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The performance of existing networks of conservation areas in representing biodiversity

Ana S. L. Rodrigues*, **Rosalind Tratt**, **Bryan D. Wheeler** and **Kevin J. Gaston**

Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

It is widely held that existing reserve systems are inadequate in representing the diversity of biological features of the regions in which they reside. Evidence for this argument has, however, derived principally from analyses of the efficiency of networks when compared with a minimum set that represents each species at least once. Here, we examine the efficiency of the system of Sites of Special Scientific Interest (SSSIs) in representing wetland plants in fen sites in the Scottish Borders, a region where reserve networks might be expected *a priori* to perform reasonably well in this regard. The results support the general contention that networks have been designated in an inefficient manner. However, examined in terms of effectiveness (measured as the gap between the representation target required and the one attained by the existing network), the SSSI system is actually a rather good way of representing diversity. This result is consistent when each of several very different representation targets is evaluated, and suggests that a more balanced approach to evaluating the performance of reserve networks should be employed, and that general statements based on existing analyses should be treated cautiously.

Keywords: biodiversity; effectiveness; efficiency; minimum set algorithms; nature reserves

1. INTRODUCTION

The establishment of networks of protected areas for conservation is an obligation placed on parties to the Convention on Biological Diversity, the Ramsar Convention on Wetlands, the Bern Convention on the conservation of European wildlife and natural habitats, the OSPAR Convention for the protection of marine environments of the North Atlantic, and on all members of the European Union (committed to the Birds and Habitats Directives). Most regions already have some system of protected areas in place, although this is obviously incipient in many cases. This begs the question of how well such networks already perform, particularly in terms of representing biodiversity. Simple representation is, in essence, the common initial goal in establishing networks of protected areas under many of these agreements, albeit of itself not sufficient to ensure long-term conservation objectives.

There have been a number of attempts to measure the performance of existing networks of protected areas (table 1). Most conclude that they are woefully inadequate. This outcome is expected in regions with less of a tradition of formal conservation, and hence where reserve systems are still poorly developed, such as India (Khan *et al.* 1997) and New Caledonia (Jaffre *et al.* 1998). However, this is perhaps a rather more surprising conclusion for other regions, such as parts of Europe (Williams *et al.* 1996; Castro Parga *et al.* 1996), Canada (Nantel *et al.* 1998), South Africa (Rebelo & Siegfried 1992; Freitag *et al.* 1998) and Australia (Pressey *et al.* 1996). Indeed, the growing number of studies reporting similar conclusions has led to a belief in some quarters that existing reserve networks in general are inherently poor. It has frequently been stated that they have been chosen in an *ad hoc* fashion (see, for example, Pressey & Tully 1994; Pressey 1994; Lombard *et al.* 1995; Freitag *et al.* 1998) and in some situations existing networks have been regarded by some as a heavy burden on efficient conservation (see, for example, Pressey & Tully 1994). Some authors have even found that existing reserves perform no better than a random choice of areas (Rebelo & Siegfried 1992). Indeed, this idea has become sufficiently well established that when Kershaw *et al.* (1994) used random sets of areas to simulate the effect of having sites already set aside for conservation, Pressey *et al.* (1996) cited this analysis as an example of how existing reserves lower the efficiency of the area selection procedure.

Even ignoring the fact that existing conservation networks were often chosen for reasons other than simply the representation of biodiversity, including other conservation objectives as well as political and financial constraints, it seems unlikely that they would almost without exception fail to some marked degree to attain the goal of embracing much of the richness of the group(s) of interest. There are two possible explanations for why they appear to perform so poorly.

First, in many published studies there is a mismatch between the actual units of conservation, which are natural and geopolitical units of land, and those units on which optimal conservation networks are determined, which are commonly grid cells for which data on the geographic occurrences of species have been mapped (see, for example, Rebelo & Siegfried 1992; Lombard *et al.* 1995; Williams *et al.* 1996; Nantel *et al.* 1998). To deal with this problem, most authors consider a grid cell as already

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*Author for correspondence (ana.rodrigues@sheffield.ac.uk).

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Table 1. *Summary of the results of examples of published studies of the performance of existing nature reserves*

study	features (no.)	selection units (no.)	geographic region	result
1	land systems (128)	cadastral units (1026)	New South Wales, Australia	the near-minimum area to represent each land system once is 5.7% of the study area. Starting with the existing reserves (3.3% of total area), 8.3% is needed
2	plants (332)	12 km × 13 km cells	Cape Region, South Africa	existing reserves (66 cells) contain no more species than predicted by a null model; 32 more sites are necessary to represent each species at least once. Only 16 cells of the 53 near-minimum set are reserves
3	plants (321), birds (47)	woods of different sizes (60)	western Norway	the 12 reserves contain 78% of plant species and 66% of bird species; 37 additional woods are necessary to include all plants. In a set of 12 sites it is possible to represent 87% of plants, or 83% of birds
4	snakes (122)	15 min × 15 min cells	South Africa	in near-minimum sets, between 63 and 78% of the selected cells contain existing reserves
5	plants (801)	10 km × 10 km cells (6330)	Iberian Peninsula	97 extra squares must be added to the reserve system (415 squares) to represent each species at least once. The near-minimum set requires 140 squares
6	land types (248)	pastoral holdings (1885)	New South Wales, Australia	it is necessary to expand the existing reserve system by at least 79% to represent each land type at least once
7	birds (218)	10 km × 10 km cells (2576)	Britain	the system of protected areas (65 cells) excludes 31 species; 20 additional cells are necessary to represent each species at least once, including 16 additional cells to represent all Red Data species
8	plants (3331)	—	Meghalaya State, NE India	reserves (1.43% of the area) are insufficient to protect the high diversity of plants; for example, 17.15% of the state endemic species occur only above 1500 m, where there are no protected areas
9	mammals (192)	15 min × 15 min cells (474)	Transvaal, South Africa	considering a cell reserved if over 50% of its area is formally protected, it would be necessary to add nine cells to the existing 36 reserves to protect each species once. The near-minimum set requires 12 cells
10	plants (3063)	—	New Caledonia	83% of the 447 threatened species do not occur in a protected area. At least five to nine times the current protected area is estimated to be needed
11	rare plants (244)	1 km × 1 km cells (456)	Newfoundland, Canada	43% of species are outside protected areas (113 cells). In a near-minimum set of 78 cells to protect all species at least once, only 13 are already reserves

Sources: 1, Pressey & Nicholls 1989*b*; 2, Rebelo & Siegfried 1992; 3, Saetersdal *et al.* 1993; 4, Lombard *et al.* 1995; 5, Castro Parga *et al.* 1996; 6, Pressey *et al.* 1996; 7, Williams *et al.* 1996; 8, Khan *et al.* 1997; 9, Freitag *et al.* 1998; 10, Jaffre *et al.* 1998; 11, Nantel *et al.* 1998.

conserved if more than a certain percentage of its area coincides with an existing reserve (for example, 55% in Rebelo & Siegfried (1992) and 50% in Williams *et al.* (1996)). A cell in which a reserve occupies less than this percentage is not considered to contain a reserve, although the species regarded as occurring in that cell will probably include all those that occur in this area of a reserve. This may distort the results of analyses of the performance of existing reserve systems. Williams *et al.* (1996) noticed this when analysing the occurrences of bird species and Sites of Special Scientific Interest (SSSIs) in 10 km × 10 km grid cells across Britain. In exploring methods for identifying additions to the network of existing conservation areas, they observed that the existing SSSI network did not embrace the occurrences of 31 bird species and that 20 additional cells would be necessary to fill the gap. However, they also found that at least 16 cells (the ones needed to fill the gap for Red Data species) already enjoyed limited SSSI cover (but this was insufficient for those cells to be scored as reserves); this result means that some of the 31 species considered to be excluded from the SSSI system may not have been so.

A second possible explanation for why existing conservation networks appear to perform so poorly is that their performance has mainly been evaluated by using measures of *efficiency* (*sensu* Pressey & Nichols 1989*a*). This is a measure of how good a system of reserves is in harbouring the maximum diversity (all the conservation features) in the minimum number of sites or total area (throughout this paper, we use 'efficiency' in this strict sense). This approach is founded on the recognition that competition between conservation and other forms of land use will often be intense, and therefore that networks of protected areas should be as small as it is possible for them to be while still attaining their objectives. Efficiency is evaluated in a relative way, and the performance of a network has usually been assessed in terms of similarity with the minimum set of sites that represents each species in the region at least once. This approach largely ignores how close the reserve network comes to attaining the general conservation objective of representing the diversity of the group(s) of interest in the study region, which is probably a more important question when evaluating their performance.

In this paper, we use an exemplar data set for plants in fens in the Scottish Borders to examine the performance of a designated set of reserves by using the efficiency-based approach and a novel alternative method. The occurrence data are derived for 'natural' areas, thereby avoiding the problem of mismatches of units of analysis and of conservation. We illustrate how misleading efficiency-based approaches may sometimes prove.

2. DATA AND METHODS

Our analyses are based on the occurrence of wetland plant species in a nationally important series of fens located in the central Scottish Borders, a region located approximately 50 km south of Edinburgh at the eastern extremity of the Southern Uplands, bounded to the north and north-east by the Moorfoot and Lammermuir Hills and to the south by the Cheviots. Here, within an area of about 30 km^2, there are almost 100 separate, small (mostly less than 5 ha) fen sites, occupying discrete waterlogged basins within a predominantly agricultural landscape. Sixty-eight of these sites (those that were accessible and which have not been badly damaged) have received a comprehensive botanical survey (for details, see Tratt 1997); of these, 16 have been notified as SSSIs by the statutory conservation agency. The presence or absence of a total of 125 wetland plant species was recorded at each site surveyed, of which 25 are nationally rare according to the criteria of Wheeler (1988).

Following previous analyses, we examine the performance of the existing protected area network (the SSSIs) in terms of capturing the biodiversity of wetland plants as represented by the 125 species occurring across all the fen sites surveyed, accepting that these protected areas may have been designated for a variety of reasons, of which this is but one (albeit an important goal). As such, and again following previous analyses, the objective is to examine how well the protected areas perform in this regard, not how well they meet the objectives of those individuals who actually designated them.

Throughout, unless otherwise stated, optimal solutions to network design problems were determined through linear integer programming by using LINDO (LINDO Systems 1996), rather than the heuristic ('near-minimum') methods more typically adopted in such analyses.

3. THE 'EFFICIENCY' APPROACH

The efficiency of the SSSI system was first assessed by the common approach of comparison with the minimum set of areas (the minimum network) that represents each species at least once. The exact minimum set was determined by solving the integer problem

minimize

$$\sum_{j=1}^{n} x_j$$

subject to

$$\sum_{j=1}^{n} a_{ij}x_j \geqslant 1, \quad i = 1,2, \ldots, m$$

$$x_j \in \{0,1\},$$

where m is the total number of species, n is the total number of sites, a_{ij} is 1 if species i is present in site j and 0 otherwise, and x_j is 1 if site j has been selected and 0 otherwise. This is known as the *set covering problem* (Balas & Ho 1980; Camm *et al.* 1996). Given that the SSSI system does not represent all species at least once (see below), the minimum set of extra sites needed to fill this gap was determined in the same way, but excluding from the analysis those areas that are SSSIs and all species that occur within them.

The selection units (sites) have different sizes; we therefore also looked for the solution to the problem of minimizing the total area needed to represent each species at least once. This is the problem

minimize

$$\sum_{j=1}^{n} c_j x_j$$

subject to

$$\sum_{j=1}^{n} a_{ij}x_j \geqslant 1, \quad i = 1,2, \ldots, m$$

$$x_j \in \{0,1\},$$

where c_j is the area of site j. As before, the minimum extra area needed to fill the representation gap in the SSSI system was also determined. Finally, all four of these analyses were repeated with only the rare species.

The results obtained from these analyses sustain the usual conclusions found in the literature about the poor performance of existing networks of protected areas in representing the diversity of biological attributes in a region (table 2). First, the SSSI system does not cover all the species; eight are not represented, including two rare ones. Second, although the SSSI system already occupies 16 sites and 45.8% of the study area, it would be possible to preserve each species once in only 13 sites or 23.4% of the area and to represent each rare species in only six sites or 14.0% of the area. Third, to fill the gaps in the SSSI system it would be necessary to add extra sites, and this implies another loss of efficiency. At least seven extra sites or an additional 9.2% of the total area are required to represent each species at least once and at least one extra site or an additional 0.2% of the area to represent each rare species once. Finally, there is a poor match between SSSIs and the optimal set of sites needed to represent each species at least once. Only five of the 13 sites in the minimum set are SSSIs, and only 13.2% of the 23.4% minimum area is classified as SSSIs.

Because the problem of minimizing the number of sites may have several equally optimal solutions, we tested the possibility of obtaining a better match between the SSSI system and a minimum set of sites. It is not possible to obtain any other set of 13 sites covering each species at least once that includes more than five SSSIs, nor is it possible to obtain another set of six sites that represents each rare species at least once that includes more than five SSSIs. For problems that minimize the area, it is highly unlikely that different equally optimal solutions exist, because the coefficients in the objective function are continuous.

The efficiency of the SSSIs can also be analysed with regard to the chronological sequence in which they were selected, because the date of each site's designation as an SSSI is known. We compared the cumulative number of

Table 2. *Performance of the SSSI system when compared with optimal minimum sets of sites*

problem	no. of sites	no. of sites classified as SSSI	% total area	% total area classified as SSSI
existing SSSI system	16	—	45.8	—
min. no. of sites to represent each species at least once	13	5	30.5	21.0
min. no. of sites to complete the SSSI system to represent each of the eight uncovered species at least once	7	—	9.6	—
min. area to represent each species at least once	15	4	23.4	13.2
min. area to complete the SSSI system to represent each of the eight uncovered species at least once	7	—	9.2	—
min. no. of sites to represent each rare species at least once	6	5	14.7	14.4
min. no. of sites to complete the SSSI system to represent each of the two uncovered rare species at least once	1	—	0.2	—
min. area to represent each rare species at least once	7	4	14.0	13.2
min. area to complete the SSSI system to represent each of the two uncovered rare species at least once	1	—	0.2	—

species represented as the number of sites or the overall area of SSSIs progressively increased with time with the maximal number that could have been represented (resulting in an optimal set) and with the expectation from choosing areas at random (figure 1) (for a similar type of analysis see Rebelo & Siegfried (1992)). The random selection was repeated 30 times. The results of this analysis again support the conclusion that the designation of SSSIs was not efficient, this time with reference to the purpose of representing all species in the region at the fastest rate. The actual trajectory of the cumulative number of species represented in the SSSIs with increasing numbers of sites (figure 1*a*) lies between that of the random model and that of the exact solution. The actual trajectory for species represented in SSSIs with increasing total area (figure 1*b*) is indistinguishable from the performance of the random model, and again noticeably poorer than the performance of the exact solution.

4. THE ‘EFFECTIVENESS’ APPROACH

The efficiency approach to determining the performance of conservation networks focuses on the comparison between the area or number of sites occupied by the existing system and that occupied by the minimum set that represents each species once (or some other specified target). Although it is implicit that the minimum set is not necessarily a definitive system of reserves, but a basic network of sites on which other considerations can be superimposed (see, for example, Pressey & Nicholls 1989*b*), in many studies it is in practice treated as the ‘ideal’ set. As a result, all dissimilarities between it and existing reserves are considered to be a demonstration of the poor performance of the existing network.

We propose that, as well as considering their efficiency, the performance of existing reserve systems should be assessed in terms of what we shall call their *effectiveness* in attaining a defined representation target for the region (figure 2). The extent of this attainment is probably the more relevant issue, if only because, regardless of their dissimilarity or otherwise to an optimal set, existing protected areas will provide the nucleus of any future developments of conservation networks (there is little likelihood of them being traded for a set of options closer to the optimum, although some have suggested this might be done; see Margules *et al.* 1994).

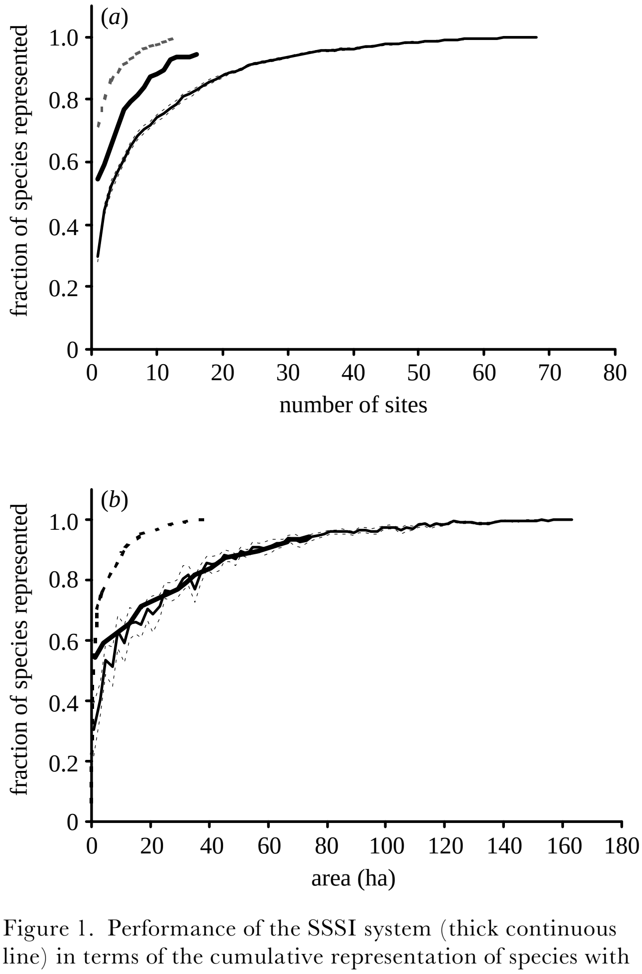

Figure 1. Performance of the SSSI system (thick continuous line) in terms of the cumulative representation of species with (*a*) increasing total number of sites, and (*b*) increasing total area, when compared with the correspondent random model (thin continuous line) and an optimal set (thick dashed line). Random models consist of 30 replicates (thin dashed lines are the limits of the 95% confidence interval), and in (*b*) data were classed in area steps of 2 ha.

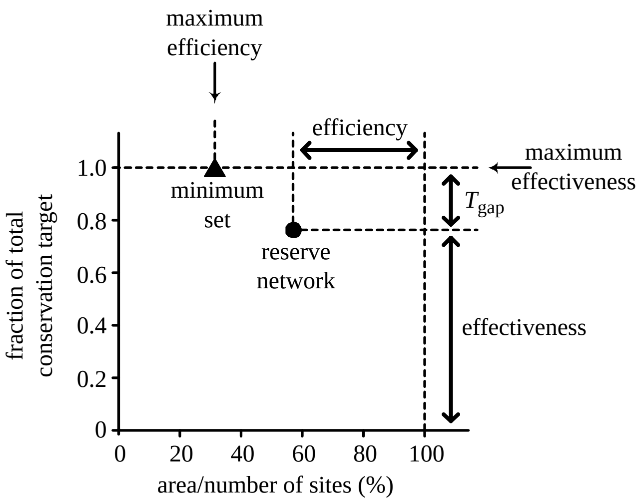

Figure 2. Illustration of the concepts of *efficiency* and *effectiveness*. *Efficiency* is larger when the area or number of sites occupied by a reserve network is smaller. Maximum possible efficiency is the one obtained by the minimum set that attains the total representation target (note that this corresponds to the minimum set that represents each species once only when considering that specific target). *Effectiveness* is larger when the reserve is closer to attaining the total representation target, i.e. when T_{gap} is smaller. Maximum possible effectiveness is reached by a set of reserves with $T_{gap}=0$. Therefore, whereas efficiency is a measure based on the size of the reserve system (y-axis), effectiveness is a measure based on its performance in terms of achieving a predetermined representation target (x-axis).

We define the gap, gap_i, in the representation of a particular species, i, in a reserve network as

$$\text{Max}\left[0, \frac{RT_{\text{total},i} - RT_{\text{reserves},i}}{RT_{\text{total},i}}\right],$$

where $RT_{\text{total},i}$ is the total representation target required for the species i, and $RT_{\text{reserves},i}$ is the representation reached in the reserve system for that species. The representation target for each species can be defined in numerous ways. Usually it has been defined as being represented once, but it can be, for example, represented five times, in 25% of its range in the study area, by 1000 individuals or by 10% of its population. Different targets can be assigned to different species, a higher target meaning a higher conservation investment to be made in the species when creating a reserve network.

The total gap, T_{gap}, of a reserve system is a value between 0 (all species reached RT_{total}) and 1 (all species totally unprotected), measured as

$$\frac{\sum_{i=1}^{m} \text{gap}_i}{m}.$$

Effectiveness is then $1 - T_{\text{gap}}$ (figure 2).

It is not the aim of this paper to determine what would be an adequate representation target for each species in the fen sites, something that should be based on a more detailed analysis of the conservation needs of each species in the region and on viability considerations (Williams 1998). As an explorative exercise, however, we considered several very different representation targets and evaluated how well the fen SSSI network performs with regard to each. T_{gap} was calculated for the targets of representing (i) all species at least once, (ii) each rare species at least once, (iii) common species at least once, rare species at least twice (or the maximum possible), (iv) common species at least once, rare species at least four times (or the maximum possible), (v) common species at least twice, rare species at least four times (or the maximum possible), (vi) common species at least 1% of range (total area of sites occupied) in the study area, rare species at least 60%, (vii) common species at least 10% of range, rare species at least 60%, and (viii) common species at least 10% of range, rare species at least 90% (figure 3*a*,*b*).

The total gap of a reserve system measures how far the system is from attaining the global representation target that is the main purpose (or one of them) for the creation of the reserves. It is not, however, a measure of how well the existing reserves have been selected. A large gap may be due to an ineffective choice but also to the fact that the representation target may be impossible to attain in a reserve system of the size of the existing one. In fact, regarding the SSSIs, the minimum sets for the more demanding targets are larger than the existing system of 16 sites and 45.8% of the total area (74.49 ha). Using the same notation as above, these minimum sets comprise (iii) 17 sites, (iv) 22 sites, (v) 27 sites, (vi) 50.0% of the total area, (vii) 50.1% of the total area, and (viii) 71.3% of the total area. In these cases, even if the SSSIs had been created with the explicit purpose of minimizing the total area or number of sites, it would have been impossible to reach the required representation targets in a system of the same size.

To adequately evaluate the effectiveness of a reserve system in terms of a defined representation target, we need to know what would be the minimum possible total gap (M_{gap}) that could exist in a system of the same size. Therefore, what we shall term the real gap (R_{gap}) of a reserve network is $T_{\text{gap}} - M_{\text{gap}}$.

Calculating M_{gap} in a system the size of the SSSI network corresponds to the problem of maximizing the effectiveness (or equivalently minimizing T_{gap}; see figure 2) subject either to selecting 16 sites or fewer, or to selecting a total area not exceeding 74.49 ha. This is the integer programming problem known as the *maximal covering location problem* (Church & ReVelle 1974; Church *et al.* 1996). However, because the objective function is not linear (because of the function Max), we use an approximation obtained by a simple greedy heuristic that in each iteration selected the site that allowed for a maximum reduction in the total gap. We estimated M_{gap} of the SSSI system for each of the above-mentioned targets (figure 3*a*,*b*). We also consider two random models (iterated 100 times), one selecting sets of 16 sites (figure 3*a*), the other sets of approximately 74.49 ha (figure 3*b*). Whereas M_{gap} corresponds to the maximum possible effectiveness that can be attained by a system with the same efficiency (same size) as the SSSI network, the random models give an indication of the expected effectiveness that would be attained if a set of sites with the same efficiency was selected randomly.

As already concluded (figure 1*b*), the SSSI system is indistinguishable from a random selection of approximately

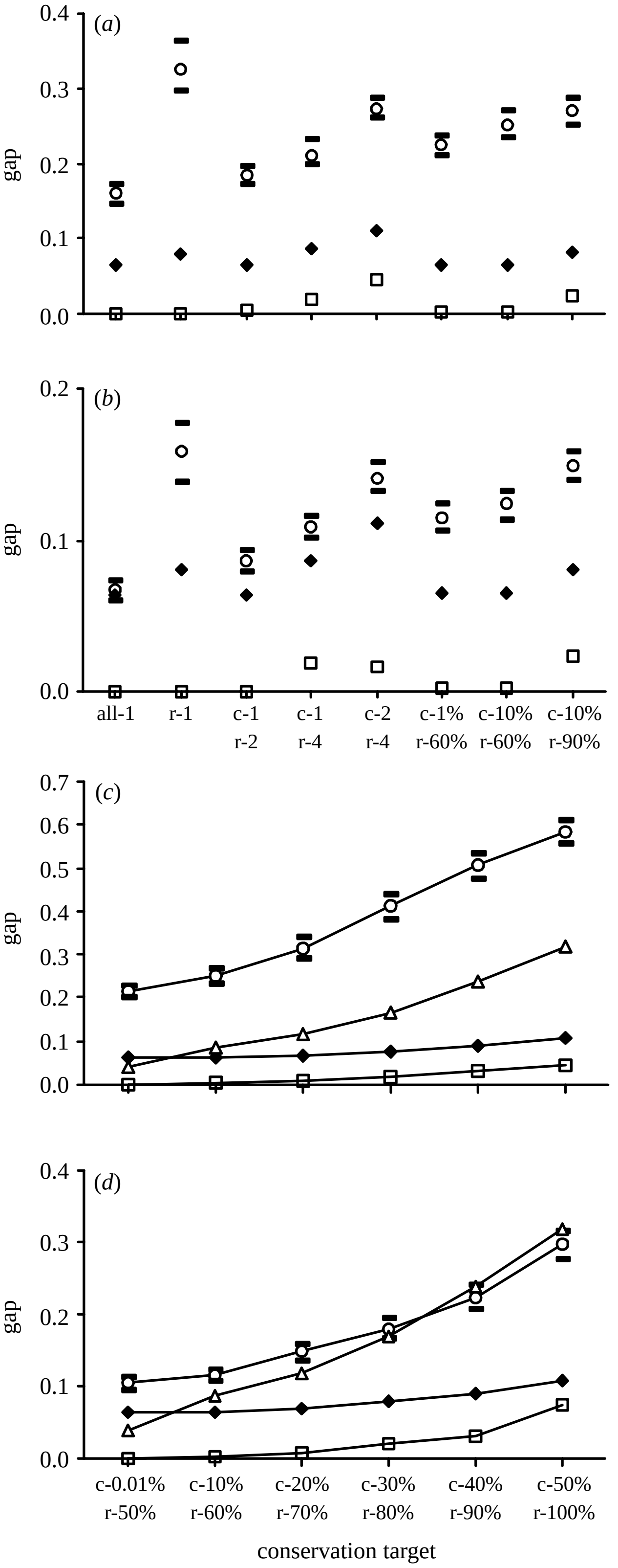

Figure 3. Performance of the SSSI system in terms of its effectiveness when evaluated according to different representation targets. In (*a*) and (*b*) the representation targets are the number of times or the percentage of range required for each species (all, all species; r, rare species; c, common species). In (*c*) and (*d*) an increasingly demanding series of targets is illustrated, expressed in terms of the relative percentage of range required for common and rare species. Parts (*a*) and (*c*) refer to analysis of the performance of the SSSI system as a network of 16 sites; (*b*) and (*d*) refer to a system of 74.49 ha. For each target T_{gap} (diamonds) and M_{gap} (squares) were calculated for the SSSI system, as well as the T_{gap} of the corresponding random model (circles indicate averages and horizontal marks indicate the limits of the 95% confidence interval, $n = 100$). The real gap, R_{gap}, is $T_{\mathrm{gap}} - M_{\mathrm{gap}}$. In (*c*) and (*d*), T_{gap} is also given for the minimum set of sites (with minimum area) that represents each species at least once (triangles).

74.49 ha when the representation target is to protect each species at least once (figure 3*b*). However, in all other situations, the SSSI system performs considerably better than any of the random models (figure 3*a*,*b*). In the situations where T_{gap} is higher, so is M_{gap}, resulting in a remarkably constant R_{gap} either considering a system of 16 protected areas (figure 3*a*) or a system no larger than 74.49 ha (figure 3*b*): the values are always between 0.054 and 0.095. In fact, the relative performance tends to increase for more demanding representation targets (a trend also found by Pressey & Nicholls (1989*b*), Pressey & Tully (1994) and Freitag *et al.* (1998)) and when disproportionate representation of rare species is required compared with common ones.

To further investigate how the performance of the SSSI network changes with more demanding representation targets we considered the series of targets (percentage of range, based on the area of the sites in which they occur) for common and rare species, respectively: 0.01 (*ca.* 0)–50%; 10–60%; 20–70%; 30–80%; 40–90%; and 50–100%. For each scenario, we calculated T_{gap} and M_{gap}, considering a system of 16 sites (figure 3*c*) and a system not larger than 74.49 ha (figure 3*d*). Again, R_{gap} is low and remarkably stable, between 0.033 and 0.064, and with a tendency to decrease. Because the gap for two random models, constructed as before, tends to increase faster than T_{gap}, the relative performance of the SSSI system is better for more demanding representation targets (figure 3*c*,*d*). We also measured T_{gap} for the optimum minimum set (minimum area) for representing each species once, the 'ideal' system when considering efficiency. In this case, the system performance becomes poorer for more demanding representation targets. According to this analysis, this set is only better than the existing system in the 0.01–50% scenario. In the most demanding scenario, its gap exceeds 0.30, three times more than T_{gap} for the SSSI network (figure 3*c*,*d*).

5. CONCLUSIONS

As judged in terms of its efficiency, the performance of the SSSI network in representing wetland plant species of fens in the central Scottish borders region is rather poor (figure 1; table 2). All 125 species, or just the rare species, can be represented at least once in notably fewer sites and in a markedly smaller area than have been designated as SSSIs, and from one to seven sites would be needed in addition to the present network to attain these ends (table 2). Likewise, the cumulative number of species represented in the SSSI network has increased more slowly with the increasing number of sites and area than could have been attained by a choice of a different set of sites and an alternative sequence of designation as protected areas (figure 1). These results would appear to confirm the general contention that conservation networks are rather poor at representing biodiversity, even in regions with relatively good networks (table 1).

This conclusion might reasonably be argued to reflect the fact that, in common with most existing networks of protected areas, a variety of criteria contributed to the designation or otherwise as SSSIs of fen sites in the central Scottish Borders region, of which the representation of plant diversity was only one. Nonetheless, when the SSSI network is considered in terms simply of its effectiveness, rather than its efficiency, in representing the plant species of the region, it performs rather well. Indeed, this conclusion is upheld when the network is evaluated according to very different representation targets. The gap between the representation achieved by the SSSI network and that potentially achievable in the same number of sites or area ranges only between 3.3 and 9.5% of the target, for a wide variety of representation targets (figure 3). In fact, that the gap is so small is perhaps surprising given the diversity of other criteria involved in the actual designation of the sites.

The poor performance of the minimum set of areas necessary to represent each species once with regard to other representation targets is a good example of the fact that what constitutes a set of sites that is optimal, or close to so being, depends on which question is asked. Although optimal in terms of efficiency and with maximum effectiveness in representing each species once, this system performs worse than the SSSI system when considering more demanding representation targets (figure 3*c*,*d*).

The contrast between results of analyses of the SSSI network based on efficiency and effectiveness suggests that more care is needed when evaluating the performance of existing networks of conservation areas. Different approaches to the same data can lead to significantly different conclusions. Efficiency is an important attribute of reserve systems. But a system should not be regarded as inherently poor solely because it does not closely match the most efficient solution to the problem of representing each species once, or the solutions to closely related problems of efficiency. Neither should the failure of a close match necessarily be interpreted as suggesting that the composition of a conservation network reflects an opportunistic approach to the acquisition of protected areas. In the data for fens, all the SSSIs are among the sites with higher species richness (for example, nine of the ten richest sites are SSSIs) and the mean area of an SSSI is almost three times that of all the other sites. Clearly, they were chosen mainly from among the richest and the largest fen sites in the region, two of the most widely used criteria in conservation evaluation (Margules & Usher 1981; Smith & Theberge 1986). This approach plainly served to generate an SSSI network that is highly effective when judged against a variety of representation targets.

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