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Robustness of reserve selection procedures under temporal species turnover

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Complementarity-based algorithms for the selection of reserve networks emphasize the need to represent biodiversity features efficiently, but this may not be sufficient to maintain those features in the long term. Here, we use data from the Common Birds Census in Britain as an exemplar data set to determine guidelines for the selection of reserve networks which are more robust to temporal turnover in features. The extinction patterns found over the 1981–1991 interval suggest that two such guidelines are to represent species in the best sites where they occur (higher local abundance) and to give priority to the rarer species. We tested five reserve selection strategies, one which finds the minimum representation set and others which incorporate the first or both guidelines proposed. Strategies were tested in terms of their efficiency (inversely related to the total area selected) and effectiveness (inversely related to the percentage of species lost) using data on eight pairs of ten-year intervals. The minimum set strategy was always the most efficient, but suffered higher species loss than the others, suggesting that there is a trade-off between efficiency and effectiveness. A desirable compromise can be achieved by embedding the concerns about the long-term maintenance of the biodiversity features of interest in the complementarity-based algorithms.

Keywords: biodiversity; complementarity; conservation; effectiveness; efficiency; turnover

1. INTRODUCTION

The prime purpose of establishing a network of protected areas for conservation is the long-term maintenance of the biological diversity of the region in question. An essential prerequisite is that biological diversity is appropriately represented in the network in the first place (Margules *et al.* 1988; Pressey *et al.* 1993). This need for representation has been strongly emphasized in recent literature on methods for the selection of reserve networks. Furthermore, it has been recognized that reserves are economically costly and, consequently, will be in direct competition with more destructive forms of land use (e.g. Bedward *et al.* 1992; Pressey *et al.* 1993). This has resulted in the development of procedures which aim at high efficiency (*sensu* Pressey & Nichols 1989) by representing the biodiversity attributes of interest in a minimum area, generally called complementarity-based methods (e.g. Bedward *et al.* 1992; Rebelo & Siegfried 1992; Williams *et al.* 1996; Csuti *et al.* 1997).

However, representation is only the first step towards achieving the final purpose of maintaining biodiversity in the long term (Williams 1998). These are not equivalent because species distribution patterns change over time and reserve networks may not necessarily continue to serve their original purpose some years afterwards (Margules *et al.* 1994). It can be argued that once a reserve network which represents all features of interest has been established, it is a matter of adequate management to ensure that those features are retained. Nevertheless, the success of management efforts and the cost of management actions may be strongly influenced by the

quality of the sites which are selected in the first place. It is expected that a more robust network of protected areas will result from selecting areas less subject to the 'natural' local extinction of features, independently of subsequent management practices.

In this study, we ask (i) how effective is a simple representation strategy (minimum set) in maintaining feature diversity over time and (ii) is it possible to predict *a priori* which sites should be selected in order to obtain a reserve network which is robust to temporal turnover in features? Although previous studies (Margules *et al.* 1994; Voininen *et al.* 1999) have addressed the first question, they did not provide many clues for the answer to the second one. Nicholls (1998) and Williams (1998) proposed strategies for improving the robustness of networks, the first by establishing a minimum population size as a required representation target for each species and the second by targeting core populations using niche-based modelling of habitat suitability; however, their effectiveness in ensuring the long-term persistence of species has not yet been tested.

In the present study, we consider the case of species as features of biodiversity and use data from the Common Birds Census (CBC) to explore the influence of temporal turnover in their occurrence for reserve selection procedures. First, we determine which variables have more influence on rates of local species extinction. Then we use this information to propose selection guidelines which aim to produce reserve networks that are more robust to such turnover.

2. DATA

The CBC, which is run by the British Trust for Ornithology, has been the main scheme by which populations of common breeding birds have been monitored in

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Table 1. *Relationship between extinction patterns in the 1981–1991 period and site species richness, species frequency and local abundance*(Logistic regression was applied to analyse each relationship. The results were interpreted using a likelihood ratio test (χ^2 -test).)

predictor variable	response variable	<i>n</i>	results
site species' richness (total number of species in a given site)	extinction rate (fraction of species that occurred in the site in 1981 but not in 1991 in relation to the number of species in the site in 1981)	56	non-significant (χ^2 -test = 0.001)
species' frequency (number of sites where the species occurred in 1981)	extinction rate (fraction of the sites from where the species disappeared between 1981 and 1991 in relation to its frequency in 1981)	94	highly significant negative relationship (χ^2 -test = 12.088; $p < 0.001$)
site number of territories (for a given species, the number of territories at a given site in 1981)	extinction probability (binary variable indicating whether the species disappeared from the site between 1981 and 1991 (1) or not (0))	1858	highly significant negative relationship (χ^2 -test = 292.177; $p < 0.001$)
site density (for a given species, number of territories per unit area at a given site in 1981)	extinction probability (binary variable indicating whether the species disappeared from the site between 1981 and 1991 (1) or not (0))	1858	highly significant negative relationship (χ^2 -test = 224.863; $p < 0.001$)

the UK (for a comprehensive description of the history and methodology of the CBC, see Marchant *et al.* (1990)). A mapping census technique (see Bibby *et al.* 1992) which provides a very accurate measure of the number of territories occupied by each species in each site during a breeding season has been employed since 1964.

In our analysis, we used CBC data for 113 species collected between 1974 and 1991 in a variable number of farmland and woodland sites. We considered eight pairs of years with years in each pair separated by a ten-year interval (1974–1984 through to 1981–1991) and analysed only those sites with good quality information in both years of a pair. Only those species for which presence or absence was recorded in both years of each pair were considered. In order to obtain a final matrix with a territory count for each species for all sites four rules were applied.

- (i) Where a species was seen but the territory count on a site in a given year was zero, the species was assumed not to be breeding but to be casually using or moving through an area.
- (ii) Where nest counts were available instead of territory counts these were considered to be equivalent.
- (iii) Three very common species (woodpigeons (*Columba palumbus*), starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*)) were eliminated from the analysis because they often were not counted systematically (and are of minimal interest here).
- (iv) Where any other species was thought to have held territory but for some reason was not counted (less than 1% of the total presence records) a density value was extrapolated from the average territory density of the respective species in the other occupied sites of the same habitat type.

The CBC data is used here as an exemplar data set to explore general reserve selection strategies and, therefore, the results should not be interpreted as an attempt to propose a new reserve network in the UK.

3. EXTINCTION PATTERNS

We used the 1981–1991 data set (97 species in 56 sites) to explore the variables which influenced the temporal patterns of species' turnover. Applying logistic regression models, we analysed the relationships between extinction and site species' richness, species' frequency (number of sites where the species occurs) and local abundance.

No significant relationship was found between the species' richness of sites and the extinction rates suffered (table 1). These results do not support a simple hot-spot strategy, based on the selection of sites with higher species richness (e.g. Prendergast *et al.* 1993; Williams *et al.* 1996), as a method of obtaining reserve networks which are more robust to temporal species' turnover.

Highly significant negative relationships between species' frequency and local extinction rates were found (table 1 and figure 1a). The observation that rare species are more prone to local extinction agrees with established ideas in this regard (Gaston 1994) and with previous results (Margules *et al.* 1994). The implication in terms of reserve selection strategies is that the occurrence of common species is more predictable than the occurrence of rare ones (in the absence of appropriate management). This means that a higher investment may be needed in order to ensure the persistence of rarer species, which may imply targeting these as priorities when allocating conservation resources. Indeed, the presence of rare species is one of the most frequent criteria for the selection of protected areas (Margules & Usher 1981; Smith & Theberge 1986).

There was also a highly significant negative relationship between local abundance, expressed either as the number of territories or as the density of a given species in a site and the probability of extinction (table 1 and figure 1b,c). These results indicate that species are more likely to disappear from sites where they are locally rarer. Again, this is an expected result, since smaller

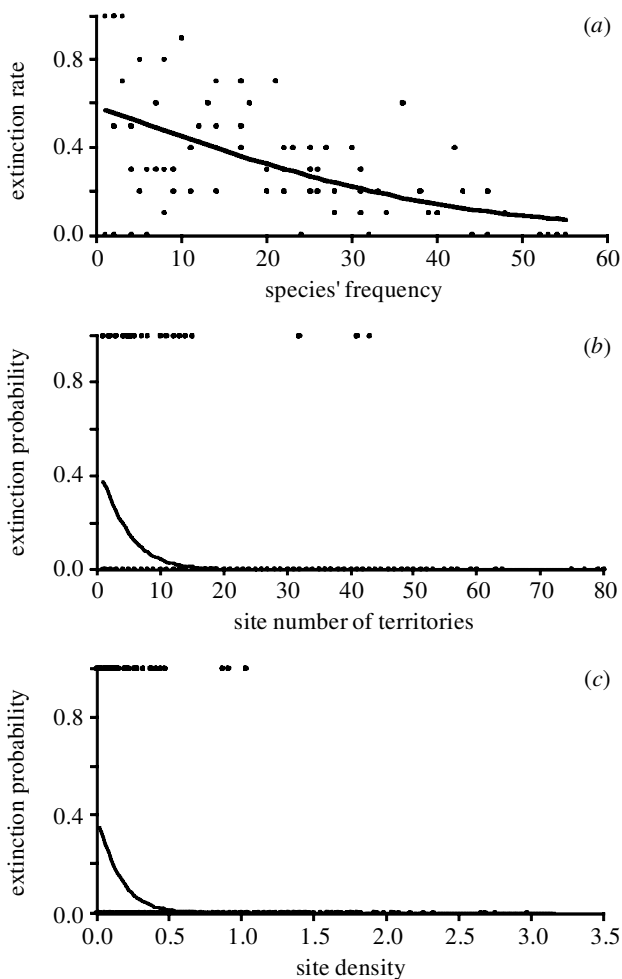


Figure 1. Extinction patterns for the 1981–1991 pair of years. (a) Relationship between the species' frequency (number of sites where the species occurs) and the extinction rate (fraction of sites from where the species disappeared between 1981 and 1991 in relation to its frequency in 1981). (b) Relationship between the number of territories in a site for a given species and the extinction probability (the probability of the species becoming extinct in that site). (c) Relationship between the site density (number of territories per hectare at a site) for a given species and the extinction probability. The relationships were analysed using logistic regressions (for more details see table 1).

populations are known to be more prone to local extinction due to demographic and environmental stochasticity and reduction in genetic variation (Caughley & Gunn 1996). Although it is unlikely that genetic considerations play a significant role for these data, the other two processes may have been important in determining extinction. The implication of these results for reserve selection procedures is that it may be possible to obtain more robust networks if species are represented in the sites where they occur in higher abundance.

The 'abundance–occupancy' relationship, a widespread attribute of species' assemblages in which locally rare species tend to be of restricted distribution and locally abundant ones tend to be widespread (Hanski 1982; Brown 1984; Gaston 1994; Gaston *et al.* 1997), implies that the negative relationships between both frequency and local abundance and the probability of extinction are connected (the 'double jeopardy' of Lawton (1993)). Those

species which occur in fewer sites in the study area may be more prone to extinction simply because, being more scarce locally, they suffer a higher probability of local extinction.

The selection units considered in this study are census plots (average area *ca.* 47 ha) which are much smaller than most nature reserves (average area of special protection areas for birds classified until March 1998 in the UK is around 6020 ha; English Nature 1998). It is therefore likely that the turnover rates observed here are considerably faster than the ones occurring in reserves. In compensation, turnover is known to increase over time (Russell *et al.* 1995) and reserves are expected to prevail far longer than the ten-year intervals considered in this study. We assumed that the turnover rates observed within the ten-year intervals in the CBC plots exhibit similar patterns to the ones observed in larger areas over longer periods and can be used to make inferences about the relative performance of different reserve selection strategies. This assumption is supported by the fact that the same patterns explored in this study (rarer species tend to be more prone to local extinction and species are more likely to persist in sites with higher local abundance) agree with previous studies (Gaston 1994; Margules *et al.* 1994; Caughley & Gunn 1996).

4. RESERVE SELECTION STRATEGIES

Using the information obtained in the previous analyses, several reserve selection strategies were proposed and tested using the data on the eight pairs of years corresponding to a ten-year interval. In each pair, the first year's data were used to select a reserve network following a specific strategy and the last year's data were used to assess the results in terms of efficiency (Pressey & Nicholls 1989) and effectiveness (Rodrigues *et al.* 1999). Efficiency is higher when the total area occupied by the network is smaller. Effectiveness is higher when the fraction of species absent from the network (the representation gap) is smaller.

For each pair of years, the average efficiency and effectiveness were also determined for 100 randomly selected networks of (approximately) a predefined area. This was done by selecting sites randomly, without replacement, until the total area was approximately that desired. We applied this procedure to a wide range of areas to establish a null relationship between efficiency and effectiveness (random model).

Five reserve selection strategies were tested.

- (i) Strategy 1: select the minimum area such that each species is represented in at least one site.
- (ii) Strategy 2: select the minimum area such that each species is represented at least by the site where it occurs in higher abundance in terms of number of territories.
- (iii) Strategy 3: select the minimum area such that each species is represented at least by the site where it occurs in higher abundance in terms of density.

The following strategies (4 and 5) are a relaxation of strategy (3) in the sense that species must be represented by the best sites where they occur in terms of density. However, instead of requiring that the best site is selected

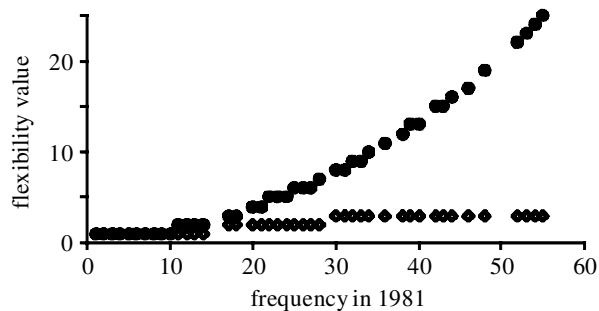


Figure 2. Conversion between the frequency of a species (number of sites occupied) and the flexibility values applied in strategies 4 (open diamonds) and 5 (filled circles), illustrated here for the 1981–1991 pair of years. The curve for strategy 5 was obtained by transforming the frequency values f_i of each species i using the equation $y_i = 2f_i + f_i^2$, then scaling the resultant y_i to a [1, 25] interval and rounding the values obtained to the nearest integer to obtain a flexibility value for i .

for each species, a higher flexibility is given in the choice for the most common species. If a species has a flexibility value of n , it means that the site selected to represent it can be chosen among the n top sites in terms of density.

- (i) Strategy 4: species are classified into three classes according to their frequency (number of sites in which they occur) in the data set: less than 15, between 16 and 30 and more than 31, with flexibility values of 1, 2 and 3, respectively (figure 2).
- (ii) Strategy 5: species have flexibility values between 1 (the rarest species) and 25 (the most frequent). These were obtained according to the curve represented in figure 2, which gives low flexibility to species with low and medium frequencies and high flexibility only to the most common ones. The maximum flexibility of 25 corresponds to approximately half the frequency of the most common species (which means that for this species the selected site can be any among the top-half best ones).

All minimization problems were solved exactly as integer linear programming problems using LINDO (LINDO Systems, Inc. 1996). In each case only one optimal solution was found (which is not unexpected since sites have different areas and there is a low probability that the exact minimum is obtained by different sets of sites).

5. RESULTS OF THE RESERVE SELECTION STRATEGIES

The random models (figure 3) reveal an intrinsic trade-off between the efficiency and effectiveness of a reserve network: the larger the area covered, the more likely it is to have a lower representation gap ten years afterwards. A possible strategy in terms of obtaining robust reserve networks could therefore be simply to select as much area as possible. However, in the limit, only by selecting the entire area could a maximum effectiveness be guaranteed *a priori*, which is obviously unrealistic.

In general, all five strategies tested performed considerably better than a random selection in terms of both effectiveness and efficiency.

Strategy 1 aims explicitly at maximizing the efficiency of a reserve network and corresponds to the most popular complementarity-based approach in the recent conservation literature (e.g. Rebelo & Siegfried 1992; Williams *et al.* 1996; Csuti *et al.* 1997). However, it always resulted in a significantly larger representation gap than the other strategies (figure 3), demonstrating that it was not possible to maximize efficiency and effectiveness simultaneously using this approach.

All of the strategies except strategy 1 addressed the lower probability of extinction in the best sites where a species occurs. Selecting the best sites in terms of number of territories (strategy 2) means selecting a larger fraction of each species' population, which makes sense in terms of long-term persistence, as reflected by the generally small representation gap obtained. However, because a high number of territories in one site is often a reflection of a larger area, this strategy tends to select larger sites and, indeed, in all situations except one this was the least efficient strategy (figure 3).

Selecting the best site in terms of density (strategy 3) may imply that very small sites are selected (Gaston *et al.* 1999), but a high density may be associated with high-quality habitat and may be a good predictor of the probability of persistence in the site. As expected, this strategy produced networks that were generally more efficient than those selected by strategy 2, but always less efficient than the minimum set. Furthermore, their effectiveness was usually high, indicating that this may provide a good compromise between efficiency and effectiveness.

Strategies 4 and 5 addressed the lower probability of local extinction of more common species to increase the flexibility of choice in those species. As expected, this always resulted in higher efficiency of the reserve networks in relation to strategy 3, although sometimes it incurred a larger representation gap (figure 3). Because of its higher flexibility, this pattern was more evident for strategy 5.

6. DISCUSSION

The results obtained in this study suggest that, in spite of its popularity in recent conservation literature, a minimum set strategy for selecting reserve networks may not be sufficient if the role of a network is to maintain species in the long term rather than simply to represent them in the present (Williams 1998). This is consistent with the results obtained by Margules *et al.* (1994; 36% species lost during an 11-year interval from the minimum set of limestone pavements which represented each plant species once, UK) and Virolainen *et al.* (1999; 16% species lost during a 63-year interval from the minimum set of lakes which represented each plant species once, Finland).

The results obtained using the other selection strategies indicate that it is possible to obtain reserve networks which are more robust to temporal turnover if species are represented in the sites where they are more likely to persist in the long term. All strategies that used this basic rule performed significantly better in terms of effectiveness than the minimum representation set (figure 3). When a higher flexibility in the selection of the best sites was allowed for the most common species (which corresponds to giving priority to the rarer species in the

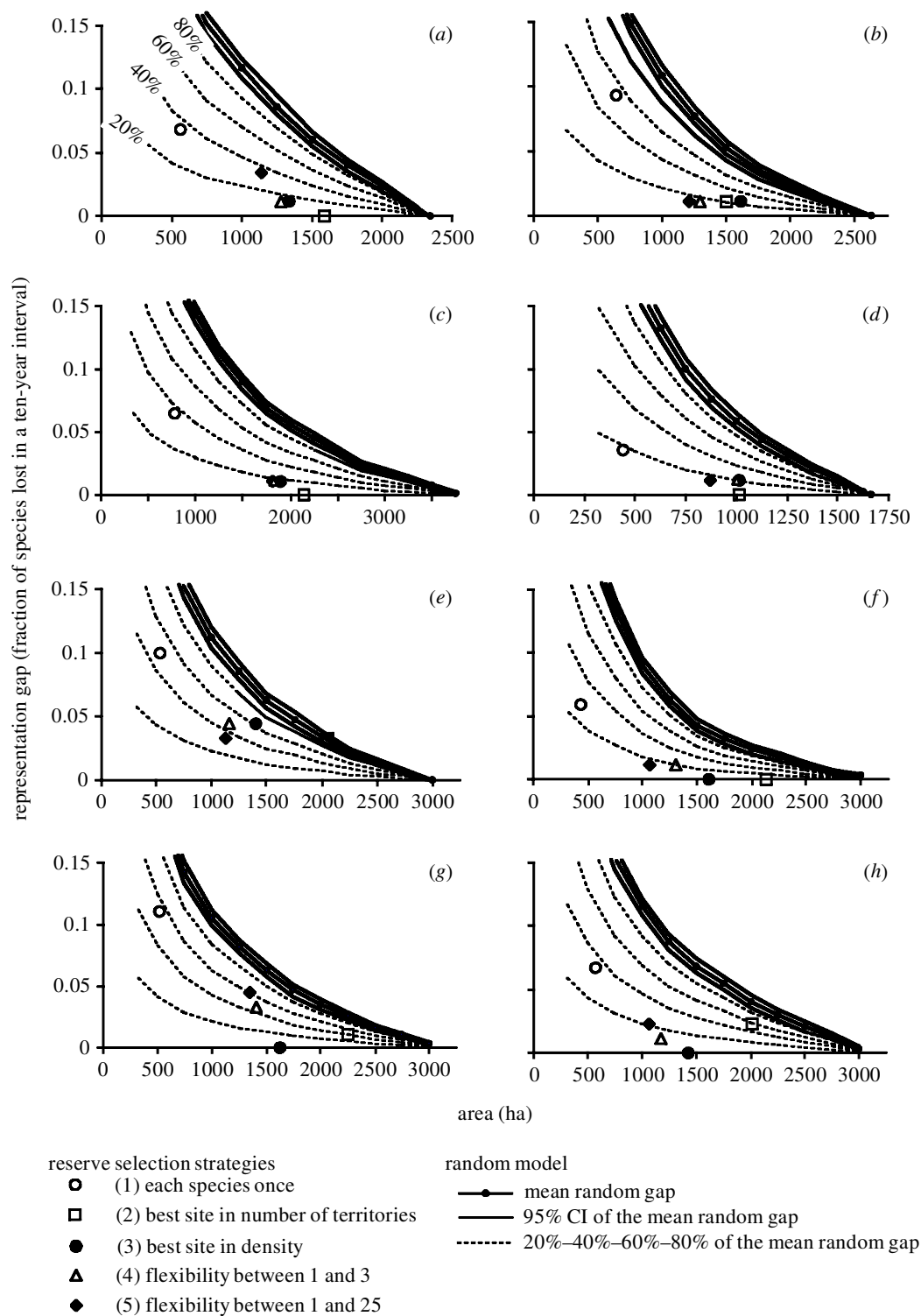


Figure 3. The results obtained for each of the reserve selection strategies tested, for each of the eight pairs of ten-year intervals considered, compared with the respective random models. For each reserve selection strategy, the data point indicates the total area occupied by the correspondent network (the smaller the area the higher the efficiency) and the representation gap (the lower the gap the higher the effectiveness). Mean gap values and 95% confidence intervals (CIs) were obtained from 100 randomly selected sites for each area. The values in parentheses refer to the number of species/number of sites. (a) 1974–1984 (88/43), (b) 1975–1985 (86/49), (c) 1976–1986 (93/64), (d) 1977–1987 (84/37), (e) 1978–1988 (90/52), (f) 1979–1989 (85/57), (g) 1980–1990 (90/55) and (h) 1981–1991 (89/56).

selection procedures), it was possible to improve the efficiency, although often by compromising some effectiveness.

Naturally, it should not be concluded from this exercise that to select the single best site is sufficient to ensure the

long-term maintenance of most species. Nevertheless, we believe that the two major guidelines presented here are of general application: species must be protected in the best sites where they occur (those that offer better

chances of long-term persistence) and the rarest species should receive a higher conservation investment. Although crude, these allow for the simultaneous integration of viability and threat concerns in complementarity reserve selection procedures (Nicholls 1998; Williams 1998).

Unsurprisingly, these two guidelines are not new in practical reserve selection exercises (see Thomas 1991). For example, the European Union Birds Directive (Council Directive 79/409/EEC of 2 April 1979) gives priority to the most vulnerable species (listed in Annex I) and established that the 'most suitable territories' for those species should be classified as Special Protection Areas. Accordingly, the European Union Habitats Directive (Council Directive 92/43/EEC of 21 May 1992) considers two levels of important species (the ones listed in Annex II and, among those, the ones classified as 'priority') and established that, in the classification of Special Conservation Areas, the density and dimension of the population of the species in each site must be taken into account. More or less systematically, conservation agencies have always been struggling to protect the best sites for the most threatened species, but there are practical constraints to be considered at the same time (Thomas 1991).

However, such a strategy is more costly than one aiming at simple representation (figure 3). This may provide an additional explanation for the observation that existing reserve networks are less efficient in representing biodiversity features than a minimum set (e.g. Rebelo & Siegfried 1992; Castro Parga *et al.* 1996), which has been interpreted as demonstrating that reserve networks have been selected in an ad hoc fashion (e.g. Pressey & Tully 1994). Less efficiency may also be a consequence of incorporating a concern for the long-term maintenance of the biodiversity features of interest in reserve selection procedures.

The results presented in this study also demonstrate that there is a trade-off between effectiveness and efficiency and that maximizing both simultaneously is unlikely to be possible. The fact that conservation planners have been emphasizing the former while scientists working in conservation research have been mainly concerned with the latter may help to explain the gap between theory and practice in reserve selection procedures (Prendergast *et al.* 1999). Effectiveness has mainly been addressed by focusing on some target species or ecosystems and selecting networks of reserves that aim at maintaining them. On the other hand, complementarity-based algorithms have been aimed at maximizing efficiency by looking for minimum sets which represent all features. There are dangers in both approaches. The first results in a biased and inefficient distribution of the conservation resources among biodiversity features, some being highly protected while others are totally unrepresented. The latter may result in reserve networks which are not robust over time and it may be sending, albeit unwittingly, the message that a minimum set is sufficient to maintain diversity when in fact it is not.

Here we have illustrated how it is possible to achieve a compromise between efficiency and effectiveness if the concerns about viability and threat are embedded in complementarity-based algorithms. This does not imply a need to hold such detailed data as the CBC, but does imply

a need to make best use of all the relevant information available. Indeed, it is often the case that when the detailed distribution data required to apply complementarity-based algorithms are available, so is other relevant information which has been overlooked in simply searching for minimum representation. This includes, for example, Red Data books, which can be used to establish priorities in terms of conservation investment, and information about the location of the best sites for at least some species, even if established qualitatively in terms of habitat quality or availability.

Reducing the gap between theory and practice in reserve selection procedures (Prendergast *et al.* 1999) will require that scientists working in conservation research give conservation planners the tools which will allow them to integrate the concerns and information that they consider to be relevant.

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