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The Roles of Spatial Heterogeneity and Ecological Processes in Conservation Planning

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Abstract

In this chapter we ask the question: To what extent does an understanding of landscape spatial heterogeneity inform conservation decisions? We answer this question in the context of two central decision-making fields within conservation biology: systematic conservation planning and population viability analysis. The conservation planning principles of comprehensiveness and representativeness are fundamentally reliant on data and concepts of compositional landscape heterogeneity. The principle of adequacy is not accommodated in conservation planning very well and it relies on an understanding of the configurational heterogeneity of the landscape. A major challenge for conservation planning scientists is to develop theory and decision support tools that incorporate ideas of population viability and spatially explicit ecological processes. Population viability analysis invariably includes spatial population processes, and as a field has largely focused on the importance of the configurational heterogeneity of landscapes. We argue that this focus might only be justified when the scale of planning coincides with either the scale of habitat heterogeneity or the scale at which small populations operate. Integrating population viability analysis into conservation planning, and showing a balanced interest in compositional and configurational heterogeneity, are important future challenges.

Introduction

Ecological heterogeneity comes in many forms ranging from the biophysical to the ecological. Substrates like soil type are highly variable but relatively static on an ecological time frame. Other aspects of heterogeneity, for example species distributions and ecological processes, can exhibit greater temporal variation. There are two components of heterogeneity: composition and configuration. Compositional heterogeneity refers to the number

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of different elements in the landscape, and configurational heterogeneity refers to the spatial arrangement of these elements. The elements can be discrete (patches) or continuous (gradients). We discuss two areas of application: systematic reserve system design and population management using population viability models.

In the field of reserve system design, the overall objective is to create a system of protected areas that conserves as much of a region's biodiversity as possible in the long term (McNeely 1994). To do this we first need to sample as much of the biodiversity as possible. Hence, an understanding of compositional spatial heterogeneity is absolutely central to reserve system design. In contrast, the role of configurational spatial heterogeneity is discussed, but poorly dealt with, in the systematic conservation planning literature.

The only way we know how to determine the adequacy of a reserve system is to assess the viability of key species. Population viability analysis (PVA) is a tool for choosing between different management options for threatened species. Traditionally, PVA has dealt with compositional heterogeneity by assuming there are only two habitat types: suitable and unsuitable. This is clearly inadequate as habitat quality will, in general, vary continuously (Franklin this volume). Configurational heterogeneity is believed to be important to the viability of populations, but the evidence is equivocal (Fahrig this volume). Ultimately good conservation planning will involve a marriage of reserve system design principles and population viability principles.

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For both reserve system design and population management, we postulate that spatial heterogeneity is relatively unimportant to conservation decision-making when the spatial scale of management (the spatial extent of typical planning actions or reserves) is significantly different to the spatial scale of the underlying heterogeneity or the population processes of the species of concern. We suggest that spatial heterogeneity is most important when its scale of variation is roughly the same as the scale of management *and* the scale of population and other ecosystem processes.

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In this paper, we will (1) describe the general reserve system design problem, (2) look at how heterogeneity at different scales has or could influence reserve system design, (3) consider the role of spatial processes in reserve system design, (4) examine how spatial heterogeneity at different scales influences conservation plans derived from population models, and (5) present an initial general framework for how we might deal with heterogeneity considerations in conservation planning.

The General Reserve System Design Problem

In its broadest sense, conservation planning is about allocating parts of a landscape to a management regime. For example, in forestry we could allocate any 50-ha compartment to one of the following: no harvesting, no harvesting and predator control, selective harvesting, clear-fell at 30-year rotation for

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woodchips, clear-fell at 70-year rotation for construction timber, conversion to native plantation, conversion to exotic plantation, or conversion to infrastructure (buildings, mills, houses). In the narrow sense, only the first two treatments would be a necessary, but not sufficient, to allocate a compartment to a reserve system. Here we will consider the more restricted question of reserve system design where parcels of land are selected for the reserve system.

The overall objective of reserve system design is to create a system of protected areas that conserves as much of a region's biodiversity as possible in the long term. To do this, we first need to sample as much of the biodiversity as possible. A simple solution is to select every parcel for the reserve system. Clearly, this is socially and economically infeasible in most regions so we add an additional objective, that of efficiency. Our economically prudent objective is to conserve as much biodiversity as possible in the long-term as efficiently as possible.

Three further notions are important here: comprehensiveness, representativeness, and adequacy (Margules and Pressey 2000). A comprehensive reserve system is one that captures every known element of biodiversity. Given our interest in efficiency, we can only hope to sample each element and we should do that in a representative fashion (i.e., the set of samples that capture each element of biodiversity should be "typical" or representative). The adequacy of a reserve system refers to how well it meets the management goal of preserving biodiversity in the long term.

These concepts define the classical reserve system design problem—referred to as "gap analysis" in the United States (Scott et al. 1993) and a "CAR reserve system" (comprehensive, adequate, and representative) in Australia (JANIS 1997). In this classic form, conservation planners take whatever data they have on any aspect of biodiversity (e.g., species distributions, habitat types, land systems) and seek to represent a fixed proportion of the original extent of each of these features in a reserve system (Margules and Pressey 2000). In this sense, conservation planning is highly reliant on patterns of heterogeneity, especially those that appear to be invariant in the short term (e.g., vegetation types, altitude, soil type, etc). Although spatial heterogeneity in species distributions and habitat types is commonly measured in landscape ecology (O'Neill et al. 1988; Haines-Young and Chopping 1996; Gustafson 1998; McAlpine et al. 2002; McGarigal, 2002), within-feature variation, which should be dealt with under the conservation planning principle of representativeness, is rarely explicitly considered in reserve system design. So that we can explore the role of spatial heterogeneity at different spatial scales in reserve system design, let us formulate the problem mathematically and consider a specific example.

The Basic Reserve Design Problem

Let the total number of sites that could be in the reserve system be m and the number of features (e.g., species, vegetation types, etc.) be represented

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by n . The information about whether or not a feature is found in a site is contained in a site-by-feature ($m \times n$) matrix \mathbf{A} whose elements a_{ij} are

$$a_{ij} = \begin{cases} 1 & \text{if feature } j \text{ occurs in site } i \\ 0 & \text{otherwise} \end{cases}$$

for $i = 1, \dots, m$ and $j = 1, \dots, n$.

Next, define a control variable (the part of the system that we control), that determines whether or not a site is included in the reserve system, as the vector \mathbf{X} with dimension m and elements x_i , given by

$$x_i = \begin{cases} 1 & \text{if site } i \text{ is included in the reserve} \\ 0 & \text{otherwise} \end{cases}$$

for $i = 1, \dots, m$.

With these definitions, the basic minimum representation problem is

$$\text{Minimize } \sum_{i=1}^m x_i \quad \{\text{minimize the number of sites in the reserve system}\}$$

$$\text{subject to } \sum_{i=1}^m a_{ij} x_i \geq 1, \text{ for } j = 1, \dots, n$$

{subject to each feature being represented at least once}

where $a_{ij}, x_i \in \{0,1\}$.

This is the integer linear programming formulation of the set-covering problem (Possingham et al. 2000). In many cases, the feature by site data is not simply zeros and ones, but could represent the number of occurrences of the feature in the site, the estimated population size of a species, or the area of a feature like habitat type. In this case, the targets for each feature are likely to be different from one. However, the basic structure of the problem remains unaltered. The key issue is that this basic approach does not explicitly deal with representativeness because we do not know if the sites captured to meet a target for a feature are representative, or typical, of that feature. To explore these ideas, let us consider a particular example.

Consider a planning area with 16 sites and 5 different features (Figure 19.1a; Table 19.1). Figure 19.1 shows the spatial location of the five features, two of which are species, represented by point data, and three of which are habitats that are mutually exclusive and cover the entire planning area. Each of the 16 sites may, or may not, be selected for the final reserve system. Table 19.1 captures all the information in the map except it ignores spatial relationships between both the sites and the habitats. Our task is to comprehensively represent each of the five features in the reserve system as efficiently as possible.

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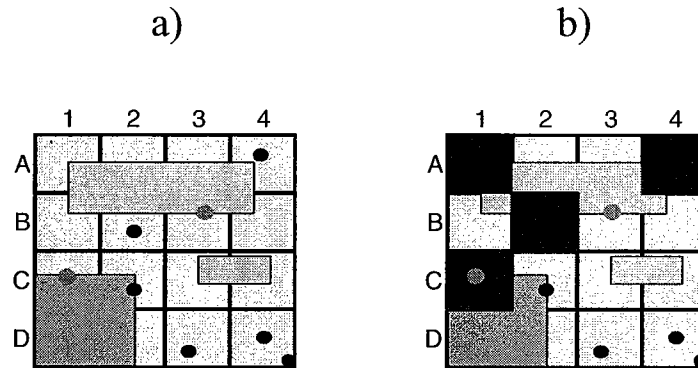


FIGURE 19.1. (a) A hypothetical planning area with 16 sites; the grid cells A1–D4. The polygons of different sizes and textures represent three different habitat types, and the black and gray dots represent populations of two species. (b) The most efficient solution that meets a 25% target coverage of each feature is highlighted by the black squares (A1, A4, B2, C1). See Table 19.1 for a representation of the map as a data matrix.

TABLE 19.1. The amount of each feature in each planning unit, and overall conservation targets, for the planning landscape described in Figure 19.1.

Site code	Features				
	Habitats			Species	
	Dash	Stripe	Dots	Gray	Black
A1	20	0	80	0	0
A2	50	0	50	0	0
A3	50	0	50	0	0
A4	15	0	85	0	1
B1	15	0	85	0	0
B2	40	0	60	0	1
B3	40	0	60	1	0
B4	10	0	90	0	0
C1	0	60	40	1	0
C2	0	30	70	0	1
C3	25	0	75	0	0
C4	35	0	65	0	0
D1	0	100	0	0	0
D2	0	50	50	0	0
D3	0	0	100	0	1
D4	0	0	100	0	2
Total	300	240	1060	2	6
25% Target	75	60	265	1	2

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Much has been written about this sort of problem. However, most authors have focused on issues such as the efficiency and speed of algorithms to solve the problem (Pressey et al 1997), whether certain types of feature can act as surrogates for other types of feature (e.g., if we conserve a sample of all habitat types will that guarantee conservation of all species; Ferrier and Watson 1996; Andelman and Fagan 2000; Ferrier 2002), and whether the reserve system is adequate in the long term (Cabeza and Moilanen 2001). We will consider a different issue and use this example to explore the role of spatial heterogeneity in reserve system design.

Because our discussion of the role of spatial heterogeneity will be couched in the context of efficient solutions to the reserve design problem, we will first need to determine what those efficient solutions are, given the data at hand. If our goal is to conserve at least one example of each feature, the classical minimum set problem, then there are several equally efficient two-site solutions to the problem displayed in Figure 19.1. For example, solution sets with two sites that meet the five targets for single representation include {B2, C1} and {C2, B3}. If we want to conserve at least 25% of the original extent of each feature, then there is only one most efficient reserve system comprising four sites {A1, A4, B2, C1} (Figure 19.1b). We will use this small sample problem to explore the role of spatial heterogeneity and the conservation of ecological processes in reserve system design.

Reserve System Design and Static Spatial Heterogeneity

Scale of Habitat Mapping

Habitat mapping is scale dependent (Davis et al. 1991; Franklin and Woodcock 1997). Exactly how many types of habitat (ecoregion, land system, vegetation) an ecologist chooses to define depends on the spatial scale at which they are working and the intended application of the data. If heterogeneity is mapped at a very coarse scale, then what appears to be a single habitat may indeed be several different habitats. For example, the striped habitat in Figure 19.1 is conserved by selecting site C1, but is this a representative sample of the striped habitat? If we look more closely, the striped habitat may comprise several types of habitat or it may contain a feature, like small rocky outcrops, that is not mapped. If those types and/or features are well mixed throughout the striped habitat (i.e. they display fine scale patchiness), then we may not miss our 25% target for each type of feature by much (Figure 19.2a). If however they display coarse-grained patchiness, then site C1 will fail to represent the variability in the striped habitat by a long margin (Figure 19.2b). This results in the selection of an unrepresentative sample of habitat and is a consequence of unmapped compositional heterogeneity.

For conservation planning, we can minimize this problem by mapping different features, such as drainage lines or rocky outcrops, at the finest scale

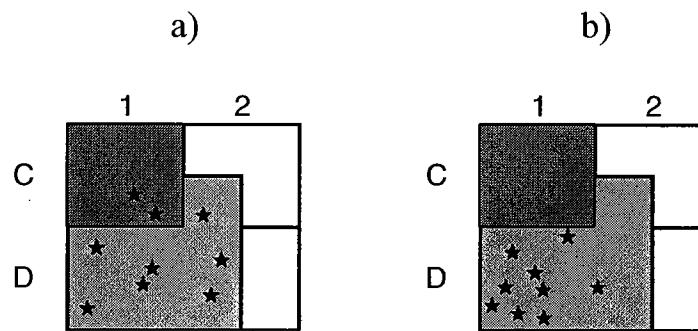


FIGURE 19.2. Enlarged section of Figure 19.1 (C1–C2–D1–D2) illustrating that (a) fine-scale or (b) coarse-scale patchiness in the location of rocky outcrops (stars) in the striped habitat affects our ability to represent this feature in a reserve planning exercise, because the compositional heterogeneity at that fine a scale is unmapped.

required. Where this is not possible, then data on biophysical features (e.g., altitude, aspect, soil type) should be combined with habitat maps to create more fine-scale heterogeneity in order for the heterogeneity to be sampled in the reserve system. This partitioning of habitats into smaller classes is facilitated by the ability of our software tools, such as geographical information system (GIS) software tools, to support different geographical data models (*sensu* Goodchild 1994), and by the use of hierarchical systems of habitat classification (Bailey et al. 1994; Küchler and Zonneveld 1988). However, it can also present a challenge because classification systems that are nested categorically do not necessarily correspond to mapped entities that are nested spatially (reviewed in Franklin and Woodcock 1997). Further, despite the proliferation of spatially referenced environmental datasets (Estes and Mooneyhan 1994; Franklin 2001), spatially explicit information on fine-scale habitat features for large regions can still be difficult (and/or expensive) to develop (e.g., Elith and Burgman 2002). From this example and discussion we can conclude that spatial compositional heterogeneity at all scales is important for conservation planning, and the issue of conserving representative samples of biodiversity features remains challenging.

The Scale of Conservation Planning Units

Although maps of biodiversity features at appropriate scales may not be as ubiquitously available as we may wish, a further issue is that the scale and positioning of the planning units (sites) used in reserve design is often quite unrelated to the underlying spatial heterogeneity. The planning unit layer may be imposed by external socioeconomic considerations—such as property boundaries—or it may be simply a “convenient” tessellation of the planning region. Limitations on algorithms to find good solutions to conservation

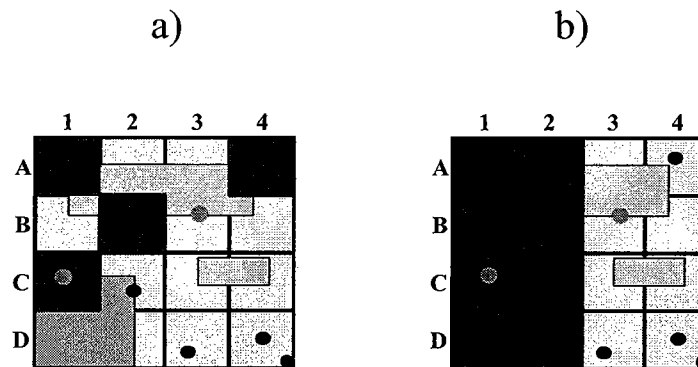


FIGURE 19.3. Optimal solutions to the reserve design problem where the planning units are defined at two different scales. (a) The same optimal reserve system for conserving 25% of every feature as in Figure 19.1. (b) The optimal reserve system for the same problem but where planning units are four times bigger, an increase in linear scaling of a factor of two. The result is reduced efficiency. See the legend of Figure 19.1 for feature descriptions.

planning problems means that tessellations with more than 100,000 planning units can be computationally difficult (although continual advances in speed and storage space of desktop computers mean this approximate upper bound is continually relaxed). This computational consideration often fixes the scale of the planning units, which in turn impacts the efficiency of solutions. For example, if the size of planning units was four times bigger in our example (Figures 19.1b and 19.3a), the most efficient solution would involve selecting 50% of the planning region, rather than 25% (Figure 19.3b).

Although an increase in the size of planning units will always make the reserve system less efficient, a coarser planning unit scale has two benefits (Pressey and Logan 1998): the reserve system is more cohesive, and the problem of representing hidden habitat and feature heterogeneity is reduced. To overcome the fragmented nature of reserve systems designed using fine-scale planning units, and thus address landscape configuration explicitly, several researchers have devised ways of incorporating spatial cohesion into the reserve design problem and have developed algorithms that implement these solutions (Bedward et al. 1992; Possingham et al. 2000).

Spatial Design in Conservation Planning

A major problem with the basic reserve design problem is that it relies only on the data in a matrix (Table 19.1) that ignores spatial relationships between planning units and hence it ignores configurational spatial heterogeneity. One solution to this problem is to include information about spatial relationships by using the boundaries that sites share with each other. The boundary length of a reserve system is an important part of the cost of

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managing that system, so it makes sense to make the boundary length as small as possible. Reducing boundary length reduces the impact of edge effects and reduces fragmentation, both of which are core conservation planning principles (Noss and Csuti 1994; Fagan et al. 1999). To include boundary length in the problem we can amend the objective in the basic reserve design problem to be a weighted sum of the number of sites selected and the boundary length of the entire reserve system

$$\text{Minimize } \sum_{i=1}^m x_i + (\text{BLM} \times \text{the boundary length of the system})$$

(which means minimize the number of sites in the reserve system and add a constant, BLM, multiplied by the boundary length of the system; Possingham et al. 2000).

If the parameter BLM (acronym for boundary length multiplier) is large, then the emphasis will be on reducing the boundary length of the reserve system. If the BLM is relatively small, then the reserve systems will have a small area with compactness given secondary consideration. For example, in our sample problem the optimal solution had four sites with a boundary length of 16 units (Figures 19.1b and 19.4a). Two solutions with one more site (less efficient in terms of the area) but with a boundary length of only 10 (more efficient from the perspective of boundary length) can be found (Figures 19.4b and 19.4c). The best solution will depend on the relative costs of boundary length and area. In practice, some method of making the reserve system spatially cohesive at a relevant management scale is essential.

Adding a consideration of reserve system boundary length in the reserve design problem is only one of many ways that space can play a role in conservation planning. Allowing for connectivity and minimizing different measures of isolation can also be included. For example, Siitonen et al. (2002) considers three measures of connectivity: the total continuous area

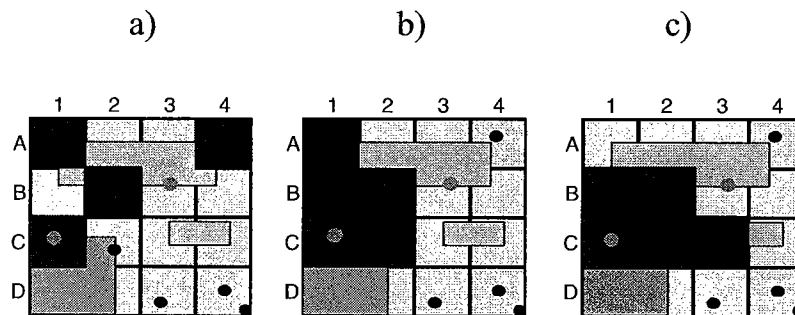


FIGURE 19.4. Three solutions to the reserve design problem where the planning objective differs. In solution (a), the focus is on minimizing area, whereas (b) and (c) are two different solutions for minimizing boundary length. See the legend of Figure 19.1 for feature descriptions.

of a single reserve, the level of isolation of that reserve from other reserves, and a measure of connectivity that assesses the size of a cluster of reserves considered to be sufficiently close to be deemed “connected.” One problem with these measures and the boundary length approach to achieving compactness and connectivity is that none are explicit about why we value compactness and/or connectivity. Ideally, the objective of the conservation planning problem would be to optimize a direct functional relationship between species viability and landscape spatial pattern. This is an active area of research that should allow more explicit configurational objectives to be incorporated into conservation planning (Frank and Wissel 2002).

Reserve System Design and Spatial Processes

Although the previous section provides insight into how issues of spatial heterogeneity can play a role in reserve system design, the focus was on pattern rather than process. There is an increasing desire to incorporate spatial processes explicitly into conservation planning, but there are few examples of this being achieved. Here we look at three situations where the boundary length problem formulation described above can be modified to take spatial processes in to account.

Consider the situation where we have data on the movement of organisms or propagules of an organism in space. Connectivity is a crucial issue in conservation biology and planning (e.g., Beier 1993; Schadt et al. 2002) and often the connectivity observed is directional. Assume that the sample planning region (Figure 19.4) is a marine planning region and prevailing currents are from left to right (west to east) (Figure 19.5a). Under this circumstance, we can see that the more compact reserve systems in Figures 19.4b and 19.4c are both preferable to the fragmented system. We also know

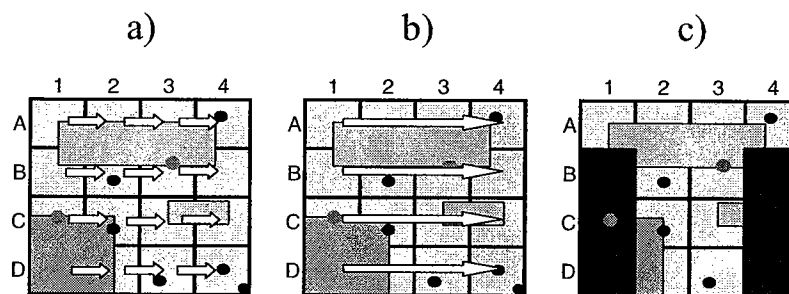


FIGURE 19.5. Two different sorts of connectivity between cells. In (a), connectivity is west-east to adjacent cells (arrows)—the solution displayed in Figure 19.4c is a good solution to this problem. In (b), propagules flow mostly to cells three sites to the east (arrows), and solution (c) is a good solution. See the legend of Figure 19.1 for feature descriptions.

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the reserve system solution in Figure 19.4c is better than that in Figure 19.4b because it has three internal boundaries that favor east-west connectivity rather than just two. If we allow the cost of free east-west boundaries that reduce connectivity to be more expensive than free north-south boundaries, then the solution in Figure 19.4c will automatically be favored over the solution in Figure 19.4b.

Having relaxed our thinking that the boundary length between two sites is the physical length of the boundary between two sites, we can now include a boundary length between any two sites in the system. For example, if we know that propagules tend to disperse three sites to the east, then we can make the “boundary length” between column 1 sites and column 4 sites large and all other boundary lengths small (Figure 19.5b). In this case, the best reserve solutions should preferentially contain sites from columns 1 and 4 if they are in the same row (Figure 19.5c).

By modifying our interpretation of what a boundary is, we can see that connectivity issues can be formulated and solved in the context of the reserve design problem. This can be achieved by describing spatial relationships between cells using “boundary lengths” that measure how favorable connections are. In essence, we have placed a cost on each site being included in the reserve system, which is reduced each time a connected site is also included in the reserve system. There are many other ways in which this could be mathematically formulated; for example, we could list pairs of sites that are favorably connected for every species and have a target for the number of favorable connections included in the reserve system for each species. We can also incorporate propagation of unfavorable spatial processes; for example, fire may preferentially move north-south across the region. If we were to spread the risk of a reserve system being affected by a single fire—risk spreading—we could put a low cost on north-south boundaries and hence favor reserve systems that are aligned east-west. The process of including spatially explicit ecological processes in reserve system design is in its infancy. Reiners (this volume) provides a detailed summary of the kinds of spatial processes that we could incorporate into conservation planning.

The full consideration of spatially explicit ecosystem processes in reserve system design will necessitate that objectives are set for the processes themselves. For example, if we know something about how land management influences the flow of nutrients through a system, or a population across a landscape, then such flows should be included in the problem formulation as part of the objective or as constraints. Although this has not occurred, we believe that such explicit incorporation of ecosystem processes into the conservation planning problem is the best way forward.

One of the most crucial processes to consider in conservation planning is spatial population processes; for example, the regular flow of migratory individuals or favored flows of natal dispersers. These need to be included in the design of reserve systems, as the issue of the long-term viability of

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species (or other features) within reserve systems that are commonly ignored. Interest in designing adequate reserve systems is increasing (Cowling et al. 1999; Cabeza and Moilanen 2001; Araújo and Williams 2000). Although a thorough discussion of the role of population modeling in conservation planning is beyond the scope of this chapter, we briefly raise some interesting issues with respect to the issue of compositional and configurational spatial heterogeneity.

Conservation Planning Based on Population Models

A properly posed reserve system design problem could include either an objective of minimum species loss or a constraint for every species to meet a specified level of viability. If we have an estimate of the number of individuals of each species in each site and we are willing to accept a target number of individuals as a surrogate for viability, then the reserve design problem remains unchanged (Pressey et al. 2003). However, a simple target number of individuals ignores the issues of fragmentation and connectivity discussed above, and we have no simple formula that adequately relates the configurational spatial heterogeneity of a reserve system to the viability of a species. In short, we have no adequate way of optimally designing reserve systems that incorporate the configurational aspects of population viability.

Population viability analysis (PVA) has been used to devise conservation plans for single species and to assess reserve systems and different sorts of landscape management (e.g., Lindenmayer and Possingham 1996). Typically, these models treat configurational heterogeneity by exploring the consequences of different patterns of just two habitats: suitable habitat and matrix habitat (Franklin this volume). The role of compositional heterogeneity with a landscape that is more than binary is less often explored, although interest in this topic is growing (Fahrig this volume).

Reviewing conservation planning using population models is beyond the scope of this paper. However, from a pragmatic perspective one question we can ask is: How often is configurational heterogeneity important to viability? In an extensive review, Fahrig (2003) suggests that the spatial pattern of habitat may rarely be important, and even where spatial pattern is a significant factor it is not always true that more fragmented systems decrease viability. So an interesting and important question is: When can we ignore spatial heterogeneity in reserve system design and still incorporate notions of viability?

In an extensive research program, Fox et al. (2004) developed population viability analysis models for 11 forest-dependent rare, threatened, or sensitive species in a forestry planning region in northeast Tasmania. The species vary from invertebrates to wide-ranging large birds, and from epiphytes to mammals. The project was designed to help Forestry Tasmania assess the viability of different species, given a range of region-wide forestry management

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scenarios including native forest harvesting and conversion of native forest to pine or eucalypt plantations. The scale of overall management is a region of about 200 km by 100 km, and the scale of operational management is a logging coupe (compartment)—about 50 ha. Intriguingly, they found that the configuration of the management was only important in one of the 11 species, and for most species simply determining the total amount of suitable habitat was sufficient to determine the viability of the species. It is worth briefly exploring why configuration was rarely important.

For wide-ranging mobile species like the Tasmanian wedge-tailed eagle, *Aquila audax*, and yellow-tailed black-cockatoo, *Calyptorhynchus funereus*—which can cross the management region in a few hours—management at the 50-ha logging unit scale is too fine to be of concern. Similarly, these species range so broadly that compositional heterogeneity is not important above and beyond the patch-matrix (uncleared-cleared forest) dichotomy. At the other end of the spectrum, with invertebrates such as beetles, each 50-ha logging coupe (area that is logged in a single event) is large enough to maintain such a large population that it is only activities at a small scale that matter. A study by Smith et al. (2000) investigated the importance of landscape configuration in a heavily forested area on the persistence of a rare carnivorous snail *Tasmaphena lamproides*. They applied a spatially explicit population viability analysis model for the species (Regan et al. 2001) to several spatial and temporal landscape configurations. They also found that at the management scale of 50–100 ha, the total amount of available habitat was sufficient to determine the species' viability and the spatial configuration was not important. These species see heterogeneity at the scale of meters. Subtle differences in forest type or other small-scale compositional heterogeneity can be quite critical, but the precise spatial relationships are unimportant because such large populations occur in small areas.

The only species for which configuration appeared to matter was the spotted-tailed quoll, which uses landscapes at the scale of a few hundred meters. This coincides with the scale of management and much of the compositional heterogeneity. Similar observations were made in a study by Smith (2000) who investigated, using population viability models, the impact of various landscape configurations and forest harvesting intensities on the persistence of two species (an invertebrate and a mammal) with vastly different life-history attributes, home ranges, and dispersal characteristics within the same landscape structure. Again, the management scale was approximately 50–100 ha. The persistence of the invertebrate was highly correlated with available habitat, while the mammal, although sensitive to available habitat, was also sensitive to changes in landscape configuration. Fahrig (1998) also predicted that habitat pattern can affect population persistence only at particular scales relative to the movement range of the organism.

These observations lead us to suggest a general framework for when we need to consider heterogeneity in conservation planning—when the scale of

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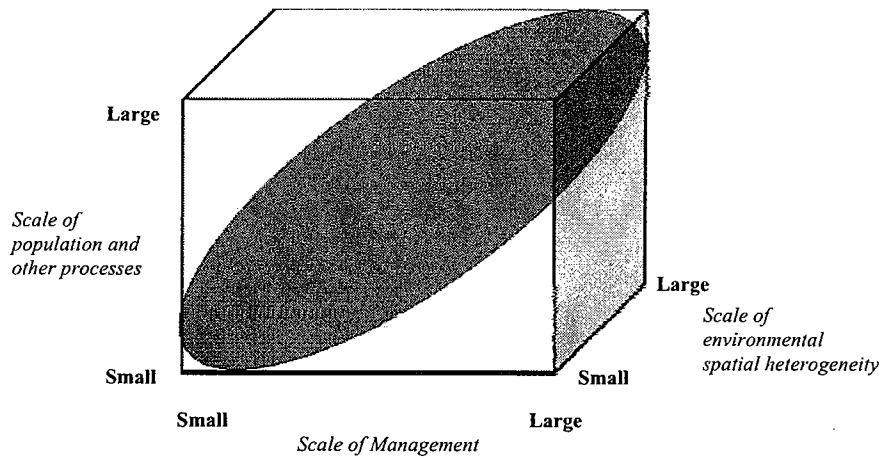


FIGURE 19.6. The circumstances where configurational heterogeneity is most important in applied conservation occurs when the scales of management, heterogeneity, and ecosystem/population processes overlap. This is found in the darker shaded region of the diagram.

management coincides most closely with the scales of spatial heterogeneity and the scale of population and ecosystem processes (Figure 19.6).

This finding is consistent with hierarchy and scaling theory (O'Neill et al. 1986; Levin 1992; Naveh and Lieberman 1994), which states that levels above the focal level of study in a (spatial, temporal, or organizational) hierarchy constrain and control the lower levels. The level below the focal level provides the details needed to explain the observed behavior of the system. The dynamics of the level above the focal level are so slow, or the spatial lag so great, that variables at that level appear constant from the perspective of the focal level. The dynamics or spatial variation at the lower level are so high-frequency that the average value is experienced at the focal level. Further, as elaborated in Turner et al. (2001), a shift in the relative importance of variables that influence a process, or even a change in the direction of the relationship, often occurs when scales are changed.

Finally, we note two recent developments in population viability analysis modeling that add important realism and will challenge our ability to understand complex interactions in a spatially heterogeneous world. First, there is increasing interest in models that expand on the patch-matrix dichotomy to include consideration of poor but suitable habitat that may, or may not, be a sink (Pulliam 1990). Weigand et al. (in press) and McAlpine et al. (submitted) have found that theoretically and empirically we sometimes need to pay attention to the spatial relationships between habitats of differing quality, not just within good-quality habitat. Second, population modelers have begun to incorporate habitat dynamics into population models (Amarasekare and Possingham 2001). This means that the compositional

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and configurational habitat heterogeneity can change through time, and the temporal patterns of configuration will become important. Under these circumstances, not only is the spatial scale of the disturbances crucial, but also how the habitat changes following those disturbances (Pickett and White 1985). Although simulation models easily incorporate patch and metapopulation dynamics overlaid on a landscape with several habitat types (Akçakaya et al. 2004), the real challenge will be developing a conceptual understanding of the whole system. This may require a complex system style approach where we seek generalizations, emergent properties, and convenient simplifications that enable us to disentangle the consequences of several spatially and temporally varying factors.

Conclusions

For conservation planning problems, there is an interplay of spatial scales that is rarely appreciated. The spatial scale of the planning unit, the underlying environmental heterogeneity, and spatially explicit ecosystem processes (including population connectivity) all interact. Although we are aware of these interactions empirically and theoretically, we are only just beginning to treat them explicitly in the more applied subfields of conservation biology, like reserve system design and population viability analysis. Understanding the importance of scale and heterogeneity in conservation planning is in its infancy. Solutions to the problems of dealing with spatial heterogeneity have been *ad hoc*; for example, by minimizing the boundary length of a reserve system. In particular, our capacity to deal with ecosystem and population processes is poorly developed. Adding compositional and configurational heterogeneity to population models is well advanced, but we have a limited conceptual understanding of the consequences of adding such complexity. This chapter has raised some of these issues and suggested some ways forward.

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