



SPATIAL POPULATION DYNAMICS IN RESERVE-NETWORK DESIGN

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Academic dissertation

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Spatial population dynamics in reserve-network design

Mar Cabeza

The Thesis is based on the following articles:

- I Cabeza, M., and Moilanen, A. (2001). Design of reserve networks and the persistence of biodiversity. *Trends in Ecology and Evolution*, 16, 242-248.
- II Cabeza, M., and Moilanen, A. (2003). Site selection algorithms and habitat loss. *Conservation Biology* (in press).
- III Cabeza, M., Araújo, M.B., Wilson, R.J., Thomas, C.D., Cowley, M. and Moilanen, A. Integrating spatial reserve design with habitat models (submitted).
- IV Cabeza, M. (2003). Habitat loss and connectivity of reserve networks in probability approaches to reserve design *Ecology Letters* (in press).
- V Moilanen, A., and Cabeza, M. (2002). Single species dynamic site selection. *Ecological Applications*, 12, 913-926.
- VI Cabeza, M., Moilanen, A. and Possingham, H.P. (2004). Metapopulation dynamics and reserve network design. In *Ecology, Genetics and Evolution of Metapopulations* (Hanski, I. And Gaggiotti, O., Eds.). Academic Press (in press).
- VII Poulin, M., Cabeza, M., and Bélisle, M. (2003). Within-site configuration in reserve design: a case study with a peatland bird (submitted).

These are referred by their Roman numerals in the text.

Contributions

The following table shows major contributions of authors to the original articles

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Study design	MC, AM	MC, AM	MC, AM	MC	AM, MC	MC, AM	MP, MC
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Empirical data gathering	-	-	**	**	*	*, **	***
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Summary

1 Systematic reserve design

Humans have been transforming the Earth during the last millennia into a patchwork of natural, human-modified, and destroyed habitats. Loss and fragmentation of habitats have become one of the most serious threats to biological diversity (Wilcox and Murphy 1985; Quinn and Hastings 1987; Cutler 1991; Burkey 1995; Pimm and Raven 2001). Presently, species are going extinct at a rate approximately 100 times the natural background rates (Smith et al. 1993; Benton 1995; Pimm et al. 1995; Pimm and Lawton 1998). Current habitat-destruction rates and the observed relationship between habitat loss and species loss suggest that extinction rates will only become higher (Saunders et al. 1991; Tilman et al. 1994; Morris 1995; Brooks et al. 1997). Therefore, conservation efforts must proceed with the understanding that only a small, critical fraction of the world's habitats may survive as natural or semi-natural areas (Soulé 1991).

Protection of habitat in reserves is a recent phenomenon, dating back only about a century, if we disregard the indirect protection of habitat, for instance as hunting reserves. Oftentimes, however, biology has played a small role in the selection of reserves and most of the decisions lack proper perspectives on conservation priorities. It follows that areas have been chosen for conservation based on availability, competition with alternative land uses, scenic value and other factors, regardless of any theoretical considerations about reserve design (Pressey 1994). These *ad hoc* decisions for setting conservation areas are an old and pervasive problem that has resulted on reserves concentrated in landscapes easiest to protect and least in need of protection (Adam 1992; Barnard et al. 1998).

During the 1970's different studies raised awareness on the need to have explicit approaches for setting conservation priorities in a more biologically sound manner (Goldsmith 1975; Ratcliffe 1977). In the early 1980's systematic conservation approaches began to be developed (e.g. Kirkpatrick 1983; Ackery and Vane-Wright 1984).

1.1 Goals and Algorithms

Reserve-network design includes two important steps: (1) the definition of explicit conservation goals for the planning region and (2) the application of optimization methods (algorithms) when selecting sites to meet the goals in the most efficient way.

The two major methodological approaches to systematic reserve design are based on (1) a scoring procedure and (2) the concept of complementarity. The so-called scoring approach focuses on the addition of one or few sites to an existing reserve network. In order to choose the best sites, scores are given to all sites according to different criteria such as species richness, presence of rare species, shape, quality of the habitat, etc. (see Margules and Usher (1981) for a review). Sites are then ranked and those with high ranks are chosen.

Nevertheless, to design entire reserve systems we need to acknowledge that the whole reserve system is different from the sum of its parts: e.g. two sites, if considered independently, may both be very valuable, however, considered together, they may be redundant if they contain essentially the same attributes.

When designing whole reserve-networks, goals have been mostly framed in terms of species representativeness (i.e. number of species included in the reserve network). When solving the problem of how to represent all the species of the region in the most efficient way (e.g. in the least number of reserves) the concept of complementarity becomes fundamental. Complementarity is a property of the sites within the matrix of sites x species (species or any other valued feature that needs to be included in the reserves, e.g. taxa, landscape types, etc.), which measures the extent to which a site, or a set of sites contributes to unrepresented features.

Complementarity-based methods were developed during the early 1980's (beginning with Kirkpatrick (1983), and simultaneously developed by several authors (Ackery and Vane-Wright 1984; Margules et al. 1988; Rebelo and Siegfried 1990)). These methods can select networks of reserves more efficiently than scoring approaches (e.g., Williams 2001).

Let us compare scoring algorithms and complementarity-based approaches with one example. Figure 1 represents the presence (marked with a cross) of 11 species in 8 candidate sites for a hypothetical system. Suppose that we could choose only one site for protection. A scoring approach that would rank the sites according to species richness (or an approach based on hotspots of richness, see e.g., Williams and Araújo (2002)) would select site 2, with a total of 7 species.

Sites	Species										
	A	B	C	D	E	F	G	H	I	J	K
1	X										X
2			X	X	X	X	X	X	X		
3		X	X	X	X	X	X				
4									X	X	X
5	X					X					
6	X	X	X								X
7	X							X	X	X	X
8	X						X				

Figure 1. Matrix showing the presence (X) of 11 species (A-K) in all candidate sites (1-8) for an hypothetical reserve design exercise.

If two sites should be selected instead of one, the scoring approach would select the next richest site, which is site 3 (6 species). Together, sites 2 and 3 represent a total of 8 species. If the goal is to select sites until all species are represented, following the ranking of sites we would add site 7 and site 6. Together, sites 2, 3, 6 and 7 represent all species. However, when the aim is to select the most efficient network (e.g. the minimum number of sites) that includes all species, we can easily see that sites 3 and 7 together would be enough to represent all 11 species (Fig. 1). Therefore, to solve the reserve-network selection problem in an efficient way, selected sites should complement one another in terms of the species they contain. It follows that the set of sites contributing most to completing the representation of all species will not necessarily include the richest site (site 2 in Fig. 1), and this, in fact, is often the case (Williams 2001; Margules et al. 2002 for reviews). It has been shown that indeed, sets of rich sites may contain no more species in total than would be expected from choosing the same number of sites at random (e.g., Williams 2001).

The problem presented in Fig. 1 may seem rather simple, however when confronted with large systems of many species and large number of sites, the optimal solutions are not evident by sight (e.g., Harrison et al. 1997: 3885 sites, 852 species).

Two common ways of defining the reserve selection problem from the perspective of complementarity-based approaches are, (1) to choose the minimum set of reserves containing all features at least once – known as the set covering problem (e.g., Underhill 1994) and (2), to maximize the number of features represented when there is a limit on the cost (or e.g. on the number of reserves that may be chosen) – known as the maximal coverage location problem (e.g., Church et al. 1996). Different optimization methods, often called reserve-selection algorithms (or area-selection, or site-selection), have been devised for solving these problems (see Box 1 and chapters I and VI for a mathematical formulation of the problems).

The optimization algorithms that have been used for solving reserve-network design problems can be classified into exact and heuristic (non-exact) methods. Exact algorithms, belonging to standard operations research techniques (such as integer linear programming), are methods which guarantee to find optimal solutions (among others: Cocks and Baird 1989; Underhill 1994; Camm et al. 1996; Church et al. 1996; Arthur et al. 1997; Rodrigues and Gaston 2002). However, reserve-selection problems are NP-complete, meaning that they cannot be solved in polynomial time, which often results in serious difficulties in finding the optimal solution for large problems. Therefore, heuristic methods are often used to obtain good, near-optimal, solutions. Non-exact optimizing approaches include the widely used simple iterative heuristic algorithms (e.g. Kirkpatrick 1983; Rebelo and Siegfried 1992; Pressey et al. 1993; Pressey et al. 1996; Van Jaarsveld et al. 1998), and stochastic global search techniques (e.g., Possingham et al. 2000; MCDonnell et al. 2002; Chapter V). Iterative heuristics execute a set of rules repeatedly, adding sites to the solution one by one. These methods use randomization only occasionally for breaking ties. Stochastic global search methods, instead, achieve good solutions by using intelligent randomization. While the latter cannot guarantee the optimality of the solution, they have been successful in solving difficult optimization problems.

Discussion about the optimality properties of reserve-selection algorithms became a central topic in reserve-design literature during the 1990's. Heuristic approaches, especially iterative heuristics, have been often preferred because of three main arguments (Rodrigues and Gaston 2002):

- good heuristics provide solutions which are only slightly sub-optimal (depending on the problem)
- exact algorithms may not be able to find solutions to large and complex (and more realistic) problems
- exact algorithms are too slow and therefore inadequate for interactive practical conservation planning

Nevertheless, the debate on what methods should be used for reserve-selection problems is no longer a central topic in reserve-selection literature. Methods continue to develop and the computational capacity of computers is continuously increasing. Currently, exact algorithms are preferred for simple problems and small systems, and heuristics are used for larger systems and when solutions are needed fast. Recently, emphasis has shifted from criticisms of computational methods to criticisms of problem definition, i.e. the identification of realistic and biologically sound conservation goals.

1.2 Conservation in a changing world

Because of limited economic opportunities for conservation great emphasis has been placed on the efficiency with which networks of reserves represent numbers of species. It has been acknowledged, however, that ultimately it is not how many species are included within a set of sites that is important for conservation, but how many will persist there for the future (Pressey *et al.* 1993; Cowling *et al.* 1999; Pressey 1999). Only recently reserve-selection studies have looked at persistence-related issues.

There is a growing awareness that the majority of systematic approaches for reserve design focus mainly on current (presence/absence) patterns of biological diversity, while disregarding ecological and anthropogenic processes (including habitat loss and fragmentation, global warming, etc.), which, in many cases, generate or threaten those patterns (Mace *et al.* 1998; Nicholls 1998). Nature is not static: population interactions in space and time determine species' distribution and persistence. Besides, populations respond to external factors in a dynamic way (MacArthur and Wilson 1963; MacArthur and Wilson 1967; Levins 1969; Quinn and Hastings 1987; Tilman *et al.* 1994; Hess 1996; Holt 1997; Hanski 1999). These factors are continuously changing in nature and strength, as human-based landscape modifications continue to expand (Mace *et al.* 1998).

Ecological theories such as island biogeography and metapopulation biology have, for instance, looked at species spatial dynamics and problems of habitat loss. Concepts from these spatial ecology theories have been used to set rules of thumb for conservation planning, which in turn have been the focus of large debates (e.g., Single Large OR Several Small reserves problem, Diamond 1975; Simberloff and Abele 1976; Simberloff and Abele 1982; Hanski and Simberloff 1997). However, it is clear that such qualitative conservation guidelines are rather simplistic generalizations and have only limited validity and theoretical support

(Hanski, 1999). Also, it is not straightforward to apply these rules for the design of real-world reserve networks when economic constraints apply.

Most reserve-selection studies during the 1980's and early 1990's were based on static presence/absence patterns which implicitly assumed that if species *i* was observed in site *j*, it will be there indefinitely. Thus, targets were often set in terms of 'single representation' (i.e. include at least one representation of each feature). From here on I refer to such simplistic approaches as 'Minimum set' (MS) approaches. Several studies have shown that such MS-designs are inadequate for ensuring species persistence (Margules *et al.* 1994; Nicholls 1998; Virolainen *et al.* 1999; Rodrigues *et al.* 2000). Species distributions are not static, and minimal reserve-design approaches cannot take species turnover into account. Empirical studies have shown, using repeated surveys at different time intervals, that a considerable number of species would be lost from hypothetical reserves selected with the static information of the earliest survey (Table 1). This is also consistent with the findings of a large number of empirical metapopulation studies that demonstrate population turnover for several species (see e.g., Hanski 1999 and references therein).

Persistence-related criticisms of systematic reserve design range from inadequate representation targets (e.g. single representation) (Nicholls 1998; Rodrigues *et al.* 1999; Rodrigues and Gaston 2001) and inadequate taxa used as biodiversity surrogates (e.g. assuming that a reserve selected to represent birds will represent also plants)(Vane-Wright *et al.* 1991; Sætersdal *et al.* 1993; Williams *et al.* 2000; Araújo *et al.* 2001), to spatially over-dispersed selected sites (increasing landscape fragmentation) (Bedward *et al.* 1992; Nicholls 1998) and selection of populations at the margins of the species' distributions (see chapter I for review). During the last 5 years, however, systematic conservation approaches have become more sophisticated and some approaches include now some criteria for persistence.

Table 1. Temporal variability in species distributions in reserves. Species turnover was assessed in the light of different surveys of the sites at different time intervals (See text). All studies based the selection on presence/absence data, except (b), which was based in different abundance(size of the populations) targets.

Study.	# Sites	# Species	Selected	% Species loss
(a) Margules <i>et al.</i> 1994 Plants in limestone pavements	77	50	18 sites	36
(b) Nicholls 1998 Mammalian herbivores, grid cells	3500	19	38-602 sites	50-25
(c) Virolainen <i>et al.</i> 1999 Aquatic plants in lakes	25	32	5 sites	18
(d) Rodrigues <i>et al.</i> 2000 Birds in census plots	56	47	556.3 ha	8

Chapter I reviews systematic reserve-design approaches at the point when the research for this thesis started. As the title suggests, (I) points out that despite the advances in algorithm development, the methods have not dealt explicitly with the main goal of reserve-networks: long-term maintenance of biodiversity. Implicit persistence criteria that have been considered were reviewed (see section ‘Persistence of biodiversity in reserve-networks’ in I). The paper also reviews issues of algorithm efficiency (and optimality) and the impact of using poor data-quality or biodiversity surrogates.

1.3 Some persistence criteria.

While simple MS approaches often use a single snapshot of presence/absence data and implicitly assume that species persist within reserves if represented, other studies have included considerations that may improve species long-term persistence. For instance, some studies have used thresholds to define the minimum size of selection units, or used abundance data instead of presence-absence data (either as thresholds to define the minimum population sizes, or for defining quantitative targets (I)). Most of these approaches thus emphasize local persistence. Bet-hedging approaches (i.e. setting multiple-representation targets for each species), instead, emphasize the regional persistence of the species (Boyce et al. 2002, (I)).

Box 1. Mathematical formulation of a generalized set covering approach

Let N be the number of sites, M the number of species, p_{ij} is an element of an $N \times M$ matrix giving the occurrence of species j in site i , S the index set of selected sites, T_j the target level for species j , c_i the cost of site i and $R_j(S)$ the representation of species j in S . Then, the objective function to be optimized is:

$$\min \sum_{i \in S} c_i$$

given that

$$R_j(S) = \sum_{i \in S} p_{ij} \geq T_j \text{ for all } j$$

Note that if $c_i=1$ we minimize the number of sites, and if c_i = ‘area of site i ’ we minimize the area of the solution (c_i may be equal to a real site cost and then we minimize the cost of the solution). In the simplest MS approaches, presence/absence data is used, in which case $p_{ij} \in \{0,1\}$, but p_{ij} can also be the probability of occurrence of the species. For the single representation problem $T_j=1$, and for the multiple representation problem $T_j > 1$.

More recent approaches have used species’ local probabilities of occurrence as a surrogate for species local persistence (Araújo and Williams 2000; Williams and Araújo 2000; Williams and Araújo 2002). Estimates of probabilities of persistence are obtained by modeling current species’ probabilities of occurrence from e.g. habitat attributes (habitat type, quality, area, etc.). Araújo et al (2002) also use a contagion measure that accounts for the number of occupied near-by sites (Box 1).

Probabilities of occurrence are generally expected to correlate with probabilities of persistence as long as the factors used to calculate probabilities of occurrence remain stable once the reserve system is set up. In a similar study as the ones shown in Table 1, Araújo et al (2002) showed that the reserves selected with the probability approach were stable in the long-term (all species were still present in the reserves). The probability approach combines local and regional persistence, by selecting either few sites of high quality or a larger number of less quality.

One major limitation of MS approaches is that they do not account for the spatial relationships between the selected sites and the consequences of spatial configuration for spatial population dynamics. Chapter II uses a theoretical approach to evaluate the long-term performance of reserve-networks in maintaining biodiversity using a model of spatial population dynamics (a metapopulation model). The study brings attention to the relevance of metapopulation concepts for conservation, putting them into the context of quantitative reserve-design. An important topic that metapopulation theory looks at is the effect of habitat loss and fragmentation to metapopulation persistence. Chapter II compares extinction rates of species in reserve-networks in two situations: when all sites remain unmodified (and therefore suitable for the species) after reserve-selection and, conversely, when the habitat in the unselected sites is lost. An important message from this study is that sites outside the reserve-network may have more importance (in terms of persistence) for what happens in the reserves than the reserves themselves.

2 Spatial population dynamics and reserve design

This thesis focuses particularly on reserve design and spatial population dynamics, and describes some new reserve-design approaches that take fundamentals from spatial ecology into account.

Spatial population dynamics in combination with a spatially structured landscape play an important role in determining the regional distribution (and persistence) of species, and therefore should be taken into account when designing reserve networks (I, II). Simple ‘Minimum-set’ reserve-design approaches tend to select tiny and scattered sites, while they overlook the long-term consequences for species persistence. Scattered reserve systems often have high edge-to-area ratios. Therefore, such reserves will be more vulnerable to edge effects and will pose problems of recolonization for species with limited dispersal ability. We showed in chapter II that when selected reserves are far apart and only one or a few representations of each species are considered, extinctions can be expected in the reserves (corresponding to the results in Table 1). However, the expected number of extinctions becomes even larger when habitat around the reserves is lost (II), because the persistence of species in reserves may be strongly dependent on sites not included in the reserve network.

Nevertheless, spatial population dynamics and effects of landscape change (including habitat loss and degradation), have mostly been ignored in reserve-network design. A group of approaches, belonging to the so-called ‘spatial reserve design’ (Possingham et al. 2000) category, provide a solution to the problem by aiming at selecting clustered

reserves. Clustered reserves have low edge-to-area ratio and therefore negative edge effects and fragmentation effects are lowered. Consequently, it is less probable that species patterns of occurrence in reserves change due to habitat loss around them (see also II).

2.1 Clustering reserves

Spatial considerations were first included in reserve-design studies by including an “adjacency rule” into a basic MS iterative heuristic algorithm (Nicholls and Margules 1993). The adjacency rule selects sites close to already selected ones, but it is only applied when ties are found in the process of iteratively adding most complementary sites to the solution. Note that clustering of reserves is not the primary goal of this algorithm variant, and that the achieved degree of additional clustering will depend on the number of ties encountered, which is often small (VI).

Possingham et al. (2000), McDonnell et al. (2002) and chapter III present different methods that aim achieved clustered reserves by minimizing a linear combination of reserve size and boundary length. A penalty for the boundary length allows giving more or less weight to the compactness of the reserve-system. When the penalty is zero, then the boundary length of the reserve system is ignored and therefore only reserve-area (or cost) is minimized (see Box 2).

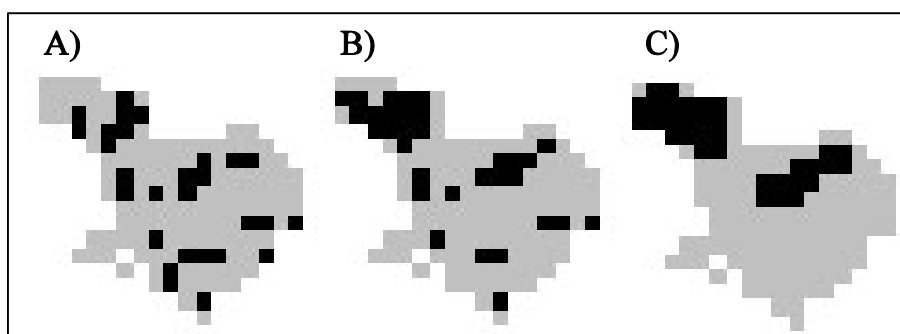


Figure 2. Reserve-design solutions for 26 species in the Creuddyn Peninsula (UK). A) Simple minimum-set solution based on presence/absence. B) Probability-based solution. C) Spatial probability-based reserve-design with a large penalty for the boundary length. Probabilities for each site in B) and C) were calculated as a function of the habitat quality and the number of occupied nearest neighbors. The target representation for each species was set to 20% of the number of occurrences (or expected number of occurrences for the probability approaches).

Box 2 A general mathematical formulation for the problem of clustering reserves

The problem formulation is similar to the problem presented in Box 1, but now the function to be optimized takes into account the boundary length weighted by a penalty b . When b tends to zero the spatial configuration of the reserve is of no consequence. With a high value for b a relatively compact reserve can be obtained.

$$\begin{aligned} \min \quad & \sum_{i \in S} c_i + bL' \\ \text{subject to} \quad & \\ R_j(S) = \sum_{i \in S} p_{ij} \geq T_j \quad & \text{for all } j \end{aligned} \quad (3)$$

In the approaches presented by Possingham et al (2000) and McDonnell et al (2002), L' equals the boundary length of the reserve network, and p_{ij} 's correspond to the presence/absence information. In chapter III the conservation targets T_j are framed in expected numbers of populations, as p_{ij} 's are based on a probability model for the presence of the species. Another difference is that L' is the ratio of reserve boundary length to reserve area instead of the boundary length alone.

Chapter III goes a step further by combining the spatial reserve problem with a ‘probabilities of occurrence’ approach (see section 1.3 of this summary). It follows that the algorithms presented in chapter III and VI are thus capable of selecting high quality habitats and compact reserve areas. The species should thus have a high probability of occurrence in the selected areas, and because the reserves are clustered, habitat loss should have a minor influence on these probabilities of occurrence (Box 2).

A dataset of 26 Lepidoptera species (22butterflies and 2 moths) from the Creuddyn Peninsula, North Wales, UK (Cowley et al. 2000), has repeatedly been used in this thesis to illustrate the novel approaches that me and my collaborators have developed. Figure 2 shows the reserves selected for this system when 500 m grid cells were used as selection units. Different reserve-selection approaches are compared. We can appreciate some differences between using presence/absence data or probability data (2a vs 2b): although some areas are commonly selected, the probability approach selects areas of higher habitat quality and/or areas that have many occupied neighbors. We can also observe that the solutions for the non-spatial problems are rather scattered (2a,b), whereas introducing a penalty for the boundary length selects two clustered areas.

Including additional constraints into the reserve selection process usually increases the cost of the solution. For instance, Possingham *et al.* (2000) have shown how using high penalties for boundary length tend to lead to solutions with more selected sites (with the largest penalty 5 times more sites were needed compared to the basic solution with no penalty). However, the increase in the cost of the

solution is highly dependent on the system (see chapter III). For instance, for the Creuddyn Peninsula system shown in Fig. (2) clustering of reserves can be achieved at very little cost (Fig. 3).

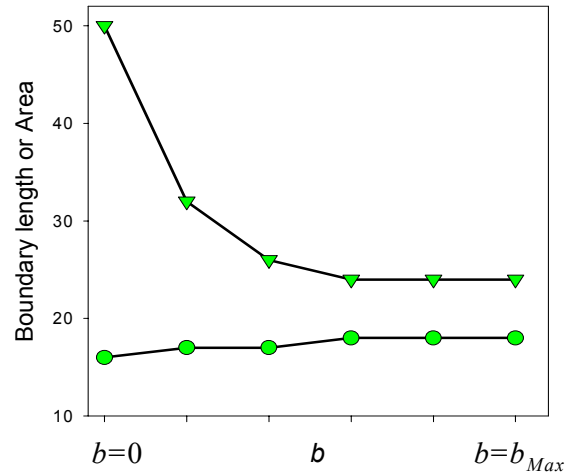


Figure 3 Cost of decreasing the boundary length of the solution. Results show the boundary length (triangles) and the number of sites (circles) at different values of b (See III and VI)

Other spatial reserve-design approaches (Briers 2002; Önal and Briers 2002) minimize either the maximum inter-site distance or the sum of inter-site distances, with the argument that if reserves are on average close together, dispersal and recolonization of nearby-sites is facilitated. Note that, for instance, minimizing the maximum inter-site distance does not guarantee that aggregated reserves will be obtained, because if there are endemisms (with a single occurrence) in the system, the distance between those endemisms will determine the minimal maximum distance.

2.2 Dynamic probabilities

The aggregation of reserves via the use of a penalty term is rather arbitrary because the desired level of clustering is determined subjectively. It follows that at a particular scale clustering may not be necessary for some species, while it may be so for others. Forcing the aggregation of the reserves may result in the unnecessary selection of low-quality sites that bridge distances between sites of higher quality. A more reasonable way of obtaining the desired level of clustering for all species is to consider separately the connectivity of the selected sites for each species.

Chapter IV presents an extension of a basic probability approach (see Section 1.3 in this Summary) that incorporates (species-specific) spatial considerations (connectivity) into the probability model. The important difference to other reserve-design probability approaches, is that this approach allows to take explicitly into account effects of habitat loss during the selection process. Let us assume that all unselected sites will be completely lost (e.g. all forest patches not selected for protection will be logged)

and therefore, only the selected sites will contribute to connectivity.

Box 3 Dynamic probability formulation

(Symbols as defined in Box 1).

The DP approach presents an important difference to previous ones (Boxes 1 and 2) in building a dependency between p_{ij} and S . For instance, in a situation of habitat loss around the reserves p_{ij} will decrease (possibly substantially) when site i loses many of its neighbors (depending on the species dispersal ability). Let us first define a connectivity measure G_{ij} for species j in site i :

$$G_{ij} = \sum_{k \in S - \{i\}} f(d_{ik}) p_{kj}(S) \quad (1)$$

where d_{ik} is the distance between sites i and k , and $f(d_{ik})$ is a decreasing function of d_{ik} . Note that G_{ij} applies to a buffer-type connectivity measure of radius r (the radius within which sites are considered around site i) by setting $f(d_{ik})=0$ for $d_{ik}>r$. Other buffer-type measures assume $f(d_{ik})=1$ for $d_{ik}<r$. Then, the local probabilities of occurrence are computed as:

$$p_{ij}(S) = f(\mathbf{h}_i, G_{ij}(S)) \quad (2)$$

in which \mathbf{h}_i is a vector of habitat variables. $p_{ij}(S)$ may be fitted (e.g. by logistic regression) to the original presence-absence information. If a species does not have a significant effect of connectivity then $p_{ij}(S)=f(\mathbf{h}_i)$. The objective function becomes:

$$\begin{aligned} \min \quad & F = \sum_{i \in S} c_i \quad (3) \\ \text{subject to} \quad & R_j(S) = \sum_{i \in S} p_{ij}(S) \geq T_j \quad \text{for all } j \end{aligned}$$

Note that, during the optimization, after changing S (e.g. by adding or removing a site) all probabilities p_{ij} have to be recomputed by iterating eqns (1) and (2) until convergence (Chapters IV and VI).

The local probability of occurrence of species j in selected site i will depend on which other sites are selected, and which is their spatial relation (Box 3). Local probabilities of occurrence have to be re-computed during the selection process, according to the selected sites and the given habitat modification expected to happen in unselected sites. For this reason the method is referred to as “dynamic probability” (DP) approach.

For comparative purposes Figure 4 shows a DP solution for the system presented in Fig (2), using the same probability model for all species (only a buffer-connectivity measure). The example presented in chapter IV, however, considers different connectivity variables and different probability models for all species.

Fig. 4a shows the results for a ‘no habitat loss situation’, and Fig. 4b for a situation of ‘complete habitat loss’. We can see that when habitat is lost, the best solution contains

reserves that are naturally clustered, as a consequence of considering the spatial configuration of reserves on the species’ probabilities of occurrence.

2.3 Explicit spatiotemporal dynamics in single-species reserve-selection

Chapter V shows how a stochastic metapopulation model can be used when selecting a network of sites for a single species. The problem addressed by this approach is slightly different than the one described above: what set of sites S maximizes the long-term persistence of a metapopulation, for a particular time-frame and given a limited amount of resources? Each site has a cost and (as in the dynamic probabilities’ approach) unselected habitat is assumed to be lost. I refer to this method as the explicit spatial population dynamics approach (ESD) later on.

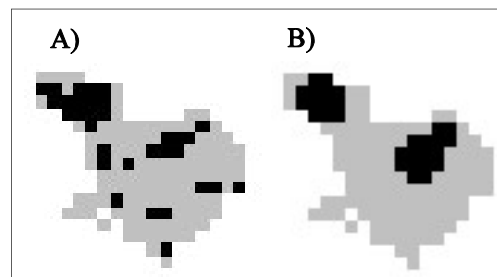


Figure 4 Sites selected (in black) with the DP approach. A) No habitat loss: unselected sites contribute to the probability of occurrence at the selected sites. B) Complete habitat loss: only selected sites contribute to the probabilities of occurrence. Note that 3a is the same as 2b

The dispersal ability of the species is probably the parameter of the metapopulation model that has the strongest effect on the spatial configuration of the selected reserves. Other factors that have to be carefully considered are the time-frame and the amount of resources. We showed how varying the objective time-frame results in intuitive changes of the solution: while long-time frames rely more on the spatial dynamics and therefore currently empty patches may be selected, at shorter time-frames more sites which are initially occupied tend to be selected. A perhaps not so intuitive conclusion follows from the consideration of different resource levels (conservation budget). It can be appreciated that increasing the amount of available resources does not result in an extension of the set of sites selected with lower budget, but instead, a different, larger and better connected reserve-selection, is often preferred. This latter result contradicts a common procedure in reserve-network design: the selection of the best set of sites with the current available resources, extending the reserves later on, when more resources are available. (See Chapters V and VI).

2.4 Within-site spatial considerations

When an area of conservation interest has not been properly surveyed, or information about species distributions is not available, landscape (or habitat) types have been used as surrogates for biodiversity (e.g., Lombard et al. 1997). Usually the habitat classes considered in reserve design are rather coarse. This means that, for instance, habitat j may be identified as present in site i independently if it occurs in an heterogeneous mix with other habitats or if it occurs in a single and large homogeneous patch within the site. In many cases, the quality of the habitat for habitat-specialists may depend on how scattered or continuous the habitat is. Remote sensing tools are useful in classifying landscape patterns and provide information that can be used alone or together with other biodiversity data for reserve-design. With remote-sensing tools getting more efficient, the mapping of detailed land classifications allows the identification of within-site spatial heterogeneity and the possibility of taking it into account, for instance, when setting conservation targets in reserve-design.

Chapter VII presents a first systematic reserve-design approach exploring the consideration of within-site spatial configuration. A trivial consequence of considering such factor is that setting larger thresholds for the minimum (within-site) habitat patch size requires larger solutions (more number of sites and more area). This is particularly true when the representation targets for each habitat type are large. The consequences for biodiversity persistence of considering different within-site habitat aggregation levels were also assessed by indirectly computing the probability of occurrence of a habitat-specialist species. In Figure 5 we can see that networks selected with larger thresholds for the (within.site) habitat patch size (empty squares) are expected to have a larger number of populations than networks

3 Discussion and Future challenges

Systematic conservation planning has mostly focused on developing algorithms for solving simple species-representation problems. More recently, however, the problems addressed have included some criteria for biodiversity persistence, for instance, by setting reasonable targets for species viability or by emphasizing the selection of 'best quality sites'. The next step has been the consideration of the spatial locations of sites, and several authors have designed tools that enable qualitative clustering of reserve-networks. Going one step further from qualitative reserve network clustering to the explicit consideration of spatial dynamics requires information on species-specific parameters of spatial population dynamics. This thesis presents two novel approaches that considered the often overlooked interaction of spatial

designed without thresholds (empty circle). However, this example does not allow drawing strong conclusions about the relative importance of within-site configuration in the context of reserve design. This is because the species' probability of occurrence depends also on other variables like site-area and isolation. For the example presented in chapter VII, these two latter variables did not correlate with within-site habitat patch size. Nevertheless, chapter VII calls for attention on to another spatial factor that has been previously ignored, which is worth of further study.

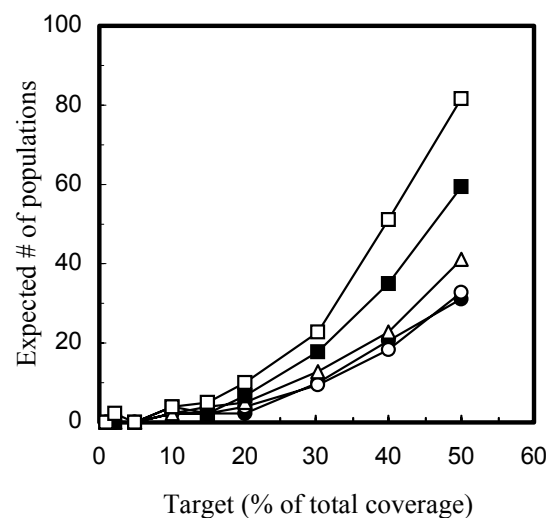


Figure 5. Expected number of occurrences of a habitat-specialist in the reserve-networks. The 5 curves belong to different increasing thresholds for the minimal patch size (25th = ○, 50th = ●, 75th = △, 90th = ■, 95th = □). See text and chapter VII.

population dynamics and landscapes dynamics, the dynamic probability approach (DP, IV) and the explicit spatial dynamics approach (ESD, V).

One factor which limits the applicability of these two approaches (especially ESD) is the availability of information to estimate all model parameters (particularly dispersal-related parameters) for all species. Nonetheless, it is reasonable to suggest that when no information is available for any of the species under consideration, qualitative clustering of reserves (as presented in III and VI) is often a desirable characteristic, at least for management reasons (i.e. the maintenance cost of a compact reserve is likely to be smaller than that of a scattered reserve), although there might also be reasons to

avoid clustering. Where catastrophes can impact large areas causing spatially correlated extinctions, it may be better to protect each species in at least two or three separate sites, rather than in clustered reserves (Hess 1996; Lei and Hanski 1997). However, if reserves are selected far apart from each other, they should then be large enough to allow species persistence independently.

This brings us to the question of what is a large reserve and what is the adequate spatial scale and size of the selection units for each different method. It has been argued that at large scales, with large enough units of selection, spatial population dynamics occur within the selection unit, and therefore we should not worry about selecting a set of sites connected together. However, the scale at which spatial dynamics play an important role varies for every species, according to the species ability to disperse and the characteristics of the habitat. Again, the DP approach (IV and VI) avoids the scale problem by fitting different probability models independently to each species, including as variables a habitat index and a species-specific measure of connectivity. For a particular species, if the size of the selection unit is much larger than the regular dispersal distance, a metapopulation-like connectivity measure is probably not explaining the distribution of the species. Instead, habitat variables alone

may be highly significant in a probability model. On the other hand, for another species with larger dispersal distances, a metapopulation-like connectivity measure may explain, together with the habitat variables, its distribution.

In all the studies presented in this thesis that consider the consequences of habitat loss, simple assumptions of how this habitat is lost were made (e.g. all unselected sites were completely lost, II, IV, V, VI). This was a necessary assumption for clarity of the results and because there was not a model for landscape change available. Future challenges for systematic reserve design include linking approaches such as DP (IV) with models of habitat change (e.g. Veldkamp and Lambin 2001). Also, there is increasing evidence that climate change may induce shifts in species ranges (Parmesan and Yohe 2003). Techniques for quantifying these shifts are currently being developed and tested. Predictions of landscape change arising from such type of modeling approaches can also be integrated into, e.g., a DP approach for selecting reserve networks that would increase the chances of species persistence as climate continues to change.

Table 2 shows a comparison of some of the different methods described here.

Table 2. Comparison of different reserve design approaches: MS (Minimum-set), MS-P (Minimum-set probability-based), BL (clustering of reserves), BL-P (probability-based clustering of reserves, III), DP (Dynamic-Probabilities, IV) and ESD (Explicit Spatial population Dynamics, V).

Approach	Data	Probability models		Accounts for Spatial pop. dynamics	Accounts for landscape change (e.g. habitat loss)
		Type	Variables		
MS	P/A / Abundance	-	-	No	No
MS-P	Probability of occurrence	Statistical model for occurrence	Habitat (quality, composition)	No	No
BL	P/A	-	-	Implicitly	No
BL-P	Probability of occurrence	Statistical model for occurrence	Habitat (quality, composition)	Implicitly	No
DP	Probability of occurrence	Statistical model for occurrence	Habitat, Connectivity	Implicitly	Yes
ESD	Probability (can include also P/A)	full model for extinction-colonization dyns	Patch size, connectivity	Explicit	Yes

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