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Spatial attributes and reserve design models: A review

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A variety of decision models have been formulated for the optimal selection of nature reserve sites to represent a diversity of species or other conservation features. Unfortunately, many of these models tend to select scattered sites and do not take into account important spatial attributes such as reserve shape and connectivity. These attributes are likely to affect not only the persistence of species but also the general ecological functioning of reserves and the ability to effectively manage them. In response, researchers have begun formulating reserve design models that improve spatial coherence by controlling spatial attributes. We review the spatial attributes that are thought to be important in reserve design and also review reserve design models that incorporate one or more of these attributes. Spatial modeling issues, computational issues, and the trade-offs among competing optimization objectives are discussed. Directions for future research are identified. Ultimately, an argument is made for the development of models that capture the dynamic interdependencies among sites and species populations and thus incorporate the reasons why spatial attributes are important.

Keywords: reserve design, biological conservation, spatial optimization, mathematical modeling

1. Introduction

Methods for systematically selecting sites (land units) for a nature reserve were first devised more than 20 years ago, beginning with the pioneering work of Kirkpatrick [1] (see also [2]). These methods sought to identify reserve systems in which biodiversity, measured quantitatively, would be represented at desired levels. These initial methods were later criticized for emphasizing representation over the long-term persistence of biodiversity (e.g., [3]). Elsewhere in the conservation literature, however, guidelines had been suggested for the spatial design of reserves to promote the persistence of biodiversity (e.g., [4]), but these guidelines, too, were subject to criticisms for a variety of reasons.

In this paper, we review how recent developments in quantitative reserve design modeling have addressed, through spatial optimization, the important issues of representation and persistence of biodiversity within reserve systems. We begin by presenting two basic mathematical programming models for optimal reserve site selection and discuss their limitations for achieving spatially coherent reserves. We next review important spatial attributes that are likely to be considered in the design of reserves. These attributes were initially proposed as design guidelines, and we briefly review the arguments, both pro and con, surrounding their use as guidelines. Third, we review the ways in which these attributes have been incorporated into recent mathematical optimization models for reserve design. Fourth, the rapid progress of optimization modeling in reserve design has been paralleled by the development of dynamic population models for evaluating reserve systems. These dynamic models are briefly discussed in terms of both the spatial attributes they address and the prospects for using them in tandem with optimization models. Finally, we conclude by discussing three other issues in reserve design modeling: uncertainty, spatial scale, and multiple objectives and trade-offs. Throughout the paper, our focus is on terrestrial reserves. Marine reserves, though, are now recognized as necessary components in a global reserve network. Marine reserves are the topic of a recent special issue: *Ecological Applications* 13(1) Supplement, 2003.

2. Reserve site-selection models

Quantitative methods for identifying an optimal or efficient set of nature reserves originated in the 1980s in the field of conservation biology. The first such methods were iterative heuristic procedures for selecting sites of land for a system of reserves. These methods sought to achieve conservation objectives typically defined as some aspect of biological diversity: the representation of all species from a list of target species (species richness) or the representation of all features such as habitat types (e.g., [1,5,6]). Frequently, priority was given to rare or endangered species or habitats. From this early work in heuristic site-selection procedures, the problem of finding a "minimum reserve set" emerged as the archetypal decision problem. The minimum reserve is the smallest set of reserve sites (in number or in total area) needed to represent all species or other features.

It was soon recognized that iterative heuristics could guarantee only approximate minimum reserve sets, not the true minimum (or global optimum). However, researchers pointed out that by formulating the problem as a zero–one integer program (IP) model, globally optimal (or "exact")

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solutions could be found by linear programming (LP) methods [7,8]. We call this IP for finding the minimum reserve set the “species set covering problem” (SSCP) because its formulation mirrors that of the earlier “location set covering problem” from facility location science [9].

2.1. Formulation of the species set covering problem

$$\text{Min} \quad \sum_{j \in J} x_j \tag{1}$$

$$\text{s.t.} \quad \sum_{j \in M_i} x_j \geq 1 \quad \forall i \in I \tag{2}$$

where i and I are the index and set of species to be represented in the reserve, respectively; j and J are the index and set of sites eligible for selection (candidate sites), respectively; M_i is the set of candidate sites j that contain species i; and $x_j = 0$ or 1; it is 1 if site j is selected for the reserve system, and is 0 otherwise.

The objective (1) minimizes the number of sites selected, and the constraint set (2) requires the selection of at least one site containing each species. Following the formulation of the SSCP IP model, a second archetypal reserve selection problem was also structured as an IP: the “maximal covering species problem” or MCSP [10,11]. In the MCSP, the total number of sites is fixed, and the number of species that can be represented is maximized.

2.2. Formulation of the maximal covering species problem

$$\text{Max} \quad \sum_{i \in I} y_i \tag{3}$$

$$\text{s.t.} \quad y_i \leq \sum_{j \in M_i} x_j \quad \forall i \in I \tag{4}$$

$$\sum_{j \in J} x_j = P \tag{5}$$

where $y_i = 0$ or 1; it is 1 if species i is represented in the reserve system (i.e., is represented in at least one site selected from the set M_i), and is 0 otherwise.

The objective (3) maximizes the number of species represented, whereas constraint set (4) enforces the condition that a species is represented only if a site containing that species is selected, and constraint (5) limits the number of sites that may be selected. A number of variations of the SSCP and MCSP have appeared, which are reviewed in [12,13]. Variations of the SSCP include minimizing total area or minimizing the total cost of sites selected instead of simply minimizing the number of sites, whereas variations of the MCSP include placing an upper bound or budget constraint on total area or total cost. In addition, constraints (2) and (4) can be adjusted so that each species is represented not once but two or more times in the reserve system. One important variation of the SSCP is the “percent area” problem, in which total area is minimized subject to a lower bound constraint placed on the percentage of area of each land or vegetation class that must be included in the reserve.

The appealing aspects of solutions – whether exact or approximate – to the SSCP, MCSP, and their variations are efficiency and cost-effectiveness. The solutions identify, respectively, the minimum (or approximate minimum) monetary investment or amount of land resources needed to achieve a specified level of biodiversity, or the (approximate) largest amount of biodiversity achievable within a particular budget or total land area. Efficient and cost-effective solutions are understandably desirable, especially when conservation resources are severely limited. The benefits of efficiency and cost-effectiveness, however, have tended to overshadow a major drawback of these reserve selection models, namely, that they do not adequately take into account the reserve system’s spatial attributes.

Solutions to the SSCP and MCSP may well be collections of scattered sites that lack spatial coherence (e.g., figure 1). Under these problem statements, the configuration of the reserve system depends entirely on the geographic distributions of species or other features in relation to site cost or site area. No consideration is given to reserve shape, edge conditions, the number of reserves created, or the connectivity and proximity of reserves to each other. Hence, although SSCP and MCSP solutions do a good job of representing species in the short term, it is highly uncertain whether these solutions would effectively support the long-term survival of those species represented at the time of site selection. Long-term persistence within scattered reserve sites is especially problematic when the surrounding matrix is inhospitable, as in the case of an urbanizing area. Persistence requires evolutionary units such as populations or metapopulation of species to be resilient to environmental fluctuations and to other intrinsic

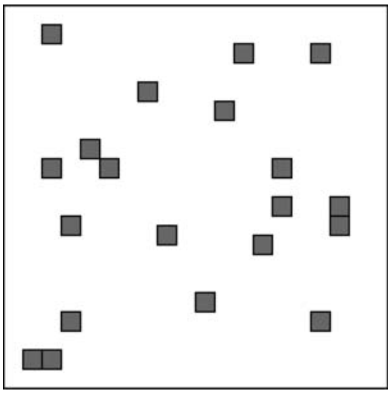

Figure 1. An optimal solution to a hypothetical minimum reserve set problem (SSCP) is shown. A minimum of 20 sites is needed to represent all species. These sites are likely to be widely scattered.

and extrinsic factors. Ultimately, persistence is promoted by heterogeneity, redundancy, and modularity of habitats and of populations [14], and reserve systems should be designed in accordance with these principles.

Several studies have used species presence/absence records collected in different times to examine how effectively a minimum reserve set would support persistence [15–17]. In each of these studies, a minimum set was identified for an initial period, and then the species contained in these sites in a later period were recorded. In each case, the result was a decline in the species richness of the reserve system. Losses of 36, 16, and 6 to 12% in the number of species present after 11, 63, and 10 years, respectively, were experienced. Cabeza and Moilanen [18] had similar results in simulation-based evaluations of hypothetical minimum reserve sets. Here, a metapopulation model was used to determine the fraction of species that would go extinct within the reserve system at different times in the future and under different assumptions of habitat loss outside of the reserve. Species losses ranged from approximately 10 to 80%.

To promote the persistence of species, ecosystem processes, and other elements of biological diversity, *spatially coherent* reserves are likely to be critically important. By spatial coherence, we mean the achievement of those spatial attributes that are thought to support natural population dynamics and support the resiliency of populations to environmental flux. Spatial coherence may also be used to describe attributes necessary for effective land management. Spatial coherence is not a one-size-fits-all standard, and no single set of spatial attributes can be ideal for all situations. The importance or desirability of different attributes depends on the conservation objectives for the reserve – those components of biodiversity that one wants to protect.

Decision models that address spatial aspects in optimizing reserve site selection have been formulated only recently. We call such models *reserve design* models, in contrast to *reserve selection* models like the SSCP and MCSP, because the former explicitly incorporate spatial attributes such as reserve shape and connectivity. However, the basic intent of both types of models is essentially the same: to protect biological diversity by selecting or arranging a subset of sites from a wider set of candidate sites. To improve clarity, we distinguish among the terms “site,” “reserve” and “reserve system.” A site is defined here as a selection unit – a piece of land (parcel or cell) that may be selected for a reserve or reserve system. A reserve is an individual, isolated site, or a contiguous cluster of multiple sites that have been selected. A reserve system is a set of multiple, spatially separate reserves. Hence, sites are the building blocks of reserves, which in turn are the components of reserve systems. In the next section, we discuss different spatial attributes that have been used to characterize a reserve or reserve system. In the following section, we review how these attributes have been incorporated into reserve design models.

3. Spatial attributes in reserve design

Diamond [4] developed six geometric design guidelines for nature reserves based on the species–area relationship of island biogeographic theory. Likening a nature reserve to an island, Diamond commented on six pairs of configurations in terms of their comparative abilities to support species persistence and diversity (figure 2): (a) a large reserve is better than a small reserve, (b) a single large reserve is better than several small reserves of the same total area, (c and d) reserves that are close together are better than reserves that are far apart, (e) reserves that are connected by wildlife corridors are better than unconnected reserves, and (f) a compact (circular) reserve is better than an elongated reserve.

Margules et al. [19], among others, were critical of Diamond’s assessment and “urged caution” in the application of these general guidelines. Two of the guidelines in particular – a single large reserve vs several small reserves, and wildlife corridors – prompted extensive debates in the literature. Indeed, all six of the criteria may be called into question for a variety of reasons. Underlying these criticisms, though, is recognition of the inherent complexity of reserve design brought about by the dynamics of species interactions and other environmental and socioeconomic factors. These complexities cannot be reduced to simple guidelines. We next consider these spatial attributes in turn and briefly discuss the major criticisms of each. The attributes are grouped under the following subheadings: reserve size, number of reserves, reserve proximity, reserve connectivity, and reserve shape. We also add to this list the concept of core areas and buffer zones (figure 2g).

3.1. Reserve size

With respect to simply the number of species that can be represented in a reserve, there is general agreement among conservation biologists that a large reserve is better than a small reserve. Soule and Simberloff [20] contend that reserve size should be based on the area necessary to support a minimum viable population (MVP) of a species, that is, the minimum number of individuals needed to guarantee a high probability of survival in the long term. If the goal is to maximize species representation, then a reserve would, ideally, need to be large enough to support an MVP for every species in need of protection. In some cases, the protection of an MVP of an “umbrella” species or MVPs of several “focal” species may be sufficient to protect MVPs of many other species [21]. The hypothesis that an MVP has a minimum area requirement is supported by the simulation experiments of Fahrig [22], who presents evidence for area-based extinction thresholds for species in fragmented landscapes. The probability of persistence is high above the threshold, but as the size of a habitat patch (or reserve) falls below the threshold, the probability of extinction increases rapidly.

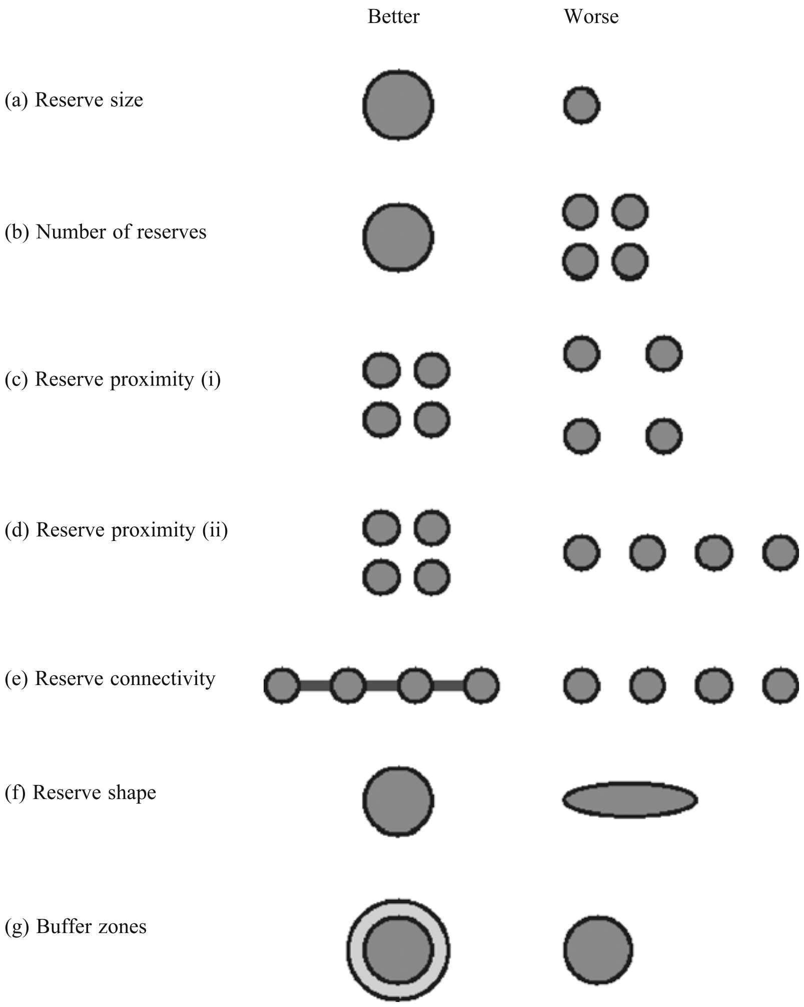

Figure 2. Proposed reserve design guidelines. (a) Reserve size: a large reserve is better than a small reserve; (b) number of reserves: a single large reserve is better than several small reserves of the same total area; (c, d) reserve proximity: reserves that are close together are better than reserves that are far apart; (e) reserve connectivity: reserves that are connected by wildlife corridors are better than unconnected reserves; (f) reserve shape: a compact (circular) reserve is better than an elongated reserve; and (g) buffer zones: a reserve surrounded by a buffer zone is better than an unbuffered reserve. Guidelines (a) through (f) are from Diamond [4].

3.2. Number of reserves

Given a fixed total area, we can ask how many reserves – one, several, or many – should be created to protect a maximum number of species. This is the question called a “single large or several small reserves” (SLOSS) and more recently a “few large or many small reserves” (FLOMS) [23]. Neither island biogeographic theory nor empirical evidence provides a clear answer to SLOSS [19,24] or to FLOMS. For example, a cluster of several small reserves might be too fragmented for large mammals, but might be well suited to the metapopulation dynamics of butterflies. Some studies suggest that several dispersed reserves contain more species than a single large reserve, but this may be due to greater habitat heterogeneity in the former [20].

Virtually no data are (yet) available for approaching this difficult question of which configuration is better for maximizing the number of species that survive in the long term. In general, one should not expect easy answers. One huge reserve might not be as effective as a similar area divided into three or four sufficiently large but distinct patches that allow averaging over environmental variability; however, further fragmentation into large numbers of tiny patches might be disastrous. Furthermore, a goal of protecting particular species, such as rare or endangered species, rather than maximizing species richness will influence the answer to SLOSS/FLOMS in particular cases.

3.3. Reserve proximity

In a system of multiple reserves, the individual reserves may be close together or far apart. Inter-reserve distance will influence the ability of species to migrate between reserves and to exist as a metapopulation. Shorter distances, it is argued, will make it easier for a species to recolonize an area where it has become locally extinct [4], and will also help prevent loss of genetic diversity due to inbreeding. On the other hand, longer distances help reduce the spread of diseases and "exotic" species between reserves, and may benefit a target species by reducing the spread of its natural enemies. In addition, longer distances increase the likelihood that some reserves will avoid the catastrophic impacts of a major disturbance (e.g., fire, hurricane). As well, longer distances may result in greater species diversity through greater habitat heterogeneity [19] and may allow species to average over environmental fluctuations that are localized in their impacts.

Does an ideal inter-reserve distance exist? Certainly, it cannot, unless there is clear agreement about what is to be protected. An optimal spacing of reserves would need to compromise between distances near enough to support recolonization and distances far enough to reduce the impacts of regional stochasticity [25]. However, as Shafer [26] points out: "The dilemma we face is that some optimal, compromise distance needed to facilitate the inter-reserve dispersal for many diverse taxa, or even one focal species, could be very different from the distance needed by that same species to thwart the agents of natural and anthropogenic catastrophic impacts" (p. 223).

3.4. Reserve connectivity

A growing concern about habitat fragmentation has prompted recognition of the importance of connectivity, both for reserve systems and for landscapes in general [27]. Alternative measures of landscape connectivity are reviewed in [28,29]. Landscape ecologists discuss two types of connectivity: structural connectivity and functional connectivity [29]. The former is equated with physical contiguity, whereas the latter is based on the behavioral responses of organisms to the landscape. A reserve that is structurally connected may or may not be functionally connected and vise versa. For example, a highway that cuts through a reserve might pose an effective barrier to a species, making the two halves functionally disconnected for that species. In contrast, reserves that are separated by distance would be functionally connected for a species that could easily travel between them. Bunn et al. [30] and Urban and Keitt [31] explore graph–theoretical representations of landscape connectivity and the use of graphs to model functional connectivity for different species.

Wildlife corridors are often mentioned as a way to provide both structural and functional connections between disconnected reserves. The pros and cons of corridors have been discussed extensively in the conservation literature [32–37]. Arguments for and against corridors run parallel to those for and against reserve proximity – facilitating migration vs the spread of diseases and disturbances. An additional benefit of corridors is that they provide habitat in and of themselves, but an additional drawback is that they can serve as bottlenecks that can be exploited by predators and poachers. In a review of 32 published wildlife corridor studies, Beier and Noss [38] found that the evidence "generally supports the utility of corridors as a conservation tool" (p. 1249), but that further generalization about whether corridors provide connectivity is difficult because functional connectivity is species specific. Whether or not functional connectivity is realized depends on design features such as length, width, degree of meander, and the presence of cul-de-sacs as well as the quality of the surrounding matrix [39,40].

3.5. Reserve shape

The shape of a reserve – whether it is compact or elongated – may be important to species survival within the reserve. Diamond [4] advocates creating compact reserves that are nearly circular in shape minimize intra-reserve dispersal distances. Compact reserves also have lower edge-to-area ratios than noncompact reserves and tend to minimize the amount of area that is subject to edge conditions. In the case of forests, edges may be subject to higher temperatures, lower humidity, and greater exposure to wind. Edge-intolerant species such as tropical songbirds are likely to have a difficult time in reserves that are both small and noncompact due to the relatively large amount of edge and small amount of interior or core area. Edge effects become most pronounced when the surrounding matrix is inhospitable. The disturbances caused by intense uses (e.g., urbanization, clear-cutting) in adjacent areas may penetrate quite far into a reserve, so that the area of suitable habitat is much less than the area within the reserve's administrative boundary [41]. Because the fraction of reserve area in the edge zone declines with reserve size for a given shape and edge zone width, compactness is probably more important for small reserves than for large ones [42].

Some evidence, however, supports noncompact reserves. Game [43] argues that in some circumstances elongated reserves provide a better equilibrium between extinction rates and rates of colonization from outside the reserve. Kunin [42] also argues for elongated reserves, but for reasons of greater species diversity: because the ranges of species exhibit spatial autocorrelation, a linear reserve would likely encompass more species than a square reserve of the same area. In addition, noncompact reserves are clearly appropriate in certain circumstances, such as the protection of riparian habitat.

A variety of shape measures or metrics have been developed in landscape ecology [44,45] and in other fields [46,47] that are applicable to reserve design. One frequently used shape attribute is compactness, which can be measured in a number of different ways including boundary length (an absolute measure), the ratio of boundary length to area (a relative measure), and dispersion (the average distance between the points in a shape and its center of mass).

3.6. Core areas and buffer zones

Core areas and buffer zones feature prominently in “biosphere reserves,” a concept that has been championed by Batisse [48–51]. Biosphere reserves seek to integrate the protection of undisturbed core habitat with benign human economic activities that would take place within one or more rings of buffer zones. The buffer zones would mitigate the negative impacts of more intense human activities taking place outside the reserve. As actual differences between core areas and buffer zones may be largely a result of reserve management and allowable land use, the core–buffer approach is part of an emerging trend in reserve design: selecting sites not for generic reserve status but for particular types of land management and protection. The effectiveness of a buffer zone depends on its width relative to what it is trying to protect. How wide should a buffer zone be? Ideal buffer widths may not be obvious because outside impacts affect different species differently: “[A]n appropriate buffer for one species may be insufficient for another species and overkill for another” ([52], p. 96).

Core areas and buffer zones have been combined with wildlife corridors in recent plans for large-scale conservation in North America [53,54]. In such plans, existing parks and refuges would be enlarged and new protected areas would be created. The resulting system would then be linked together by an expansive network of wildlife corridors and surrounded by buffer zones.

The ecological consequences of following any of Diamond’s [4] guidelines are likely to be varied and complex. Because a mix of desired and undesired outcomes may result, each guideline can be expected to have advantages and disadvantages for achieving conservation objectives. In short, general rules of thumb for reserve design cannot be derived from ecological principles, except perhaps that larger reserves are better than smaller reserves.

If we expand reserve design objectives to also address socioeconomic issues, the picture becomes even less clear. Different spatial configurations do different things, not only on the basis of conservation outcomes, but also with respect to cost and other socioeconomic concerns. For example, larger reserves may promote ecological objectives better than smaller reserves, but the larger size tends to come at a higher monetary cost or opportunity cost of foregone land uses. In addition, the social and cultural impacts of setting aside land, such as the displacement of people and disruption of traditional ways of life, may rise as the size of the reserve grows. The practicalities of managing a reserve may also cause some spatial attributes to be favored over others, possibly in conflict in ecological considerations. For example, it is typically easier to manage a large contiguous area than to manage multiple smaller areas, and this (nonbiological) consideration could push the SLOSS decision toward the single–large extreme. Likewise, reserve maintenance and security (e.g., perimeter fences and enforcement of antipoaching laws) tend to be easier when the length of a reserve’s boundary is lower, favoring compact reserves.

4. Using reserve design models to control spatial attributes

Although universal design guidelines are problematic, the spatial attributes themselves are inherent in any reserve design problem. The six attributes discussed above have had a significant influence on thought in reserve planning and decision making and offer a useful framework for approaching reserve design modeling. Even as guidelines were debated, the creation of spatially coherent reserves was recognized as important for both ecological success and a host of socioeconomic and political reasons. In particular, developers of iterative heuristics for the SSCP acknowledged that the spatial properties of the minimum reserve set might need to be improved. A variety of decision rules for making spatial improvements were added to the procedures. For example, Nicholls and Margules [55] proposed selecting the site nearest to previously selected sites to increase site-to-site proximity. This rule was triggered only in the event of a tie in the number of new species that the new site would contribute. Briers [27] strengthened this proximity rule by devising a more sophisticated distance-based heuristic that did not rely on ties. In another effort, Bedward et al. [56] developed a nine-step heuristic that allowed unneeded portions of sites to be excluded and allowed new sites to be added to increase connectivity and rationalize reserve boundaries. Recently, Siitonen et al. [57] developed a multiobjective heuristic for selecting reserve sites to optimize spatial conservation criteria such as patch connectivity, continuous area, and area of old-growth forest protected, in addition to nonspatial criteria.

While these and other modifications to iterative approaches for solving the SSCP were being made, parallel efforts were under way to incorporate spatial attributes explicitly within mathematical programming models. The purpose here was to realize a level of control such that a spatial attribute could be achieved to the degree desired or not achieved, as appropriate, for the reserve system. Spatial attributes may be addressed in one of two ways in mathematical programs: with maximization or minimization *objectives* for achieving as much or as little of a spatial attribute as possible, or with structural *constraints* for guaranteeing (or preventing) a particular level of an attribute to be realized. This type of objective-and-constraint formalization is seen in the IP models for the SSCP and MCSP (above), and spatial reserve design models typically have extended these two basic formulations by adding new spatial objectives and/or constraints. In the years after Underhill’s [8] publication of an IP for the SSCP, more than a dozen reserve design models have been formulated as mathematical programs.

In the remainder of this section we return to the six spatial attributes discussed above and describe how each has been stated as an objective or as a constraint for use in a mathematical programming model. The corresponding mathematical expressions are stated in stand-alone fashion for each attribute, although it should be kept in mind that these expressions would need to be combined with some of the expressions (1)–(5), as appropriate, to form a complete reserve design model for representing species or other features. In addition to reserve design models, we also mention other spatial optimization models that have been developed for land-use planning and civil engineering applications. Researchers in these fields have developed site-selection models for housing developments, landfills, and other land uses (e.g., [58–60]). These "land allocation" models, as they are often called, are relevant here because they incorporate many of the same spatial attributes important to reserve design, such as proximity, compactness, and contiguity. Models for forest management form another category of spatial optimization model. Spatially explicit optimization modeling of forest harvesting schedules dates back at least 25 years, although the inclusion of habitat considerations is more recent [61–63]. A review of forest models is beyond the scope of this paper, but several of the references below and in section 5 indicate the growing overlap between reserve design and the management of forests and other natural resources.

4.1. Reserve size

In variations of the SSCP and MCSP models, the total area of the reserve system was, respectively, minimized or constrained by an upper bound. In reserve design models, the total area has been either maximized, when viewed as a surrogate for conservation value [64], or minimized, when viewed as a surrogate for cost [65,66]. This is achieved using as an objective

$$\text{Max or Min} \quad \sum_{j \in J} a_j \, x_j \tag{6}$$

where a_j is the area of site j. Total area has also been constrained, either by placing a bound on the sum of the areas of selected sites [67] or by limiting the number of sites selected [68,69]. Limiting the number of sites is equivalent to constraining total area when all sites have equal area, but is otherwise a surrogate for total area. An area constraint, in turn, may be used as surrogate for a budget constraint. An area constraint would take the form

$$\sum_{j \in J} a_j x_j \leq A \tag{7}$$

where A is an upper bound on total area. Depending on the problem, expression (7) could also be written using " = " or "≥." Hence, reserve size can be controlled by including a straightforward area-based objective or constraint within the model. Some models do not address area explicitly, but instead allow reserve system size to be determined by the tension between other criteria such as cost and species representation (e.g., [70,71]) or cost and connectivity (e.g., [72,73]).

4.2. Number of reserves

Whereas a straightforward objective or constraint can control total area, this does not necessarily enable the user to control the actual number of reserves created, which may depend on accidents of site adjacency. Ideally, though, the user would be able to specify the number of reserves created (e.g., three reserves) given a particular total area (e.g., 30 sites). Alternatively, the user might want to minimize the number of reserves given a fixed total area to minimize fragmentation of the reserve system. Researchers have found ways to control this attribute in two special cases. First, when reserves are required to be circular or rectangular, the location of the centroid of each reserve and the size of each reserve (a function of radius or side length) can be optimized. The number of reserves is then determined by specifying the number of centroids to locate [74]. Second, candidate reserves that are not adjacent and do not overlap can be created in advance, possibly as multisite clusters, and treated as selection units [64]. An expression such as (1) or (5) can then be used to control the number of reserves selected. The control of other attributes, such as reserve shape, can also help to limit the number of reserves. Minimizing or placing an upper bound on the reserve system's boundary length or requiring a buffer zone to surround the core tends to result in one or several larger reserves rather than many smaller reserves. However, these proxies offer only indirect and incomplete control over the number of reserves.

Williams [75] formulated a land allocation model that gives the user direct control over the number of reserves. In this model, which uses concepts from graph theory, the reserve system is forced to be a single contiguous group of sites unless "disconnections" are allowed. A constraint enables the user to specify the allowable number of disconnections $(q-1)$ for the reserve system, which serves as an upper bound on the number of reserves realized (q) for the given total number of sites selected (P).

A further complication involves the size of each individual reserve. For example, three reserves having a combined area of 30 sites could have individual areas of 10, 10, 10 or 28, 1, 1. Because of the potential for wide variation, it would be desirable to control area in addition to number. To our knowledge, though, this problem has not yet been addressed in reserve design models except when candidate reserves are delineated a priori as in Rothley [64]. Delineating reserves a priori is a potentially useful but relatively unexplored approach. Here, candidate reserves of suitable size and shape would be generated in advance as clusters of candidate sites, and the optimization model would select from among these reserves. Generating all possible candidate reserves might be a practical impossibility for combinatorial reasons, except in very small problems, but the key would be to generate enough candidate reserves for sufficient flexibility and for optimality to have meaning. This approach has been used with some success in models for political districting [76] and for land allocation [59,77].

4.3. Reserve proximity

Several ways to control the distances between individual sites or reserves in a reserve system have been developed. The motivation here has been to select sites or reserves that are closer together (for reasons given in section 3.3) than they would normally be in, for example, a solution to the SSCP. The sum of inverse pairwise distances between reserves was maximized in [64] by using the model form

$$\text{Max} \quad \sum_{j \in J} \sum_{k > j} 1/d_{jk}\, u_{jk} \tag{8}$$

$$\text{s.t.} \quad u_{jk} \le x_j \qquad \forall j \in J; \forall k \in J, k > j \tag{9}$$
$$u_{jk} \le x_k$$

where d_{jk} is the distance between candidate reserves j and k, and u_{jk} = 0 or 1; it is 1 if candidate reserves j and k are both selected, and is 0 otherwise. The constraint set (9) enforces the definition of the binary u_{jk} variables.

Nalle et al. [69,78] minimized the sum of distances between all pairs of selected sites by using a quadratic objective function

$$\text{Min} \quad \sum_{j \in J} \sum_{k > j} d_{jk}\, x_j\, x_k \tag{10}$$

Onal and Briers [79] also minimized the sum of pairwise distances, but used the linear model form

$$\text{Min} \quad \sum_{j \in J} \sum_{k > j} d_{jk}\, u_{jk} \tag{11}$$

$$\text{s.t.} \quad u_{jk} \ge x_j + x_k - 1 \quad \forall j \in J; \forall k \in J, k > j \tag{12}$$

where constraint (12) enforces the definition of the u_{jk} variables. Under objective (10) or (11), combined with constraint set (2), the result is a relatively tight cluster of sites that represents all species (e.g., figure 3a). Onal and Briers [79] also minimized the maximum intersite distance (or "diameter") of the reserve system, which placed greater emphasis on avoiding extreme outlying sites (e.g., figure 3b). This was done using the model form

$$\text{Min} \quad D \tag{13}$$

$$\text{s.t.} \quad D \ge d_{jk}\left(x_j + x_k - 1\right) \quad \forall j \in J; \forall k \in J, K > j \tag{14}$$

where D is a nonnegative continuous variable that takes on the value of the maximum intersite distance. Constraint (14) enforces the definition of D.

In the "flyway" models of Malcolm and ReVelle [80] and Williams et al. [81], sites are selected to support long-distance bird migration in a particular direction such as north–south. Here, the allowable distance between successive habitat sites or "stepping stones" is limited by an upper bound that reflects the distances birds would be expected to fly between stops for feeding and resting. This proximity requirement was modeled by "directed conditional covering" constraints of the form

$$\text{s.t.} \quad x_j \le \sum_{k \in F_j} x_k \quad \forall j \in J \tag{15}$$

where F_j is the set of sites k that are within a specified distance and direction of site j. Constraint (15) says that if site j is selected, then at least one other site k within the desired distance and direction relative to j must also be selected.

Another approach to proximity is to not control it directly, but to capture its effect on population size. In the model of Hof and Flather [74], which seeks to maximize the expected total population size of a single species, the population of each reserve is modeled as a probabilistic function of inter-reserve distance. In optimizing population size, this model delineates reserves that are the most advantageous distances apart. This basic approach has also been used in other models that address population dynamics directly (see section 5).

4.4. Reserve connectivity

As mentioned above, connectivity may be characterized as structural or functional. Functional connectivity may be achieved by enforcing some level of proximity among sites, although structural connectivity may also be needed. Nalle et al. [69,78] maximized structural connectivity by maximizing the number of adjacent pairs of sites in the reserve (e.g., figure 3c), using the quadratic objective function

$$\text{Max} \quad \sum_{j \in J} \sum_{k \in B_j,\, k > j} x_j\, x_k \tag{16}$$

where B_j is the set of sites k that are adjacent to (share a boundary with) j. This objective (16) maximizes the number of adjacent site pairs selected. We note that this objective can also be written linearly by adding appropriate constraints, in a form similar to (8) and (9):

$$\text{Max} \quad \sum_{j \in J} \sum_{k \in B_j, k > j} u_{jk} \tag{17}$$

$$\text{s.t.} \quad u_{jk} \le x_j \qquad \forall j \in J;\ \forall k \in B_j, k > j \tag{18}$$
$$u_{jk} \le x_k$$

Because structural connectivity can be realized by creating a single compact and contiguous reserve, these attributes (number of reserves and reserve shape) can serve as indirect ways to control structural connectivity. Strict contiguity (e.g., figure 3d), though, has not been emphasized in reserve design models thus far (but see papers by Cerdeira et al. and by Onal and Briers in this issue). However, in land allocation, several methodologies have

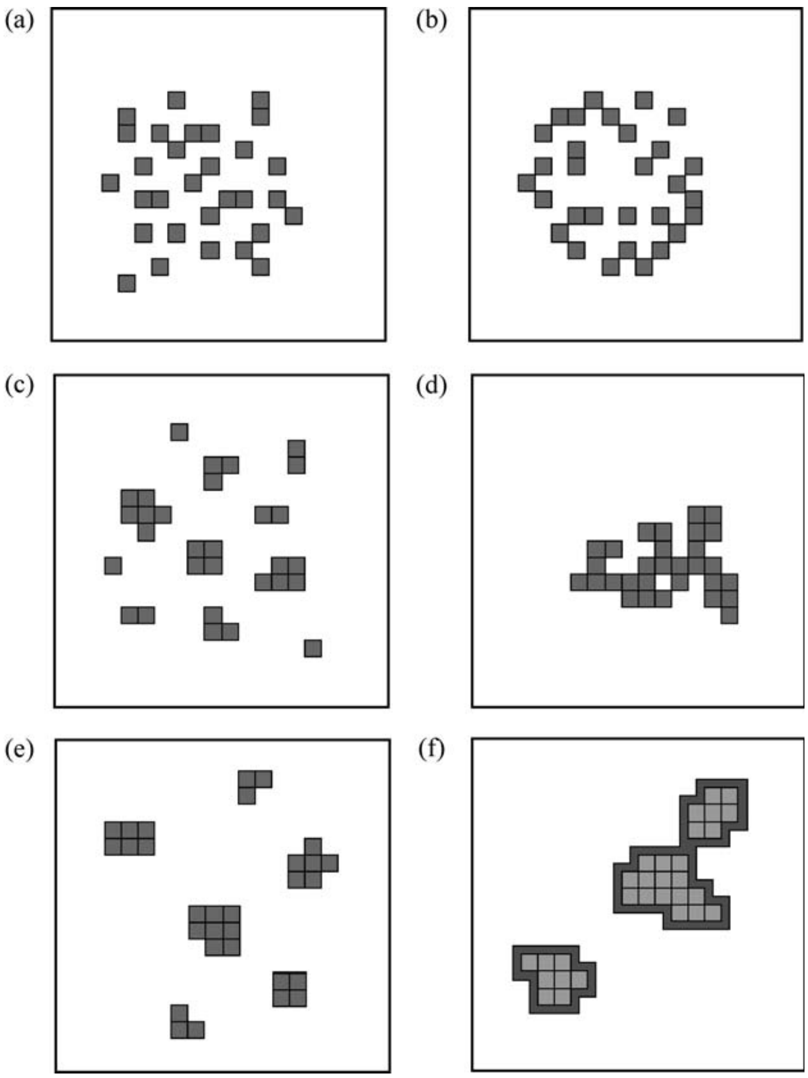

Figure 3. Diagrams are shown of reserve systems that represent all species but also have improved spatial coherence in comparison to the minimum reserve set shown in figure 1. The number of sites needed to represent all species is larger than in the minimum reserve set because a spatial objective or constraint is imposed (30 sites are shown, in comparison to 20 sites in figure 1). (a) Proximity: minimize the sum of distances between all pairs of selected sites; (b) proximity: minimize the diameter of the reserve system; (c) connectivity: maximize the number of adjacent pairs of selected sites; (d) connectivity: create a single, contiguous reserve; (e) shape: minimize the total boundary length of the reserve; (f) establish core areas and buffer zones (additional area is shown for buffer zones).

been developed for identifying an optimal contiguous region [59,75,77,82,83]. We expect these land allocation methods to be applicable to reserve design.

The related problem of physically connecting a set of existing reserves with wildlife corridors has been addressed by Sessions [72] and Williams [73] using the concept of "Steiner trees" from network optimization. Sessions developed a shortest-path-based heuristic for minimizing the amount or cost of land needed to provide a corridor link between each reserve and every other reserve. Williams [73] developed an IP model for this same problem and added a second objective of minimizing the amount of unsuitable habitat included in the corridor system. Jordan [84] proposed using network reliability theory to evaluate how successfully corridor systems would be expected to facilitate migration. Although wildlife corridors have received significant attention in the conservation literature, optimization modeling for corridor design is relatively unexplored.

4.5. Reserve shape

The shape attribute that has been most frequently modeled is compactness, as defined by the total boundary length of the reserve or reserve system. McDonnell et al. [65] (see also [85]) used a quadratic objective function to minimize boundary length (e.g., figure 3e):

$$\text{Min} \quad \sum_{j\in J} b_j x_j - \left(2\sum_{j\in J} \sum_{k\in B_j, k>j} sb_{jk}\, x_j x_k \right) \tag{19}$$

where b_j is the boundary length of site j and sb_{jk} is the length of the shared boundary between adjacent sites j and

k. In this objective (19), the boundary length of the reserve system is calculated by adding the boundary lengths of the selected sites and then subtracting twice the length of boundaries shared by selected sites that are adjacent. Fischer and Church [66] also minimized total boundary length, but used a linear model form similar to (17) and (18):

$$\text{Min} \quad \sum_{j \in J} b_j x_j - \left(2 \sum_{j \in J} \sum_{k \in B_j, k > j} sb_{jk} u_{jk} \right) \tag{20}$$

$$\text{s.t.} \quad u_{jk} \leq x_j \qquad \forall j \in J; \forall k \in B_j, k > j \tag{21}$$
$$u_{jk} \leq x_k$$

A third way to formulate the boundary minimization objective is

$$\text{Min} \quad \sum_{j \in J} \sum_{k \in B_j, k > j} sb_{jk} v_{jk} \tag{22}$$

$$\text{s.t.} \quad v_{jk} \geq x_j - x_k \qquad \forall j \in J; \forall k \in B_j, k > j \tag{23}$$
$$v_{jk} \geq x_k - x_j$$

where $v_{jk} = 0$ or 1; it is 1 if the shared boundary of adjacent sites j and k is part of the reserve system's perimeter, and is 0 otherwise. Note that v_{jk} must take on a value of 1 if j is selected but not k, or vice versa. Constraints (23) enforce the definition of the v_{jk} variables. This formulation appeared in Onal and Briers [86].

Hof and Flather [74] controlled shape by requiring reserves to be either circular or rectangular. Another way to control shape is to delineate reserves with acceptable shapes a priori (as discussed in section 4.2), although, again, this is relatively unexplored. Optimization models that incorporate shape have also been developed in land allocation. Most often used has been compactness as defined by either (i) boundary length [58], (ii) the product of boundary length and diameter [59], or (iii) the ratio of squared diameter to total area [77]. Other shape restrictions include bounding all selected sites by an enclosing rectangle of specified dimensions [87] and requiring the set of selected sites to form a convex shape [83]. Hence, boundary length and certain shapes (circles, rectangles) have been controlled in reserve design models, and land allocation models offer other approaches for controlling shape.

4.6. Core areas and buffer zones

Three optimization models have been formulated for selecting distinct core areas and buffer zones [68,70,71]. These models allow a site to be selected for the core only if all other surrounding sites are selected as either buffer sites or other core sites. In this way, the user may specify one or more buffer zone rings to surround the core. For example, a single ring would comprise the sites that are edge- and corner-adjacent to the candidate core site(s), whereas a double ring would include the first ring plus additional sites adjacent to the first ring. This basic core–buffer relationship was modeled using the constraints

$$\text{s.t.} \quad z_j \leq x_k \qquad \forall j \in J^c, \forall k \in S_j \tag{24}$$

where $z_j = 0$ or 1; it is 1 if site j is selected for the reserve core, and is 0 otherwise; J^c is the set of candidate core sites; and S_j is a set that includes site j plus those sites k that surround j and would need to be selected either as buffer sites or as other core sites to give j core status. This buffer zone requirement was found to promote (but not guarantee) compactness and contiguity (e.g., figure 3f). Because buffer zones mitigate complex impacts and dependencies between the core and the matrix, this way of modeling buffer zones should be viewed as just an initial step.

4.7. Solution methods

Collectively, these approaches to spatial reserve design modeling represent substantial progress beyond the basic SSCP and MCSP models. These approaches enable model users to assemble reserve systems that have attributes needed for spatial coherence. Because of the binary yes/no aspect of selecting sites and representing species, most of the above reserve design models have been formulated as discrete optimization models. As seen above, the same types of yes/no decision variables are common to many of the models, suggesting the possibility of mixing and matching spatial objectives and constraints between models. The ability to mix and match gives the user needed flexibility to formulate custom models for new reserve design problems from existing "parts." Many of the spatial attributes discussed above were able to be modeled using linear expressions, although other attributes were stated nonlinearly. Some, such as connectivity and boundary length, have been modeled in both linear and nonlinear forms. Linear expressions are often preferred because linear optimization problems have the potential to be solved to exact optimality, whereas nonlinear problems tend to be difficult or impossible to solve exactly. The use of nonlinear expressions, however, may be advantageous for heuristics because a nonlinear form may obviate the need for additional variables and constraints while being no less tractable for the heuristic than the corresponding linear form.

These two basic types of solution methodologies – exact methods and heuristics – have each been widely used in applications of reserve design models. Heuristics, such as "greedy adding," together with sophisticated "metaheuristics," such as simulated annealing, tabu search, genetic algorithms (see [88]), and heuristic concentration [89], are typically used for large problem instances or for problems that contain nonlinear expressions. Heuristics and metaheuristics, as the names imply, can guarantee only approximate solutions and may not find a global optimum. Within this category we also include methods tailored to nonlinear problems, such as "reduced-gradient algorithms," which can guarantee local optima but not global optima. Heuristics were used in applications of the models of Sessions [72], Hof and Flather [74], and Williams et al. [81], whereas metaheuristics were used in applications of the models of Clemens et al. [71], McDonnell et al. [65], and Nalle et al. [69,78].

In contrast, exact methods – typically LP/IP – can in principle find provably optimal solutions and will do so if allowed to run to completion, although very large problems may not be solvable in reasonable amounts of time. Exact (LP/IP) methods were used in applications of the models of Williams and ReVelle [68], Rothley [64], Williams and ReVelle [70], Williams [73], Malcolm and ReVelle [80], Onal and Briers [79], and Fischer and Church [66]. Another exact method, implicit enumeration, has been used to solve land allocation problems [59,77] and political districting problems [76], although to our knowledge it has not yet been used for reserve design. Implicit enumeration algorithms must be custom-coded for a particular model or problem statement and tend to work best when "bottleneck" (max-min or min-max) objectives are used [e.g., expressions (13) and (14)].

The issue of which approach is best – exact or (meta)heuristic methods – has been debated in the case of the SSCP, MCSP, and their variations [90–92]. This debate has shown, on the one hand, that (meta)heuristic methods will continue to be useful tools for a variety of reasons, including the need to solve large problems, if only approximately; the need for flexibility, that is, for quickly identifying many near-optimal solutions [93]; and convenience of use within decision support systems. On the other hand, the range of problems amenable to exact solution using LP/IP will continue to grow in parallel with the growth trend in computing power, making exact methods increasingly attractive. Thus, both approaches will continue to be used, depending on the nature of the problem and on the needs of those solving it.

The advantages and disadvantages of exact and (meta)heuristic methods also apply to reserve design models. Relative to the SSCP and MCSP, however, the modeling of spatial attributes typically makes the optimization problem larger (more variables and constraints) and more difficult to solve. For example, an SSCP comprising 2,000 sites and 200 species might solve in a minute or less using commercial LP/IP software. The same problem with an added boundary length requirement would be much larger and would likely take much longer – perhaps several hours or more – to solve using the same software. The modeling of spatial attributes may also entail nonlinear expressions, which would necessitate the use of (meta)heuristics. Spatial modeling turns out to be as much an art as a science, and the same attribute can often be modeled in different ways, as seen above (see also [94]). Hence, in reserve design modeling the solution method of choice depends not only on the nature of the problem and on the needs of those solving, but also on the way the problem is modeled.

5. Reserve design models and population dynamics

Most of the reserve design models discussed above are static in that site-selection decisions are based only on information from a single period (e.g., species presence/absence data). Such models ignore the dynamic aspects of species and sites. Ecological regions are systems of sites with interacting populations that "reseed" one another over space and time. For example, if site A has a high biodiversity value, but neighboring sites B and C are removed as sources, the value of A will be diminished. Multiplied over thousands of sites and hundreds of species, these interactions within the landscape become enormously complex. Conservation decisions regarding the fate of one site will affect populations in other nearby sites, possibly in unpredictable ways. These complexities admit no easy answer for addressing the goal of long-term persistence. Indeed, achievement of the spatial attributes reviewed above may be thought of as a surrogate for spatial coherence used in response to the difficult prospect of capturing ecological complexities directly within a decision model. Yet, spatial surrogates may not be adequate, and the inherent complexities argue ultimately for basing reserve design models on the dynamic interdependencies of ecological regions. Decisions for achieving spatial coherence in reserves ought to be based on the reasons why spatial attributes are important.

Characterizing complex dynamics is the purpose of spatially explicit population models (SEPMs), which model a species' dispersal and colonization among habitat sites in the landscape. The history of SEPMs in ecology stretches back several decades and may be summarized in terms of three modeling paradigms: (i) diffusion approaches (e.g., [95,96]), (ii) metapopulation approaches (e.g., [97–100]), and (iii) individual-based approaches (e.g., [101,102]). As a class of models, SEPMs are now also recognized as descriptive and predictive tools for land management and conservation (e.g., [103,104]). Beissinger and Westphal [105] discuss the prospects of using SEPMs and other types of demographic models to manage endangered species.

In the last decade, population-dynamic models have been used in a variety of ways to evaluate alternative habitat configurations and to identify optimal systems of habitat sites for protection. Typically, the evaluator or objective has addressed some aspect of species persistence. Several definitions of persistence have been used, including population size at equilibrium (e.g., [106]), population size at time T in the future (e.g., [107]), time to system-wide extinction (e.g., [23]), and probability of system-wide extinction (e.g., [108]). Recent population-dynamic models are discussed below in terms of three principal directions of research. A full review of such models and their results in particular applications is beyond our scope, but we highlight several examples within each research direction, with a focus on problem statements and on the spatial attributes incorporated in the models.

5.1. Research direction 1

The first direction of research comprises models that use dynamic simulations to assess how different habitat configurations would influence the metapopulation persistence of a single species. Adler and Nuernberger [109] evaluated several different spatial placements (clumped, equidistant, or randomly spaced) of a fixed number of identical circular sites. Day and Possingham [108] evaluated several alternative habitat systems composed of sites that varied not only in location, but also in size and shape. Etienne and Heesterbeek [23] compared a system of a few large sites to one with many small sites having t0he same total area; in each case, sites were equidistantly spaced on a regular grid. A fourth study [110] broadened this basic approach to address multiple species. Here, plant species richness was measured at equilibrium for alternative patterns of habitat fragmentation in tropical rain forests. Total habitat area was held (approximately) constant in four scenarios in which the size and number of reserve sites ranged from many small identical square habitat patches to fewer larger squares randomly located in the landscape.

The common approach of these four modeling efforts was to evaluate and compare several prespecified reserve configurations to see which performed best. However, because these configurations represented only a small fraction of all possible configurations, the likelihood that one of the tested configurations was a global optimum was low. Although these approaches give insight into the efficacy of particular patterns (and thus are useful for critiquing the prospect of applying Diamond's [4] guidelines in particular cases), they do not use optimization modeling and are not really methods for selecting reserve sites.

5.2. Research direction 2

The second direction of research extends the first by combining dynamic simulation modeling with optimization modeling. Here, an optimization model is used to select reserve sites, whereas simulations are used for one or both of two purposes. First, simulations are used to determine parameter values, such as distance-based dispersal coefficients, or to determine functional forms, such as extinction probability functions, for use in the optimization. Second, simulations are used to evaluate reserve systems once they have been identified through optimization. In this research direction, the optimization model is usually static with respect to time but captures species dynamics in an equilibrium sense. As before, the objective of the optimization and what the simulation evaluates is the persistence of a single species. The model of Hof and Flather [74] belongs in this category but was discussed in the previous section because of its explicit treatment of several spatial attributes.

Hof and Raphael [106] developed an LP model to identify the amount of habitat to retain in each of multiple sites to maximize the total population of northern spotted owls. The model's constraints addressed both site adjacency (connectivity) and carrying capacity relationships and also limited the total amount of habitat that could be set aside. Parameters used in the LP model related population size to habitat area and habitat connectivity, and were based on the results of a simulation model. LP-derived optimal solutions were evaluated using the simulation model, which predicted what the actual (equilibrium) population would be for each LP solution.

Haight et al. [111] formulated a mathematical programming model to select new protected habitat to add to an existing reserve system to minimize the risk of population extinction for kit foxes. Simulations with a population model were used to estimate extinction risk as a function of the amount and quality of habitat protected. In the optimization model, this nonlinear risk function was minimized, subject to a budget constraint that limited the amount of new habit that could be selected. Extinction risk vs cost trade-off curves were developed for two spatial scenarios, one in which new candidate habitat was contiguous to an existing reserve and one in which new habitat was spatially isolated. In a related effort, Haight et al. [112] developed a nonlinear programming model to add habitat to eight existing reserves, each of which had its own kit fox population. The objective was to maximize the expected number of reserve populations (out of eight) that survived over a specified time horizon, subject to a budget constraint on habitat selection. Again, a population model was used to characterize extinction risk as a function of habitat area and quality. A reduced-gradient algorithm was used to solve the optimization component of each of these methodologies.

Also falling within this category is the model of Rothley [67], who formulated a two-objective IP for selecting a reserve system to protect a metapopulation of a predator species (hawk). One objective was to maximize the total predator population at equilibrium within the reserve system; the other was to maximize the percentage of individual selected sites (reserves) in which the predator appeared at equilibrium. A constraint limited the total area of reserves that could be selected. This model used predator–prey dynamics (Lotka–Voltera equations) to determine the equilibrium sizes of predator and prey (vole) populations within each reserve, based on birth rates, death rates, and reserve area. Hawk migration was also modeled, and the ability of hawks to colonize reserves was based on inter-reserve distance. This model was applied to a series of synthetic example problems in which five or ten circular candidate reserves of varying areas were placed at random locations in the landscape.

5.3. Research direction 3

In the third direction of research, population dynamics are embedded within spatially and temporally explicit optimization models. A particularly compelling aspect of this approach is that site selection is driven largely by the dispersal of individuals or populations among sites, so that the spatial attributes of the reserve system result directly from intersite migration in conjunction with population growth and decline over time. This is in contrast to the second research direction in which species dynamics are captured in an equilibrium sense, but, like approaches in the other two directions of research, models in this third direction have focused on the population of a single target species. This general type of model has appeared in several papers by Hof, Bevers, and coauthors, and two examples are discussed. A full review of their recent work in this area is beyond our scope but is provided in two books [113,114].

Bevers et al. [108] formulated an LP for identifying a management policy for each site in each period to maximize the expected total population of black-footed ferrets at a specified year T in the future. Constraints tracked the expected population in each site over time, based on site carrying capacity, intersite dispersal of ferrets, and releases of captive-bred ferrets into the wild. Site management involved scheduling the application of rodenticide to control the population of prairie dogs, the primary prey of ferrets.

Hof et al. [115] formulated a similar LP for determining the optimal selection of protected habitat to set aside for black-tailed prairie dogs. In this model, the objective was to maximize the total size of the prairie dog population, summed over all sites and all periods. Constraints tracked the dispersal of individuals among sites where the probability of successful dispersal declined with intersite distance. The per-site population in any period was limited by the site's carrying capacity. The total area of land that could be protected was constrained by an upper bound.

In a third example of this direction of research, Moilanen and Cabeza [116] developed a site-selection procedure for a single species of butterfly. The objective was to minimize metapopulation extinction risk over a specified time horizon, where this risk was defined as the mean yearly probability of metapopulation extinction. Optimization was done using a genetic algorithm combined with a local search procedure. This metaheuristic systematically generated reserve systems (combinations of reserve sites) and improved on prior systems based on the results of a simulation model that was used to evaluate each system in terms of metapopulation extinction risk. This risk was characterized in terms of local site extinction and intersite colonization, which in turn were defined as nonlinear functions of site area and site isolation. A budget constraint limited the total monetary amount that could be spent on site acquisition.

5.4. Modeling challenges

The tandem use of optimization models and SEPMs has great potential for reserve design but also poses substantial modeling and computational challenges. First, further work is needed to extend single-species population models to multiple species models so that the persistence of biological diversity in a reserve can be addressed [25]. Capturing population dynamics can be difficult even for a single species, and these difficulties are naturally compounded for many interacting species. In addition, parameter estimation in the SEPM component adds a layer of uncertainty to the results of the optimization component, which may already contain some level of uncertainty (see section 6.1).

The methodologies discussed in this section indicate that combining SEPMs and optimization models for a single species can be done in basically one of two ways. First, the two models can be run separately and in sequence: an optimization model is used to delineate or select alternative reserve systems, and an SEPM is then used to evaluate each system in terms of its effectiveness in achieving a population objective (research direction 2). Under this approach, it may be practical to evaluate only a small portion of the full “solution space” of all possible reserve systems, making it likely that a global optimum would be missed. The second way is to embed an SEPM within a temporally explicit optimization model that selects sites to optimize a population objective (research direction 3). Here, a much larger portion (possibly all) of the solution space could potentially be considered, although, as a result, the time needed to find an (approximate) optimal solution could be much longer.

These two ways of combining SEPMs and optimization models can in principle be extended to reserve design for multiple species (one example is [110]). In practice, however, computational challenges arise due to the potential nonlinearity and large size of models needed to capture multispecies population dynamics within a discrete-site framework. The ability to solve reserve design optimization problems on desktop computers tends to decline rapidly as problem size grows beyond a few tens of thousands of variables and constraints (depending on the model formulation and solution method). This same number of variables, however, is more suggestive of a lower limit to the size of SEPMs, and many SEPMs are much larger than this. Thus, finding the right balance of spatial and temporal resolution – the number of candidate sites or cells and the number of periods to model – may be problematic. Metaheuristics evidently offer the most promise for finding at least approximate solutions to reserve design problems that incorporate multispecies population dynamics.

6. Discussion and areas for future research

In this paper we have identified three basic modeling approaches for assembling land for a reserve system:

reserve site-selection models, reserve design models, and spatially explicit simulation–optimization models. Reserve site-selection models focus on the representation of biological diversity, defined in terms of species richness or other conservation features, but do not address spatial attributes. Reserve design models seek not only to represent biodiversity but also to give the reserve system some measure of spatial coherence to promote the persistence of biodiversity and to address management considerations. Spatially explicit simulation–optimization models seek to identify reserve configurations and management actions that best support the persistence of a single species, based on population dynamics. Here, spatial attributes such as site connectivity influence migration and colonization. A key challenge is to extend this type of model to multiple species. A variety of problem statements have been articulated under each modeling approach, and researchers have responded with an equally diverse set of model formulations and solution methodologies. In the rest of this section, we explore some remaining spatial issues not discussed above.

6.1. Uncertainty

Reserve design models are data intensive, typically requiring multiple layers of quantitative biological, economic, and spatial data for the region of study. The above discussion of models has supposed that all of the data needed to run a model would be available. Yet, data sets are frequently incomplete or out-of-date, and the accuracy even of current data may be uncertain. Given that conservation analysts and planners may have no choice but to work with imperfect information, how can reserve design models utilize uncertain or incomplete data? In the case of reserve site-selection models, two approaches have been developed to utilize uncertain or probabilistic species presence/absence data. Haight et al. [117] formulated a model to maximize the number of species represented with a specified level of *reliability*, subject to a constraint on total area. The models of Polasky et al. [118] and Camm et al. [119] maximized the *expected number* of species represented given a fixed total area. These two approaches are compared in [120]. Like other reserve selection models, these models do not include spatial attributes other than total area. To our knowledge, reserve design models that utilize probabilistic presence/absence data and also optimize spatial attributes have not yet been formulated; such models provide an opportunity for future research.

Uncertainty in the presence or absence of species in sites corresponds to uncertainty of representation in the reserve. However, another fundamental uncertainty is the uncertainty of long-term species persistence. In the case of a single species, uncertainty of persistence has been addressed in some of the dynamic population models discussed in section 5 (e.g., minimizing extinction risk [116]). In the case of multiple species, methods for selecting reserve sites based on probabilistic estimates of persistence have been proposed by Araujo and Williams [121], Williams and Araujo [122,123], and Araujo et al. [124]. These methods use presence/absence of data as a starting point, but also include other factors that affect the likelihood of persistence, such as: migration, colonization, and contagion between nearby sites; source–sink dynamics; and other intrinsic and extrinsic threats (e.g., human activities). In these approaches, at least some spatial factors were incorporated implicitly (e.g., “contagion scores”), but it is worth investigating whether explicit spatial optimization would be beneficial here.

Uncertainty also exists with respect to extrinsic factors that affect the availability and suitability of sites for inclusion in a reserve. Landscapes change over time as a result of natural and human disturbances. Climate change and habitat fragmentation are two phenomena that will increasingly affect the mix of species and the general ecological functioning of reserves in unpredictable ways. Ideally, the locations and boundaries of reserves would be adjustable over time, as needed, in response to both changing conservation needs and a changing environment. This seems implausible, though, especially in areas where the amount of land available for reserves declines every year. Will those sites not protected now still be available in the future? Costello and Polasky [125] developed a stochastic IP model for the problem of selecting reserve sites over time in the face of uncertain future land availability to maximize the number of species represented within a budget. This model does not address spatial attributes, but spatial aspects are important for reasons of both species persistence and economics (the value of as yet unprotected sites may rise in response to a reserve located on nearby sites). The optimal selection of sites over time for achieving spatial attributes is therefore suggested as another area of future research.

6.2. Spatial scale

Most of the reserve models discussed above rely on preexisting selection units (candidate sites) for building reserves and reserve systems. Candidate sites may be the cells of a regular grid, typically rectangles or hexagons, or may have the irregular geometries of hydrologic units or cadastral parcels. Sites may range in size from less than a hectare (e.g., butterfly patches used in [116]) to 10,000 km^2 or more (e.g., one-degree longitude by one-degree latitude cells used in [126]). Many modeling applications have used sites whose sizes are between these two extremes, for example: 1-km^2 quadrangles [78]; 160-km^2 quadrangles [11]; and 635-km^2 hexagons [127].

The reserve design models reviewed in section 4 tend to operate independent of scale. Any one of these models can solve a problem with N large sites just as easily as a problem with N small sites. However, recent studies have shown that the sizes and shapes of sites have profound implications for the efficiency with which conservation objectives can be achieved and also for the effective design and functioning of reserve systems [42,128,129]. Different species function at different spatial scales [130,131], so a particular size or scale of sites will have different implications for the persistence of different species. Of principal concern is whether the scale of sites is appropriate for what is to be protected. As Kunin [42] points out, "the 'optimal' design of a nature reserve must depend on the spatial scale at which the question is asked" (p. 374).

To illustrate these points, consider a hypothetical 20 by 20 landscape of 400 candidate sites. First, suppose that we solve the SSCP site-selection model [(1) and (2)] and find that all species can be represented by selecting 12 sites. Let us then say that each block of four sites is aggregated in a single larger site, giving us a 10 by 10 grid of 100 candidate sites. Suppose we solve the SSCP again and find that only six of the larger sites are needed to represent all species. This second solution has half as many sites as the first solution but has twice the total area. The first solution with 12 small sites is therefore more efficient than the second solution with six large sites, but the 12-site solution could ultimately turn out to be less effective in supporting species persistence. The point here is that the two solutions came from the same model and the difference between them is solely a result of a difference in site size.

The scale of sites is also important for assessing the relative importance of different spatial attributes for use in reserve design models. For example, if large sites are used, each site may operate effectively as a stand-alone reserve, making high levels of aggregation or connectivity between sites less critical than if smaller sites are used. Smaller sites, on the other hand, may provide more flexibility for fine-tuning reserves with respect to shape attributes. The spatial configuration of a reserve system also depends on the underlying pattern of candidate sites in the landscape. What does the site map look like? Is 100% of the landscape eligible to be selected, or are candidate sites dispersed within a mosaic of unavailable land? If many candidate sites are dispersed, it may be impossible to achieve a compact or highly connected reserve. Hence, with respect to the spatial attributes of a reserve system and their implications for species representation and persistence, the results of the model depend strongly on the type of sites used as input.

6.3. Multiple objectives and trade-offs

The fundamental trade-off in reserve design is between cost (or the resources available for conservation) and what can be conserved. As indicated above, different variations of this trade-off have been considered (see also [132]). In reserve site-selection models this trade-off is modeled by a cost minimization objective or a budget constraint (or surrogate) combined with an objective or constraint for achieving species richness. In reserve design models, these trade-offs between cost and species representation are augmented by trade-offs involving spatial attributes. For example, as the level of connectivity among sites increases relative to the SSCP solution, one of two things is expected to happen. Either the cost (or area) needed represent all species must increase, or the number of species represented by a fixed cost (or area) must decline. In spatial optimization approaches that use SEPMs, this three-way trade-off becomes a two-way trade-off between cost and long-term persistence because the reserve's (optimal) spatial characteristics are determined implicitly.

In general, trade-offs inevitably exist between any set of competing objectives that influence conservation decisions. For example, Williams [73] examined trade-offs between cost and the amount of unsuitable land in wildlife corridors; Nalle et al. [69,78] examined trade-offs between proximity and connectivity; and Rothley [64,67] looked at trade-offs between total hawk population and the percentage of reserves containing hawks. As seen in these and other reserve design models, trade-offs can be explored by formulating the model multiobjectively, that is, by explicitly articulating two or more objective functions. The field of multiobjective optimization offers methods for identifying trade-offs in a systematic way and for making these trade-offs explicit (e.g., [133,134]). Multiobjective methods are intended to generate a variety of "noninferior" alternatives rather than just a single optimal solution. Each noninferior alternative can be thought of as a solution that would be optimal for a particular prioritization or weighting of the objectives. Noninferior solutions are desirable because they cannot be improved upon in all objectives simultaneously. An improvement can be made in one objective (e.g., reducing cost) only by sacrificing another objective (e.g., increasing the amount of unsuitable land). The most common multiobjective method used is the "weighting method," which is a straightforward extension of single-objective optimization. In the weighting method, each objective is multiplied by a numerical weight, and all objectives are then added together into a single grand objective. For example, the weighted objective used in [73] for minimizing cost and minimizing unsuitable area was

$$\text{Min} \quad \lambda \sum_{i \in J} c_j x_j + (1-\lambda) \sum_{j \in J} r_j x_j \tag{25}$$

where c_j is the cost of site j, r_j is the area of unsuitable land in j, and λ is a weight coefficient specified by the user, $0 \leq \lambda \leq 1$. The weighted problem is solved multiple times for a range of weightings (values of λ) to generate different noninferior solutions that place different emphases on each of the objectives. The weighting method can be used with both exact and heuristic procedures. When used with heuristics, the resulting solutions are approximations of the noninferior solutions that would have been found had an exact method been used. Multiobjective methods have already been applied in promising ways to reserve design, and their use is likely to increase as conflicts between human land uses and conservation become more acute.

7. Summary

The need to efficiently protect species and other aspects of biological diversity inspired the development of optimization models for reserve selection. Although these models provide some baseline for making conservation decisions, they lack the ability to control the spatial attributes of reserves. Recognition of the importance of spatial attributes for the long-term persistence of species diversity and other conservation features, as well as for socioeconomic feasibility, has prompted the development of reserve design models for delineating spatially coherent reserves. The attributes important to spatial coherence include reserve size, number of reserves, proximity, connectivity, shape, and core areas and buffer zones. The ability to control these attributes within an optimization framework may be critical to the successful functioning of reserve systems. In this paper, we have reviewed decision models for reserve design in terms of how the models control spatial attributes. Some reserve design models have built on reserve site-selection models for representing species or other features but have also included additional objectives or constraints for controlling spatial attributes. Other models have sought to protect a single target species and have allowed dynamic factors such a migration and colonization to dictate the optimal spatial properties of the reserve system.

Reserve design problems have been modeled as linear programs, integer programs, and nonlinear programs. They have been formulated as static models encompassing a single period or equilibrium state, or as dynamic models optimized over multiple periods. They have been solved to exact optimality using LP/IP methods or to approximate optimality with heuristics and metaheuristics. Multiobjective methods provide an important new dimension for reserve design modeling by enabling the analysis of tradeoffs. As a relatively new field, reserve design modeling has benefited from other areas of applied operations research, including land allocation, facility siting, and dynamic systems analysis. These areas have extensive experience with spatial optimization and have much to offer. Two issues caution for care in applying reserve design models and in interpreting their results: uncertainty in the accuracy of data and of future conditions and the spatial scale of selection units.

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