8

Optimization of landscape pattern

8.1 Introduction

Wu and Hobbs (2002) state that:

> A fundamental assumption in landscape ecology is that spatial patterns have significant influences on the flows of materials, energy, and information while processes create, modify, and maintain spatial patterns. Thus, it is of paramount importance in both theory and practice to address the questions of landscape pattern optimization . . . For example, can landscape patterns be optimized in terms of both the composition and configuration of patches and matrix characteristics for purposes of biodiversity conservation, ecosystem management, and landscape sustainability?

Physical restructuring of landscapes by humans is a prominent stress on ecological systems (Rapport *et al.* 1985). Landscape restructuring occurs primarily from land-use conversions or alteration of native habitats through natural resource management. A common faunal response to such land-use intensification is an increased dominance of opportunistic species leading to an overall erosion of biological diversity (Urban *et al.* 1987). Slowing the loss of biodiversity in managed systems will require interdisciplinary planning efforts that meld analysis approaches from several fields including landscape ecology, conservation biology, and management science. Again from Wu and Hobbs (2002), "Such studies are likely to require theories and methods more than those in traditional operations research (e.g., different types of mathematical programming), as well as the participation of scientists and practitioners in different arenas."

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The objective of this chapter is to review emerging methods from this set of disciplines that allow analysts to make explicit recommendations (prescriptions) concerning the placement of different features in managed landscapes. We will refer to this general set of methods as "spatial optimization." As used here, spatial optimization refers to methods that capture spatial relationships between different land areas in the process of maximizing or minimizing an objective function subject to resource constraints. We will begin with a terse review of the state-of-the-science in spatial optimization and then proceed to a discussion of prominent research questions in need of attention.

8.2 State-of-the-science in spatial optimization

In our view, four basic approaches have been taken to address optimization of landscape pattern: adjacency constraints (with augmentation), spatial enhancement of the reserve-selection problem, direct spatial-optimization approaches, and automated manipulation of simulation models. We will review each of these in turn.

8.2.1 Adjacency constraints

In the forestry literature, the predominant perception of spatial considerations has been that of adjacency relationships. Concerns regarding adjacent timber harvests emerged from legal and regulatory restrictions on the effective size of harvests – if two seemingly legal-size clearcuts, for example, occur within a short time of each other in adjacent areas, the effective size of the clearcut may not be legal. The basic formulation for avoiding adjacent harvests is:

$$X_1 + X_2 \leq 1,\ X_1, X_2 \in (0, 1)$$

where the X_1 and X_2 are binary (integer) management prescriptions that have harvests within the prohibited time limit of each other, for areas that are adjacent. If "n-tuples" (triplets, quadruplets, etc.) of mutually adjacent areas can be defined for $i = 1, \ldots, I$, then:

$$\sum_i X_i \leq 1,\ X_i \in (0, 1)\ \forall i$$

can cover the set. Many other sophistications are possible. These approaches require that the management variables be binary (integer), and considerable effort has been expended towards solution of these problems – typically with heuristic methods such as tabu search or simulated annealing (see, for example, Martell *et al.* 1988, Murray and Church 1995, Boston and Bettinger 1999).

Because the original motivations for the clearcut size limits included concerns for aesthetics, wildlife habitat, water quality, and so forth, addressing adjacency constraints has often been interpreted (or even advertised) as addressing those underlying concerns. Adjacency constraints are most clearly applicable when the problem is avoidance of adjacent management actions, per se. They do not necessarily address any other spatial relationship. However, there have been a few recent attempts at augmenting the basic adjacency formulation that show more promise in addressing the underlying ecological problems (see, for example, Bettinger *et al.* 1997, Barrett *et al.* 1998, Falcao and Borges 2001). We will not discuss this approach further here, because we believe that as spatial relationships in addition to adjacency are captured, this approach becomes a special (simple) case of direct spatial optimization or heuristic manipulation of simulation models, as described below.

8.2.2 Spatial enhancement of the natural reserve-selection models

It has been said that the next great challenge for conservation science is the design and implementation of comprehensive and ecologically adequate reserve networks (Lubchenco *et al.* 2003, Williams *et al.* 2004). Because conservation reserve areas are rare (at least in areal extent) and human impacts on natural ecosystems are increasing, there is a growing realization that when there are alternative locations for reserve lands the choice should be, in some sense, optimal (Pressey *et al.* 1993, Reid 1998). Quite a large body of literature has developed based on the set-covering formulation (Toregas and ReVelle 1973) applied to the natural reserve-selection problem (see, for example, Williams and ReVelle 1997, Polasky *et al.* 2001, and Rodrigues and Gaston 2002). The basic formulation is as follows:

$$\text{Minimize:} \quad \sum_i c_i X_i$$

$$\text{Subject to:} \quad \sum_{i \in \Omega_j} X_i \geq k_j \quad \forall j$$

$$X_i \in \{0, 1\} \quad \forall i$$

where $X_i = 1$ if site i is selected and 0 if site i is not selected for the reserve system, c_i = the cost of selecting site i for the reserve network, Ω_j = the set of sites that contain species j, and k_j = the number of sites required for adequate representation of species j ($k = 1$ for the most basic set-covering problem; $k > 1$ if some degree of redundancy is desired).

Because the choice variables are often defined in a fairly spatially explicit manner, this formulation is sometimes referred to as a form of spatial

optimization. This provides a good opportunity for us to draw a distinction between "spatially explicit optimization" (of which this is an example) and what we refer to as "spatial optimization," which (as defined above), refers to methods that capture spatial *relationships* between different land areas in the process of maximizing or minimizing an objective function subject to resource constraints.

Just as attempts have been made to augment the adjacency constraint formulation, recent contributions in the literature (for a review see Williams *et al.* 2004) have endeavored to add spatial relationships to the set-covering reserve selection model (some examples are Possingham *et al.* 2000, Nalle *et al.* 2002, Onal and Briers 2002, 2003, Fischer and Church 2003). And, similar to our point about the augmented adjacency constraint formulation, we will not discuss this approach further here, because we believe that as spatial relationships are captured, this approach will be best described as being one of the next two approaches.

8.2.3 Direct approaches to spatial optimization

The basic approach that we favor is to directly include the spatial relationships of concern in a formulation that is focused on the optimization of landscape pattern, per se. We would characterize the approach as having a closed-form formulation with a formal solution method. Hof and Bevers (1998, 2002) explore a number of formulations along these lines, including static models, dynamic models, models of spatial autocorrelation, and models of sustainability. Other authors that have taken relatively direct approaches include Nevo and Garcia (1996), Farmer and Wiens (1999), and Loehle (1999).

As an example, wildlife habitat fragmentation (spatial division into disaggregated patches) is a common concern with regard to placement of timber harvests. The approach is to directly model the wildlife population growth and dispersal patterns that make habitat connectivity (nonfragmentation) important. This is a dynamic problem where management activities must be scheduled over time, wildlife habitat (determined by forest age) must be tracked as forest stands age and grow, and different wildlife species respond differently to those habitats. The method is related to the classic "reaction-diffusion models" (Skellum 1951, Kierstead and Slobodkin 1953, Allen 1983).

First, the land is divided into cells, where the cell could be scaled to the ecology of the species (e.g., average home range or territory size) or could be scaled simply to provide adequate spatial resolution for the optimization problem. Then, a set of choice variables is defined for each cell, each of which represents a complete scheduled management prescription. For example, each prescription could define the time periods for harvesting the given celone, including

a no-harvest option. Any harvest would reset the forest age class to zero, and would change the habitat for each wildlife species accordingly. Initial forest age classes are assigned to each cell, as well as initial population numbers for each wildlife species included.

The following definitions will be used for the further discussion of these approaches: i indexes species, k indexes the management prescription, h indexes the cells, as does n, t indexes the time period, q_h = the number of potential management prescriptions for cell h, T = the number of time periods, X_{kh} = the area in cell h that is allocated to management prescription k, K_h = the total area in cell h, S_{iht} = the expected population of species i in cell h at time period t, a_{ihtk} = a coefficient set that gives the expected carrying capacity of animal species i in cell h at time period t, if management prescription k is implemented (based on forest age class), N_{ih} = the initial population numbers for species i in cell h, and g_{inh} = the probability that an animal of species i will disperse from cell n in any time period to cell h in the subsequent time period. This includes a probability for $n = h$, so that the g_{inh} sum to one for each combination of h and i. In addition, r_i is the "r value" of population growth rate (net of mortality not related to dispersal) for species i, and F_{it} is the total population for species i in time period t.

The simplest objective function would be to maximize a given species' expected total population:

$$\text{Maximize } \sum_t F_{it} \quad \text{for a given } i$$

The minimum population over all time periods (m), for a given species could be maximized as follows:

$$\text{Maximize } m$$

$$\text{Subject to } m \leq F_{it} \quad t = 1, \ldots, T \quad \text{for a given } i$$

Or, a weighted (V_i) sum of multiple species' populations could be maximized:

$$\text{Maximize } \sum_i V_i \left(\sum_t F_{it} \right).$$

Many other objective functions are also possible. The basic constraint set for such a model is:

$$\sum_{k=1}^{q_k} X_{kh} = K_h \quad \forall h \tag{8.1}$$

$$S_{ih0} = N_{ih} \quad \begin{matrix} \forall i \\ \forall h \end{matrix} \tag{8.2}$$

$$S_{iht} \leq \sum_k a_{ihtk} X_{kh} \quad \begin{matrix} \forall i \\ \forall h \end{matrix} \qquad (8.3)$$

$$t = 1, \ldots, T$$

$$S_{iht} \leq \sum_n g_{inh} \left[(1 + r) S_{in(t-1)}\right] \quad \begin{matrix} \forall i \\ \forall h \end{matrix} \qquad (8.4)$$

$$t = 1, \ldots, T$$

$$F_{it} = \sum_h S_{iht} \quad \begin{matrix} \forall i \\ \forall t \end{matrix} \qquad (8.5)$$

$$0 \leq X_{kh} \leq K_h \quad \begin{matrix} \forall k \\ \forall h \end{matrix} \qquad (8.6)$$

This model is linear, with continuous variables, and can be solved with standard solution software. Equation (8.1) limits the total management prescription allocation to the area in each cell. The management prescriptions are defined with no action in the first time period ($t = 0$), which is used simply to set initial conditions. Equation (8.2) sets the initial population numbers for each species, by cell. The S_{iht} (expected population by species by cell, for each time period) is determined by whichever of Equation (8.3) or Equation (8.4) is binding. Constraint set of Equation (8.3) limits each cell's population to the carrying capacity of the habitat in that cell, determined by forest age classes. The constraint set of Equation (8.4) limits each cell's population according to the growth and dispersal from other cells and itself in the previous time period. The growth and dispersal characteristics of each species are reflected by the parameters in constraint set of Equation (8.4). The constraint set of Equation (8.4) adds up the expected value of the population dispersing from all cells in the previous time period to the given cell in the given time period. It is important to note that whenever Equation (8.3) is binding for a cell, some of the animals assumed to disperse into that cell are lost because of limited carrying capacity. Reaction–diffusion models assume that organisms dispersing into unsuitable regions will perish. This mechanism provides a probabilistic basis for the expectation that mortality (beyond the nondispersal-related mortality accounted for in the r value) occurs in proportion to the usage of inhospitable surroundings. Thus, actual population growth is determined by a combination of potential growth, dispersal, and spatially located carrying capacities determined by the management prescription allocations. The constraint set of Equation (8.5) defines the total population of each species, in each time period. And finally, the constraint set of Equation (8.6) limits the choice variables to be between zero and the area in each cell.

Hof and Bevers (1998, 2002) applied this basic type of model structure to problems of habitat placement for the black-footed ferret, which also

accounted for release schedules of captive-born animals. As a follow up, it was applied to the black-tailed prairie dog, accounting for population-dependent dispersal behavior. Hof and Bevers also modified this structure to account for water-borne seed dispersal and for habitat edge effects, converted the model to optimize the location of control measures in managing exotic pests, and applied these basic ideas to problems other than organism management (especially stormflow management and fire management).

8.2.4 Heuristic manipulation of simulation models

The primary criticism that can be leveled at the approaches in the previous section is that there are limits to the complexity of ecological relationships that can be captured in a closed-form optimization formulation. An alternative that has been suggested by several authors (see, for example, Haight and Travis 1997, Boston 1999, Jager and Gross 2000, Calkin *et al.* 2002) is to start with a more complex ecological model and use heuristic procedures to direct repeated predictions with different management regimes, hopefully converging on a near-optimum.

A number of ecological modeling approaches are available to serve this purpose, including empirical models derived from statistical estimation (e.g., Morrison *et al.* 1987), analytical models that have exact solutions derived from a few fundamental mathematical relationships (e.g., Lande 1987), and simulation models derived from mechanistic mathematical relationships whose number and complexity requires that solutions be explored numerically with digital computers (e.g., Fahrig 1997). Because empirical models tend to be correlative in nature and have not performed well in prediction (Block *et al.* 1994), and because analytical models tend to become intractable in all but the simplest cases of spatial heterogeneity (Fahrig 1991), simulation modeling has become the method of choice for management problems (Simberloff 1988). It is hard to provide a general formulation for this approach because it depends on the simulation model chosen.

The primary shortcoming of this approach is, of course, that the outcome is only "the best" alternative from among the landscape layouts investigated. Even with a large number of layouts, near-optimality is not assured. To demonstrate the point, suppose we have 100 land units (for example, in a 10×10 grid). Even if we must consider only one action (versus none), with no scheduling component, there are still 2^{100} or 1.2676×10^{30} possible spatial layouts. Even if 99.9999999 percent (all but a trillionth) of the layouts can be eliminated as undesirable, we still have 1.2676×10^{21} options. Even if there are a trillion layouts that are acceptable, we only have a 7.886×10^{-13} ($1 \times 10^{9} \div 1.2676 \times 10^{21}$) chance of hitting an acceptable

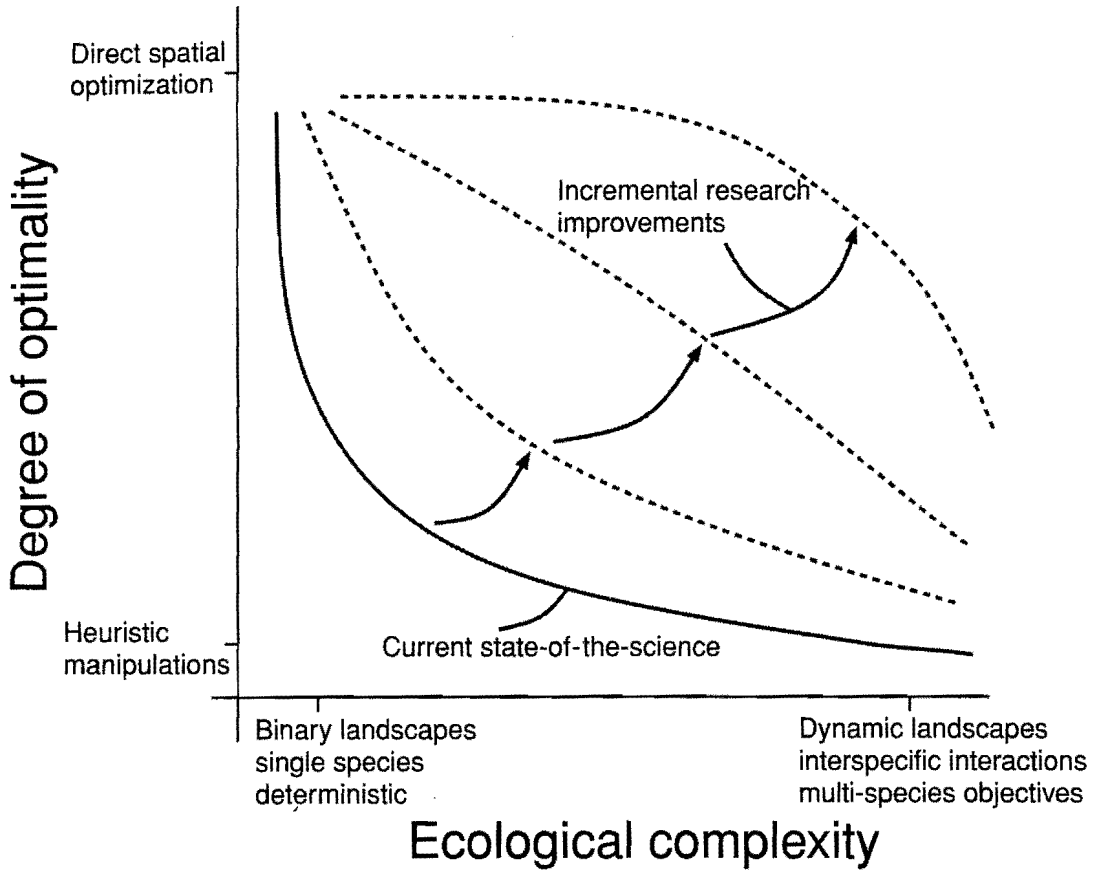

FIGURE 8.1
The trade-off between degree of optimality assured and the ecological complexity captured

solution if we randomly arrange our management actions. This suggests the need for optimization procedures in all but the simplest spatial problems. In addition, the implicit response surface may or may not be convex, such that a solution that appears to be near-optimal may actually not be at all.

Thus, the choice is between a precise optimum to a simplified model and an approximate optimum to a more precise model. Figure 8.1 depicts this trade-off and how it might change as progress is made in this research area. We have previously drawn the analogy between these two alternatives and the two alternatives faced early in the US space program between the X-15 plane and the Mercury program rocket as the direction for future manned space exploration (von Braun *et al.* 1985). The simulation approach, like the Mercury rocket, can do more immediately (especially in terms of ecological complexity and uncertainty). The closed-form optimization, however, is more like the X-15 plane in that it is of the basic structure that we would eventually like to get to (it finds global optima and is of the mathematical form that most closely captures the concept of landscape pattern optimization in the first place). Like the choice

faced by the US space program, it is really hard to say which approach might be the most fruitful in the long run, and both are probably worth researching until proven otherwise. In a given planning application, the answer may depend on the questions being asked and the circumstances surrounding the planning problem. For example, habitat placement choices may be limited because the pattern of land development has reduced the configuration possibilities (Saunders *et al.* 1991). When habitat-placement options are restricted to a small set, simulation modeling may offer a very useful approach for ranking alternative configurations. If, however, placement choices are numerous, then formal spatial optimization may be more useful in determining a layout that really is "the best" given the objectives and constraints of the planning problem. Joint use of both strategies as in Hof and Raphael (1997) or Haight *et al.* (2002) might offer planners the opportunity to take advantage of both the ecological detail captured by simulation models and the analytical power of formal spatial optimization to select the best solution.

A very pragmatic version of the heuristic approach that is commonly applied is to use simulation modeling to evaluate population response to alternative landscapes a posteriori. Management choices are thus made by ranking a small number of landscape alternatives according to some criterion (e.g., organism abundance, persistence) and selecting the strategy that ranks highest. This use of simulated predictions in conservation planning has been termed "relative ranking" by Turner *et al.* (1995) and is a form of prescriptive planning because the result specifies a habitat arrangement that will "best" address some set of management objectives. This approach is severely limited (as just discussed) by the small number of landscape layouts investigated (Conroy 1993).

8.3 Critical research questions

It should be fairly clear from the preceding section that the state-of-the-science in optimization of landscape pattern borrows heavily from the operations-research or management-sciences fields. Thus, ecology in general and landscape ecology in particular could probably benefit from more utilization of management-science methodology. It should be pointed out that the flow of knowledge also goes the other way. The study of natural processes has inspired several heuristic procedures in optimization. In particular, a class of heuristic solution algorithms called "genetic algorithms" (Reeves 1993) solves mathematical programming problems by emulating evolutionary processes. In the heuristic search, new trial solutions are created by "mating" previous solutions so as to emphasize positive traits much like natural selection promotes evolution in natural systems. Another example is "simulated

annealing" (Reeves 1993) which was originally developed to simulate the annealing process of cooling metals, but which is now commonly used as an optimization search routine. There is sufficient interest in this line of thought that an advertisement appeared in OR/MS Today (April 1999), the online version of the INFORMS magazine of the Institute for Operations Research and the Management Sciences, for an endowed chair in industrial and systems engineering at a major university that focused on "the design of sustainable man-made systems drawing upon understanding of efficiencies of natural systems" and "the introduction of efficiencies from natural systems to industrial operations." At any rate, our focus here is on the application of optimization to manage natural systems (and not the other way around).

8.3.1 Randomness

The most glaring weakness in the state-of-the-science in spatial optimization is in the treatment of stochastic variables. In Hof and Bevers (1998), we treat randomness with "chance constraint" formulations that assume normal distributions, and knowledge of the means and variances for all random variables (as well as the spatial covariances between them). With knowledge of random variable distributions, stochastic programming as well as Monte Carlo and other numerically intensive approaches may show promise in both evaluating the impact of risk on optimization model solutions and in modifying those solutions to better account for the randomness in the systems being modeled. This knowledge allows rigorous analysis of random variables, but we must admit that it is rarely available in real-world resource management and planning problems.

In order to discuss the less rigorous possibilities, let us make sure that a few definitions are clear. Under conditions of "risk," we face randomness in the systems that we must manage, but we have knowledge of the probabilities of the possible outcomes, and we know the effects that our alternative courses of action have on those probabilities. Under "uncertainty" we do not know the probabilities or the effects of our potential actions on those probabilities. And, there is a third condition, usually referred to (rather unsympathetically) as "ignorance," where we do not even know what outcomes are possible with our alternative courses of action. Obviously, uncertainty is more difficult to deal with than risk, and ignorance is more difficult than uncertainty. Analytical approaches are quite potent in managing risk, but are less so with uncertainty and ignorance. Stochastic programming, Monte Carlo simulations, expert systems, etc. all need information on probabilities of outcomes in order to manage randomness rigorously. The fundamental research problem for landscape (and other) ecologists is to reduce ignorance and uncertainty, but we often must

manage systems that are inherently stochastic so that the best we could ever hope to do is convert ignorance and uncertainty into risk. At least, if the problem can be so-reduced, it is conducive to rigorous analysis. Under conditions of significant uncertainty or ignorance, there is really not very much that can be done analytically to spatially optimize landscape pattern.

The best that can probably be done from a management viewpoint is to diversify the land management portfolio in the short term, and use that as a start to an adaptive management process (Walters and Holling 1990) in the long term. This approach is quite analogous to how a portfolio manager diversifies a client's investments in order to reduce the chance of a catastrophic loss. The two basic principles of diversifying a land management portfolio in the short term are: (1) within areas that are subject to the same random events, we should do different things that will respond differently to those random events, and (2) when we do the same things in different areas, we should do them far enough apart that they are subject to different random events.

In both cases, the objective is to reduce the random variability of system response by diversifying what we are doing across elements that are relatively noncovariant (that have covariances that are smaller than the variances of the individual elements). We can dó this (imperfectly) without knowing the actual variances or covariances, but just knowing that landscapes are spatially autocorrelated, such that areas are more independent the farther they are away from each other. This diversification also presents a good beginning for an adaptive management process where we use management actions as experiments so as to learn more about the systems that we are managing. By diversifying our approach to management, we will learn more, sooner. It will be critical that monitoring systems be put into place if we are going to learn anything from these "management experiments" (monitoring will be discussed as a separate research need below). With this approach, we will adapt our management strategy as we go along, learning what we can in a continuous process. Thus, research is integrated with management in this approach to dealing with uncertainty and ignorance.

8.3.2 Organism movement

The second most obvious set of research questions emanates from the most fundamental reason that spatial pattern matters in ecological systems – the fact that organisms move around on the nonhomogeneous landscape. The recognition that environmental heterogeneity and organism movement (in particular organism dispersal) interact to affect population dynamics has been key to what Turchin (1998) called a ". . . paradigmatic shift from the aspatial equilibrium view . . . to a spatially explicit view." Unfortunately,

organism movement is poorly understood and is an extremely difficult area of empirical research (Clobert *et al.* 2001), particularly at the landscape scale (Harrison and Bruna 1999). It may seem trivial to highlight species movement as a knowledge gap given its oft-cited importance, but we would be remiss not to emphasize the need for more empirical data regarding how (e.g., random or biased diffusion), when (e.g., what ecological conditions promote dispersal), and to what degree (e.g., how often and how far) species move in landscapes.

Techniques for studying animal movement are less well developed than are methods for estimating demographic parameters (Turchin 1998). Choice of methods will depend to a large degree on whether one needs to quantify the movement paths or simply the population-level pattern of redistribution. The kind of movement data required will be dictated by the information needed to address the planning problem. For example, quantifying species-specific search rules used to locate vacant territories would require information on the actual movement paths taken by individual organisms. Alternatively, estimating the distribution of dispersal distances or the resistance of the interpatch environment to movement may only require information on the rate and directionality of population spread. Turchin (1998) and Clobert *et al.* (2001) provided a comprehensive review of data collection and analysis methods that are appropriate for both types of questions.

Although the use of new approaches to study species movement will extend our abilities to prescribe landscape configurations, the spatial and temporal extent of conservation plans often make it very difficult to detect population response, replicate conservation treatments, and identify mechanisms underlying population change. These problems pervade empirical testing of conservation plans and they have been addressed with several atypical research protocols. Carpenter (1990) reviews pre- and post-treatment time-series analyses to infer nonrandom change in system response. Similarly, Hargrove and Pickering (1992) outline the use of "quasi-experiments" to take advantage of natural disturbances that alter habitat configuration. An approach directed specifically at increasing replication is to repeat unreplicated studies in different systems (Carpenter 1990). Such an approach can be approximated by accumulating the efforts of others and analyzing independent research efforts with meta-analysis procedures (Arnqvist and Wooster 1995). And again, where replication and experimental controls within the planning problem are feasible, active adaptive planning (Walters and Holling 1990) could provide opportunities for stronger inferences from management experiments.

8.3.3 Monitoring of spatially explicit plans

Even if landscape planners had access to complete information on species movement, a more fundamental empirical gap is the paucity of tests

of spatially explicit conservation plans. An especially critical need is for well-designed and active monitoring programs that are linked to plan implementation. Monitoring information is needed to assess the success or failure of a given plan, to test basic ecological concepts upon which the plan is based, and to identify the mechanisms underlying population response to habitat prescriptions (Hansson and Angelstam 1991). For example, critical thresholds have been demonstrated theoretically, but there have been very few attempts to establish the existence of critical thresholds in field studies of species distribution and abundance (but see With and Crist 1995 and Trzcinski *et al.* 1999).

Regardless of the protocol used, it is critical that a more concerted effort be directed at designing and implementing monitoring strategies that allow conservation plans to be tested (Havens and Aumen 2000). Because long time periods are required to quantify species response to modified landscapes, researching the relative merits of alternative monitoring designs will be difficult. Wennergren *et al.* (1995) offer an intriguing suggestion for researchers – use spatially explicit population models to test the ability of alternative monitoring designs to predict the consequences of habitat layouts prior to implementing them in the field. Failure to devote more effort toward monitoring will perpetuate our current reliance on untested concepts and will heighten the contention and uncertainty that surrounds the use of planning models to derive spatially explicit habitat prescriptions.

8.3.4 Multiple species/community level models

Another important theoretical gap concerns how one prescribes habitat layouts that are relevant to the broader species assemblage occupying the landscape. The discussion above was limited to the response of individual populations to varying habitat arrangements, avoiding the issue of conflicting habitat requirements among multiple species. Even if planning models could be developed for some suite of species inhabiting the planning area, the feasibility of deriving habitat prescriptions that are relevant to the group is questionable due to species interactions. The extension to biodiversity conservation as a whole is even less clear (Turner *et al.* 1995).

Moving from single-species to multi-species conservation planning is certainly difficult and we know of no definitive strategy. One approach that has emerged repeatedly is the use of indicator species (related incarnations include keystone, umbrella, or focal species) to reflect the status of the overall species assemblage. Unfortunately, indicators are often chosen opportunistically (e.g., well-studied and well-surveyed taxa). Tests of this strategy using broad taxonomic groups (e.g., birds, mammals, butterflies) have not supported its general applicability (Flather *et al.* 1997). However, rejection at broad taxonomic levels should not preclude the search for indicators among finer sets

of species. MacNally and Fleishman (2002) are developing statistical modeling approaches to defining efficient sets of indicator species within taxonomic groups (e.g., butterflies) that are showing promise, at least among butterflies. A more refined search to identify life-history attributes that could serve to group species based on critical vital rates (e.g., reproductive potential, dispersal ability) may offer an alternative approach to defining indicators because species that share similar life histories may respond to habitat geometry in a similar fashion (see Noon *et al.* 1997). In a slight variation of this approach, mathematical taxonomy and ordination techniques (Gauch 1982) could be used to define clusters of species based on measured life-history attributes such that the species pool for a given planning area is partitioned into sets that may be similarly sensitive to habitat arrangement effects.

8.3.5 Synthesis

Even though theoretical developments in spatial ecology are relatively recent, theoretical research on the concepts reviewed in this chapter has far outpaced empirical research. The disparity between theory and empirical research has resulted in a baffling array of models and results that can appear contradictory to conservation planners (de Roos and Sabelis 1995). Consequently, the lack of theoretical synthesis is an important knowledge gap hindering the application of these concepts in conservation planning. There is a need to summarize how different modeling approaches and parameterizations affect habitat prescriptions so that domains of applicability can be recognized by those who develop and implement conservation plans. In the absence of a more comprehensive synthesis, landscape planners will continue to be reluctant to implement the habitat prescriptions derived.

Although synthesis may lack the intellectual excitement associated with new theoretical developments, it is nonetheless important. We identify two broad approaches to theoretical synthesis. The first is through structured reviews of the literature. This will not be an easy task. There are numerous nuances to spatial planning models that can quickly overwhelm attempts to distill rules for application (de Roos and Sabelis 1995). It is not uncommon for models of similar ecological phenomena to reach divergent conclusions (e.g., compare the conclusions reached by Hill and Caswell 1999 and Fahrig 1998 regarding the importance of habitat arrangement in facilitating population persistence). Part of the problem is that both structure and parameterization differ among models, making it difficult to determine what is causing the variability in model results. It is this complexity that may render traditional narrative reviews for theoretical synthesis flawed, suggesting that the more structured analyses formalized in meta-analysis might be better suited to

identifying common patterns among published models (Arnqvist and Wooster 1995).

A second approach to synthesis involves the systematic manipulation of specific models using sensitivity analysis (Conroy *et al.* 1995). This would involve the quantification of model response following purposeful and systematic alteration of model parameters (singly and in combination). Comprehensive exploration of model behavior under a wide range of ecologically relevant parameter settings is important for at least two reasons. First, it can help identify those aspects of species life history or habitat arrangement that are critically important for understanding population response to landscape changes. Second, it can determine whether there are fundamental shifts in habitat arrangements in response to relatively small changes in the parameter space.

8.4 Conclusion

The most fundamental research need in optimizing landscape pattern is the ability to better capture the relevant ecological relationships in an optimization analysis. The other chapters in this book provide summaries of the state-of-the-science in the most important research areas in landscape ecology. Thus, an appropriate concluding remark would be that research in spatial optimization of landscape pattern should strive to capture the state-of-the-science described elsewhere in this book, wherever appropriate. Also, the other chapters identify the most pressing research questions in landscape ecology, so obviously the future challenge will be to continue to capture this landscape ecology research in spatial optimization models.

A natural reaction to the idea of optimizing spatial pattern across a landscape is that we simply do not know enough about ecological systems to actually optimize them. Indeed, we will probably never know as much about ecology as we would like to. Our reaction is that it is important to apply spatial optimization in the context of an adaptive learning process (as we have noted previously). We will probably never have a level of knowledge that is adequate to find a permanent optimal strategy for a managed ecosystem in a one-time optimization analysis. On the other hand, an adaptive management process that does not take advantage of optimization methods is much less likely to make progress either in learning about the ecological system or in managing it.

Applied in a careful, learning process, spatial optimization of landscape pattern has the potential to illuminate new hypotheses for landscape ecology research as well as providing a mechanism to apply landscape ecology research in landscape management. We will close this chapter as we began it, with a quote from Wu and Hobbs (2002): "Research into the spatial optimization

of landscape pattern . . ." as it relates to ecological structure (e.g., species distribution, community composition) and function (e.g., disturbance spread, species dispersal) across landscapes, ". . . presents a new and exciting direction for landscape ecology." We definitely hope so.

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