

A COMPARISON OF RESERVE SELECTION ALGORITHMS USING DATA ON TERRESTRIAL VERTEBRATES IN OREGON

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(Accepted 25 January 1996)

Abstract

We compare the number of species represented and the spatial pattern of reserve networks derived using five types of reserve selection algorithms on a set of vertebrate distribution data for the State of Oregon (USA). The algorithms compared are: richness-based heuristic algorithms (four variations), weighted rarity-based heuristic algorithms (two variations), progressive rarity-based heuristic algorithms (11 variations), simulated annealing, and a linear programming-based branch-and-bound algorithm. The linear programming algorithm provided optimal solutions to the reserve selection problem, finding either the maximum number of species for a given number of sites or the minimum number of sites needed to represent all species. Where practical, we recommend the use of linear programming algorithms for reserve network selection. However, several simple heuristic algorithms provided near-optimal solutions for these data. The nearoptimality, speed and simplicity of heuristic algorithms suggests that they are acceptable alternatives for many reserve selection problems, especially when dealing with large data sets or complicated analyses. © 1997 Published by Elsevier Science Ltd. All rights reserved

INTRODUCTION

The resources that can be devoted to the conservation of biodiversity are limited. Existing nature reserves constitute a small fraction of total area, and there are limited funds available to expand the current system of reserves. In addition, many existing natural areas managed for conservation were selected not for their biological value but because of their scenic beauty or because they had no obvious economic value (Pressey, 1994). Given these facts, it is critical that conservation resources be utilized efficiently so that most, if not all, species and ecosystems are represented in a limited reserve network. As Margules *et al.* (1988) observed, you cannot manage nature reserves to preserve elements of biodiversity if they are not included in the reserve network in the first place.

A number of approaches to the problem of selecting which sites to include in a reserve network have been suggested. A common approach for the site selection problem is to use a stepwise (iterative) algorithm (e.g. Kirkpatrick, 1983; Ackery & Vane-Wright, 1984; Margules et al., 1988; Pressey & Nicholls, 1989; Rebelo & Seigfried, 1990; Vane-Wright et al., 1991; Bedward et al., 1992; Nicholls & Margules, 1993; Kershaw et al., 1994; Margules et al., 1994; Lombard et al., 1995; Williams et al., 1996). The "greedy" (richness-based) algorithm starts with the site containing the most species and sequentially includes sites that add the most additional species. The greedy algorithm has the advantage of speed and simplicity. In addition, by design, it incorporates the principle of complementarity (Pressey et al., 1993). Other stepwise algorithms, "raritybased" algorithms, choose sites in order of the rarity of species they contain or weight heavily species with small distribution. Rarity-based algorithms tend to be more effective than the richness-based greedy algorithm in finding the minimum number of sites necessary to represent all species at least once (Kershaw et al., 1994). A somewhat different approach to the site selection problem is to make use of spatial patterns in the data. Starting from a given solution, such as the greedy algorithm, an

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improved solution may be found by searching for substitute sites in the neighborhood of the original solution. This operation forms the basis of the "simulated annealing" algorithm.

As has been noted by a number of authors, heuristic algorithms may not find an optimal solution to selecting a reserve network (May, 1990; Vane-Wright et al., 1991; Underhill, 1994; Camm et al., 1996; Pressey et al., 1996a; Williams et al., 1996). Optimal solutions to the reserve network problem can, at least in theory, be found by application of integer programming algorithms developed in operations research, such as linear programming-based branch and bound algorithms. These algorithms have been applied to the design of a reserve network in several studies (Cocks & Baird, 1989; Saetersdal et al., 1993; Church et al., 1996; Willis et al., 1996). When the number of potential reserve sites is large or the stated objective is more complex than representing a species once, a branch and bound algorithm may not find a solution in a reasonable amount of time (Pressey et al., 1996a).

The purpose of this paper is to compare the performance of different types of reserve selection algorithms: (a) greedy richness-based algorithms; (b) rarity-based algorithms; (c) a simulated annealing algorithm; and (d) a branch-and-bound algorithm. A linear programmingbased branch and bound solution is, by definition, an optimal (efficient) solution to the reserve network selection problem, which provides a benchmark to measure the performance of other algorithms. However, because it may not be possible to find a solution for large or complex problems using a branch-and-bound algorithm, it is important to understand how well or poorly alternative methods work. In general, we would like to know both the speed with which a solution is found and how close the solution is to optimal. We compare the performance of 19 algorithms on terrestrial vertebrate species distribution data for the State of Oregon (USA) on the basis of both rates of richness accumulation and the total number of sites required to represent all species at least once.

DEVELOPMENT OF THE SPECIES DISTRIBUTION DATA BASE FOR OREGON

Distribution maps for 426 species of terrestrial vertebrates that breed in the State of Oregon were developed as a part of a pilot program of a cooperative national biodiversity mapping effort in the United States, known as the Biodiversity Research Consortium. We selected this subset of all species for analysis because their distributions are the best known. Observations of animals in the field, often accompanied by voucher specimens, form the basis of our knowledge of species distributions (Udvardy, 1969). Distribution maps can be developed from locality records in a number of different formats. A simple approach to data modelling interpolates distribution patterns by placing a boundary around marginal records for a taxon. Grid-based maps record the occurrence of a species in cells of a regular grid (e.g. Sharrock, 1976; Udvardy, 1981). This format makes it possible to record specific information about the species in each grid cell. We created grid-based distribution maps, using a coverage of 635 km² hexagons, that were developed for the US Environmental Protection Agency (White et al., 1992). There are 441 sampling units that completely or partly overlap the political borders of Oregon. The reserve selection algorithms discussed here are not limited by either the taxa, number of species in the data set, or any particular spatial unit of analysis. Many geometric, political or economic spatial units, as well as many different taxa, have been used with site selection algorithms (e.g. Margules et al., 1988; Bedward et al., 1992; Kershaw et al., 1994; Williams, 1994). Distributional information for species (or other elements of biodiversity, such as land systems) is the only data requirement for this type of spatial analysis.

Relatively few regions in Oregon have been intensively surveyed, so many sites (hexagons) lack occurrence records. In constructing the distribution maps, a method of interpolating the probable presence of a species between confirmed records of occurrence was used. The probability of a species occurring in a site (hexagon) was given one of three ratings: (1) confident-a verified sighting of the species in the site has occurred in the two past decades; (2) probable-the site contains suitable habitat for the species, there have been verified sightings in nearby sites, and in the opinion of a local expert, it is highly probable that the species occurs in the site; and (3) possible—no verified sightings have occurred in the site, the habitat is of questionable suitability for the species, and in the opinion of a local expert, the species might occur in the site. The ranking of possible is highly speculative. Only the classifications of confident and probable were used to assign the presence of a species in a site. All distribution maps were circulated to local experts for review prior to use of the species data base in this analysis.

DESCRIPTION OF ALGORITHMS

subject to

The reserve site selection problem can be represented formally as follows:

$$\operatorname{Max}\sum_{i\in I} y_i \tag{1}$$

$$\sum\nolimits_{j \in N_i} x_j \ge y_i \quad \text{for all } i \in I$$

$$\sum_{i \in I} x_j \le k \tag{3}$$

(2)

$$y_i = (0, 1) \quad \text{for all } i \in I \tag{4}$$

$$x_j = (0, 1) \quad \text{for all } j \in J, \tag{5}$$

where $J = \{j \mid j = 1,...,n\}$ denotes the index set of candidate reserves from which to select, and $I = \{i \mid i = 1,...,m\}$ denotes the set of the species to be covered. The set N_i , a subset of J, is the set of candidate reserves that contain species *i*. The variable $x_j = 1$ if site *j* is selected, 0 if site *j* is not selected. Constraint (3) limits the total number of sites selected to no more than *k*. The variable y_i will be one except when $x_j = 0$ for all *j* in N_i (since constraint (2) will force $y_i = 0$ in that case). In words, constraint (2) enforces that the species not be counted as preserved if none of its sites is selected. The following algorithms represent different ways of finding solutions to this problem.

Greedy (richness-based) algorithms (algorithms 1-4)

In the richness-based greedy algorithm, the first site chosen is the one that has maximal species richness. Inclusion of more sites is done so that at each step, the inclusion of the next site adds the most additional species to those already represented. When two or more sites add the same number of additional species, several procedures can be used to break ties. In algorithm 1, when there is more than one site that yields that maximum number of additional species at a step, we choose the first site encountered (i.e. the site with the lowest site number). In algorithm 2, for each site that yields that maximum number of additional species at a step, we choose the site with the highest range-size rarity score (see below) for the complementary species (Williams, 1994). The algorithm can be modified to check for within-set redundant choices, i.e. sites selected that are found at subsequent steps to contribute no unique species (Williams et al., 1996). In these data, no redundant site selections were found.

Where computationally feasible, the optimal solution is guaranteed by enumerating all possible combinations of sites. In this data set, complete enumeration is practical with four sites or fewer. Algorithm 3 begins with the complete enumeration solution through four sites. Beyond this point, a greedy algorithm (algorithm 1) is used.

Algorithm 4 begins with a greedy algorithm (algorithm 1) as an initial solution. After completing the greedy solution, the algorithm attempts to solve a Lagrangian dual formulation of the reserve site selection problem. Initial dual multipliers are chosen, based on the greedy solution, and the numerical technique known as subgradient optimization (Fisher, 1981) is used iteratively to update the dual multipliers. At each iteration, a feasible solution to the problem is generated. If it is better than the current solution (the greedy solution at first), then the current solution is replaced by this improved solution. This technique has the added feature that it generates a bound on the optimal solution, allowing us to know the maximum deviation that the current solution can be from the optimal solution. This heuristic algorithm is phase one of a two-phase exact branch and bound algorithm described in Downs and Camm (1996).

Rarity-based algorithms

Rarity weight algorithms (algorithms 5 and 6)

These algorithms weight site selection by the relative rarity of the fauna in each site (e.g. Rebelo & Seigfried, 1990; Williams et al., 1993; Kershaw et al., 1994). A score is calculated for each site based on: (1) the number of species; and (2) how infrequent the species are among all the sites. In the algorithm weighting richness by inverse range-size rarity (algorithm 5), each species is scored as the inverse of the number of sites in which it occurs. In the algorithm weighting richness by the inverse square of range size (algorithm 6), each species is scored as the inverse of the square of the number of sites in which it occurs. The site score is the sum of the component species scores. The selection algorithm proceeds by selecting the site with the highest score. The scores are then recalculated with the represented species removed, and the site with the highest new score is then selected. This process is continued until all species have been represented.

Progressive rarity algorithms (algorithms 7–17)

We used 11 algorithms that are based on the algorithm described by Margules et al. (1988). The first sites selected are those that contain species unique to that site (i.e. occur in no other sites). Next, a site containing the least frequent unrepresented species (i.e. those species occurring in just two sites if there are any, if not, in three sites, etc.) is chosen. If there are ties, the different algorithms use a number of different rules for which sites to select next. The rules used and the order in which these rules are used are described in Table 1. Algorithms 9-17 contain a random selection rule. Each of these algorithms was run 100 times. Results reported are for the best of the 100 runs. Algorithms 8-17 check for and eliminate redundant sites. In addition, algorithm 8 reorders the sites in the chosen set to maximize the number of species covered at each step.

Simulated annealing (algorithm 18)

This algorithm begins with the complete enumeration solution through four sites. Beyond this point, an algorithm consisting of a spatially explicit variation of simulated annealing methods is used (Kirkpatrick et al., 1983; Press et al., 1992). For each n greater than 4, an initial or "seed" set of n sites was determined by choosing the first four sites to be those found by complete enumeration and then using a greedy algorithm (algorithm 1) to determine an additional n-4 sites. Additional seed sets were then chosen by fixing all possible combinations of 2 of the initial seed set sites and then determining the remaining n-2 sites using algorithm 1. This process yields a number of distinct seed sets up to the number of possible combinations of two sites taken from a set of nsites. Annealing was then performed on each of these seed sets by setting a radius about each site in the seed set and randomly searching the space within this radius.

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A.	Description of the rules used in the algorithms
1. 2.	Unique: choose sites with a species that is unique to that site. Next Rarest: choose a site containing the next least frequent unrepresented species (i.e. those species occurring in inst two sites if there are any if not in three sites etc.)
3.	Greatest Number of Next Rarest: choose the site containing the greatest number of the next least frequent unrepresented species
4.	Next Next Rarest: choose a site containing the next next least frequent unrepresented species.
5.	Greatest Number of Next Next Rarest: choose the site containing the greatest number of the next next least frequent
6	<i>Richest</i> : choose the site with the highest number of unrepresented species.
7.	Percent Richest: choose the site with the highest percentage of unrepresented species out of the total number of
0	species in the site.
8.	<i>Total Rarity</i> : choose the site with the highest sum of rarity values for all unrepresented species, where the farity value for a species is the inverse of the number of sites containing the species
9.	Average Rarity: choose the site with the highest average rarity value for all unrepresented species.
10.	Random Selection: site is randomly chosen from eligible sites.
<u> </u>	First Encountered: choose the first site encountered (lowest number site).
B .	Algorithm Description (order of application of rules).
Algorithm 7:	
(a) (b)	Unique. Greatest Number of Next Rerest: ties broken with Richness and further ties broken with First Encountered
(c)	Repeat (b) until all species have been represented.
Algorithm 8:	
(a)	Unique.
(D)	Greatest Number of Next Karest: ties broken with Greatest Number of Next Next Karest, further ties broken with First Encountered
(c)	Repeat (b) until all species have been represented.
(d)	Selected sites are re-ordered to maximize complementary richness at each step.
Algorithm 9:	
(a)	Unique. Next Rarest: ties broken with Random Selection
(c)	Repeat (b) until all species have been represented.
Algorithm 10:	
(a)	Unique. Next Parent: tion broken with Dichest further tion broken with Pandam Selection
(0) (c)	Repeat (b) until all species have been represented.
Algorithm 11:	
(a)	Unique.
(b) (c)	Next Rarest: ties broken with Average Rarity, further ties broken with Random Selection. Repeat (b) until all species have been represented
Algorithm 12:	Repeat (b) until an species have been represented.
(a)	Unique.
(b)	Next Rarest: ties broken with Total Rarity, further ties broken with Random Selection.
Algorithm 13	Repeat (b) until all species have been represented.
(a)	Unique.
(b)	Next Rarest: ties broken with Next Next Rarest, further ties broken with Random Selection.
(C)	Repeat (b) until all species have been represented.
(a)	Unique.
(b)	Next Rarest: ties broken with Percent Richest, further ties broken with Random Selection.
(c)	Repeat (b) until all species have been represented.
(a)	Unique
(b)	Next Rarest: ties broken with Richest, further ties broken with Next Next Rarest, further ties broken with Random
	Selection.
(c) Algorithm 16:	Repeat (b) until all species have been represented.
(a)	Unique.
(b)	Next Rarest: ties broken with Richest, further ties broken with Total Rarity, further ties broken with Random
	Selection.
Algorithm 17	Repeat (0) until all species have been represented.
(a)	Unique.
(b)	Next Rarest: ties broken with Richest, further ties broken with Next Next Rarest, further ties broken with Total
(c)	Rarity, further ties broken with Random Selection. Repeat (b) until all species have been represented.

As the algorithm progressed the search radius was decreased analogously to the decrease in temperature in classical annealing. Because the simulated annealing algorithm takes advantage of spatial correlations between the seed sets and optimal solution sets, the effectiveness of the algorithm is inversely proportional to the distance between the members of the seed sets and the desired solution set members.

Branch and bound algorithm (algorithm 19)

Optimal solutions for the mathematical model of the reserve selection problem may be solved using a linear branch-and-bound algorithm. programming-based Initially, the linear programming (LP) relaxation of the integer programming model (that is, the binary restrictions replaced by lower and upper bounds of 0 and 1) is solved. If the LP relaxation is an integer, the optimal solution has been found. If one (or more) of the variables is fractional, branching takes place. A branch is the creation of two new problems (nodes), one with the fractional variable set to 0 and the other with the fractional variable set to 1. The LP relaxation for each of the new problems is solved and the process repeated until all nodes under consideration have been fathomed. A node is fathomed if its solution is infeasible, is an integer, or has a value worse than the current incumbent integer solution.

The basic branch-and-bound process described above can be computationally intense. However, intelligent preprocessing of problem data and algorithmic improvements make the solution of relatively large problems feasible. As an example of preprocessing for the reserve selection problem, if two or more species are located in the exact same set of locations, only one of them needs to be explicitly represented in the model (with an objective function coefficient equal to the number of such species). This simple scheme reduces the number of coverage constraints from 426 to 368 in the Oregon data, a reduction of roughly 14% in the row size of the model. Algorithmic enhancements, such as logical and cost-based variable pegging (fixing a variable permanently to 0 or 1 in the branch-andbound), are helpful. The software package LINDO used in this work uses a cost-based pegging scheme.

Often, it is useful to find multiple combinations of sites that yield optimal or near-optimal solutions. Finding multiple solutions can be done by resolving the model with a constraint that prevents the original solution from being chosen. Using this method repeatedly allows us to find as many solutions, ranked in order of declining number of species represented, as desired (Camm *et al.*, 1966).

RESULTS AND ANALYSIS

The main results of the algorithm comparison using data on all 426 breeding terrestrial vertebrate species in

Oregon are reported in Table 2. The rows of Table 2 represent the different number of reserve sites included in the reserve system, starting with one site and continuing up to the total number of sites necessary to represent all 426 species in the reserve system at least once. The results of different algorithms are reported in different columns. Each entry in the table corresponds to the number of species covered in the reserve system selected by an algorithm for a given number of reserve sites. Figure 1 graphs the accumulation curve for a subset of the algorithms.

The results of the branch and bound algorithm (algorithm 19) are reported in the last column of Table 2. The branch and bound algorithm solution gives the maximum number of species that can be covered with a given number of sites for these data and the minimum number of sites needed for complete representation of all species. This solution represents a useful benchmark with which to compare the performance of other algorithms. Not only can we judge relative performance of various algorithms but we can also judge how close an algorithm comes to the optimal solution.

Most of the species in Oregon can be represented in a reserve system with relatively few sites. In the branchand-bound solution (algorithm 19), over 90% of the species can be represented with five sites (384/426), and over 95% of the species can be represented with 10 sites (406/426). Beyond 10 sites, adding an additional site yields an increase of only one or two species in all of the richness based algorithms. To represent all of the species in the state at least once in the reserve system requires selecting only 23 of the total of 441 sites. Like many temperate regions, the majority of species in Oregon have fairly wide spatial distribution after interpolation. Over 63% of species are located in more than 100 sites and less than 10% of the species are located in 10 sites or fewer. There are seven species that are located in a single site.

The rapid accumulation of species in relatively few sites, in contrast to the larger number of sites needed for complete representation, has implications for conservation planning. Noss (1987) has suggested that most species may be represented in relatively few areas representing major habitat types (the "coarse filter"), while the conservation needs of the small number of species not represented in those areas are best addressed on an individual basis (the "fine filter"). The results presented here offer another way of identifying a few areas in which most species are thought to be represented. These areas could form the nucleus of a network of ecosystem reserves. The identity and conservation needs of species not represented in the network could be examined to determine if they could be conserved in less ambitious ways.

One pattern that emerges from Table 2 is the different relative performance of greedy richness-based and raritybased algorithms. Greedy richness-based algorithms do relatively well at finding large numbers of species when

Table 2. Species accumulation table

Alg. no. Site no.	1 Simple Greedy	2 Greedy w/Rarity Tie-Break	3 Enumeration and Greedy	4 Greedy w/Subgradient Optimiz.	5 Inverse Rarity Weight	6 Sq. Inverse Rarity Weight	7 Progressive Rarity
	254		254	254		224	
1	254	254	254	254	221	224	224
2	306	306	318	306	290	290	290
3	347	347	356	356	330	305	330
4	365	365	374	374	354	345	345
5	379	379	384	384	363	357	357
6	388	388	390	388	372	361	361
7	394	394	394	394	376	365	365
8	398	398	398	400	380	373	373
ğ	401	401	402	403	388	381	379
10	404	401	402	403	396	396	381
10	404	406	406	406	300	401	386
11	400	400	400	400	399	401	200
12	408	408	408	408	401	405	390
13	410	410	410	410	403	405	391
14	412	412	412	412	405	407	392
15	414	414	414	414	407	409	394
16	415	416	415	416	410	411	397
17	416	417	416	417	414	413	407
18	417	418	417	418	416	414	415
19	418	419	418	419	418	416	416
20	419	420	419	420	420	418	417
21	420	421	420	421	421	421	420
22	421	422	421	422	422	423	422
22	421	422	421	422	422	425	422
23	422	423	422	423	424	425	424
24	425	424	423	424	425	420	420
25	424	425	424	425	420		
26	425	426	425	426			
27	426		426				
							1.4
Alg. no. Site no.	8 Progressive Rarity	9 Progressive Rarity	10 Progressive Rarity	11 Progressive Rarity	12 Progressive Rarity	13 Progressive Rarity	14 Progressive Rarity
Alg. no. Site no.	8 Progressive Rarity	9 Progressive Rarity	10 Progressive Rarity	Progressive Rarity	12 Progressive Rarity	13 Progressive Rarity	Progressive Rarity
Alg. no. Site no.	8 Progressive Rarity 254	9 Progressive Rarity 224	10 Progressive Rarity 224	Progressive Rarity 224	12 Progressive Rarity 224	13 Progressive Rarity 224	Progressive Rarity 224
Alg. no. Site no.	8 Progressive Rarity 254 303	9 Progressive Rarity 224 290	10 Progressive Rarity 224 290	Progressive Rarity 224 290	12 Progressive Rarity 224 290	13 Progressive Rarity 224 290	Progressive Rarity 224 290
Alg. no. Site no.	8 Progressive Rarity 254 303 343	9 Progressive Rarity 224 290 330	10 Progressive Rarity 224 290 330	Progressive Rarity 224 290 330	12 Progressive Rarity 224 290 330	13 Progressive Rarity 224 290 330	Progressive Rarity 224 290 330
Alg. no. Site no. 1 2 3 4	8 Progressive Rarity 254 303 343 360	9 Progressive Rarity 224 290 330 345	10 Progressive Rarity 224 290 330 345	Progressive Rarity 224 290 330 345	12 Progressive Rarity 224 290 330 345	13 Progressive Rarity 224 290 330 345	Progressive Rarity 224 290 330 345
Alg. no. Site no. 1 2 3 4 5	8 Progressive Rarity 254 303 343 360 377	9 Progressive Rarity 224 290 330 345 357	10 Progressive Rarity 224 290 330 345 357	11 Progressive Rarity 224 290 330 345 357	12 Progressive Rarity 224 290 330 345 357	13 Progressive Rarity 224 290 330 345 357	14 Progressive Rarity 224 290 330 345 357
Alg. no. Site no. 1 2 3 4 5 6	8 Progressive Rarity 254 303 343 360 377 387	9 Progressive Rarity 224 290 330 345 357 361	10 Progressive Rarity 224 290 330 345 357 361	11 Progressive Rarity 224 290 330 345 357 361	12 Progressive Rarity 224 290 330 345 357 361	13 Progressive Rarity 224 290 330 345 357 361	14 Progressive Rarity 224 290 330 345 357 361
Alg. no. Site no. 1 2 3 4 5 6 7	8 Progressive Rarity 254 303 343 360 377 387 392	9 Progressive Rarity 224 290 330 345 357 361 365	10 Progressive Rarity 224 290 330 345 357 361 365	11 Progressive Rarity 224 290 330 345 357 361 365	12 Progressive Rarity 224 290 330 345 357 361 365	13 Progressive Rarity 224 290 330 345 357 361 365	14 Progressive Rarity 224 290 330 345 357 361 365
Alg. no. Site no. 1 2 3 4 5 6 7 8	8 Progressive Rarity 254 303 343 360 377 387 387 392 396	9 Progressive Rarity 224 290 330 345 357 361 365 367	10 Progressive Rarity 224 290 330 345 357 361 365 373	11 Progressive Rarity 224 290 330 345 357 361 365 367	12 Progressive Rarity 224 290 330 345 357 361 365 367	13 Progressive Rarity 224 290 330 345 357 361 365 373	14 Progressive Rarity 224 290 330 345 357 361 365 373
Alg. no. Site no. 1 2 3 4 5 6 7 8 9	8 Progressive Rarity 254 303 343 360 377 387 392 396 400	9 Progressive Rarity 224 290 330 345 357 361 365 361 365 367 375	10 Progressive Rarity 224 290 330 345 357 361 365 373 381	11 Progressive Rarity 224 290 330 345 357 361 365 367 368	12 Progressive Rarity 224 290 330 345 357 361 365 367 375	13 Progressive Rarity 224 290 330 345 357 361 365 373 381	14 Progressive Rarity 224 290 330 345 357 361 365 373 381
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Alg. no. Site no. 1 2 3 4 5 6 7 8 9 10 11	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 384 387	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374	12 Progressive Rarity 224 290 330 345 357 361 365 365 367 375 379 382	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 384 387
Alg. no. Site no. 1 2 3 4 5 6 7 8 9 10 11 12	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405 407	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 385 387	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405 407 409	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 400 403 405 407 409 411	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 400 403 405 407 409 411 412	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409
Alg. no. Site no. 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 400 403 405 407 409 411 413 415	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 374 378 379 380 384	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411
Alg. no. Site no. 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 400 403 405 407 409 411 413 415	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 412
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 400 403 405 407 409 411 413 415 417	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405 407 409 411 413 415 417 419	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396 403	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405 407 409 411 413 415 417 419 421	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411 414	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410 418	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396 403 405	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414 416	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413 414 416	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414 417
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 400 403 405 407 409 411 413 415 417 419 421 422	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411 414 417	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410 418 419	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396 403 405 407	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414 416 418	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413 414 416 418	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414 417 418
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 400 403 405 407 409 411 413 415 417 419 421 422 423	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411 414 417 419	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410 418 419 420	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396 403 405 407 410	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414 416 418 419	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413 414 416 418 421	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414 417 418 419
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Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 400 403 405 407 409 411 413 415 417 419 421 422 423 424 425 426	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411 414 417 419 420 423 424	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410 418 419 420 423 425 426	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396 403 405 407 410 412 415 417	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414 416 418 419 422 424 426	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413 414 416 418 421 423 425 426	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414 417 418 419 420 423 425
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405 407 409 411 413 415 417 419 421 422 423 424 425 426	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411 414 417 419 420 423 424 426	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410 418 419 420 423 425 426	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 379 380 384 387 396 403 405 407 410 412 415 417 419	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414 416 418 419 422 424 426	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413 414 416 418 421 423 425 426	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414 417 418 419 420 423 425 426
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405 407 409 411 413 415 417 419 421 422 423 424 425 426	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411 414 417 419 420 423 424 426	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410 418 419 420 423 425 426	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396 403 405 407 410 412 415 417 419 421	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414 416 418 419 422 424 426	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413 414 416 418 421 423 425 426	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414 417 418 419 420 423 425 426
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Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405 407 409 411 413 415 417 419 421 422 423 424 425 426	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411 414 417 419 420 423 424 426	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410 418 419 420 423 425 426	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396 403 405 407 410 412 415 417 419 421 422 423	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414 416 418 419 422 424 426	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413 414 416 418 421 423 425 426	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414 417 418 419 420 423 425 426
Alg. no. Site no.	8 Progressive Rarity 254 303 343 360 377 387 392 396 400 403 405 407 409 411 413 415 417 419 421 422 423 424 425 426	9 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 380 382 385 400 405 407 408 411 414 417 419 420 423 424 426	10 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 402 404 406 407 410 418 419 420 423 425 426	11 Progressive Rarity 224 290 330 345 357 361 365 367 368 371 374 378 379 380 384 387 396 403 405 407 410 412 415 417 419 421 422 423 426	12 Progressive Rarity 224 290 330 345 357 361 365 367 375 379 382 384 386 398 401 402 406 414 416 418 419 422 424 426	13 Progressive Rarity 224 290 330 345 357 361 365 373 381 383 385 387 390 404 409 411 413 414 416 418 421 423 425 426	14 Progressive Rarity 224 290 330 345 357 361 365 373 381 384 387 389 391 405 409 411 413 414 417 418 419 420 423 425 426

contd.

Alg. no. Site no.	15 Progressive Rarity	16 Progressive Rarity	17 Progressive Rarity	18 Enumeration and Simulated	19 Branch and Bound	
				Annealing		
1	224	224	224	254	254	
2	290	290	290	318	318	
3	330	330	330	356	356	
4	345	345	345	374	374	
5	357	357	357	384	384	
6	361	361	361	390	390	
7	365	365	365	395	395	
8	373	373	373	398	400	
9	381	381	381	403	403	
10	384	384	384	405	406	
11	387	387	387	407	408	
12	389	389	389	409	410	
13	391	391	391	411	412	
14	405	405	405	413	414	
15	410	408	410	415	416	
16	412	410	412	417	418	
17	414	412	414	418	419	
18	415	413	415	419	420	
19	418	416	418	420	422	
20	419	418	419	421	423	
21	422	419	422	422	424	
22	424	420	424	423	425	
23	425	423	425	424	426	
24	426	425	426	425		
25		426		426		
26						
27						





Fig. 1. Species accumulation curve.

the number of sites is restricted so that not all of the species can be covered. Rarity-based algorithms do well at finding a near-minimum number of sites needed to cover all species.

Greedy richness-based algorithms (algorithms 1-4) are near optimal, in the sense of covering a near-maximal

number of species, when the number of sites selected is between six and 15. All of these richness-based algorithms are within two species of the maximum number of species throughout this range. Between two and five sites, algorithms 1 and 2 fall well short of achieving the maximum number of species represented. The gap between the solutions for algorithms 1 and 2 and the optimal solution is 12 species at two sites, 11 species at three sites, nine species at four sites, and five species at five sites. Algorithms 3 and 4 are optimal or near-optimal for a small number of sites, with the exception of algorithm 4 for two sites. In fact, algorithm 4 is optimal for one, three, four, five, eight and nine sites. However, none of the four algorithms does well at finding the minimum number of sites necessary to represent all species. All four algorithms need 26 or 27 sites to represent all species, which is more sites than needed by other algorithms included in the study, with one exception.

In contrast, many of the rarity-based algorithms (algorithms 5-17) represent the entire set of species in 24 sites. These algorithms place a high priority on sites that contain species with narrow distributions even though they may not contain a large number of species. Since many of these sites must be included in order to cover all species, rarity-based algorithms are relatively efficient in finding the minimum number of sites to represent all species (Kershaw et al., 1994). Rarity-based algorithms, however, do not represent as many species as do simple richness-based algorithms when the number of sites is not close to the number needed to represent all species (Williams & Humphries, 1994). In general, rarity-based algorithms will not fare well in choosing reserve networks with many species when the number of sites allowed is small and where sites with rare species do not coincide with sites with numerous species.

Algorithms 9–17 were also used in a recent study by Pressey *et al.* (1996) using data from New South Wales Western Division. Table 3 shows a comparison of the relative efficiency of algorithms on the Oregon and Western Division Data in finding the minimum number of sites necessary to represent all species. Both the minimum values and the average values are reported. In general, the algorithms performed relatively better on the Oregon data than they did on the Western Division data. Using the Oregon data, the average over the nine algorithms for the minimum number of sites to represent all species was 24.8 sites, only 7.7% above the minimum number of sites (23). Over all 100 runs for each of the algorithms, the average number of sites needed to represent all species was 25.9 sites, 12.7% above the minimum. Using the Western Division data, the average over the nine algorithms for the minimum number of sites to represent all species was 63.7 sites, 17.9% above the minimum number of sites (54). Using all runs, the average number of sites needed to represent all species was 67.2 sites, 24.4% above the minimum. With the exception of algorithm 12, those algorithms that performed well (poorly) in the Oregon data did well (poorly) in the Western Division data. Algorithm 12 needed only 24 sites to represent all the species in Oregon but needed 66 sites to do so in the Western Division. Algorithms 10, 13, 15, 16 and 17 also needed only 24 sites in Oregon but all of these algorithms needed less than 60 sites in the Western Division. Algorithms 9 and 14 needed 25 sites in Oregon and the high 60s in the Western Division. Algorithm 11 did relatively poorly in both data sets, indicating that the average rarity rule is not an effective selection rule.

The advantages of both richness and rarity algorithms may be obtained to a large extent by combining them sequentially (Williams, 1994). Algorithm 8 is equal to the best of the rarity algorithms for obtaining representation of all species with relatively few sites, and yet by re-sequencing for complementary richness, it achieves a higher species accumulation rate.

The simulated annealing algorithm (algorithm 18) is either optimal or near-optimal for cumulative richness through the entire range of sites. Up to four sites, algorithm 18 uses complete enumeration of all combinations and by definition finds the maximum number of species covered. For these data, the simulated annealing algorithm is able to find optimal solutions beyond four sites as well (at five, six, seven and nine sites). The simulated annealing algorithm is usually midway between the optimal solution and the solution for a greedy algorithm beyond nine sites. In order to represent all species, the simulated annealing algorithm needs 25 sites.

 Table 3. Comparative results of nine algorithms for complete representation of all species in Oregon and New South Wales Western Division data

Algorithm	Orego	n Data	Western Division Data		
	Minimum Number of Sites	Average Number of Sites	Minimum Number of Sites	Average Number of Sites	
Optimal Solution	23		54		
Algorithm 9	25	28.12	69	75.47	
Algorithm 10	24	24.65	57	59.75	
Algorithm 11	29	33.09	79	86.94	
Algorithm 12	24	25.69	66	68.37	
Algorithm 13	24	24.00	59	62.33	
Algorithm 14	25	25.00	67	71.68	
Algorithm 15	24	24.00	59	60.25	
Algorithm 16	24	24.71	58	59.65	
Algorithm 17	24	24.00	59	59.98	

A key concern in conservation planning is flexibility (Pressey et al., 1993). Having flexibility in choosing sites for the reserve network may be important because constraints may preclude certain combinations of sites from being selected. In the Oregon data, there are usually many different combinations of the same number of sites that represent the maximum number of species. In Table 4, using the branch-and-bound algorithm, we report the number of combinations of sites that yield the optimal solution for reserve networks from one site to 23 sites (full representation). Other algorithms, e.g. simulated annealing, are also capable of finding multiple solutions in cases where they find an optimal solution. There is a unique optimal reserve network when the number of sites is four or less. Also, there are few combinations that are even close to optimal. For example, for two sites, there is only one combination of sites that represents 317 species, one less than optimal, and only one combination of sites that represents 316 species. Somewhat surprisingly, there is also a unique optimal combination with eight sites, though here there are numerous combinations that yield near-optimal results. On the other hand, when the number of sites is more than 10, with the exception of 19 sites, there are more than 100 combinations of sites that yield the optimal solution. In the case of 12 sites, there are more than 1000 combinations that yield the optimal solution.

In Fig. 2, we show the irreplaceability values for the various sites in Oregon. Irreplaceability is the percentage of all fully representative sites in which each individual site occurs (Pressey et al., 1994). There are 144 solutions (combinations of sites) that completely represent all species in the minimum number of sites. Note that 19 out of 23 sites show up in all solutions and have irreplaceability values of 100%. If we allow a larger number of sites to be reserves (e.g. 24 or 25 sites), the irreplaceability values for the sites that do not contain a species located in a single site will fall below 100%. Any combination of sites that involves selecting all 19 sites labeled with 100% in Fig. 2 and one site from each of the following sets of hexagons (each identified with its 5 digit label) constitutes an optimal path: (a) 24651 or 24652 (50%); (b) 24520, 26425 or 26860 (33.3%); (c) 26647, 26967, 27073 or 27177 (25%); (d) 25029, 25030, 25152, 25153, 25274 or 25275 (16.7%).

In Fig. 3a, we show the spatial pattern of the reserve network solution for two algorithms, the branch and bound algorithm (algorithm 19) and the squared inverse rarity weight algorithm (algorithm 6) for 10 sites and for full representation. The squared inverse rarity weight algorithm solution is fairly representative of the spatial pattern of the solution of most of the rarity-based algorithms. For 10 sites (Fig. 3(a)) there is not much overlap between the solution of the branch-and-bound algorithm and the squared inverse rarity weight algorithm. Only three of the 10 site choices coincide and several choices lie in different parts of the state. The squared inverse rarity weight algorithm tends to pick

Table 4. Number of optimal solutions

Number of Reserve Sites	Number of Solutions		
1	1		
2	1		
3	1		
4	1		
5	5		
6	7		
7	12		
8	1		
9	12		
10	11		
11	200+		
12	200+		
13	200+		
14	200 +		
15	200 +		
16	200+		
17	200 +		
18	200+		
19	12		
20	108		
21	200 +		
22	200 +		
23	144		

sites with species with restricted ranges, while the branchand-bound algorithm tends to pick areas that have many complementary species. In contrast, at complete representation of all species in the reserve network, Fig. 3(b), 19 site choices can be the same for both algorithms. (Since there are multiple solutions for the branch-andbound algorithm, there is some flexibility on which sites are included.) Two more site choices are adjacent and one more site choice is two sites apart. With complete representation, all sites containing species with restricted ranges tend to be chosen by all algorithms, leading to a convergence of spatial patterns.

In Fig. 3(c), we show the 10 sites that individually have the greatest number of species. Notice that all of these sites are clustered together in one part of the state. It is interesting to note that only one of these sites is chosen by the algorithms both at 10 sites and at full representation. These maps clearly show the importance of complementarity vs. species richness in designing a reserve system (Williams *et al.*, 1996).

One concern with using relatively complex algorithms like the branch and bound or the simulated annealing algorithm is that it may take so long to find a solution with these algorithms that using them on real conservation problems is not practical. This concern did not turn out to be a problem in our analysis conducted with the Oregon data. Using a 486 PC and a commercial software package (LINDO), it took 23.4 min to find the complete branch-and-bound algorithm solution for the maximum number of species that could be covered from



Fig. 2. Irreplaceability values for sites in Oregon.

one site up to full coverage (23 sites). The maximum time to find a solution for any given number of sites was 4.7 min for six sites. In 16 out of 23 cases, an optimal solution for a given number of sites was found in less than 1 min. Using more specialized software or a more powerful computer would shorten these times further. How much larger the data set can be in terms of sites or number of species or how much more complex the objective can become before the branch and bound approach becomes impractical is still an open question. In a problem with 1885 sites and 248 attributes (land systems), finding an optimal solution took 10 days on a SUN IPX workstation (Possingham et al., 1993), though the solution time was reported to be cut to 10 h more recently (Possingham, pers. comm.). The simulated annealing algorithm also found a solution within a reasonable period of time. Complete enumeration is the time consuming part of the approach. Up to four sites, the solution takes c 2.5 min. At four sites, it takes almost 2 h (119 min) to find the solution. However, beyond four sites, the time taken to find a path using simulated annealing is < 1 min for any given number of sites.

At the other extreme, the simple richness and rarity algorithms take just 4-5 s (or 8 s with within-set redundancy checks at each step) on a 486 PC. Computing time is not an issue when using these algorithms, even with very large data sets.

DISCUSSION

Reserve selection algorithms can be used to find efficient combinations of sites capable of representing a group of species in a region. The analysis yields results that are indicative of combinations of areas that may be high priority for conservation. This analysis, however, does not address issues of the size, shape, or quality of a natural area necessary to maintain viable species populations or functional ecosystems. No information is available in this data set about habitat condition in different sites. Field surveys are needed to confirm the conservation value of potential reserve sites. Further, landscape context should be considered during natural area design (Noss, 1987). Additional factors, such as acquisition and management costs, political constraints



Fig. 3a. Branch-and-bound (algorithm 19) and square inverse rarity weight (Algorithm 6): 10 sites.

and proximity to other reserves may also need to be addressed when recommending a natural area network in a real-world context (Pressey *et al.*, 1996).

For simplicity, we have assumed that a species is represented in the reserve network if it is contained in at least one selected site. A more conservative approach would be to modify the algorithms to require multiple representations of each species (Williams *et al.*, 1996), or to require that a certain percentage of the species geographic range be represented. Algorithms can also be modified to give preference to sites in proximity to one another, increasing the opportunity for landscape linkages (Nicholls & Margules, 1993).

Many regions have existing natural reserves, which can be factored into the analysis. The effectiveness of the current reserve network can be evaluated by looking at coverage of the existing network and by comparing reserve networks both with and without a constraint to include the current reserve sites. Further, if the biological potential of a currently degraded site can be modelled, one can assess the contribution that restoring a particular site would have. In the Oregon data, the hexagonal grid cells used to develop species distribution maps are larger than most natural areas. Quantifying the representation of species in existing natural areas will require higher resolution maps. Such maps are being developed for the Gap Analysis Program (Scott *et al.*, 1993; Scott & Csuti, 1997) by linking species to a higher resolution (100 ha minimum mapping unit) vegetation cover type map. While various algorithms are useful in identifying a minimum set of areas in which all species are predicted or known to be represented, we do not mean to imply that natural and semi-natural lands outside of nature reserves do not play an important role in maintaining regional species and ecosystem diversity (Scott *et al.*, 1990).

The combined terrestrial vertebrate data set used here represents only a small subset of all species, albeit ones about which we have the best distributional information. Several recent studies (Prendergast *et al.*, 1993; Saetersdal *et al.*, 1993; Lawton *et al.*, 1994; Williams & Gaston, 1994) have pointed out that areas of species richness ("hotspots") for different major taxa may not coincide, raising questions about the appropriateness of selecting a reserve network based on only a few major taxa. There is a difference, however, between selecting



Fig. 3b. Branch-and-bound (algorithm 19) and square inverse rarity weight (Algorithm 6): full coverage.

hotspots for a taxon, whose species lists are often spatially correlated (Fig. 3(c)), and selecting a set of areas in which most or all species of the taxon are represented. These areas reflect dissimilar species lists, often the result of dissimilar environments. Complementary areas may be relatively depauperate, but are included because of maximally different species content. As a result, we hypothesize that a set of areas in which one major taxon is completely represented may also do a good job representing the diversity of unrelated taxa. Further analysis of the Oregon data set by some of us (Kiester, Huso and Sahr) supports this hypothesis among terrestrial taxa (vertebrates, trees and butterflies).

The number of sites needed to represent all species in a taxon varies greatly. Large-bodied, mobile species that are habitat generalists and have a wide geographic distribution need the fewest sites to be fully represented. Taxa that exhibit high beta and gamma diversity require a greater proportion of sites to represent all species in the region. In Natal, South Africa, all 570 bird species can be represented in 27 out of 166 quarter degree grid squares by an iterative richness algorithm, while all 65 carnivore and ungulate species can be represented in nine sites. In contrast, plant species, that show much higher inter-site turnover due to their lower mobility and greater habitat specificity, require 140 of the 166 sites to represent all 6111 species. The 400 species of grasses require 51 sites to be fully represented (M. Kershaw, pers. comm.). When woodlands were selected iteratively in Norway, only 20% of the total area was needed to incorporate all bird species, compared to 75% to include all plant species (Saetersdal *et al.*, 1993).

Ideally, an evaluation should be made at a distinct biogeographic level to minimize the problem of giving equal weight to endemic species vs. those widely distributed outside of the region. Both Hunter and Hutchinson (1994) and Lesica and Allendorf (1995) argue the merits of protecting peripheral populations of widespread species. Regional conservation requirements may make it valid, in some cases, to target conservation of species that are rare in the region but common elsewhere—for example to represent ecotypic variation (Rebelo, 1994). In general, however, we feel that conserving species that are locally rare but common elsewhere should not take precedence over conserving species that are globally rare. A practical solution to this



Fig. 3c. Sites of maximum species richness.

problem would be to apply a consistent criterion to eliminate species peripheral to the region of analysis or to base measures on data for rarity at the global scale (Williams *et al.*, 1996). In reality, most practical conservation decisions are made at national or other political levels. Sensible processing of the data, and choice of scale to be used can help to avoid some of these potential problems. We recognize the limitations inherent in carrying out a reserve selection exercise for a political unit, rather than for a biologically defined region, and intend to pursue bioregional analyses when data for surrounding states become available.

It should be noted that the data we used are still being edited and refined. Also, the data have not yet been subjected to field validation. Species lists for units of analysis (i.e. hexagons) are largely predicted rather than confirmed lists. A similar data set, developed for 419 terrestrial vertebrates in the State of Idaho (USA), was used to predict species lists for natural areas for which there were existing species lists based on field observation. Comparison of predicted and observed lists indicated a 11% omission error and a 21% commission error (Scott *et al.*, 1993), although some commission errors may reflect species difficult to detect. We expect similar levels of accuracy in Oregon. When an actual reserve is created, it may contain a different set of species than did the (hexagon) site. Given complementarity, the potential contribution of other sites will change and a new analysis should be performed to select additional sites.

CONCLUSIONS

A wide range of approaches to selecting reserve networks has been explored and methods for finding optimal solutions are now available. However, as Pressey *et al.* (1996*a*) point out, there are a number of practical constraints that are likely to be encountered in developing a reserve network for any jurisdiction (e.g. land tenure, habitat quality, costs, social attitudes, political opposition). Incorporating these constraints makes the job of finding a solution more difficult. Work remains to be done in devising methods to solve for optimal solutions in more complex problems and in assessing the relative performance of various algorithms (Pressey *et* *al.*, 1996*a*). The existence of alternative paths to satisfactory reserve systems gives land use planners and decision makers the flexibility (Pressey *et al.*, 1993) needed to balance conservation goals with competing land uses.

The work of Kirkpatrick (1983) and others has demonstrated the practicality of iterative methods of reserve selection for achieving the conservation goal of representing the maximum number of species or land classes in a constrained reserve network. Here, we have compared a number of approaches to reserve network selection and described the strengths and limitations of each. We agree with Underhill (1994) that linear integer programming algorithms, such as branch-and-bound algorithms, are most likely to find optimal solutions to the reserve selection problem. Simpler heuristic algorithms can, however, come very close to the optimal solution in the right circumstances. Their speed and convenience for interactive analysis, when used in software programs such as WORLDMAP (Williams, 1994), will continue to make them a valuable conservation tool.

ACKNOWLEDGEMENTS

Data compilation and some analyses reported here are a part of the Oregon Gap Analysis Program, US National Biological Service. This work was supported by the Biodiversity Research Consortium (BRC), a group of US government agencies, academic and non-governmental institutions performing coordinated research on biodiversity assessment and management methods. The BRC acknowledges the support of Cooperative Research Agreement PNW 92-0283 between the USDA Forest Service and Oregon State University, Interagency Agreement DW12935631 between the US EPA and the USDA Forest Service, and the USDA Forest Service, Pacific Northwest Research Station. We thank Brian Garber-Yonts and Michael Jaspin for research assistance, and Eleanor Gaines for directing development of the species distribution database. Oregon State Agricultural Experiment Station Technical Paper No. 10997.

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