Selecting networks of nature reserves: methods do affect the long-term outcome

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Data on vascular plants of boreal lakes in Finland were used to compare the efficiency of reserve selection methods in representing four aspects of biodiversity over a 63 year period. These aspects included species richness, phylogenetic diversity, restricted range diversity and threatened species. Our results show that the efficiency of reserve selection methods depends on the selection criteria used and on the aspect of biodiversity under consideration. Heuristic methods and optimizing algorithms were nearly equally efficient in selecting lake networks over a small geographical range. In addition, a scoring procedure was observed to be efficient in maintaining different aspects of biodiversity over time. However, the random selection of lakes seems to be the most inefficient option for a reserve network. In general, reserve selection methods seem to favour lakes that maximize one aspect of diversity at the time of selection, but the network may not be the best option for maintaining the maximum diversity over time. The reserve selection methods do affect the long-term outcome but it is impossible to recommend one method over the others unequivocally.

Keywords: heuristic methods; nature conservation; optimization algorithms; reserve selection; scoring methods

1. INTRODUCTION

The options for conservation are diminishing steadily as intact nature areas are reduced and competition with alternative land uses increases (Pressey *et al.* 1993). Nature reserves should be as representative as possible of all levels of biodiversity, although the selection of reserves depends not only on biological criteria but also on political and economic criteria. If the protection of biodiversity is to be successful, limited resources for nature conservation must be used effectively. This will depend on the degree of success with which biodiversity can be measured for the purposes of conservation planning (Pressey *et al.* 1993; Williams *et al.* 1993). A simple measure of biodiversity is species richness. Reserve selection can also be based on rare and threatened species or restricted range diversity (e.g. Williams *et al.* 1996). Most recently, conservationists have become interested in taxonomic diversity, which measures the relative diversity within whole floras and faunas (e.g. Faith 1992; Kershaw *et al.* 1995).

In the past, the selection of nature reserves has been based on ad hoc decisions depending on a specific purpose and such features as recreational value, scenery or unsuitable areas for economic purposes have been determining factors (Margules & Usher 1981). Recognition of the limitations of ad hoc decisions has led to the development of systematic procedures for selecting reserves (Pressey *et al.* 1993). All reserve selection

methods share a common objective of efficiency. They have been designed to select reserve networks that afford the most protection of biodiversity for the least cost, e.g. purchase cost, reserve size or number of sites (Pressey *et al.* 1993; Caughley 1994).

The number of species varies over time because of the colonization and extinction of species. Therefore, a site that is rich in species at a given point in time may not be the best choice for protecting species in the long term. The success of reserve networks will depend on the degree of care taken in locating individual reserves. Each individual site should maintain viable populations and communities (e.g. Kirkpatrick 1983; Margules *et al.* 1994). Margules *et al.* (1994) found that 14 Ingleborough limestone pavements selected by a heuristic method did not maintain 41 original plant species after 11 years. However, the entire reserve selection literature is almost devoid of any attention dedicated to the notion of viability. Previously used scoring procedures concentrated on individual sites by using ranking systems to determine the significance for protection. Among the most commonly used scores were species richness, rarity, diversity, size and naturalness (Margules & Usher 1981). However, scoring procedures have a serious limitation: any set of highest ranking sites duplicates some attributes many times and may miss others (Pressey & Nicholls 1989).

The more recent reserve selection methods have not concentrated on individual sites but, instead, on the problems of combining sites into networks (e.g. Kirkpatrick 1983; Pressey *et al.* 1993). These methods apply the principles of complementarity, flexibility and irreplacability (Vane-Wright *et al.* 1991; Pressey *et al.* 1993, 1994).

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Complementarity refers to the degree to which an area contributes unrepresented species to a network. Flexibility refers to a range of alternative networks with the aim of reaching the objective of full representation. Irreplaceability is defined as the potential contribution of a site to a specific reservation goal and the extent to which the options for reservations are lost if the site is lost. Iterative heuristic methods emphasize these principles (Kirkpatrick 1983; Margules *et al.* 1988; Pressey *et al.* 1993, 1996, 1997). Kirkpatrick (1983) introduced an iterative method that progresses in a stepwise manner until all species, communities or habitats are preserved to a predetermined level. Margules *et al.* (1988) presented another heuristic method which selects sites containing rare species. Iterative heuristic methods give priority order for the selected sites.

Algorithms developed in operations research 30 years ago can find optimal solutions to reserve selection problems (e.g. Cocks & Baird 1989; Camm *et al.* 1996; Church *et al.* 1996; Pressey *et al.* 1996, 1997). These optimization algorithms identify a set of sites which afford the most protection for the least cost, e.g. reserve area. However, optimization algorithms give no priority order for the selected sites.

Reserve selection methods have usually been tested with data collected at one point in time (Margules *et al.* 1988, 1994). In this study, we used long-term empirical data on vascular plants of boreal lakes and applied several methods to the problem of selecting nature reserves at a fine geographical scale: simple scoring procedures, heuristic methods, optimization algorithms and random selection. We tested viability, although algorithms were never exactly intended to deliver viability since they have always been constructed on the basis of current distributions only. However, viability is the goal of conservation and, thus, we compared the efficiency of the methods in representing species richness, phylogenetic diversity (Faith 1992), restricted range diversity (Kershaw *et al.* 1995) and threatened species (e.g. Rassi *et al.* 1992) over 63 years. This study is unique in that we used data from 63 years ago in comparison with current data to consider the theoretical success rate had we used a particular method at the time of selection.

2. MATERIAL AND METHODS

(a) Study sites

Field data on vascular plants restricted to lakes were collected from 25 lakes in central Finland (62° N, 26° E) in 1933–1934 (Metso 1936). We surveyed the lakes using the same methods as Metso (1936). The lakes were surveyed from a boat and onshore in July–August 1996. The time spent in studying each lake was proportional to the length of the shoreline. However, we spent more time in locations such as shallow coves where the vegetation belt was broad. The survey results are relatively reliable as the number of vascular plants in boreal lakes is generally very low. The total area of the lakes was 748 ha, ranging from 0.2 to 140 ha for individual lakes. Only 57 vascular plant species are found in lakes of southern boreal phytogeographical regions (Hämet-Ahti *et al.* 1998). In our study, the total number of aquatic plant species in the lakes was 32 in 1933–1934 and 28 of the original species were found in 1996 (see table 1).

Among the most common genera were *Eleocharis* (three species), *Potamogeton* (seven), *Ranunculus* (three) and *Sparganium* (three).

(b) Phylogenetic diversity, restricted range diversity and degree of threat

The analysis focused on efficiency of reserve selection methods in representing different aspects of diversity: the number of species, phylogenetic diversity, restricted range diversity and the number of threatened species.

Phylogenetic diversity was calculated using the formula $G = \text{minimum, over all } i, j \text{ in } s \text{ of } 0.5(D_{x,i} + D_{x,j} + D_{i,j})$ (Faith 1992), where G is the increase in phylogenetic diversity with addition of a species x to an already protected subset s consisting of species i and j . The distance $D_{i,j}$ between two taxa i and j is the sum of the lengths of the branches on the path between them (species, genus, family, order, class and division based on Hämet-Ahti *et al.* (1998)). As detailed phylogenetic information about plant species was unavailable, the terminal branches were extended to the same distance from the root of the tree (anagenetic evolutionary model) (Faith 1992, 1994; Humphries *et al.* 1995). This model favours the earliest diverging taxa (e.g. Williams & Humphries 1996). The phylogenetic diversity of lakes was expressed as a percentage of the total score (70) for the entire classification of all 32 species and it averaged 49% in 1933–1934 and 47% in 1996.

Widespread species will always occur with restricted species. Restricted range diversity was based on a rarity score of species, i.e. the sum of the inverse number of sites in which the species is found (Kershaw *et al.* 1994, 1995). Restricted range diversity of a lake is the sum of the individual species rarity scores and it is given as a percentage of the total scores (7.46) for all 32 species. The restricted range diversity of lakes averaged 17% in 1933–1934 and 22% in 1996.

Species were classified according to their occurrence within the southern boreal phytogeographical region and their national threat category modified from International Union for the Conservation of Nature and Natural Resources (IUCN) threat categories: common, moderately abundant, locally uncommon, insufficiently known, rare, regressed, vulnerable and endangered species (Rassi *et al.* 1992; IUCN 1993; Rossi & Kuitunen 1996; Hämet-Ahti *et al.* 1998). Among the vascular plants were two vulnerable species (*Juncus supinus* (Moench) and *Ranunculus peltatus* (Schränk)) and three regressed diminishing species (*Nymphaea tetragona* (Georgi), *Potamogeton praelongus* (Wulfen) and *Ranunculus lingua* (L.)). We used current species status of species to classify the species also seen in 1933–1934.

The most threatened species are often seen as the most immediate priority (Williams 1996). However, focusing on threatened species now could restrict the diversity in the future (Kershaw *et al.* 1995). Assuming that most species will become threatened in the future we categorized all but the most common species to a category of threatened species. The total number of threatened species was seven in 1933–1934 and five in 1996. The number of threatened species of a lake was expressed as a percentage of the seven species.

(c) Reserve selection methods

The analysis was performed with a computer program designed to select networks of lakes by using different reserve selection methods. The cost of reserve selection was defined as the number of lakes in a network. The maximum number of lakes in a network was arbitrarily set to six (24% of the lakes)

Table 1. Vascular plants of 25 boreal lakes that persisted (×), became extinct (–) and colonized (+) over 63 years

species	study site																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Alisma plantago-aquatica</i>	×	×	×	×	×	–	×	×		×	×	×	×	–	×	–	×	+		×	+				+
<i>Alopecurus aequalis</i>	×		×															–							
<i>Callitriche</i> sp.		–						–				×			×										
<i>Eleocharis acicularis</i>	–		–	–																					
<i>Eleocharis palustris</i>	×	×	×	×	×	–	–	–		×		+		×	–	+		–							+
<i>Equisetum fluviatile</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	–	×	×
<i>Glyceria fluitans</i>	–	×	+	–						×	–														
<i>Iris pseudocarus</i>	×		×	+	+		×	+		+							+	+							
<i>Isoetes lacustris</i>	–	+	×	×	×	+		+	+	×	×	×		×	–			–	–						
<i>Juncus bulbosus</i>																									
<i>Lobelia dortmanna</i>	–	×	×	×	×					×				–											
<i>Lysimachia thyrsiflora</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
<i>Myriophyllum alterniflorum</i>	×	×	×	×	×	×	–		+	×	×	–				–	+		×	+					+
<i>Nuphar lutea</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
<i>Nymphaea candida</i>	×	–	×	×	×	–	×	×	+	×	×	–	×	–		×				+					
<i>Nymphaea tetragona</i>	×	+	+			×	×	+	×	×	×	×			×	+	×	×	×				×		
<i>Phragmites australis</i>	×	×	×	×	×	×	×	×	×	×	+	×	×	×	×	×	×	×		×		×	×	×	×
<i>Polygonum amphibium</i>	–	×	×	–	–	–																			
<i>Potamogeton perfoliatus</i>	×	×	×	×	×	×	+	×	×	×	+	×			+	+	+	+							
<i>Potamogeton alpinus</i>	+	+	+	+	+	+	+	×	×			+	+		×	×		–	×		–				+
<i>Potamogeton berchtoldii</i>		×					+									+	+	+		×					
<i>Potamogeton gramineus</i>																–									
<i>Potamogeton natans</i>	×	×	×	×	×	×	×	×	+	×	×	×	+	×	×	×	+	+	×	×	×	+		+	
<i>Potamogeton praelongus</i>	–							×	×																
<i>Ranunculus lingua</i>	×	+	–																						
<i>Ranunculus peltatus</i>	–	×	×	×	–	×				–	×	–													
<i>Ranunculus reptans</i>	×	–	×	×	×		–			+	–	+													
<i>Schoenoplectus lacustris</i>	×	×	×	×	×	×	–			×	–	×	+	–	×			–		–					
<i>Sparganium gramineum</i>	×	×	×	×	×	×	×	×	×	×	×	×		–	×	+	×	×	×	×	×	×	+	+	+
<i>Sparganium minimum</i>	–	×	×		–	–		–	–			–		–	–	–	–		–	–	–	–	–	–	–
<i>Utricularia intermedia</i>			–																–						
<i>Utricularia vulgaris</i>	+	×	×	–	–	+	+	×	+	–	×	×	×		×	×	×	×	×	+			+		×

and the number was enough to protect all species in 1933–1934 and 1996 if chosen correctly. The computer program used four aspects of diversity as selection criteria. The program calculated the cumulative number of species, phylogenetic diversity, restricted range diversity and the number of threatened species for each selected lake network in 1933–1934 and 1996. For each of the four criteria, a priority set of lakes was separately selected by using a scoring procedure, a heuristic method, an optimization algorithm and random selection as follows.

The scoring procedure selected lakes in descending order of scores and, in the case of ties, selected the smallest lake and then, in the case of further ties, randomly. The heuristic complementarity method used a computer program which first selected a lake with the highest score and removed species of the selected lake from further selections. The scores of lakes were then recalculated. Next, it selected the lake. The selection was repeated with the highest new scores. In the case of ties, the program selected the smallest lake or used random selection. When the selection was based on the degree of threat, the program selected the lake with the largest number of most threatened species. The selection was repeated until all of the most threatened species were selected. Next, the program proceeded downwards and then repeated the selection process with the next category of threat (Kershaw *et al.* 1995). In the case of ties, the program selected the lake with the largest number of next threatened species.

The computer program searched all the possible combinations of lakes and selected the optimal combination of lakes which contained the maximum score and the minimum total area. In the case of ties, the program selected the first combination found.

The results of reserve selection may have occurred by chance. We tested the success of different methods by comparing each selected lake network with the results of random selections. We used 19 random selections to calculate a 95% empirical confidence interval.

3. RESULTS

The number of species, phylogenetic diversity, restricted range diversity and the number of threatened species increased in relation to the lake area and the number of lakes in a network in both 1933–1934 and 1996. The smallest number of lakes needed to sample all species was five (167 ha) in 1933–1934 and four (145 ha) in 1996. We found that 88% of the original species richness, 91% of the phylogenetic diversity, 68% of the restricted range diversity and 71% of the threatened species persisted over the 63 years. Our results showed that the selected lake networks contained up to 100% of the total number of species in 1933–1934, but that these networks maintained less than 84% of the original species over the 63 years.

Figure 1. Persistence of vascular plants in boreal lakes. Lake networks were selected from 1933 data by using three reserve selection methods: the scoring method (left-hand column), heuristic method (centre column) and optimizing algorithm (right-hand column). The figures show the cumulative percentages of (a) the number of species, (b) phylogenetic diversity, (c) restricted range diversity and (d) the number of threatened species in networks of one to six lakes in 1933 and persistence of the species in lake networks in 1996. The dashed line indicates the maximum, average and minimum scores obtained by random selections. In some figure parts only the average or maximum scores can be seen. The solid line indicates the maximum possible percentages of species, phylogenetic diversity, restricted range diversity and threatened species in 1996. See the text for further explanations.

The differences between methods were noticed when lakes were evaluated with the 1996 data. The efficiency of heuristic methods and optimizing algorithms varied depending on the selection criteria used. The heuristic method and the optimizing algorithm based on restricted range diversity were the most efficient methods when the goal of reserve selection was to maintain high species richness (figure 1a). All three methods based on restricted range diversity can be used to select lake networks that maintain the highest phylogenetic diversity over 63 years (figure 1b). However, the scoring procedure based on the number of threatened species is the most efficient method of selecting lakes with high restricted range diversity (figure 1c). The same procedure was also efficient in selecting lakes to protect threatened species in addition to the heuristic method based on the number of species (figure 1d). The heuristic method based on phylogenetic diversity was particularly poor at representing species richness, phylogenetic diversity and restricted range diversity (figure 1a–c). Even average random selection produced a better result.

4. DISCUSSION

Our study of the vascular plants of boreal lakes in central Finland did not result in a single answer as to the best method of selecting nature reserves. It showed that the efficiency of reserve selection methods depends on the selection criteria used and on the aspect of biodiversity under consideration (see also Williams 1999). Many reserve selection methods seem to favour lakes that maximize different aspects of diversity at the time of selection, but the network may not be the best option for maintaining maximum diversity over time. We also agree with Kershaw *et al.* (1995) that the selection of reserves should not be based on the results of a single method but on a comparison of results obtained by different methods.

Data from our study on boreal lakes suggest that the success of reserve selection depends on the method used and on the conservation goal. For instance, to protect areas with an originally low number of species, we should maximize restricted range diversity. To protect nature areas with a large number of species at the edge of their

distribution range, we should maximize the number of threatened species. In terms of overall efficiency heuristic methods and optimizing algorithms seemed to be equally efficient in selecting lake networks in 1933–1934. The results for all four aspects of diversity were better than maximum random selection. In addition, the scoring method appeared to be more efficient than average random selection.

Different indices of biodiversity vary in use at different scales. Kershaw *et al.* (1994) stated that species richness of Afrotropical antelopes may be a reasonable surrogate measure for taxonomic diversity. We obtained similar results with vascular plants of boreal lakes in Finland. According to Pressey *et al.* (1993) taxonomic diversity is generally insufficient for decisions on actual reserve boundaries at a local scale. More recent research has focused on *p*-median diversity which measures representations of character combinations (Faith 1994; Humphries *et al.* 1995; Williams & Humphries 1996).

This study was based on one set of data with a limited number of vascular plants and, therefore, different results may be obtained by using different taxa, land types or geographical locations. Pressey & Nicholls (1989) showed that iterative analyses were more efficient than scoring procedures for data on 118 vascular plants of 432 wetlands in New South Wales. Similar results have also been noted for Afrotropical antelopes (Kershaw *et al.* 1994) and snakes in South Africa (Lombard *et al.* 1995). Studies on limestone endemic flora in South Africa (Willis *et al.* 1996), vertebrates in Oregon (Csuti *et al.* 1997) and land types in New South Wales (Pressey *et al.* 1997) found that iterative and optimization algorithms can be equally efficient.

In practice, priority areas for conservation are chosen with regard to many conflicting values (Williams *et al.* 1993). The selection of reserves depends largely on political and economic criteria and, therefore, the development of reserve selection methods may be useless if the methods are not applied to real-world conservation problems (Vane-Wright 1996). Despite this, the objectives of a reserve network should be clear when choosing a reserve selection method (Kershaw *et al.* 1994; Pressey *et al.* 1996; Williams 1996).

We conclude that reserve selection methods do affect long-term outcomes, but it is impossible to recommend one method over the others. It would be useful to have a more detailed long-term assessment of which methods are likely to perform better or worse under given conditions or conservation goals. In any case, this type of work requires much repetition in order to detect truly superior methods.

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