species compiled by the U.S. Environmental Protection Agency Office of Pesticide Programs (6). These data, which are essentially the same as those used in (1), record by county the occurrence of all plants and

animals protected or proposed for protection under the Endangered Species Act, as of 1995. The data cover a total of 911 species, subspecies, and populations and 2851 counties.

The corresponding county-level data on 1992 agricultural land values, in dollars per acre, have been compiled by the U.S. Department of Agriculture (7). Although it would be preferable to have the value of undeveloped land, the value of agricultural land, which reflects land market conditions, is a reasonable proxy. Values are available for 2822 counties in the species distribution list. We estimated the 29 missing values, which occur mainly in counties with minimal agricultural land, using values from previous years, neighboring counties, or both.

The goal of the analysis presented here was to compare optimal site selection when the loss is measured by the number of sites with optimal site selection when the loss is measured by the cost of the sites. To make this comparison, we assumed that all species within a county were covered in a site of unit area. Because the size of the unit area serves only to scale cost, for convenience, we took it to be 1 acre. More importantly, this assumption implies that all species within a county can be covered in the same unit area. In reality, not all of the endangered species within a county co-occur in the same site, and different species require reserves of different size for survival. In practice, the design of reserve sites, which is the subject of a large

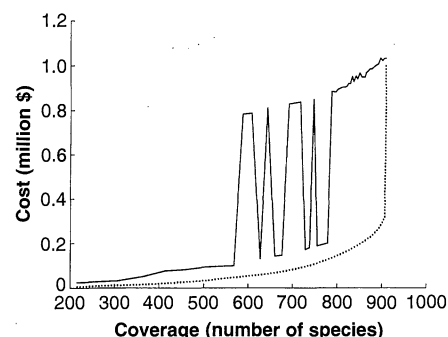


Fig. 1. Cost versus coverage for site-minimizing (solid curve) and cost-minimizing (dotted curve) solutions.

A. Ando, Resources for the Future, 1616 P Street, NW, Washington, DC 20036, USA.

J. Camm, Department of Quantitative Analysis and Operations Management, University of Cincinnati, Cincinnati, OH 45221, USA.

S. Polasky, Department of Agricultural and Resource Economics, Oregon State University, Corvallis, OR 97331, USA.

A. Solow, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.

*To whom correspondence should be addressed. E-mail: asolow@whoi.edu

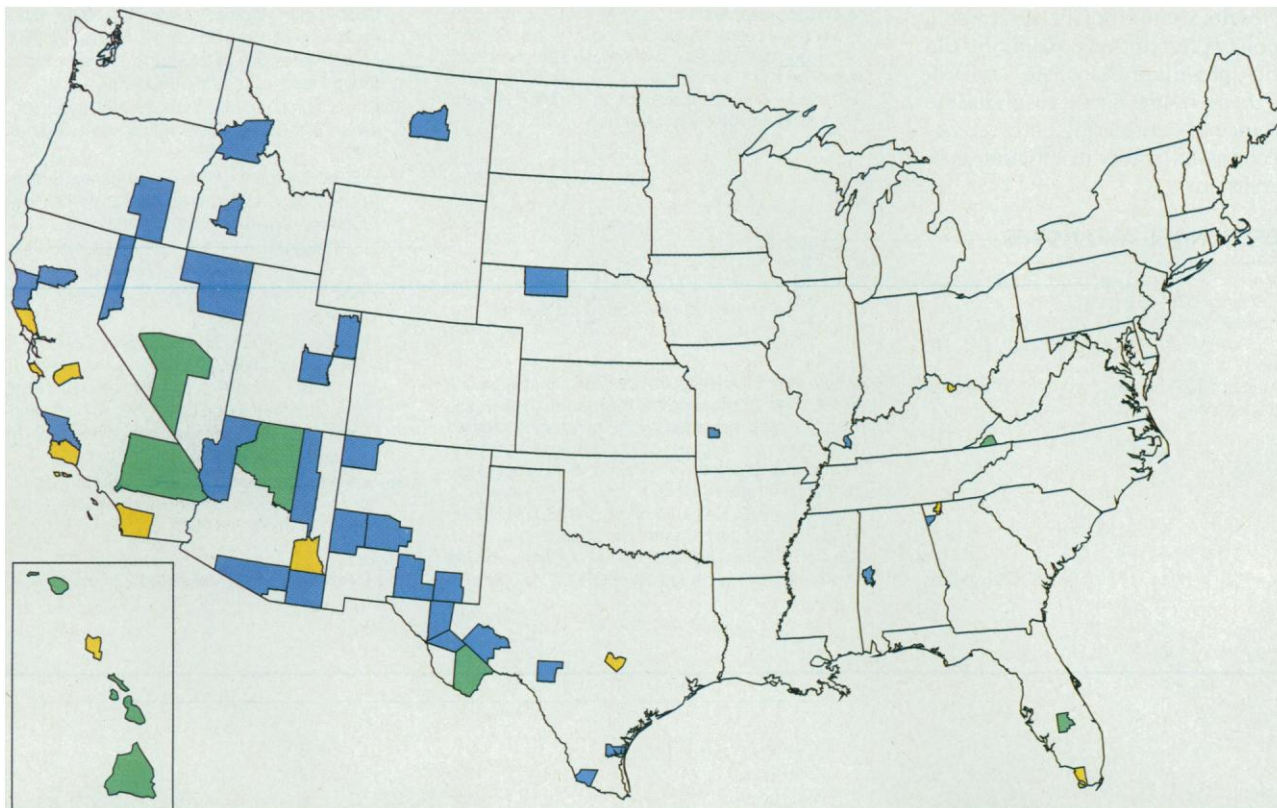


Fig. 2. Selected sites for coverage of 453 species in the United States. Sites in the site-minimizing solution only are shown in blue, sites in the cost-minimizing solution only are shown in yellow, and sites in both solutions are shown in green.

and growing literature (8), requires detailed information about species distributions and range requirements.

We began our analysis by finding the optimal solution for each of a range of values of the site-number constraint and calculating the cost of the solution. The results in terms of cost and coverage are shown in Fig. 1. For example, the cost of covering 453 species, which can be achieved by selecting a minimum of 20 sites, is \$75,700. On the other hand, the cost of covering all 911 species, which can be achieved by selecting a minimum of 212 sites, is \$1,020,600. It is often possible to attain the same level of coverage with different sets of sites of equal number. For example, a coverage of 453 species can be achieved by 33 different sets of 20 sites. As a result, cost is not uniquely defined. For example, the cost of covering 453 species in 20 sites ranges from \$74,749 to \$79,049. The solutions presented in Fig. 1 were selected without regard to cost.

A striking feature of Fig. 1 is its oscillatory behavior for coverage between about 650 and 800 species. Within this range, it is possible to achieve increased coverage at a reduced total cost. This effect occurs because sites selected to achieve one level of coverage need not be selected to achieve a higher level of coverage. If coverage is in-

creased by dropping particularly expensive counties and adding less expensive counties, total cost may fall. This behavior is particularly pronounced because of the extremely high estimated land value in San Francisco County, which is an order of magnitude larger than the next highest value. As San Francisco County is added to and dropped from the set of selected sites, total cost rises and falls markedly.

Next, the cost-minimizing solution was found for each of a range of coverages. The results are also shown in Fig. 1. As expected, the cost of this solution is less than the cost of the solution that minimizes the number of sites. For example, for coverage of 453 species, the cost of this solution, which includes 41 counties, is \$22,582. This value is around 30% of the cost of achieving the same coverage by minimizing the number of sites. Alternatively, if the conservation budget is fixed at \$100,000, the cost-minimizing solution covers about 750 species, whereas the site-minimizing solution covers only about 590 species. The difference in cost is even more marked when the site-minimizing solution includes San Francisco County, which only enters the cost-minimizing solution at the last step to achieve complete coverage. To make the comparison without the dominating effect of San Francisco County, we repeated the

analysis under the extreme assumption that land in San Francisco County is free. For coverage of up to about 700 species, the cost of the cost-minimizing solution is 25 to 50% of the cost of the site-minimizing solution. As coverage increases beyond 700 species, the relative difference in cost declines until, at complete coverage, the cost of the cost-minimizing solution is 93% that of the site-minimizing solution. This convergence is due to endemism: To cover a species endemic to a single county, both solutions must contain that county.

The locations of the sites selected under the two solutions (with San Francisco entered at full cost) for coverage of 453 species are shown in Fig. 2. Although the two solutions are similar, the cost-minimizing solution includes sites in the Inner-Mountain West and the Midwest that are not included in the site-minimizing solution. Although these sites are not especially rich in species, this deficiency is offset by their low cost. In areas common to both solutions, the cost-optimal solution achieves efficiency by avoiding costly sites and selecting nearby sites that have fewer species but are less costly. By including twice as many sites at 30% of the cost, the cost per site under the cost-minimizing solution is less than one-sixth of that under the site-minimizing solution.

These results should not be interpreted as actual policy prescriptions. As in (1), the experiments presented here are stylized. However, these results serve to underline the importance of considering both ecological and economic factors in efficient species conservation.

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3. Formally, an optimal solution to the SCP is found by solving the following: Minimize

$$\sum_{j \in J} c_j x_j$$

subject to

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

where $J = \{j \mid j = 1, \dots, n\}$ is the index set of

candidate reserve sites, $I = \{i \mid i = 1, \dots, m\}$ is the index set of species to be covered, N_i is the subset of J that contain species i , c_j is the loss associated with selecting site j , and $x_j = 1$ if site j is selected and 0 otherwise. An optimal solution to the MCP is found by solving the following: Maximize

$$\sum_{i \in I} y_i$$

subject to

$$\sum_{j \in N_i} x_j \geq y_i \text{ for all } i \in I \text{ and } \sum_{j \in J} c_j x_j \leq b$$

where $y_i = 1$ if species i is contained in at least one of the selected sites and b is the maximum allowable loss. If loss is measured by the number of selected sites, then $c_j = 1$ for all j . If loss is measured by the cost of the selected sites, then c_j is the cost of establishing a reserve in site j .

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10 November 1997; accepted 23 February 1998

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