
The Application of Neutral Landscape Models in Conservation Biology

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Abstract: *Neutral landscape models, derived from percolation theory in the field of landscape ecology, are grid-based maps in which complex habitat distributions are generated by random or fractal algorithms. This grid-based representation of landscape structure is compatible with the raster-based format of geographical information systems (GIS), which facilitates comparisons between theoretical and real landscapes. Neutral landscape models permit the identification of critical thresholds in connectivity, which can be used to predict when landscapes will become fragmented. The coupling of neutral landscape models with generalized population models, such as metapopulation theory, provides a null model for generating predictions about population dynamics in fragmented landscapes. Neutral landscape models can contribute to the following applications in conservation: (1) incorporation of complex spatial patterns in (meta)population models; (2) identification of species' perceptions of landscape structure; (3) determination of landscape connectivity; (4) evaluation of the consequences of habitat fragmentation for population subdivision; (5) identification of the domain of metapopulation dynamics; (6) prediction of the occurrence of extinction thresholds; (7) determination of the genetic consequences of habitat fragmentation; and (8) reserve design and ecosystem management. This generalized, spatially explicit framework bridges the gap between spatially implicit, patch-based models and spatially realistic GIS applications which are usually parameterized for a single species in a specific landscape. Development of a generalized, spatially explicit framework is essential in conservation biology because we will not be able to develop individual models for every species of management concern.*

Aplicación de Modelos de Paisaje Neutros en la Biología de la Conservación

Resumen: *Los modelos de paisajes neutros derivados de la teoría de percolación en el campo de la ecología de paisaje, consisten en mapas cuadriculados en los que se genera la distribución de hábitats complejos por medio de algoritmos aleatorios o fractales. Esta representación de la estructura del paisaje es compatible con el formato de los sistemas de información geográfica (SIG) que facilitan la comparación entre paisajes teóricos y reales. Los modelos de paisaje neutros permiten la identificación de umbrales críticos de conectividad, que se pueden utilizar para predecir cuando se fragmentarán los paisajes. El acoplamiento de modelos de paisaje neutros con modelos poblacionales generales, por ejemplo la teoría de metapoblaciones, proporciona un modelo nulo para generar predicciones de la dinámica poblacional en paisajes fragmentados. Los modelos de paisaje neutros tienen la siguiente aplicación en la conservación: (1) incorporación de patrones espaciales complejos en modelos de (meta) poblaciones; (2) identificación de la percepción de la estructura del paisaje por las especies; (3) determinación de la conectividad del paisaje; (4) evaluación de las consecuencias de la fragmentación del hábitat en la subdivisión de poblaciones; (5) identificación del dominio de la dinámica metapoblacional; predicción de umbrales de extinción; (7) determinación de las consecuencias genéticas de la fragmentación del hábitat y (8) diseño de reservas y manejo de ecosistemas. Este marco de referencia general y espacialmente explícito llena el vacío entre modelos espacialmente implícitos, basados en parcelas, y aplicaciones. SIG espacialmente realistas que generalmente consideran a una sola especie en un paisaje específico. El desarrollo de un marco de referencia general y espacialmente explícito es esencial en la biología de la conservación, ya que no es posible elaborar modelos individuales para cada especie.*

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Introduction

Habitat fragmentation is a central issue in conservation biology (Soulé 1986; Rolstad 1991; Harrison 1994; Wiens 1996) and has been implicated in the greatest extinction event on Earth in over 65 million years (Wilcox & Murphy 1985). Although loss of habitat poses the greatest threat to maintaining biodiversity, the effects of fragmentation are more insidious. Fragmentation results in the subdivision and decreased area of habitat, increases the potential for edge effects, and changes the surrounding habitat matrix, all of which may reduce the continuity or connectivity of the landscape and thus threaten the survival of sensitive species (Rolstad 1991). Fragmentation effects are so evident, so amply documented, that we appear to have overlooked a rather fundamental question: when do landscapes become fragmented? This is one of the primary concerns of conservationists; yet, conservation biology offers no formal theory to predict when habitat fragmentation occurs.

Instead, theory focuses on the consequences of spatial subdivision for biodiversity and the persistence of populations. Metapopulation theory has become a major theoretical underpinning of conservation biology (Hanski & Gilpin 1991; Caughley 1994; Meffe & Carroll 1994; Hanski & Simberloff 1997). Metapopulation structure—subdivided populations linked by dispersal that balances extinctions and recolonization of patches—figures prominently in the design of reserves (Quinn & Hastings 1987) and in the management of threatened populations (e.g., Beier 1993; LaHaye et al. 1994; Hanski et al. 1995). From a conceptual and analytical standpoint, metapopulation models are appealing because they offer a simple way to view and model a spatially complex world. As a legacy of island biogeographic theory, metapopulation theory holds to a binary view of the world, of patches embedded within an inhospitable, or at least an “ecologically neutral” (Wiens et al. 1993), matrix of non-preferred habitat. Because anthropogenic destruction of habitat dramatically fragments the landscape into small, disconnected patches of habitat (e.g., Krummel et al. 1987; Gardner et al. 1993), patch-based models would seem apt descriptors of the resulting population dynamics.

The problem is that this patch-based view of the world, although analytically tractable, does not encompass the full range of spatial complexity inherent in real systems. Metapopulation models assume populations are contained within discrete habitat patches, but this is an oversimplification for most systems where it is difficult to delineate population boundaries. Habitat patches are not oceanic islands; individuals of many species can move through the habitats that comprise the matrix, which may differentially affect colonization success (e.g., Cummings & Vessey 1994; Gustafson & Gardner 1996). Habitat fragmentation may or may not produce spatial differentiation in the dynamics of populations (Wiens 1997b). Spe-

cies confined to a newly fragmented habitat do not necessarily function as a metapopulation; poor dispersal abilities may prevent the species from recolonizing habitat patches following extinction (Hanski & Gilpin 1991).

“Metapopulation” has become synonymous with any spatially subdivided population (e.g., Hastings & Harrison 1994), which is a broader definition than originally accommodated by metapopulation theory (Levins 1969; 1970). Spatial subdivision is a necessary, but not sufficient, condition for metapopulation dynamics. In fact, there are several conditions that are necessary for metapopulation persistence (Hanski et al. 1995). Metapopulations occupy what Wiens (1997b) refers to as the “Goldilocks Zone.” The notion is that there is a critical patch geometry and a critical dispersal rate that is neither too much (patches are not too isolated, dispersal is not too frequent) nor too little, but “just right.” Despite its widespread application in conservation, the assumptions or conditions underlying metapopulation theory are rarely tested to determine whether the population of management concern is functioning as a metapopulation (Harrison 1991; 1994; Doak & Mills 1994; Hastings & Harrison 1994).

How do we manage populations that are subdivided but are not, strictly speaking, metapopulations? A broader modeling framework is needed, one that incorporates landscape complexity beyond simple patch-based models and which can encompass a range of population dynamics including metapopulation structure. Landscape ecology has emerged as a discipline whose primary focus is the analysis of the ecological consequences of environmental heterogeneity or patchiness (Turner & Gardner 1991). Given that metapopulation theory and landscape ecology both deal with the consequences of patchiness, Hanski and Gilpin (1991) proposed that the “fusion of metapopulation studies and landscape ecology should make for an exciting scientific synthesis.” Landscape structure may often be an important component of metapopulation dynamics (Fahrig & Merriam 1994; Wiens 1997a). Variation in patch quality, boundaries between patches, the nature of the mosaic (patch context), and overall landscape connectivity may influence the dynamics of local populations and the way in which local populations are linked by dispersal (Wiens 1997a). Dispersal also defines the scale at which individuals perceive landscape structure and whether a landscape is connected or whether a species is likely to be affected by fragmentation (Wiens & Milne 1989; Wiens et al. 1993; With 1994; Pearson et al. 1996). Individual movement is thus the most important unifying theme in both metapopulation dynamics and landscape ecology (Wiens 1997a).

Despite the obvious applications of landscape ecology for conservation biology, and vice versa, the synthesis between the two disciplines has barely begun (Wiens 1997a). As a first step toward forging a link between these

fields, my objective in this paper is to introduce conservation biologists to a recent theoretical development in the field of landscape ecology. Neutral landscape models (Gardner et al. 1987; Gardner & O'Neill 1991) show promise of providing a spatially explicit framework for modeling (meta)population dynamics. Landscape maps are constructed as grids in which cells are identified by habitat type or some other landscape feature; this raster format is therefore compatible with management applications tied to geographical information systems (GIS). Neutral landscapes are constructed with simple algorithms that generate complex habitat distributions. When coupled with generalized population models, such as metapopulation theory, neutral landscapes provide a spatially explicit framework for modeling population dynamics in fragmented landscapes. Currently, population models are coupled with GIS-generated landscapes (spatially "realistic" models, Hanski 1994a) to understand how actual or projected land-use change affects some threatened or endangered species (e.g., Bachman's Sparrow, [*Aimophila aestivalis*]; Pulliam et al. 1992). These species-specific models are thus a special case of the more general modeling framework I propose; neutral landscapes provide null models for predicting when habitat fragmentation occurs and is expected to affect population dynamics. The development of a generalized, spatially explicit framework in conservation biology is essential given that we will be unable to develop individual models for every species of management concern. I describe the different types of neutral landscape models that have been generated and how these have been used in various ecological applications. I then outline a protocol for coupling these landscape models with metapopulation models. Finally, I discuss the implications of neutral landscape models for conservation biology.

Neutral Landscape Models

Neutral landscape models are derived from percolation theory, which developed from the study of the flow of liquids through lattices of material aggregates (Orbach 1986). Neutral landscape models have been applied to

understand the statistical properties and connectivity of heterogeneous systems (Feder 1988). For ecological applications, artificial landscapes were conceived as percolation maps in which habitat could be assigned to occupy some proportion, b , of cells (Gardner et al. 1987; Gardner & O'Neill 1991). These landscapes are generated with analytical algorithms and thus are "neutral" to the biological and physical processes that shape real landscape patterns. Neutral landscapes provide a useful model for the study of ecological responses to landscape patterns because they are based on the movement, flow, or rate of spread that characterize a diverse array of biological processes (e.g., resource utilization by species, O'Neill et al. 1988; Lavorel et al. 1995; species coexistence, Gardner et al. 1991; Lavorel et al. 1994; Palmer 1992; spread of disturbance, Turner et al. 1989). They are thus well suited for providing a spatially explicit framework for modeling population responses to landscape change.

Simple Random Landscapes

The first generation of neutral landscapes were simple random maps created by randomly assigning habitat to a proportion, b , of the grid map (Gardner et al. 1987; Gardner & O'Neill 1991; Fig. 1). The number of available habitat cells on a particular landscape is thus bm^2 , where m is the number of cells along one side of the landscape grid (number of rows or columns). Although patch structure is not explicitly defined in the construction of such landscapes, it emerges nonetheless from the aggregation of habitat cells to form clusters or patches. Patches are defined by aggregation size or "neighborhood rule" (Fig. 2). For example, the simplest definition of a patch is determined by the "nearest-neighbor rule;" the neighborhood includes the four adjacent cells (Rule 1, Fig. 2). The "next-nearest neighbor" rule includes the nearest neighbors, plus the four diagonal cells; each cell thus has eight neighboring cells (Rule 2, Fig. 2). Larger neighborhood rules include cells that are not immediately adjacent, but are still considered part of the "neighborhood" in defining patch structure (e.g., Rule 3, Fig. 2). The rationale behind this is that highly vagile species or those with good dispersal abilities are able to cross

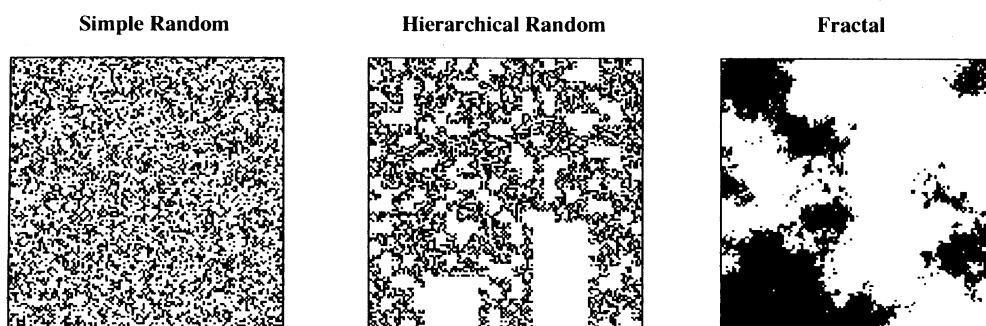


Figure 1. Examples of neutral landscape models. The proportion of available habitat (h) is 0.33 in all maps (shaded cells). For the hierarchical random map, h varies across three levels as $h_1 = 0.85$, $h_2 = 0.75$, and $h_3 = 0.50$ ($h_1 \times h_2 \times h_3 = 0.33$).

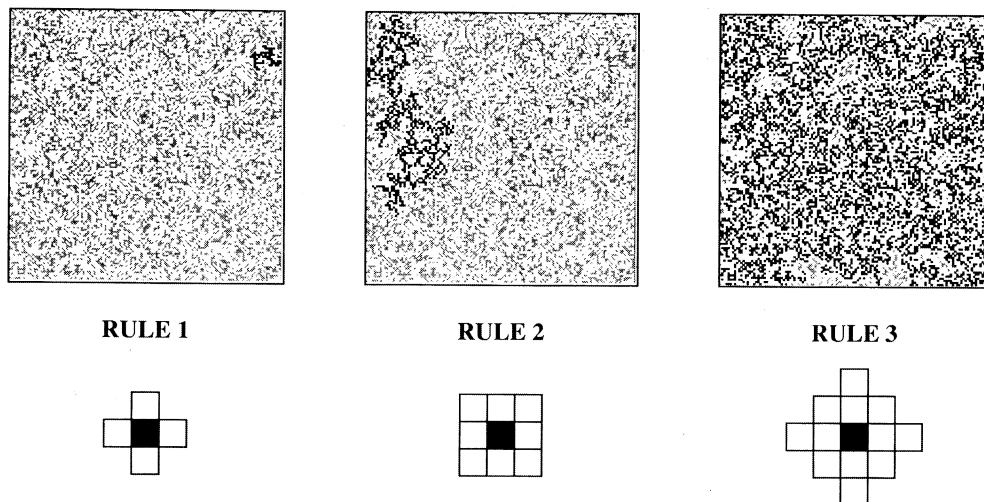


Figure 2. Connectivity of a landscape comprised of 35% habitat using different neighborhood rules. The landscape is connected and contains a single cluster that “percolates” across the map only when neighborhood Rule 3 is used as in this example.

“gaps” in available habitat and thus might link non-adjacent cells in a neighborhood of utilized habitat (e.g., Dale et al. 1994; With & Crist 1995; Pearson et al. 1996).

The use of neighborhood rules provides a species-centered definition of landscape structure, permitting patch structure to be identified at a scale appropriate to the organism in question. This is analogous to the concept of “ecological neighborhoods” (Addicott et al. 1987) and is based on dispersal distances, movement rates through habitat, or the “willingness” of individuals to cross gaps of nonhabitat. This information can be difficult to obtain in the field, but neighborhood rules provide a means of modeling animal movement in a reasonable fashion and can be used to compare the effects of land-use practices and habitat fragmentation on various groups of species that differ in dispersal ability.

In discussions of fragmentation effects, it is not clear at what point the landscape became fragmented, particularly from the standpoint of the target species. One of the most significant contributions of neutral landscape models has been the identification of critical thresholds in landscape connectivity, which defines quantitatively the point at which the landscape becomes fragmented. Imagine a completely forested landscape. If forest habitat is randomly removed a cell at a time, the landscape becomes riddled with gaps, but the landscape remains connected as long as habitat cells are adjacent (if the nearest-neighbor rule is used) and form a continuous cluster that stretches from one end of the landscape to the other (Fig. 3). With continued deforestation the removal of a single cell is enough to break the continuous cluster into two separate clusters. At this point, the landscape is suddenly disconnected. This is the critical threshold (b_{crit}), which is predicted by percolation theory to occur on a random landscape when $b = 0.59$ for the nearest-neighbor rule (Fig. 2). Above the threshold, habitat destruction merely results in a loss of habitat area (Andrén 1994). Below the

threshold, landscape connectivity is disrupted and the landscape is dominated by small, isolated clusters of habitat; the landscape is fragmented.

The threshold value, and thus whether or not the landscape is fragmented, depends upon the scale at which species perceive patch structure. Highly vagile species are represented with larger neighborhood rules and perceive the landscape as connected across a greater range of habitat loss (Gardner et al. 1991; With & Crist 1995; Pearson et al. 1996). The critical threshold for these species will thus be lower. For example, $b_{crit} = 0.30$ for species able to cross gaps of unsuitable habitat (Rule 3); such a species would not perceive the landscape as fragmented until habitat comprised $<30\%$ (Plotnick & Gardner 1993).

Percolation theory strictly deals with binary systems—habitat versus nonhabitat—just like metapopulation theory, thus providing a common framework for linking these modeling approaches. Neutral landscapes need not be restricted to a single habitat type, however, and proportions of multiple habitat types can be specified ($b_1 + b_2 + \dots + b_n = 1$, where $n =$ number of habitat types). On random maps each habitat will percolate at the corresponding b_{crit} for the specified neighborhood rule. Such heterogeneous landscape maps more closely approximate environmental complexity (e.g., Fig. 4). Heterogeneous landscape maps permit the modeling of complex interactions between species characteristics, such as habitat affinity, and features of the landscape, such as the abundance and quality of different habitat types (With & Crist 1995; With et al. 1997). Critical thresholds in species’ responses to habitat fragmentation result from the interaction of species characteristics with landscape structure. For example, habitat specialists, regardless of dispersal abilities, are more likely to be affected by loss of habitat than a disruption of landscape connectivity (With & Crist 1995). Simulation experiments

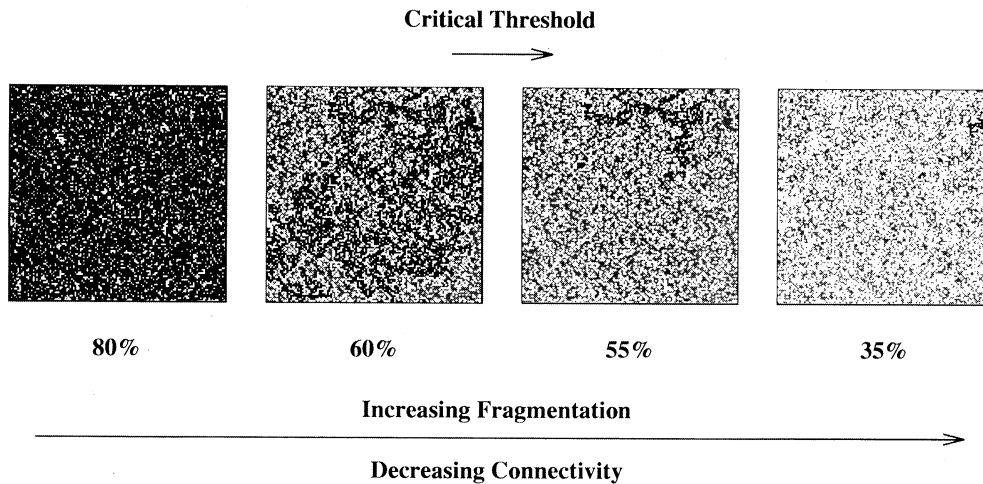


Figure 3. Critical threshold in landscape connectivity. As the proportion of available habitat (shaded cells) is reduced, connectivity—the occurrence of a percolating cluster—is disrupted, producing small, isolated clusters of habitat across the landscape. The largest patches (defined by the nearest-neighbor Rule 1, see Fig. 2) are the dense black areas in each landscape.

on neutral landscapes help identify scenarios where threshold effects could occur for a given species or group of species that share similar life-history characteristics or dispersal strategies. Simulation experiments, conducted as a factorial design for all levels of the model parameters, permit the exploration of the model state space and provide a simple means of identifying statistically significant factors, or combinations of variables, that affect population distributions and persistence (With et al. 1997). This makes it possible to tease apart the specific landscape features that affect the structure and dynamics of populations.

Hierarchical Random Landscapes

Much of the conceptual appeal of metapopulation theory lies in its recognition of hierarchical structure in natural systems (“population of populations,” Levins 1970). Resources are generally patchy in distribution and this patch structure may be manifested across scales in a nested hierarchy of patches within patches (Kotliar &

Wiens 1990). Natural landscapes exhibit scale-dependent changes in pattern (Krummel et al. 1987; O’Neill et al. 1991). Species may respond to resource distribution at different levels within the hierarchical patch structure of the landscape, as determined by their perceptual grain—the finest scale at which they respond to heterogeneity—and their spatial extent—the broadest scale at which the species interacts with heterogeneity, usually determined by dispersal distances (Kotliar & Wiens 1990; With 1994). Thus, it is important to identify the spatial scaling of habitat across the landscape and to determine the scales at which species are interacting with landscape structure. For example, habitat fragmentation may have different consequences for biodiversity if it occurs at fine versus broad scales. Fine-scale fragmentation poses a greater risk to landscape connectivity than the same reduction of habitat at a coarser scale (Rolstad 1991; Pearson et al. 1996). Habitat destruction at a broad scale obviously produces gaping holes in the landscape, but some large, contiguous tracts of habitat are left intact which helps promote overall landscape connectiv-

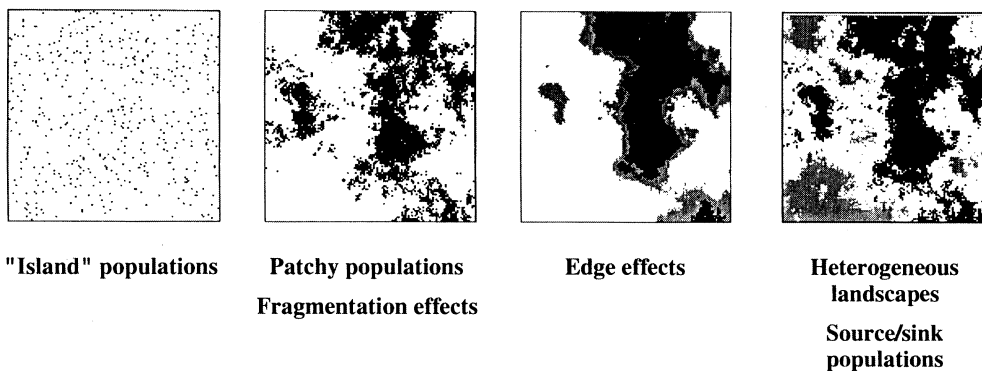


Figure 4. Application of neutral landscape models to various conservation scenarios. Management of small, discretely patchy populations (“island” populations) might be modeled with simple random maps. For the study of fragmentation effects or populations that have a spatially complex distribution

(patchy populations), fractal landscapes provide more appropriate models. Edge effects can also be addressed in fractal landscapes by designating a “habitat halo” around the primary habitat. In addition, heterogeneous landscapes comprised of >1 habitat type or source/sink population can be modeled with neutral landscapes (fractal landscape example shown here).

ity. Small, isolated “clear cuts” are more insidious because these whittle away at the percolating cluster. The removal of a single critical cell of habitat breaks the percolating cluster into two separate clusters and results in a disconnected landscape.

Hierarchically structured landscape models reflect the inherent patch structure of natural landscapes (O'Neill et al. 1992; Lavorel et al. 1993; Gardner et al. 1993; Fig. 1). Hierarchical neutral landscapes are generated using a fractal algorithm referred to as “curdling” (Mandelbrot 1983). The number of scales across which pattern varies is set by specifying a number of hierarchical levels, L , within the map. The proportion of habitat that occurs within each level is set independently as $b_1 \dots b_L$. This is a recursive procedure; the availability of habitat at one level constrains the availability of habitat at finer scales. For example, 60% of the landscape could be covered by forest at the coarsest scale (b_1), and 80% of those cells could contain forest at an intermediate level (b_2), and perhaps 40% of the L_2 cells will contain forest at the finest scale (b_3). The available habitat across the landscape is thus the combined probabilities, $P = b_1 \times \dots \times b_L$; in the previous example, $P = 0.6 \times 0.8 \times 0.4 = 0.192$. If habitat is absent at the coarsest scale, it will not be found at finer scales either. Subtle patterns of landscape fragmentation can be created by adding “whey” to the “curds” and seeding habitat with a proportion, q , at each of the finer levels (Pearson et al. 1996). Available habitat is now calculated as:

$$P = [b_1 \times b_2 \times b_3] + [b_1 \times (1 - b_2) \times q_3] + [(1 - b_1) \times q_2 \times b_3] + [(1 - b_1) \times (1 - q_2) \times q_3].$$

Fractal Landscapes

The neutral landscapes assumed complete spatial independence among cells; habitat types exhibited no spatial autocorrelation, although b obviously affects the probability that adjacent cells will be similar. In reality habitat is distributed with some degree of spatial contagion across landscapes. Fractal algorithms can generate neutral mod-

els of landscape patterns with simple control over spatial autocorrelation (Petigen & Saupe 1988; Palmer 1992; With et al. 1997; Fig. 1). Although two-dimensional fractals may be generated in various ways, we have used the midpoint displacement algorithm outlined in Saupe (1988) to generate fractal landscapes. For the purposes of this discussion, it will suffice to understand that a 3-dimensional surface—a topographical map—is created. The “ruggedness” of the topography depends upon the degree of correlation among habitat cells, H . The fractal dimension of the landscape is $D = 3 - H$; landscapes with little spatial autocorrelation (low H) will have an extremely variable surface (sharp peaks adjacent to deep valleys) that is more volume-filling and hence $D \rightarrow 3$ (Fig. 5). Extremely complex landscapes can thus be generated in a systematic fashion, just by varying H . As a consequence, the effects of habitat fragmentation can be assessed across a gradient of habitat clumping (H) and abundance (b).

Habitat is assigned to the continuously varying surface of fractal landscapes by making slices along an “elevational gradient” and assigning the range of elevations (which are the cell values) encompassed by the slice to a particular habitat type. The proportion of a particular habitat represented on the landscape is determined by the range of elevations encompassed in each slice; if 40% of the elevational range is captured by the slice, then 40% of the landscape will be comprised of that habitat. This produces a contour map. Habitat is assigned along a gradient and thus certain habitat types will always be adjacent (e.g., habitats 1 and 2, habitats 2 and 3, but not habitats 1 and 3). This models the transition of ecotones in natural landscapes or can be used to explore edge effects by designating a small proportion of habitat adjacent to a primary habitat (e.g., $b_2 = 0.05$ and $b_3 = 0.35$ in Fig. 4).

Fractal landscapes have been applied to the consequences of fragmentation for biodiversity (Palmer 1992) and subdivided populations (With et al. 1997). Scale-dependent effects on species coexistence were found in fractal landscapes. In extremely fragmented landscapes

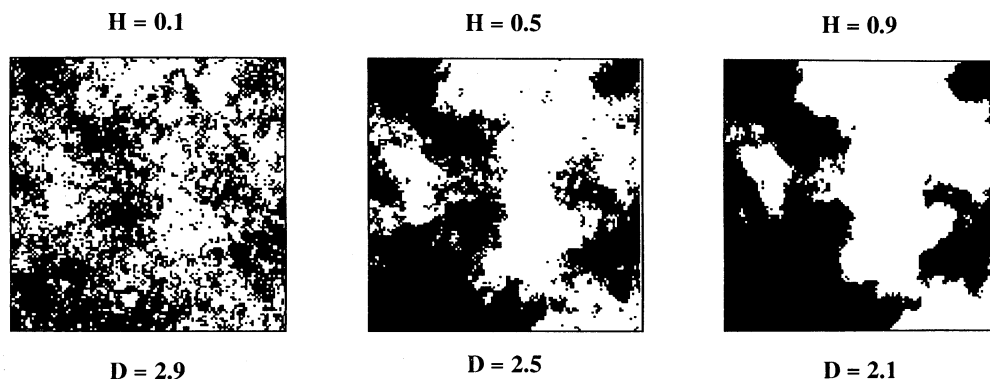


Figure 5. Topography of fractal landscapes. These maps illustrate how changing the spatial autocorrelation among habitat cells (H) affects the spatial patterning and hence the fractal dimension (D) of landscapes ($D = 3 - H$).

(high D), more plant species were able to coexist at the finest scale (within individual cells) than in more clumped landscapes (Palmer 1992). Species richness at the scale of the entire landscape was lower in fragmented than in clumped landscapes, however. Factors that operate at different scales may affect population distributional patterns. Populations were more likely to be subdivided at the landscape scale on fractal maps (with intermediate levels of spatial dependence, $H = 0.5$), and population distributions were determined primarily by species' habitat affinities and habitat quality (With et al. 1997). At finer scales on fractal landscapes, however, population structure was influenced by the relative abundance of habitat and the interaction of species' habitat affinities with habitat quality.

A Generalized, Spatially Explicit Framework

Because metapopulation models define a narrow range of population dynamics (i.e., the "Goldilocks Zone"), Hastings and Harrison (1994) formulated a more general theoretical framework called the " p -state, i -state model," which was initially developed by Metz and Diekmann (1986). Parameters that describe the condition of individuals (i -state) could be numbers of individuals or allele frequencies, and the state of the population as a whole (p -states) could be described as the fraction of patches that are in particular i -states. The model is among the most general models in population biology—virtually all models in population biology are among its special cases—and the point of defining a model at this level of generality is that it provides a single framework for integrating and comparing different population models. Nevertheless, this model is spatially implicit; the spatial arrangement of habitat is ignored, but allows for very general assumptions about patch sizes and dispersal.

Conceptually, then, one might extend this framework to an " l -state, p -state, i -state" model. In this case, l is a landscape containing a group of populations under consideration or fraction of landscape in various p -states, p is an individual population (or a local site, such as a grid cell) on the landscape, and i is an individual organism. Functions at higher levels constrain parameter states at lower levels (e.g., habitat distribution, an l -state, affects habitat of individual cells, a p -state), and patterns at higher levels may be obtained by aggregating information from lower levels. This facilitates the translation of patterns and processes across levels of organization. In the model, functions can be derived that describe the relations among l , p , and i -states; for example, an l -state describing the mean population size is a function of a p -state variable (number of individuals in each population). The state parameters specified at each level depend upon the question of interest. The utility of such a model lies in its versatility. In practice, it is necessary to limit the

number of parameters so that the model is analytically tractable. With computer-based simulation modeling, the number of parameters under simultaneous consideration can be greatly increased and more complex problems addressed. Metz and Diekmann (1986) characterized different population modeling approaches based on the " p -state, i -state" framework, one of which they classified as " i -state configuration models," which refer particularly to simulation models that take into consideration the life-history characteristics of individuals in heterogeneous environments (DeAngelis & Gross 1992).

Coupling Metapopulation Models and Neutral Landscape Models

Lande (1987) adapted the phenomenological metapopulation model of Levins (1969) to territorial populations on a random landscape. This model is spatially implicit; the landscape is assumed to be binary, in which suitable territories of a fixed size are randomly distributed in an unsuitable matrix. By incorporating demographic parameters and the dispersal range of individuals searching for territories, Lande derived the "demographic potential" of the population, a single parameter that described the maximum occupancy of territories at equilibrium. Territorial populations exhibited extinction thresholds, determined by their demographic potential and the proportion of suitable territories available on the landscape. Species with high demographic potential (good dispersers, high reproductive output), for example, can withstand considerable habitat loss before the population crashes. The application for conservation biology is obvious and Lande's model has been used to illustrate how habitat fragmentation would impact the Northern Spotted Owl (*Strix occidentalis caurina*). The population is predicted to go extinct once old-growth forest covers <20% of the landscape (Lande 1988; Lamberson et al. 1992).

Lande's model has the basic form of an l -state, p -state, i -state model, where the equilibrium occupancy of territories (local sites or patches) across the landscape (p^* , an l -state) was determined for a single (meta)population. In this application individual territories or "patches" are p -states that can be occupied by a single breeding pair with proportion p (a p -state). The demographic potential of the (meta)population (k , an l -state) is based on individual parameters such as the lifetime reproductive output of individual females (R_0 , a function of i -state parameters such as age-specific birth and death rates, and age at first reproduction) and the dispersal range (m , another i -state) of juveniles searching for a suitable, unoccupied territory. Persistence of the population on the landscape (p^*) depends upon the availability of suitable habitat (b , an l -state) and the demographic potential of

the population (k). The equilibrium occupancy of suitable habitat is positive ($p^* > 0$) only if b exceeds the threshold value determined by the life-history and dispersal abilities of the species. The extinction threshold is the minimum proportion of suitable habitat required for population persistence on the landscape; below this, the population goes extinct. Species with low reproductive output and poor dispersal abilities (low k) are predicted to go extinct much sooner (at higher values of b) than species with high demographic potentials. For example, a species with $k = 0.2$ is only able to occupy 20% of habitat patches even when the landscape is entirely suitable ($b = 1.0$). Such a species is predicted to go extinct when 20% of the landscape has been destroyed ($b = 0.8$). A species with $k = 0.6$, on the other hand, would persist on the landscape until $b = 0.4$.

This model, while analytically tractable, can not deal with the spatial complexity of real systems. Thus, Lande suggested that "the prediction of extinction thresholds for real populations may be most accurately accomplished by incorporating these principles into computer models that explicitly account for habitat quality and spatial distribution and the influence of these factors on the dispersal behavior and life history parameters of individuals" (Lande 1987:634). We are now in the process of linking neutral landscapes and metapopulation models (K. A. With and A. W. King, unpublished data). Because landscape structure affects dispersal success (the probability of successfully colonizing unoccupied habitat patches or territories in Lande's model), the introduction of spatial complexity (e.g., a function of b and H for fractal landscapes; Fig. 5) should affect the predicted value of extinction thresholds. Preliminary results suggest that populations persist longer on fractal landscapes than predicted by Lande's model. Fractal landscapes are inherently more clumped than random landscapes and thus remain connected across a greater range of habitat loss. Dispersal success is thus higher on fractal landscapes, even when habitat is scarce, and populations are able to persist across a greater range of habitat loss than populations on random landscapes.

Applications for Conservation Biology

What new insights can be gained by developing a synthesis between conservation biology and landscape ecology? The importance of landscape pattern and connectivity in structuring metapopulation dynamics suggests that current metapopulation theory could be enhanced by incorporating spatially explicit theory from landscape ecology (Wiens 1996). The challenge of modeling metapopulation dynamics in a spatially complex environment has been tackled by a variety of modeling approaches, (e.g., Wu & Levin 1994; Hanski 1994b; Possingham &

Davies 1995). These models however, are typically parameterized for a specific management application (e.g., LaHaye et al. 1994; Liu et al. 1995; Hanski et al. 1995; Hanski et al. 1996), which may ultimately limit their generality in other systems or even other species within the same system (e.g., Liu et al. 1995). The coupling of (meta) population models with neutral landscape models shows promise of providing a generalized, spatially explicit framework, thus cultivating the synthesis envisioned by Hanski and Gilpin (1991). Neutral landscape models can contribute to the following applications in conservation biology.

Representation of Complex Spatial Patterns in (Meta)Population Models

Algorithms used to generate artificial landscapes provide a simple means of generating environmental complexity in a number of ways (e.g., Figs. 1 and 4). Neutral landscape models enable one to vary systematically aspects of landscape structure such as relative habitat abundance, spatial contagion ("clumping" of pattern and thus patch-size distributions), or amount of edge. This permits the exploration of the effects of fragmentation across a range of severity and spatial complexity. Neutral landscapes offer a more holistic view of landscape structure by dealing with the intact landscape (Pearson et al. 1996). Landscapes are not dissected into discrete elements such as patches, matrix, and corridors. Rather, patch structure emerges from the interaction (e.g., movement responses) of organisms with environmental complexity, enabling "species' perceptions" of landscape structure.

Identification of Species' Perceptions of Landscape Structure

The patch-structure of the landscape is defined by species' area requirements and their propensity for movement (Wiens et al. 1993; Dale et al. 1994; With & Crist 1995; Pearson et al. 1996). This permits an organism-centered definition of landscape structure, which is necessary if we are to adopt meaningful and effective conservation strategies (Hansen & Urban 1992). The consequences of land-use change and fragmentation can be simultaneously addressed on the same landscape for a multitude of species with different dispersal capabilities and life-history traits. For example, Dale et al. (1994) identified species likely to be extirpated following forest fragmentation in the tropics based on the area requirements and the "gap-crossing" ability of these species (i.e., their willingness to cross areas of unsuitable habitat). Not only can the effects on target species be addressed, but it might then be possible to identify the circumstances under which other populations, not currently of management concern, become threatened.

Determination of Landscape Connectivity

The key to metapopulation persistence is to maintain landscape connectivity, a functional cohesion among habitat patches across the landscape. Neutral landscape models predict the occurrence of critical thresholds in habitat fragmentation, abrupt transition ranges where small losses of habitat have dramatic, and potentially dire, ecological consequences (Gardner et al. 1993; With & Crist 1995; Pearson et al. 1996). Threshold effects are "a major unsolved problem facing conservationists" (Puliam & Dunning 1994:193). The potential for threshold effects should be a principal concern in the evaluation of management strategies in fragmented landscapes.

Evaluation of the Consequences of Habitat Fragmentation for Population Subdivision

Habitat fragmentation does not always produce metapopulation structure, but may nevertheless have important implications for the spatial structure of populations. The most obvious effects of landscape structure are on dispersal among habitat patches. Dispersal affects colonization rates, whether patches are connected, and thus whether subpopulations function as a metapopulation. Thus, predicting "exactly how the translation from individual movements to population distribution and interactions should be accomplished is one of the most vexing problems confronting a metapopulation-landscape synthesis" (Wiens 1997a:52-53). We have modeled individual movement in heterogeneous, simple random landscapes (i.e., mosaics of three habitats) as a percolation process to identify the point at which populations became subdivided (With & Crist 1995). The results of this simulation exercise demonstrated that this "threshold" between continuously distributed and patchy populations depended upon the relative abundance of preferred habitat, the relative habitat affinities of species (e.g., whether a habitat generalist or specialist), and the dispersal range of the species. Subsequent modeling work on heterogeneous fractal landscapes, with habitats of varying quality, indicated that different factors may simultaneously operate at both fine and broad scales that affect population distributional patterns (With et al. 1997). It is important to remember that patchiness does not always matter, particularly if habitat is abundant, dispersal distances are greater than the scale of fragmentation, the species is a generalist, the species has a myopic view of the landscape and can only detect patches over short distances, or if habitat patches are ephemeral (Fahrig 1988; With & Crist 1995; Wiens 1997b).

Identification of the Domain of Metapopulation Dynamics

Where is the "Goldilocks Zone?" In highly connected landscapes (e.g., above the critical threshold), the entire

landscape may function as a single population, in which case, metapopulation theory is no longer relevant (Wiens 1997a). At the other extreme, if the landscape is highly fragmented and populations are subdivided, it may be possible to treat each patch as a separate unit (e.g., individual reserves). Thus, the domain of metapopulation dynamics may fall somewhere in the vicinity of the percolation threshold, where the explicit spatial arrangement of patches and inter-patch movements are most important.

Prediction of Extinction Thresholds

Far from enhancing population persistence, spatial subdivision may drive some species to extinction if they do not have the demographic potential and dispersal abilities to exploit patchy habitats. Extinction thresholds are determined by the interaction between landscape structure, demography, and dispersal; it is not yet clear to what extent extinction thresholds are related to critical thresholds in landscape structure and population subdivision. The ability to predict which species will go extinct, and when, under various scenarios of land-use change may ultimately be the most critical application of neutral landscape models in conservation. As outlined previously, this can be accomplished by coupling neutral landscapes with metapopulation models, such as that derived by Lande (1987) for territorial populations.

Determination of the Genetic Consequences of Habitat Fragmentation

Dispersal is not the only process affected by landscape structure. As individuals move, they take their genes with them and thus ultimately gene flow among populations can be affected by habitat fragmentation. Green (1994) used a simple random landscape to demonstrate that genetic variability within a population was highly sensitive to changes in landscape connectivity. Below the critical threshold, a regional population became subdivided and genetic drift increased genetic variability among populations. Again, the critical region where this occurred depended upon the neighborhood function (area of gene flow) and pattern of dispersal.

Guide Reserve Design and Ecosystem Management

At the landscape scale, patch-based theory (i.e., theory of island biogeography) is being used to design reserve networks and in the management of entire ecosystems. Corridors have been implemented as an obvious solution to the problem of maintaining connectivity in an increasingly fragmented world. Why then have corridors become one of the most hotly debated issues in conservation (Mann & Plummer 1995)? Although habitat corridors linking populations or individual reserves may facil-

itate the dispersal of some species (e.g., large carnivores or ungulates), the presumed effectiveness of corridors remains controversial (Hobbs 1992). The notion of landscape connectivity is perhaps being taken too literally. Connectivity need not entail physical linkages between patches; it is the functional connectivity—patches linked by dispersal—that is ultimately important. In a patch-based view of the world, corridors are appealing because they provide a physical bridge linking habitat islands across a matrix sea. Given that landscapes are habitat mosaics and that species can traverse the “matrix,” corridors may not be discrete structures. Gustafson and Gardner (1996) used hierarchical random neutral landscapes to model the effects of dispersal on patch colonization rates across heterogeneous landscapes. Areas that facilitated movement, and thus functioned effectively as corridors, tended to be diffuse and difficult to identify from structural features of the landscape. Another holdover from patch-based theory is the assumption that flows between patches are linear and symmetrical. Spatial complexity may reduce colonization success when individuals must follow convoluted pathways or are trapped in “cul-de-sacs” (Gustafson & Gardner 1996). Asymmetry in dispersal between patches arises because of patch context; an isolated patch may have a high proportion of dispersers which successfully reach a neighboring patch, but if the neighbor is part of a network of patches, only a small fraction of dispersers from this neighboring patch may reach the more isolated one. These applications from neutral landscape models underscore the importance of elaborating reserve design from the standpoint of overall landscape connectivity and within the context of entire landscape mosaics rather than isolated patches (Pressey et al. 1993; Hobbs et al. 1993).

Conclusions

Whatever the scale of management, the pervasive theme in conservation is connectivity. Connectivity is a fundamental feature of neutral landscape models. Besides providing quantitative predictions as to when landscapes become disconnected, neutral landscapes offer a sophisticated way of modeling spatial complexity. The coupling of neutral landscape models with (meta)population models helps bridge the gap between spatially implicit, patch-based models and spatially “realistic” simulation models based on GIS applications (e.g., BACHMAP, Pulliam et al. 1992). It is important to remember, however, that neutral landscape models are merely tools, abstractions that help us understand in general terms how spatial complexity affects ecological processes such as dispersal, population dynamics, and species persistence. As with any model, care must be exercised in deciding which type of neutral landscape to apply in a given management context (Fig. 4), how it is designed (e.g., are

the grid cells to be square or hexagonal?), and what the underlying assumptions are regarding movement that are ultimately used to define landscape structure. For example, determination of the critical threshold depends on the lattice geometry of the neutral landscape (Plotnick & Gardner 1993), the specific algorithm used to generate the landscape (random vs fractal; With et al. 1997), and the way dispersal is modeled (e.g., different neighborhood rules; Plotnick & Gardner 1993; With & Crist 1995; Pearson et al. 1996). These assumptions all have the potential to affect one’s assessment of the consequences of habitat fragmentation for populations. The best application is to make “comparative and qualitative statements about the likely population responses to a set of potential or real landscape alterations” (Dunning et al. 1995:9). Although we still may be unable to make quantitative predictions about the effects of landscape change on populations, the development of a generalized spatially explicit framework by integrating metapopulation theory with neutral landscape models may lead to new insights in the conservation management of threatened populations.

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