

Incorporating connectivity into reserve selection procedures

Robert A. Briers*

Institute of Biological Sciences, Edward Lhwyd Building, University of Wales, Aberystwyth, Ceredigion SY23 3DA, UK

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Abstract

Methods for selecting sites to be included in reserve networks generally neglect the spatial location of sites, often resulting in highly fragmented networks. This restricts the possibility of dispersal between sites, which for many species may be essential for long-term persistence. Here I describe iterative reserve selection algorithms which incorporate considerations of reserve connectivity and evaluate their performance using a data set for macroinvertebrates in ponds. Methods where spatial criteria were only invoked when ties between sites occurred did not perform significantly better than a simple greedy algorithm in terms of reserve connectivity. An algorithm based on a composite measure of species added and changes in reserve connectivity produced a reserve network with higher connectivity, but needed more sites to represent all species. A trade-off between connectivity and efficiency may be inevitable, but the costs in terms of efficiency may be justified if long-term persistence of species is more likely. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The protection of biological diversity commonly entails the establishment of a series of protected areas or reserves, in order to conserve species or habitat types. Many methods have been proposed to facilitate the selection of the sites to be included in a reserve network from the range of candidate sites, typically aiming to represent all species in the minimum number of sites. Heuristic, iterative algorithms, based on a series of rules (e.g. Pressey and Nicholls, 1989; Kershaw et al., 1994), integer linear programming (ILP; Willis et al., 1996; Rodrigues et al., 2000a) and simulated annealing (Posingham et al., 2000) have all been employed in reserve selection problems. Heuristic algorithms have the advantage of speed and simplicity, but may not always result in optimal solutions, i.e. reserves that include more sites than is necessary to represent all species (Csuti et al., 1997; Pressey et al., 1997). ILP methods are guaranteed to produce an optimal solution, provided that the problem is analytically tractable (Rodrigues et al., 2000a), whereas simulated annealing can produce a

range of alternative solutions, but both methods are significantly more computationally intensive.

The spatial location of selected reserve sites has been generally neglected in the design of reserve selection procedures, yet it may be critical in the long-term persistence of species in reserves, by allowing dispersal of individuals between sites. There has been a growing realisation in recent years that fragmentation of habitats often leads to the formation of metapopulations (Hanski and Gilpin, 1997), where species existing in habitat fragments persist over a regional area by balancing the extinction of local populations with the establishment of new populations elsewhere. Many species inhabiting the fragments of habitat that are to be protected by inclusion in a reserve network may require some degree of dispersal and colonisation of new sites for long term regional persistence, even if they do not exist in the colonisation–extinction balance envisaged in metapopulation models (Harrison, 1994). If a reserve network is highly fragmented, this restricts opportunities for dispersal between sites leading to poor performance of the reserve network if there is turnover of local populations (Rodrigues et al., 2000b).

Nicholls and Margules (1993) introduced a modified rarity-based heuristic algorithm which included a step to ensure that if there was a tie between candidate sites, the

* Corresponding author. Tel.: +44-1970-623111 ext. 4427; fax: +44-1970-622350.

E-mail address: rob@aber.ac.uk

site nearest to a site already selected is chosen. This does not address the overall connectivity of the reserve network, and may result in long thin reserve networks, which may not always be desirable (Possingham et al., 2000), although it is equally possible to envisage situations where high connectivity would be disadvantageous, such as limiting the potential spread of disease or exotic species between sites. Reserve connectivity is difficult to incorporate into ILP approaches to site selection, due to the non-linearity introduced by such considerations (Possingham et al., 2000; A.Rodrigues, personal communication) and hence other approaches may be required in order to address this problem. Rothley (1999) applied multi-objective programming to the problem of selecting reserves. Alternative solutions based on maximising different criteria (in this case connectivity, total area of the reserve and rare species representation) were produced and a ranking system used to assess which was the best overall solution based on a trade off between alternative criteria. Possingham et al. (2000) presented a modified simulated annealing method which included a constraint to minimise the boundary length of the reserve network relative to its area. Here I develop simple extensions of iterative reserve selection algorithms that incorporate considerations of the spatial location of selected sites and compare the performance of the algorithms on a data set for the occurrence of freshwater pond invertebrates at sites in Oxfordshire, UK.

2. Methods

2.1. Description of algorithms

Details of the steps involved in the algorithms are given in Table 1. In all cases the target was to represent all species at least once in the reserve network in the minimum number of sites (the set covering problem, Rodrigues et al., 2000a). A single population is unlikely to be sufficient to allow a species to persist in the long term, but if the reserve sites are clustered this increases the likelihood that colonisation of new sites could occur.

The first three algorithms are derivatives of the greedy (richness-based) algorithm. In algorithm 1 (Greedy), the sites are chosen sequentially, based on the number of species not currently represented in the network that are added by each site. Ties between candidate sites are broken based on the level of representation i.e. the site containing the set of species that are represented least frequently in the currently selected sites is chosen, and subsequently by random selection if any ties remain.

Algorithms 2 and 3 are similar to algorithm 1, with the exception that an extra step has been added to break ties. In algorithm 2 (Greedy/Neighbour) ties are broken by selecting the site which is nearest to a currently selected site. This is the greedy equivalent of the rarity-based algorithm introduced by Nicholls and Margules (1993). Algorithm 3 (Greedy/Maximum connectivity)

Table 1
Description of rules and algorithms used in reserve selection procedures

Rule	Description
A: Description of rules used in algorithms	
<i>Richness</i>	Choose site containing the highest number of species not already represented in the network
<i>Representation</i>	Choose site supporting species with the lowest total representation in the reserve network, i.e. the number of times the species present at the site have been represented in the sites already selected
<i>Neighbour</i>	Choose site which is nearest to a site already selected
<i>Maximum connectivity</i>	Choose site which maximises the mean connectivity of the reserve network, \bar{C}
<i>Maximum $s\Delta C$</i>	Choose site with the maximum value of $s\Delta C$ i.e. the number of unrepresented species added by the site multiplied by the change in connectivity resulting from the addition of the site to the network
<i>Maximum s of neighbours</i>	Find all sites within specified maximum distance, d_{\max} of currently selected sites and select site with the highest number of unrepresented species
<i>Random</i>	Choose site at random from sites available for addition to network
B: Descriptions	
Algorithm 1 (Greedy)	<i>Richness</i> , ties broken by <i>Representation</i> , further ties by <i>Random</i> Repeat until all species represented
Algorithm 2 (Greedy/Neighbour)	<i>Richness</i> , ties broken by <i>Neighbour</i> , further ties by <i>Representation</i> , further ties by <i>Random</i> Repeat until all species represented
Algorithm 3 (Greedy/Maximum connectivity)	<i>Richness</i> , ties broken by <i>Maximum connectivity</i> , further ties by <i>Representation</i> , further ties by <i>Random</i> . Repeat until all species represented.
Algorithm 4 ($s\Delta C$ selection)	(a) Select first site based on <i>Richness</i> (b) Subsequent sites selected by <i>Maximum $s\Delta C$</i> , ties by <i>Representation</i> , further ties by <i>Random</i> . Repeat (b) until all species represented.
Algorithm 5 (Distance based selection)	(a) Select first site based on <i>Richness</i> (b) Subsequent sites selected by <i>Maximum s of neighbours</i> , ties by <i>Representation</i> , further ties by <i>Random</i> . Repeat (b) until all species represented or no more sites are within specified d_{\max} .

has ties broken by selecting the site which maximises overall connectivity between sites. Here connectivity is defined not in terms of direct connections between sites, such as habitat corridors, but rather by the distances between sites. There are many ways in which connectivity between sites can be represented. In this study, connectivity, C is expressed as

$$\sum_{j>i} \exp^{-d_{ij}}$$

where d_{ij} is the distance between sites i and j . The number of sites included in the reserve network influences the value of connectivity, and different algorithms may select different number of sites for inclusion in the reserve. Therefore, here I will use an alternative measure, the mean connectivity \bar{C} , i.e. C/n , where n is the number of sites in the reserve network. This measure has a range of 0–1.

In Algorithm 4 ($s\Delta C$), the site containing the maximum number of species is selected first. Selection of sites at each subsequent step is based on a composite measure, $s\Delta C$. For each candidate site for selection, the number of species that the site would add (s) is multiplied by the change in C that would result from the addition of the site (ΔC). The site with the maximal value of $s\Delta C$ is added to the network, with ties broken by standard methods (Table 1). Because of the inclusion of an exponential term relating to inter-site distances in the expression defining C , there is a strong down-weighting of distant sites, even if they add a larger number of species. The distribution of dispersal distances of many organisms is commonly modelled as a negative exponential function (McCallum, 2000) and hence this definition of connectivity is appropriate when the goal is to maximise the chances of dispersal between sites.

Algorithm 5 (Distance-based selection) starts by selecting the site with the maximal species richness. At subsequent steps, all the candidate sites within a specified maximum distance (d_{\max}) from the selected sites are located and the site adding the maximum number of unrepresented species is added. This process is repeated until all species are represented or no more sites are within the specified distance, with ties broken as above. Different values of d_{\max} were used in the selection process to examine how this affected the resultant reserve networks.

2.2. Data set used

The data set to which the algorithms are applied is for the occurrence of freshwater macroinvertebrates in ponds in Oxfordshire, UK. This is derived from the Oxfordshire Pond Survey carried out between 1989 and 1990 by Pond Action (Table A3.8 in Pond Action,

1994b). One hundred and thirty sites, which had grid references given in the original reports, were used in this study and a total of 256 species of macroinvertebrate were recorded from these sites. Further details of the sites and survey methodology are given in Pond Action (1994a,b). Not all pond sites within Oxfordshire were surveyed in this study, and the actual number of ponds within Oxfordshire is considerably higher than would appear from this survey (approximately 2–3000, J. Biggs, personal communication). However for the purpose of this analysis it was assumed that the survey was systematic, and no intervening sites were present. In practice the reserve selection approaches detailed here should only be applied when all sites in a given area are included, in order to give accurate measures of connectivity and inter-site distances. In this example, distances between nearest neighbours are much exaggerated due to the nature of the survey and consequently values of connectivity and d_{\max} should be seen as illustrative only, rather than having direct biological relevance to dispersal of invertebrates between the ponds.

2.3. Comparison of algorithms

The results of applying the different algorithms to the data set were assessed in terms of their effectiveness [how close the algorithm comes to attaining the specified target, in this case the proportion of species represented in the network (Rodrigues et al., 2000a)], efficiency (i.e. the number of sites required to attain a given target of representation) and the connectivity of the final reserve network.

3. Results

3.1. Comparison of results from different algorithms

The results of applying the different algorithms to the Oxfordshire Pond Survey data set are summarised in Fig. 1. The spatial location of the sites selected by algorithm 1 (Greedy) and algorithm 4 ($s\Delta C$) is shown in Fig. 2 to illustrate which sites were selected by different approaches. In terms of their effectiveness, all the algorithms achieved the specified target of representing all species at least once in the reserve network, with the exception of the distance-based algorithm when d_{\max} was small. This was a result of there being no sites with unrepresented species within d_{\max} of the sites selected. A range of values of d_{\max} were used in the selection process and following initial changes in the number of species represented with increasing d_{\max} , the level of representation remained static regardless of the value of d_{\max} used until d_{\max} equalled 52 000 m, when full representation was achieved (Fig. 1).

The number of sites required to reach full representation (i.e. the efficiency of the algorithms) is identical for the greedy algorithm and its derivatives (31 sites, algorithms 1–3, Fig. 1, 2) and the rate of species accumulation

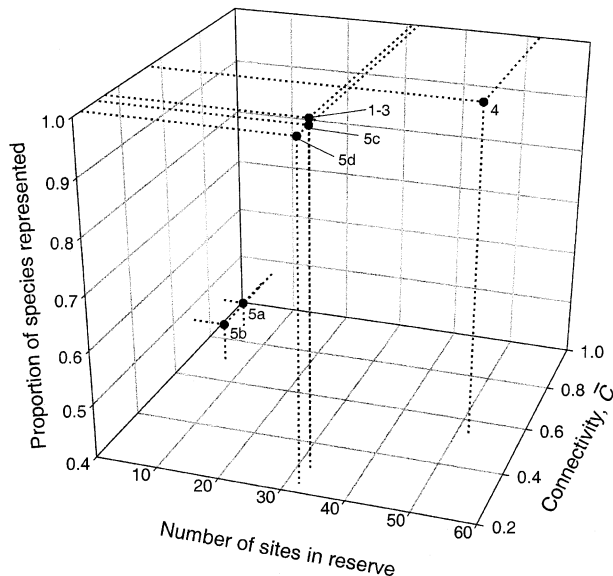


Fig. 1. Summary diagram of results of applying algorithms to the Oxfordshire Pond Survey data set. Number of sites in reserve is a measure of algorithm efficiency and the proportion of species represented algorithm effectiveness. See text for definition of connectivity. Algorithms are numbered according to Table 1. Letters a–d after algorithm 5 refer to different values of d_{\max} : a = 5000 m, b = 10000 m, c = 52000 m, d = 54000 m.

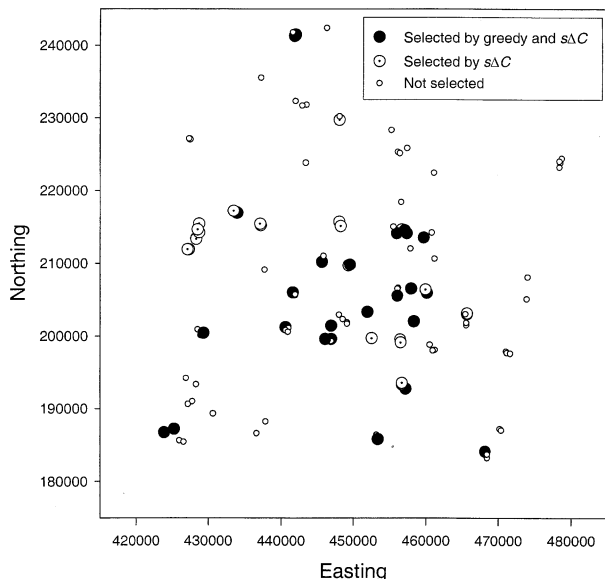


Fig. 2. Spatial distribution of pond sites selected by different algorithms. Sites are labelled according to whether they were selected by the algorithm 1 (Greedy) or 4 ($s\Delta C$) or neither. All sites selected by algorithm 1 were also included in the network of sites selected by algorithm 4. Figures on the axes are British National Grid References in metres. Size of sites is not to scale: symbols of sites not selected have been reduced in size to aid clarity.

is very similar between algorithms (Fig. 3). The distance-based algorithm (values of $d_{\max} \geq 52000$ m) required one more site than the greedy derivatives to represent all species. Although the results with values of d_{\max} of 52000 and 54000 m are identical in terms of the final number of sites selected, there is some variation in the rate of species accumulation (Fig. 3) and connectivity (Fig. 1) resulting from selection of different sites at certain points in the selection process. In contrast to the other algorithms, selection based on $s\Delta C$ required a significantly higher number of sites (52) to represent all species, and accumulated species at a slower rate than the other methods (Fig. 3).

In terms of mean connectivity of the reserve network, $s\Delta C$ based selection performed better than any of the other algorithms (Fig. 1). Mean connectivity values for the other algorithms were very similar, with the exception of distance-based selection with small d_{\max} , which had high values of connectivity, but did not represent all species (Fig. 1).

4. Discussion

The results of applying the different algorithms demonstrate a trade-off between efficiency and effectiveness, and increases in reserve connectivity. Algorithms 1–3 (greedy and derivatives) resulted in identical reserve networks when applied to this data set. However, although the final set of sites selected and rate of accumulation were identical, the order in which the sites were selected varied between algorithms as a result of the different procedures used to break ties. In this case, the identical results from these algorithms derive from the particular characteristics of the data set. However,

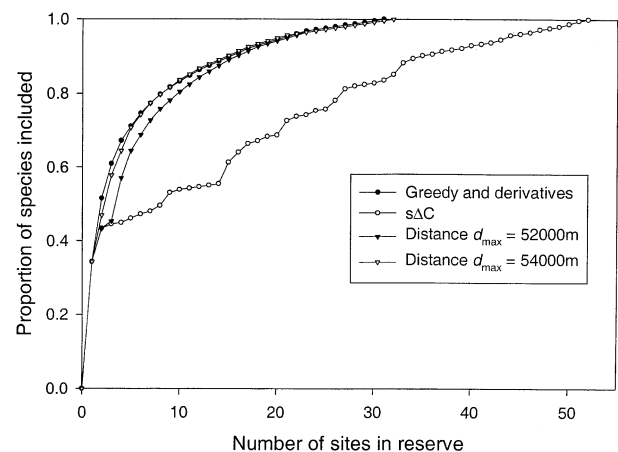


Fig. 3. Cumulative representation of species with increasing number of sites for the different algorithms applied to the data set. Only one line is shown for the greedy algorithm and derivatives (algorithms 1–3) as they followed identical trajectories. The curves for distance based selection with small d_{\max} are also excluded as they did not achieve full representation.

this result points to a potential weakness of these algorithms in that the considerations of the spatial location of the sites only come into play when ties between sites occur. If no ties result during the selection process, the algorithms incorporating spatial criteria will produce identical networks to the simple greedy algorithm. An alternative method of incorporating connectivity into greedy type algorithms would be to define an initial rule which selects for example the top 10% of sites in terms of species richness, from which choices could be made based on spatial criteria.

In contrast, $s\Delta C$ and distance-based selection methods incorporate spatial criteria explicitly at a higher level in the algorithm. This results in costs in terms of efficiency or effectiveness relative to the other procedures considered.

For distance-based selection with values of d_{\max} greater than or equal to 52 000 m the selected network of sites represents all species in a similar number of sites to the greedy algorithms. However the connectivity of the final network is not markedly different from the greedy algorithm, which does not include consideration of spatial location of sites, suggesting that in this case the use of distance-based selection methods does not result in any benefit in terms of reserve connectivity over simpler methods such as the greedy algorithm. At smaller values of d_{\max} , the algorithm fails to represent all species and hence effectiveness is lower, although the rate of accumulation is similar to that of the greedy algorithms (Fig. 3) and values of connectivity are higher (Fig. 1). In this case the high values of d_{\max} required to reach full representation are due to the nature of the survey data to which the algorithms were applied (not all sites in the area were surveyed), combined with a significant number of species present at only one site. These sites must by definition be included in the reserve network, regardless of their spatial location in relation to the other sites. This accounts for the outlying sites selected by all algorithms (Fig. 2). Given that a significant number of rare species (in this case defined as species which only occupy a small number of sites over a regional area) is a common characteristic of most communities (Gaston and Blackburn, 2000) this may be an inevitable problem for reserve selection procedures that take into account spatial location of sites.

One advantage of distance-based selection is that it is possible to use biological information regarding dispersal distances of organisms to inform the selection of an appropriate value of d_{\max} . However, this information is not generally available for all species that are to be conserved in the reserve and hence surrogate information for a focal species or a conservative estimate of dispersal distances of all species may be used instead. Alternatively, d_{\max} could be set with reference to the connectivity of the original sites, with the aim of preserving the original characteristics of the sites in terms of connectivity (Boothby, 1997).

Selecting sites using the $s\Delta C$ algorithm resulted in a cost in terms of efficiency (i.e. the number of sites required to reach the target is nearly double that for the greedy algorithm). Despite this, the algorithm does achieve the goal of representing all species at least once, and has a benefit in terms of higher reserve connectivity than the other algorithms. The algorithm is constrained to represent all species and hence isolated sites which contain rare species are included in the network (Fig. 2). As this method is based on a composite measure, there is some loss of transparency in the selection process. This may be disadvantageous in situations where the explicit decisions behind selection of certain sites may have to be defended (Nicholls and Margules, 1993). However, it is the only approach of those considered here that allows simultaneous consideration of connectivity and species representation.

It would be straightforward to construct alternative forms of the composite measure on which selection is based other than the simple product used here. Alternative measures of connectivity would also result in different reserve networks. This would enable the user to apply different relative weightings to the change in connectivity and the number of species added to the site, allowing a range of alternative reserve scenarios to be explored. Clearly, the results of reserve selection algorithms only provide solutions which can be seen as starting points for real-world planning of reserve networks (Bedward et al., 1992; Pressey et al., 1993; Prendergast et al., 1999). This process is subject to additional constraints such as land ownership or economic factors which must also be taken into account when designating areas for conservation (Prendergast et al., 1999). However, by incorporating biological considerations such as the importance of dispersal for persistence, the practical utility of such algorithms may be improved.

4.1. Application to conservation of ponds

Here, the algorithms are applied to a data set for macroinvertebrates in ponds. There is evidence that a metapopulation perspective is appropriate for many invertebrate species in ponds (Jeffries, 1994; Briers and Warren, 2000). Therefore, selection of pond sites for conservation must include considerations of the spatial location of sites (Biggs et al., 1994; Boothby, 1997). Many areas have large numbers of pond sites (e.g. Boothby and Hull, 1997) and conservation strategies typically cannot hope to conserve all sites. Previous consideration of strategies for pond conservation have been based either on the connectivity of sites (Boothby, 1997), which ignores the identity of the species present in the sites to be conserved, or on focal species of particular conservation interest. For ponds within Oxfordshire, a “Top 50” list of sites has been drawn up on the

basis of macroinvertebrate and macrophyte rarity scoring and the presence of nationally rare or protected species (mainly crested newts, *Triturus cristatus* Laurenti) (J. Biggs, personal communication). Of the 34 Oxfordshire Pond Survey sites within the “Top 50”, between 50 and 60% were selected by the algorithms. The highest number of sites was selected by the $s\Delta C$ algorithm, but this is due at least in part to the larger number of sites required to represent all species. The Oxfordshire Pond Survey sites included in the “Top 50” had a value of mean connectivity similar to that given by greedy algorithms (0.36), but only represented 191 of the 256 species present across all sites. Therefore, although the algorithms replicate to a certain extent the results of classifications based on other criteria, the approaches detailed here attempt to improve upon such methods by combining considerations of site connectivity and species identity in the selection of sites.

5. Conclusions

Overall, it appears that in order to ensure that highly connected reserve networks are produced by reserve selection procedures, algorithms that have explicit consideration of the spatial location of sites are required, rather than approaches where spatial criteria only come into play in a secondary context, such as the derivatives of the greedy algorithm. There is clearly a trade-off between reserve connectivity and efficiency and effectiveness of reserve selection procedures (Nicholls and Margules, 1993; Rothley, 1999; Possingham et al., 2000). The results of applying the algorithms illustrate the costs and benefits of attempting to incorporate different selection criteria, which can be used to help explore the consequences of alternative real-world scenarios. The importance of dispersal between sites for population persistence will vary between taxa, but there is evidence that temporal population turnover in reserve fragments may be significant for taxa other than pond invertebrates (e.g. Margules et al., 1994; Rodrigues et al., 2000b) and hence connectivity of individual sites may be a critical consideration for the persistence of species in reserve networks. Therefore, the costs in terms of efficiency or effectiveness would be justified if the reserve is more likely to support viable populations in the long term.

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