

Neutral Models: Useful Tools for Understanding Landscape Patterns

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8.1 Introduction

A neutral model is a minimum set of rules required to generate pattern in the absence of a particular process (or set of processes) being studied. The results of the neutral model provide a means of testing the effect of the measured process on patterns that are actually observed (Caswell 1976). If observed patterns do not differ from the neutral model, then the measured process has not significantly affected the observed pattern. Conversely, when results differ from model predictions in a way that is consistent with a particular process, then strong evidence for the importance of this process has been obtained. Several authors have argued that formulation of a proper neutral model is necessary for hypothesis testing, because data often exhibit nonrandom patterns in the absence of the causal mechanisms of interest (Quinn and Dunham 1983). This approach has been discussed extensively in the field of community ecology (e.g., Conner and Simberloff 1984, 1986; Haefner 1988) as well as other areas of biology (Nitecki and Hoffman 1987).

Neutral models are useful in landscape ecology, a field of ecology that emphasizes the complex relationships between landscape pattern and eco-

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logical process (Turner 1989, Gardner and O'Neill 1991). Processes, such as disturbance, can produce landscape patterns by changing the abundance and location of habitat patches (Baker 1992). Likewise, patterns have important effects on ecological processes. For example, habitat fragmentation affects metapopulation dynamics (Holt et al. 1995), gene flow (Ballal et al. 1994), and dispersal (Santos and Telleria 1994). The purpose of this chapter is to demonstrate the usefulness of neutral models to landscape ecology by discussing how neutral models (1) assist the investigator in understanding patterns in spatial data and (2) are useful for generating maps for quantifying the effect of landscape pattern on ecological processes.

8.2 A Simple Neutral Model

Neutral models help landscape ecologists understand relationships between measures of spatial pattern and landcover abundance. A simple neutral model designed to explore the effect of changes in the abundance of a habitat on the spatial pattern of landcover (Gardner et al. 1987) was derived from the principles of percolation theory (Stauffer and Aharony 1992). The complex patterns generated by simple random maps and the insights provided by percolation theory were proposed as sufficient to test the importance of landscape process on observed landcover patterns.

To understand the effect of changing habitat abundance on measures of spatial pattern, Gardner et al. (1987) used the following simple neutral model consisting of a few straightforward rules:

1. Generate a map of 100×100 grid cells.
2. For each cell, randomly assign the presence or absence of landcover to each grid cell with probability P . Thus, P represents the proportion of the map occupied by the landcover type of interest. In this chapter, P represents the proportional abundance of suitable habitat; the abundance of unsuitable habitat is $1 - P$.
3. For each map, quantify the spatial pattern of landcover by recording the number, size, and shape of habitat patches.

This model is "neutral" in the sense that there is no process governing the spatial distribution of landcover; i.e., the distribution is random. Figure 8.1 shows examples of maps produced using this model. A set of nine landscapes having values of P ranging from 0.1 to 0.9 were produced. Patch-based metrics (e.g., the number of patches, mean patch size, and the area of the largest patch), as well as the amount of edge measured as the total number of cells along the perimeter of all patches, were recorded.

We defined a *patch* as a cluster of adjacent cells of the same habitat type, allowing a theoretical organism to visit all the cells of the patch without having to cross any cells of unsuitable habitat. The rule used to connect cells and define patches is important because it affects both the number and size

P = 0.4



P = 0.6



P = 0.8

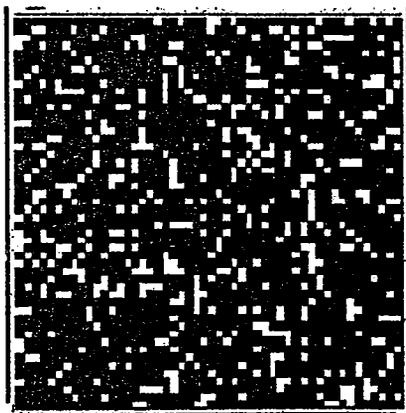


FIGURE 8.1. Simple random maps (100 × 100 cells) having different proportions (P) of suitable (black) habitat.

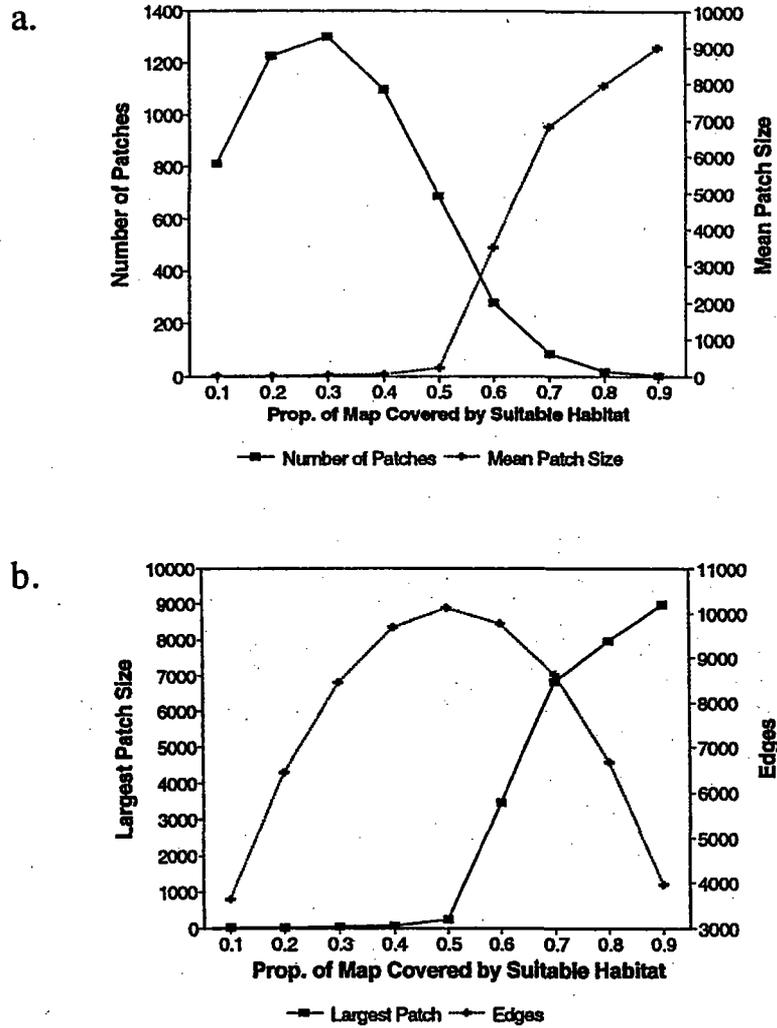


FIGURE 8.2. Landscape metrics for suitable habitat in simple random maps. Units for mean patch size, largest patch size, and edge are number of cells. *Edge* is defined as the number of cells bordering at least one cell of a different cover type. A "four-neighbor" rule was used to identify the patches (i.e., diagonal cells were not considered connected).

of patches. Some applications of percolation theory specify that habitat cells belonging to the same patch must be adjacent on the four cardinal directions. Habitat cells touching on the diagonals (subcardinal directions) are not considered to be connected. This type of rule is called a four-neighbor, or nearest-neighbor rule. The analyses and results presented here

used the four-neighbor rule. An eight-neighbor rule would allow organisms to move to cells on the diagonal; therefore, connecting cells in the subcardinal directions would be included as part of a habitat patch.

All of the patch-based measures were dependent on P . As P increased from its lowest value, the number of patches of suitable habitat increased initially, but patch number began to decline above $P > 0.3$ as small patches began to coalesce (Figure 8.2a). The process of patch coalescence causes mean patch size to increase simultaneously (Figure 8.2a). Likewise, the amount edge increased initially as the number of patches increased, but declined as patches coalesced and the map became filled with suitable habitat (Figure 8.2b). The area of the largest patch increased slowly between $0.1 \leq P \leq 0.5$, then it increased rapidly at higher values of P (Figure 8.2b). This behavior indicated the presence of a critical threshold near $P = 0.59$. A *critical threshold* is a region in parameter space where a small change in the parameter produces a relatively large change in the measured response. In this case, a small change in P in the region $0.5 \leq P \leq 0.6$ produced a large change in the area of the largest patch.

The existence of such critical thresholds is an important contribution of percolation theory to our understanding of spatial patterns. This theory states that if we identify patches with the four-neighbor rule, 50% of very large maps randomly generated with $P = 0.5928$ will have a single, large habitat patch (i.e., the percolating cluster) that will span the entire map (Stauffer and Aharony 1992). If the eight-neighbor rule is used to identify habitat patches, then the critical threshold for P is equal to 0.4072 (see Plotnick and Gardner 1993 for a discussion of critical thresholds for different neighborhood rules). O'Neill et al. (1988) have demonstrated that these patch-definition rules can be used to study the effect of P on landscape connectivity. Pearson et al. (1996) used different neighborhood rules to compare the connectivity of landscapes for organisms with different dispersal capabilities. For example, a species with limited vagility (e.g., a snail) was represented by a four-neighbor movement rule, while a more vagile species (e.g., a mouse) was represented by an eight-neighbor rule. The critical values for landscape connectivity were lower for the eight-neighbor rule than for the four-neighbor rule.

Ecologists and land managers should be aware of the existence of these thresholds because they show that the relationship between habitat abundance and spatial pattern is nonlinear, especially near a critical threshold. This theory implies that small changes in abundance and landscape pattern might have little effect if the habitat is especially abundant or, in some cases, very rare. However, if the habitat is near a threshold level, then a small change in habitat abundance might change a previously connected landscape into a fragmented one. A manager might be caught by surprise when small reductions in habitat (e.g., due to management or economic development), that previously had little effect on a population, suddenly resulted in a population crash. In percolation theory, the threshold values

are dependent on the neighborhood rule used to define patches. Therefore, it is important to realize that the "threshold value" must be defined with respect to a given taxon or ecological process because organisms and processes vary in their ability to move across a patchy landscape (O'Neill et al. 1988, Pearson et al. 1996).

The simple neutral model states that in the absence of specific landscape processes that affect the distribution of landcover, the number, size, and shape of patches will change as a function of the fraction of landscape occupied by the landcover type of interest (Gardner et al. 1987). These simple random models also have been used to compare data from actual landscapes. Gardner et al. (1991) found that the spatial pattern of habitat maps of forests in Georgia (USA) was similar to randomly generated maps when the proportion of forest (P) was ≥ 0.6 . At $P < 0.6$, the spatial pattern of forest often differed from that of random maps. They concluded that the many processes that shape landscapes—including human alterations, local variations in topography and soils, the distribution of biota, and the frequency and severity of disturbances—act together to produce "unique" patterns of landcover. Use of random maps as neutral models revealed that the patterns of deforestation in landscapes where more than 40% of the forest had been lost were nonrandom and likely driven by the interactions between land-use choices and environmental characteristics such as topography and soil fertility.

8.3 Hierarchical Neutral Landscapes

The use of simple random maps as neutral models is based on the null hypothesis that there are no significant processes affecting the spatial pattern of landcover. In nature, spatial pattern often is structured by many factors, and ecologists may desire a model that is neutral to a specific set of factors while considering the organizing effects of other processes on landscape pattern. Gardner and O'Neill (1991) have described a method of producing maps that vary in levels of contagion; allowing the user to control pattern at a single spatial scale. However, real landscapes often exhibit shifts in spatial patterns as the spatial extent of the landscape being studied increases (O'Neill et al. 1991). For example, broad-scale differences in geology may affect abiotic properties of soils and/or hydrology that in turn, will significantly affect broad-scale changes in vegetation. Thus, the variation in geological patterns may be an important consideration for predicting the broad-scale patterns of vegetation. Ecologists interested in the spatial patterns of disturbance and plant succession also require neutral models that can generate random patterns at fine scales (i.e., the disturbance-succession scale) while allowing users to control the broad-scale variation of landcover types (i.e., geological constraints). Models for generating *hierarchical neutral landscapes* satisfy these needs

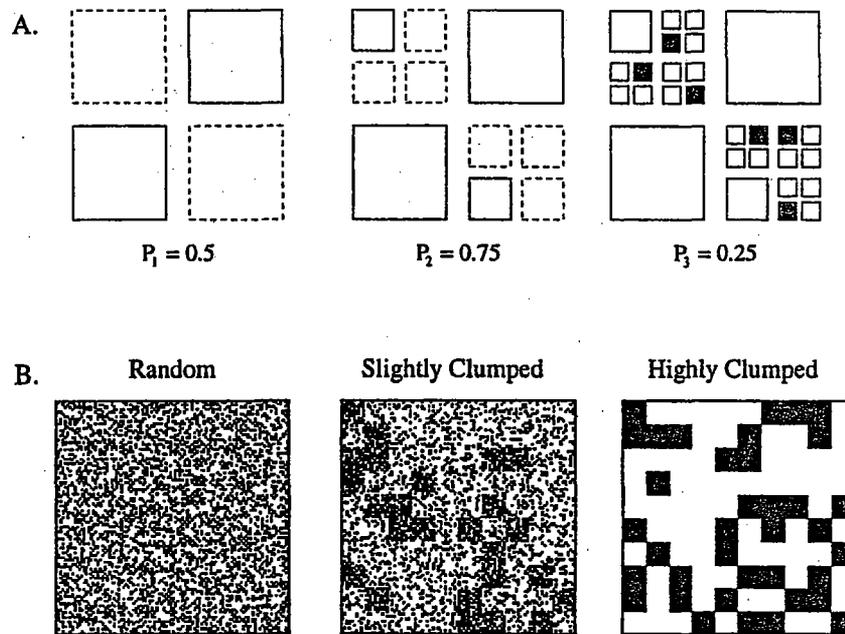


FIGURE 8.3. Method for making a hierarchical neutral map (A; see text) and examples of three maps produced using this method (B). In (A), dashed lines indicate division randomly selected to contain habitat in hierarchical levels 1 and 2. Shaded cells at the finest scale, level 3, contain suitable habitat. Each map in (B) has $P = 0.375$.

by creating random maps with control over pattern at successively finer spatial scales.

Hierarchical neutral models produce scale-dependent patterns by specifying the proportion of habitat present at several hierarchical scales. For example, a 100×100 cell map may be divided into four equal sized regions (50×50 cells). The proportion of these regions that contain suitable habitat is specified as P_1 (see Figure 8.3a). Next, each of these regions can be divided into four subregions of 25×25 cells each. The proportion of these subregions that contain suitable habitat is P_2 . Finally, specify the proportion of cells within a subregion with suitable habitat (P_3). The proportion of cells containing suitable habitat for entire map is the product of these three P values ($P_1 \times P_2 \times P_3$). Altering the relative magnitude of these proportions (or changing the number of hierarchical levels) changes the scale of variation. This technique allows the user to produce random maps that vary in the abundance and dispersion (clumping) of habitat (Figure 8.3b).

Hierarchical neutral maps have been used to better understand the interactions between P and spatial pattern at different scales. Lavorel et al.

(1993) found that spatial structure (e.g., spatial organization) depends on the relationship between spatial pattern and P . Patches tend to be larger on hierarchical maps than on random maps when $P >$ critical threshold. When $P <$ critical threshold, patches were smaller on hierarchical maps than on random maps. The relationship between P and spatial structure likewise influences the consequences of landscape change experienced by species requiring the changing habitat. Pearson et al. (1996) used hierarchical maps to demonstrate how P interacts with spatial pattern to affect habitat fragmentation (or connectivity) for different species. For a given value of P , landscapes with a fine-scale, random pattern of habitat were more likely to be fragmented than landscapes having some spatial organization (e.g., clumping). This work illustrates how species with different dispersal abilities vary in their sensitivities to a given pattern of habitat loss. With respect to habitat fragmentation, the species with limited dispersal ability were the most sensitive to changes in pattern and abundance of habitat, whereas vagile species were generally more tolerant (see Dale et al. 1994 for a similar analysis of real landscapes). Fractal geometry has been used to describe the hierarchical structure of real landscapes (Palmer 1988; Milne 1991, 1992, this volume). Hierarchical neutral maps based on fractal geometry have been used to study insect movements (Johnson et al. 1992) and species coexistence (Palmer 1992).

8.4 Fractal Landscapes

The simple neutral and hierarchical neutral models discussed above produce binary maps composed of cells showing the presence and absence of a single habitat type. Real landscapes frequently have gradients rather than abrupt changes in habitat suitability. That is, habitat quality often varies in a more continuous, rather than discrete, manner. This continuous variation is not represented in a binary map but can be simulated by maps having grid cells of two or more types (e.g., gradient maps). Maps showing semicontinuous variation in habitat suitability can be produced using techniques from fractal geometry. One technique for producing fractal maps employs algorithms based on fractional Brownian motion of a two-dimensional random walk. This technique produces maps with varying amounts of spatial autocorrelation. Consider a sequence of steps X , with the value of the current step equal to X_t . If each successive step ($X_{t+1} - X_t$) of the random walk is drawn independently from the Gaussian distribution, the resulting sequence of steps is a Brownian motion. Fractional Brownian motion is produced by introducing the parameter H , which controls the correlation between successive steps (Saupe 1988; Plotnick and Prestegard 1993). H can assume values over the interval (0, 1). When $H = 0.5$, steps are not correlated; when $H < 0.5$, steps are negatively correlated; and when $H > 0.5$, steps are positively correlated. Although the fractional Brownian

motion algorithm generates random numbers (see Saupe 1988), a map can be produced by assigning the values obtained from the random walk (i.e., X_i) to grid cells by scaling the results to the mean and range of the generated sequence.

This technique was used to study the consequences of varying spatial patterns of ^{137}Cs contamination in a Tennessee reservoir. While the total amount of contaminant in the reservoir was generally known, its dispersion in space was not. The spatial pattern of contamination could affect the strategies for detecting sites with high contaminant levels ("hot spots") and strategies for cleanup of ^{137}Cs . The degree of spatial autocorrelation in contaminant levels was unknown, so maps that varied in their levels of autocorrelation were produced in an effort to study the effect of spatial variation on the effectiveness of various sediment sampling schemes. Three values of H (0.01, 0.05, and 0.75) were used to produce three fractal maps of ^{137}Cs inventory for the reservoir (FRAC01, FRAC50, FRAC75, respectively; Figure 8.4). FRAC01 had the least amount of spatial autocorrelation. That is, cell values in this map were only weakly correlated with adjacent cell values. FRAC50 showed a moderate degree of spatial autocorrelation, and FRAC75 showed a high degree of spatial autocorrelation. These numbers were scaled to a reservoir-wide mean ^{137}Cs inventory of 225 picocuries per square centimeter for each map.

The degree of spatial autocorrelation affected the level of sampling intensity needed to detect hot spots of contamination. The spatial pattern of contamination could be detected accurately in maps with a large degree of spatial autocorrelation using relatively few samples. As autocorrelation declined, the number of samples required to achieve the same degree of accuracy increased dramatically. This investigation also compared the fractal maps to maps of ^{137}Cs contamination that incorporated hydrody-

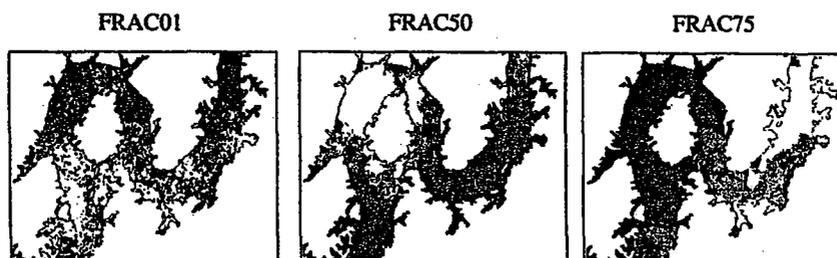


FIGURE 8.4. Neutral maps of semicontinuous values of ^{137}Cs contamination in a Tennessee reservoir. These fractal maps were produced using a model of fractional Brownian motion in a two-dimensional random walk. The map FRAC01 has little or no spatial autocorrelation. FRAC50 has moderate levels, and FRAC75 has high levels of autocorrelation. Darker areas have lower levels of contamination; light areas are highly contaminated.

dynamic mechanisms of sediment deposition. ^{137}Cs in solution is often bound to fine particles, such as clay, by a static charge. Therefore, hydrodynamic mechanisms that influence the particle-size distribution of sediments consequently affect the concentration of contaminants in sediments. Comparison of the fractal maps, which were neutral with respect to sediment deposition, to the sedimentation maps demonstrated that sediment deposition produced patterns quite different from those of the neutral fractal maps. For example, maps produced by the sedimentation models had positive spatial autocorrelation in contaminant levels within zones having similar processes of deposition, but little or no correlation between zones having different sedimentation processes. This investigation documented that sampling strategies that incorporated some stratification with respect to sedimentation zones were most effective in mapping contamination and detecting hot spots that may require cleanup.

8.5 Neutral Landscapes and Population Responses to Habitat Fragmentation

Landscape pattern is the result of many ecological processes, and pattern, in turn, directly affects processes. One of the most noticeable effects of pattern on process is the effect of habitat fragmentation on the rate of population growth and the probability of extinction. We found neutral models to be particularly useful in investigating the relationships between habitat loss and fragmentation on biological diversity in human-dominated landscapes of the Southern Appalachian Mountains. The following paragraphs describe results from this research.

Habitat fragmentation is complicated by the fact that both the abundance and spatial pattern of habitat vary among landscapes. For example, consider a landscape covered by 20% suitable habitat. This habitat can be arranged in a few large patches (relatively unfragmented), many small patches (highly fragmented), or in a mixture of large and small patches. Moreover, landscape characteristics can impose structure on habitat patchiness. For example, floodplains provide corridors of undeveloped habitat that maintain habitat connectivity, but an interstate highway may form a barrier to dispersal by bisecting the landscape and exacerbating the isolation of habitat fragments. Topographic patterns affect the arrangement of xeric and mesic habitats. Thus, there are many possible ways that habitat can be spatially arranged in a landscape.

Any set of real landscapes will contain only a limited number of these possibilities. This reality limits the ability of ecologists to investigate the effects of habitat fragmentation empirically because a full range of combinations of P with different spatial patterns usually is not available. Field biologists often are constrained by the small set of "unique" landscapes in which habitat pattern and abundance are observed. Theoretical experi-

ments involving simulation models are useful for testing hypotheses concerning our limited understanding of the effects of landscape pattern on processes. These experiments, in turn, help the investigator put empirical data from a few unique landscapes in a broader conceptual framework.

Changes in landcover result in changes in both the abundance and spatial pattern of habitat. Such changes undoubtedly affect the population dynamics of native species; however, all species using a particular habitat may be differentially affected by these changes. Species that differ in their patterns of survival, fecundity, and dispersal will respond differently to habitat loss and fragmentation. For example, species having large area requirements and limited vagility are impacted more by fragmentation than species that disperse well and can live in small isolated patches. To incorporate the varying responses of species to landcover change, we developed a spatially explicit model that simulates population dynamics on habitat maps. This model can represent species that differ in the three life-history characters listed above (Pearson et al., unpublished manuscript). The purpose of the model was to provide a means of comparing the response of species with different life-history strategies to changes in the abundance and spatial pattern of suitable habitat. Rather than providing predictions about the population dynamics of specific species, the model was used to determine which landscapes could support populations that employ a particular life-history strategy (e.g., high dispersal-high survivorship versus low dispersal-low survivorship). We also determined which life history strategies were most sensitive to landscape changes occurring in the Southern Appalachians.

We used model simulations to rank landscapes in the Southern Blue Ridge province with respect to their ability to support species with a suite of different life histories. Maps derived from remotely sensed images of real landscapes were also used, but these maps encompassed a limited number of combinations of habitat abundance and pattern. Therefore, neutral models for generating maps were used to produce maps that had the same levels of abundance (P) but different spatial arrangements of habitat (Table 8.1,

TABLE 8.1. Landscape metrics and population response for six habitat maps generated for the population dynamics model. Percent habitat occupied is the occupation rate after 10 time steps and the mean of 10 replicate simulations

	Percent suitable	Number of patches	Mean patch size	Landscape shape index	Percent habitat occupied
Map 5 Actual	36	104	3.75	9.14	23.90
Map 5 Random	36	288	1.36	23.98	0.20
Map 5 Clumped	36	6	65.30	2.95	49.30
Map 8 Actual	53	38	17.20	7.26	44.20
Map 8 Random	53	24	24.00	25.86	1.70
Map 8 Clumped	53	2	288.60	3.32	54.00

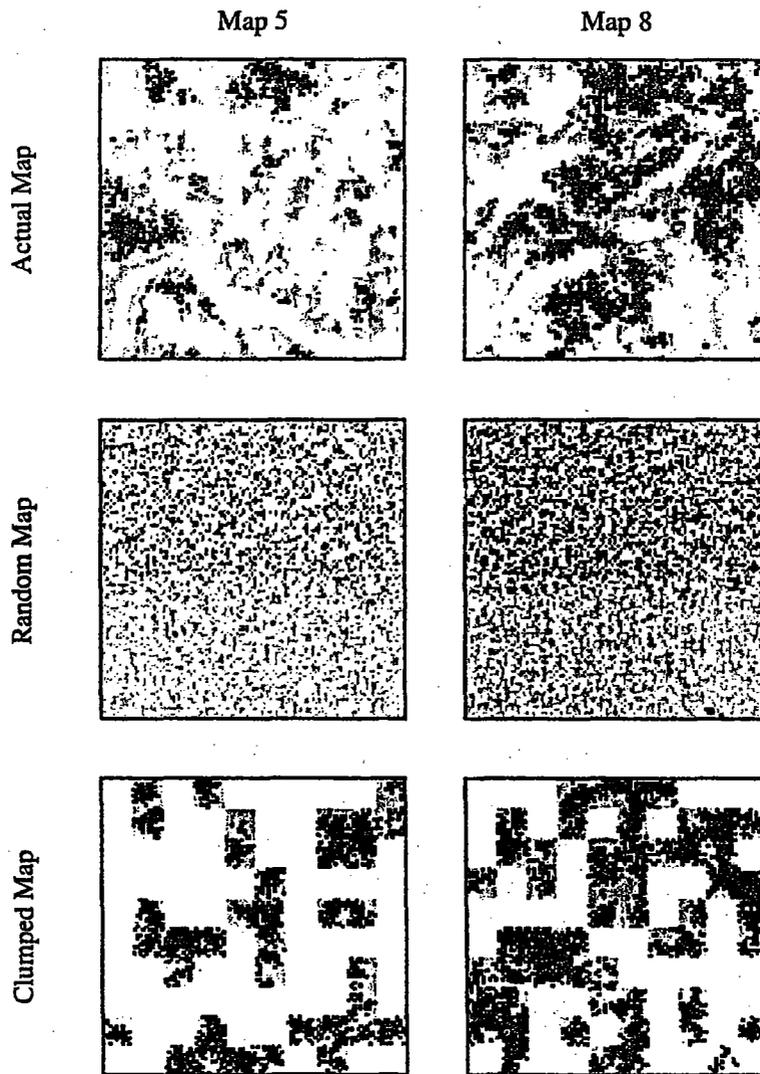


FIGURE 8.5. Actual and generated maps of forest habitat used in a simulation study of population dynamics. Maps in the same column have the same P but different spatial patterns (Map 5, $P = 0.36$; Map 8, $P = 0.53$). The actual maps were derived from actual landcover maps. The random and clumped maps were produced using methods described for hierarchical neutral maps. In all maps, white cells represent unsuitable habitat. Shaded cells represent suitable habitat that is either occupied (black) or unoccupied (grey) by a population. The maps show patterns of occupancy after 10 time steps of a model simulating the growth of populations of an annual plant with moderate fecundity and limited dispersal ability (see Table 1).

Figure 8.5). Landscape metrics, used to quantify these spatial pattern of suitable habitat, were calculated using FRAGSTATS (McGarigal and Marks 1995; see Hargis et al. [this volume] for a further discussion of landscape metrics).

The population dynamics model was used to simulate populations of an annual plant having a life-history strategy of moderate fecundity and limited dispersal, similar to that of *Trillium erectum*, a common mesic forest species in the Southern Appalachian Mountains. At the beginning of each simulation, 33% of cells of suitable habitat were selected at random and marked as occupied. The percentage of suitable cells that were occupied after 10 time steps was recorded and compared for each map (Table 8.1). Rates of occupation greater than 33% indicated growing populations, while rates lower than 33% indicated declining populations.

This life-history strategy was strongly affected by the spatial pattern of habitat. The populations increased on actual Map 8 but declined on actual Map 5 (Figure 8.5). It declined on both random maps and increased on both clumped maps. Analysis of variance confirmed that spatial pattern ($F_{2,56} = 1924.0$, $r^2 = 0.95$) had a stronger effect than habitat abundance ($F_{2,56} = 122.4$, $r^2 = 0.02$). Moreover, the occupation rate was correlated with mean patch size across all maps ($r = 0.68$, $P < 0.01$; Figure 8.6). The exception to this

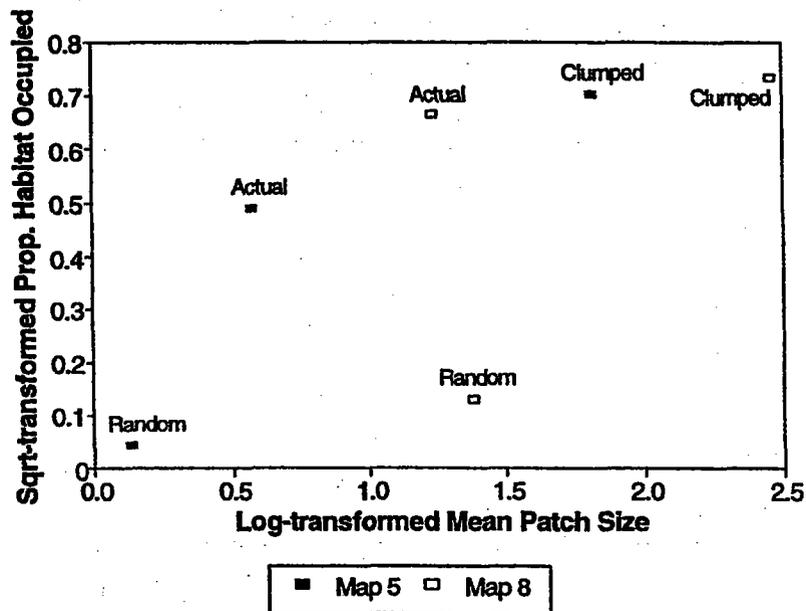


FIGURE 8.6. Relationship between percentage of suitable habitat occupied by population and mean patch size. Occupation rate is square-root transformed, and patch size is log-transformed.

relationship is found with the random Map 8 (Figure 8.6), indicating that patch shape was also important. The patches in this map were more complex (cf. landscape shape index, Table 8.1) than those in the actual and clumped maps. This understanding between the interaction of landscape pattern and population dynamics would not have been possible if the analysis had been limited to the actual maps in which habitat abundance and pattern were confounded. The neutral maps made available additional comparisons that revealed the relatively greater importance of habitat pattern as manifest in patch size and shape.

8.6 Summary

Neutral models are useful for testing whether a particular hypothesized mechanism is needed to explain an observed pattern. They are useful in landscape ecology, a field that attempts to understand the complex relationships between landscape patterns and ecological processes. The relationship between landscape processes and observed patterns can be tested rigorously only if the expected pattern in absence of the process is known. Real landscapes can be compared to maps produced from neutral models to test hypotheses related to proposed mechanisms (processes) that control habitat abundance and spatial pattern. Neutral models can produce maps that vary in their complexity and control over spatial pattern at different scales. Obviously, pattern also affects processes. Neutral models can be used to produce maps having habitat patterns not observed in the limited number of real landscapes available to a researcher. Maps of real and theoretical landscapes can be used as input to spatially explicit models to help ecologists explore the implications of landscape patterns for ecosystem processes, population dynamics, and management decisions.

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