17
Ecological Implications of Landscape Fragmentation

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Introduction

Understanding the effects of extensive and rapid changes in land-use patterns on the distribution and abundance of organisms is an important ecological issue (Burgess and Sharpe 1981; Forman and Godron 1986; Risser et al. 1984; Wiens et al. 1985; Naiman et al. 1988; Lubchenco et al. 1991). Although many physical and biotic factors, such as topography, disturbance, and resource gradients, are associated with habitat fragmentation, the direct effects of human activities (O'Neill et al. 1988a), on the size, shape, and the spatial arrangement of habitat types are particularly important (Krummel et al. 1987; Odum and Turner 1990). Sudden changes in broad-scale patterns have been predicted (Gardner et al. 1987) from gradual change in land-use, producing patterns which may be very sensitive to future disturbances (Franklin and Forman 1987).

The effects of patch size, isolation, and regional abundance on forest bird communities were assessed by van Dorp and Opdam (1987) in 235 small (0.1-39 ha) deciduous woodlots. Woodlot size was the best single predictor of species number and probability of occurrence. While regional levels of abundance affected the probability of occurrence of avifauna in all woodlots, interior species were affected most by the degree of woodlot isolation. Bolger et al. (1991) compared the species-area relationship in unfragmented chaparral habitat with that in urban chaparral fragments and found rapid population extinction of resident bird species as the habitat was fragmented. Because more abundant species persist longer in fragmented landscapes, species remaining in small fragments do not reflect the original diversity of biota in the unfragmented landscape (Bolger et al. 1991).

Recent theoretical and empirical studies indicate that a multi-scaled,

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Methods

Generating Simple Random Ma

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A cluster or habitat patch is
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hierarchical approach may be needed to relate landscape pattern and process. Systematic examination of a number of different landscapes (O'Neill et al. 1991a, 1991b) has shown that landscape patterns shift as the grain and extent of the data set change. On all of the landscapes examined, the small-scale patterns of biota (e.g., distribution of individual plants) are superimposed on the broader-scale patterns of abiotic variables (e.g., soils, topography, climate, etc.). Because there is a multitude of factors which affect biota, and because these factors are distributed across a hierarchy of scales, the nature of community persistence must be analyzed and interpreted at more than one scale (Rahel 1990).

As human effects accelerate, a general approach is needed to characterize spatially heterogeneous systems and understand what makes different species sensitive to landscape fragmentation (Lubchenco et al. 1991). This chapter examines the effect of scale-dependent changes in spatial patterns by: 1) generating a series of simple random and hierarchically structured maps; 2) comparing the results with patterns of forest habitat from digitized landscape data; and 3) simulating two consumer populations with different life history characteristics. The effect of spatial patterns on population abundance (number of sites and spatial extent of habitat utilized) were compared to determine how abundance of biota can be predicted from scale-dependent changes in landscape patterns.

Methods

Generating Simple Random Maps

Two-dimensional random maps were formed by creating arrays with M columns and M rows and randomly setting the M^2 elements of the array to 1 with a probability of P, or to 0 with a probability of (1.0 - P). Array elements set to 1 represent suitable habitat, while elements set to 0 represent sites that are unsuitable. Figure 17.1a shows an example of a random map size of M = 64 and P of 0.64, with the dark pixels representing areas of suitable habitat. Large random maps will have an average of PM^2 suitable sites, S, and 1 - PM^2 unsuitable sites. The patterns of simple random maps were characterized by generated arrays with M fixed at 216 (46,656 total sites) and P ranging from 0.3 to 0.8 (Table 17.1).

A cluster or habitat patch is defined as a group of suitable sites which have at least one common edge along the vertical or horizontal directions of an array but not along the diagonals (i.e., each suitable site has four possible neighbors). The number, size, and shape of clusters are known to change as a function of P, with rapid changes occurring near the critical probability, p_c, when the largest cluster extends, or percolates, from one

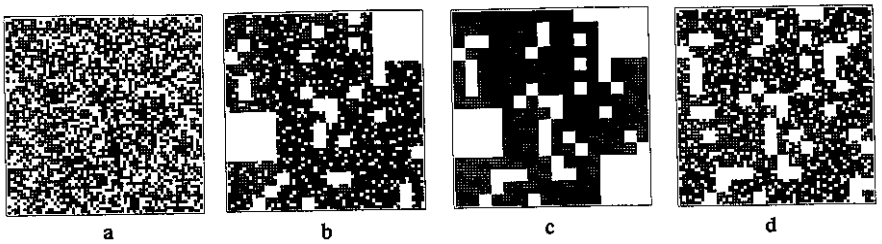

Figure 17.1. Four randomly generated maps with 64 rows and columns (4,096 individual sites). All four maps have a total fraction of suitable sites, P, of 0.64. The dark sites represent locations of suitable habitat: (a) a simple random map; (c-d) three-level hierarchically random maps with different level-dependent probabilities of site suitability. The probabilities are: (b) $p_1 = p_2 = p_3 = 0.861$; (c) $p_1 = p_2 = 0.8$ and $p_3 = 1.0$; (d) $p_1 = 1.0$, $p_2 = p_3 = 0.8$.

edge of the grid to the other. The value of p_c for extremely large maps has been determined to be 0.5928 (Stauffer 1985) when exactly 50% of the observed maps have clusters that extend from one edge to the other. Although percolation on an individual map is a discrete phenomena, the probability of percolation can be estimated by sampling many maps at the same value of P. Analysis of arrays generated by percolation theory has provided a means of applying these methods to ecological systems (see Gardner et al. 1992).

Generating Hierarchically Structured Maps

The recursive algorithm for generating hierarchical structured random maps is derived from methods of fractal geometry referred to as curdling (Mandelbrot 1983), since the process transforms an initially uniform distribution of material into many small clumps of high density (Feder 1988). Our adaptation of this algorithm requires the specification of the number, L, of successively finer scales within the map; the number of units, m_i, within each level, I (i = 1...L); and the fraction of units, p_i, that are randomly designated as units that contain suitable habitat. Units at the finest level, L, are sites whose values have been set to 1. The recursive procedure for generating a three-level hierarchical map ($L = 3$) is summarized in Fig. 17.2. A matrix of (m_1 x m_1) elements is created with the elements randomly set to 1 with a probability of p_1. Each element that is set to 1 is subdivided into an (m_2 x m_2) matrix and these $(m_2)^2$ elements are randomly set to 1 with a probability of p_2. The process is repeated a third time by subdividing those elements set to 1 at level 2 into an (m_3 x m_3) matrix and randomly setting to 1 the elements at this finest resolution with a probability of p_3. Because sampling is performed without replacement, the algorithm produces a random hierarchical map with a total

Table 17.1. Characteristics of two

	Map[b]			
P	ΣC	LC	ΣE	
0.3	6030.0	30.4	39300.0	
0.4	5040.0	70.0	45000.0	1
0.5	3140.0	307.0	46900.0	11
0.54	2340.0	927.0	46700.0	49
0.56	1940.0	2480.0	46300.0	199
0.58	1580.0	5460.0	45800.0	425
0.6	1250.0	15700.0	45100.0	553
0.62	994.0	24900.0	44300.0	358
0.64	780.0	27600.0	43400.0	297
0.66	614.0	29300.0	42300.0	265
0.68	470.0	30700.0	4100.0	243
0.7	365.0	31900.0	39700.0	227
0.72	282.0	33100.0	38000.0	213
0.74	208.0	34200.0	36300.0	201
0.76	147.0	35300.0	34400.0	191
0.78	100.0	36200.0	32600.0	182
0.8	79.0	37200.0	30500.0	174

[a] The results are means of 5 replicate maps sites per map).

[b] The means characteristics of the maps ar number of clusters; LC, the number of site edge (the total number of non-habitat si correlation length (see text for details).

[c] SAW and DAP are results of simulations an Annual Plant, respectively (see text for of sites visited during the simulation by SA ξ^2 is the correlation length of visited or po

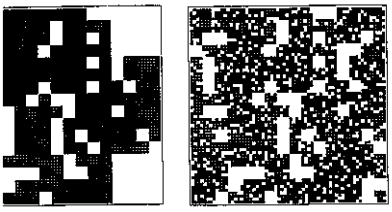

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Table 17.1. Characteristics of two populations on simple random maps.[a]

	Map[b]				SAW[c]		DAP[c]	
P	ΣC	LC	ΣE	ξ^2	V_2	ξ^2	V_2	ξ^2
0.3	6030.0	30.4	39300.0	5.7	3.0	1.3	4.2	0.8
0.4	5040.0	70.0	45000.0	17.1	2.4	1.0	2.0	0.5
0.5	3140.0	307.0	46900.0	117.0	8.6	4.8	20.0	3.5
0.54	2340.0	927.0	46700.0	498.0	25.8	17.6	51.6	5.1
0.56	1940.0	2480.0	46300.0	1990.0	17.0	13.3	239.0	16.1
0.58	1580.0	5460.0	45800.0	4250.0	51.2	29.7	625.0	28.1
0.6	1250.0	15700.0	45100.0	5530.0	65.0	68.5	204.0	8.6
0.62	994.0	24900.0	44300.0	3580.0	27.6	17.9	2500.0	29.6
0.64	780.0	27600.0	43400.0	2970.0	60.8	53.9	6270.0	70.3
0.66	614.0	29300.0	42300.0	2650.0	1060.0	1030.0	8740.0	131.0
0.68	470.0	30700.0	4100.0	2430.0	1660.0	1410.0	8290.0	168.0
0.7	365.0	31900.0	39700.0	2270.0	5070.0	3410.0	13000.0	556.0
0.72	282.0	33100.0	38000.0	2130.0	9470.0	4230.0	16700.0	688.0
0.74	208.0	34200.0	36300.0	2010.0	14200.0	3760.0	17700.0	17990.0
0.76	147.0	35300.0	34400.0	1910.0	14500.0	2910.0	18000.0	28070.0
0.78	100.0	36200.0	32600.0	1820.0	22400.0	3390.0	15500.0	3410.0
0.8	79.0	37200.0	30500.0	1740.0	27300.0	2870.0	21600.0	4880.0

[a] The results are means of 5 replicate maps with dimension, M, of 216 by 216 (M^2 = 46,656 sites per map).

[b] The means characteristics of the maps are P, the proportion of suitable sites; ΣC, the total number of clusters; LC, the number of sites in the largest cluster; ΣE, the total amount of edge (the total number of non-habitat sites adjacent to each habitat site); and ξ^2, the correlation length (see text for details).

[c] SAW and DAP are results of simulations of a Self-Avoiding Walker and the Dispersal of an Annual Plant, respectively (see text for details of simulation methods). V_s is the number of sites visited during the simulation by SAW and the number of sites populated by DAP. ξ^2 is the correlation length of visited or populated sites for SAW and DAP, respectively.

Generating Hierarchically Structured Random Maps

A three-level hierarchical map with 64 rows and 64 columns (4,096 individual sites, s) is iteratively generated by:

Step 1: Forming a $m_1 \times m_1$ matrix with $(m_1)^2$ sites, then randomly setting individual sites to 1 with probability p_1 and to 0 with probability $(1.0 - p_1)$;

Step 2: Each site set to 1 in Step 1 is subdivided into $m_2 \times m_2$ sites. The finer-grained sites are randomly set to 1 with probability p_2, and to 0 with probability $(1.0 - p_2)$; and

Step 3: The procedure is iterated a final time by further subdividing those sites set to 1 in Step 2 into $m_3 \times m_3$ sites. These finest-grained sites are then set to 1 with probability p_3, and to 0 with probability $(1.0 - p_3)$.

The overall dimension of the hierarchically structure map, m, will be equal to $m_1 \times m_2 \times m_3$, and the overall probability, p, will be equal to $p_1 \times p_2 \times p_3$. Three hierarchically structure maps are illustrated in Figure 17.1.

Figure 17.2. Recursive procedure for generating a three-level hierarchically random map.

number of sites, M^2, equal to $(m_1 \times m_2 \times m_3)^2$, a total fraction of suitable sites, P, equal to $(p_1 \times p_2 \times p_3)$, and the total number of suitable habitat sites, S, will be $(m_1 \times m_2 \times m_3)^2(p_1 \times p_2 \times p_3)$.

Figure 17.1 compares a simple random map (Fig. 17.1a) with three hierarchically random maps (Fig. 17.1b-d). All maps in Figure 17.1 have M = 64 (4,096 individual sites) and P = 0.64. In addition, the values of L and m_i for the three hierarchical maps has been fixed at 3 and 4, respectively. Figure 17.1b shows a self-similar hierarchical map (i.e., the pattern is the same at each level) with p_i = 0.861 (0.861^3 = 0.64). The fact that identical values of the m_i and p_i produce a self-similar map is confirmed by observing that exactly two empty "units" are found at each hierarchical level. Figure 17.1c shows a hierarchical map with m_i and m_2 = 0.8, while m_3 = 1.0 (i.e., all sites are suitable at the finest scale if the units at higher levels are also suitable). Figure 17.1d shows a hierarchical map with the m_1 = 1.0 and m_2 and m_3 = 0.8.

If we fix L = 3 and require that the m_i are identical, it is possible to generate a number of hierarchical maps to compare with the random maps. We chose to generate 7 maps with P = 0.64, M = 216, and L = 3. The 7 maps are produced by limiting the permutations of the p_i's to combinations of (1.0, 1.0, 0.64), (1.0, 0.8, 0.8), or (0.86, 0.86, 0.86).

The LUDA Maps

The U.S. Geological Survey (USGS) digital land-use and land-cover data base (LUDA) provides a spatial description of landscapes across the United States (Fegeas et al. 1983). The
and Space Administration (U2
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into 1 of 37 Level II (Fegeas
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Seven quadrangles were select
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ranged from a P of 0.27 to 0.9
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Method of Map Analysis

A computer program was writte
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calculates for each map: S, the
fraction of map sites that are s
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and $\sum E$, the total amount of e
adjacent to each habitat site).
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The mean squared radius, R_s^2, a
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The information provided for R
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64 columns (4,096 individual sites, s) is

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a three-level hierarchically random map.

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States (Fegeas et al. 1983). The data originate from National Aeronautics and Space Administration (U2/RB-57 high-altitude aerial photo coverage taken in the 1970s, and from these photos, land-cover types were delineated into 1 of 37 Level II (Fegeas et al. 1983) land-cover categories. The minimum polygon (patch) size of forested land in the LUDA data base is 16 ha, based on the provision that the minimum width of a polygon must be greater than 400 m. Because the original USGS data divides the 1:25,000 quadrangles into 24 separate sections, a special computer program was written to reformat the arc and node topological elements of the polygons and remove section boundaries that arbitrarily dissect polygons along those boundaries.

Seven quadrangles were selected from the LUDA data to form a transect from southern Georgia to northeastern Tennessee. Each quadrangle was sub-sampled by selecting 5 maps, each with M = 216, from the northeast, southeast, northwest, southwest, and central portion of each quadrangle. The forested regions of each map were analyzed and compared with the random and hierarchical maps. The percent forested habitat of the 35 LUDA maps ranged from a P of 0.27 to 0.94, and the total number of habitat patches ranged from 9 to 279.

Method of Map Analysis

A computer program was written to analyze the spatial patterns of simple random, hierarchically random, and actual LUDA landscapes. This program calculates for each map: S, the number of suitable habitat sites; P, the total fraction of map sites that are suitable ($P = S/M^2$); $\sum C$, the total number of clusters or patches of suitable habitat; LC, the size of the largest cluster; and $\sum E$, the total amount of edge (the total number of non-habitat sites adjacent to each habitat site). In addition to these metrics, the mean squared radius of patches was estimated as a measure of habitat dispersion. The mean squared radius, R_s^2, also called the "radius of gyration" (Stauffer 1985), is calculated by enumerating the number, s, and position, r, of individual sites within a given cluster:

$$2R_s^2 = \sum_{i,j} \frac{|r_i - r_j|^2}{s^2} \qquad (17.1)$$

The information provided for R_s^2 for each cluster can be used to estimate the correlation or connectivity length, ξ, of the entire map. Because ξ is the average distance of two sites belonging to the same cluster, the average

value of $2R_s^2$ for all clusters is weighted by the size and frequency distribution of the clusters to estimate the squared correlation length for the map:

$$\xi^2 = \frac{2\sum_s R_s^2 s^2 N_3}{\sum s^2 N_s} \qquad (17.2)$$

where N_s is the number clusters of size s per site.

Simulating Two Types of Consumer Populations

The generation of simple random and hierarchically random maps provides a spatial description of habitat resources for simulating the patterns of growth and dispersion of organisms. We performed simulations by using a set of rules which describe the patterns of habitat utilization and spread of different consumer populations, and analyzed the final patterns of abundance at the conclusion of the simulations. The population-specific rules for habitat utilization and spread consisted of: 1) the probability, i, of spread from a populated site to adjacent suitable sites; 2) the probability, e, per unit time and per site for local extirpation of the population (the expected residence time of a population at a site will be $1/e$); and 3) the probability, h, that the local site will be unsuitable for recolonization after a local population has been extirpated. If h = 0.0, the sites will be unaffected by colonization, if h = 1.0, then resources are permanently depleted and the site cannot be recolonized. Values of h between 0.0 and 1.0 indicate that colonization diminishes (but does not deplete) local resources, lowering the probability of reestablishment.

Although these rules are probabilistic, certain combinations of parameters will produce deterministic results. For instance, when i is small and e and h are set to 0.0, the population will slowly spread into all sites within a cluster. When i, e, and h are equal to 1.0, then the population spreads very rapidly throughout the cluster, destroying sites as it moves, much like a forest fire. Therefore, we chose two sets of parameters that produced different spatial dynamics. The first consumer populations (SAW) had values of i, e, and h of 0.8, 1.0, and 1.0, respectively. The high value of i causes rapid spread to adjacent suitable sites, but site colonization lasts for only one time step (e = 1.0) and sites cannot be recolonized (h = 1.0). The landscape dynamics of SAW are much like a self-avoiding walk and similar to a herd depleting resources as it moves through a landscape. The second population (DAP) had values of i, e, and h of 0.8, 0.25, and 0.25, respectively. DAP is similar to a weedy, annual plant that moves quickly to adjacent sites (i = 0.8), has a moderately low probability of local extinction (e = 0.25), and may frequentl
0.25).

Simulations were begun by
initializing a single map site
recording the spread of the p
patterns of abundance at the
were initialized at a single site,
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were performed for each map

The Map Patterns

The total number of clusters,
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ranging from 0.3 to 0.8 and M
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0.5928, is evident in the sudden
4 PC; LC increased nearly thre
P = 0.6, and the number of c
0.58 to 994 at P = 0.62. The
as a percent of available habitat
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Changes in ξ^2 with increasin
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$$\frac{{}^{2}s^{2}N_3}{{}^{2}N_s} \qquad (17.2)$$

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(e = 0.25), and may frequently recolonize previously occupied sites (h = 0.25).

Simulations were begun by defining the parameters of i, e, and h, initializing a single map site near the center of the map at random, recording the spread of the population through time, and analyzing the patterns of abundance at the end of 200 time steps. Because populations were initialized at a single site, and because the rule for growth is restricted to adjacent sites, the upper limit of population size is set by the size of the cluster that is randomly selected by the initialization process. Five iterations were performed for each map and population type.

The Map Patterns

The total number of clusters, $\sum C$, the size of the largest cluster, LC, the total amount of edge, $\sum E$, and the correlation length, ξ, were calculated as measures of pattern for 5 replicate simple random maps with values of P ranging from 0.3 to 0.8 and M (the number of rows and columns in the map) equal to 216 (Table 17.1). The effect of the critical threshold, p_c = 0.5928, is evident in the sudden changes in $\sum C$ and LC near that value of 4 PC; LC increased nearly three-fold from 5,460 at P = 0.58 to 15,700 at P = 0.6, and the number of clusters declined rapidly from 1,580 at P = 0.58 to 994 at P = 0.62. The effect was even more dramatic if expressed as a percent of available habitat. At P = 0.56, only 10% of available habitat was found in the largest cluster (% = $LC/(M^2P)$), while at P = 0.6, 56% of available habitat is present in one large cluster. The total amount of edge, $\sum E$, reached a maximum at 0.5, and declined gradually as P increased.

Changes in ξ^2 with increasing P were more complex (Table 17.1; Fig. 17.3a). For values of P below 0.5, clusters were small, consequently the correlation length was also small. The aggregation of clusters that occurred above the critical threshold caused ξ^2 to increase rapidly, reaching a maximum at P = 0.6. Values of ξ^2 then declined as the cluster became dense and was confined by the boundary of the map, resulting in a decrease in the average distance between sites.

Differences in P among maps caused a corresponding change in the number and size distribution of clusters on the map (Stauffer 1985). We controlled for this effect by generating a set of hierarchically random maps with P fixed at 0.64 (Table 17.2). Although the total fraction of available habitat was the same among maps, the differences in pattern were large. The total number of clusters, $\sum C$, showed a nearly 300-fold change from a low of 2.6 for the hierarchical map with p_is of (0.64, 1.0, 1.0), to a high of 779 for the simple random map. Differences in the amount of edge, $\sum E$,

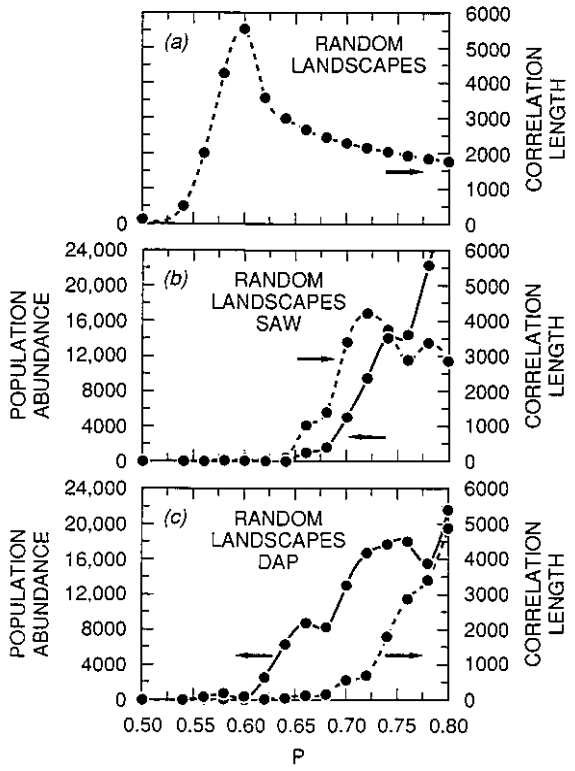


Figure 17.3. The correlation length (dashed line) and landscape abundance (solid line) for: (a) habitat patterns of simple random maps and the simulation of two organisms types; (b) SAW; and (c) DAP. See text for details of simulation procedures.

were also large. The simple random map and the hierarchical map with p_is of (1.0, 1.0, and 0.64) had the greatest amount of edge, while the hierarchical map with p_is of (1.0, 1.0, and 0.64) showed nearly 30-fold fewer edges. The size of the largest clusters, *LC*, did not differ greatly among maps (ranging from 23100 to 30200), although smaller *LC*s were observed when p_1 <1.0 and larger *LC*s occurred when p_3 <1.0. Because the correlation length was affected most by the size of the largest cluster, the values of ξ^2 did not differ greatly among maps (Table 17.2). When p_1 and p_2 equal 1.0 and p_3 = 0.64, the pattern of the hierarchical map was nearly identical to the simple random map.

The landscape pattern of forest patches extracted from the LUDA quadrangles (Table 17.3 and Fig. 17.4) showed greater variation than the precisely defined simple random and hierarchically random maps. Total number of clusters peaked near 0.5. The *LC* increased with increasing *P*(Fig. 17.4b), but declined gradually at p_c. The amount of total edge was

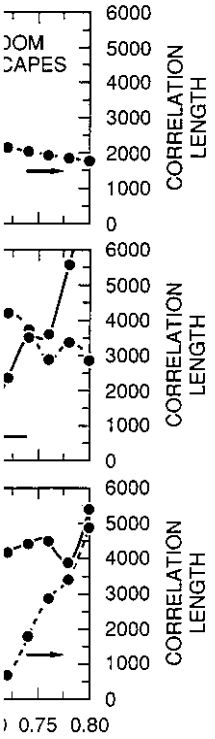
Table 17.2. Characteristics of
0.64.[a]

				Ra
				Map[b]
P	Σ*C*	*LC*	Σ*E*	
0.64	779.0	27500.0	43400.0	
				Hier
P_1	P_2	P_3	ΣC	LC
0.64	1.0	1.0	2.6	23100.0 1
1.0	0.64	1.0	27.4	24500.0 7
1.0	1.0	0.64	662.0	28000.0 44
1.0	0.8	0.8	60.8	30200.0 27
0.8	0.8	1.0	3.4	29100.0 4
0.8	1.0	0.8	43.0	29200.0 25
0.86	0.86	0.86	14.0	29700.0 20

[a] The results are means of 5 replicate m
sites per map). The hierarchical maps a
P, the fraction of suitable sites, is equa
fraction of suitable sites is calculated as

[b] The means characteristic of the maps a
number of clusters; *LC*, the number of si
(the total number of non-habitat sites ac
length (see text for details).

[c] SAW and DAP are results of simulatio
an Annual Plant, respectively (see text fo



landscape abundance (solid line) for: imulation of two organisms types; (b) procedures.

d the hierarchical map with p_is nt of edge, while the hierarchi- ved nearly 30-fold fewer edges. ıot differ greatly among maps aller *LC*s were observed when <1.0. Because the correlation largest cluster, the values of ξ^2 7.2). When p_1 and p_2 equal 1.0 al map was nearly identical to

s extracted from the LUDA ved greater variation than the ırchically random maps. Total *LC* increased with increasing The amount of total edge was

Table 17.2. Characteristics of random and hierarchical maps when P = 0.64.[a]

Random Map

		Map[b]			SAW[c]		DAP[c]	
P	ΣC	LC	ΣE	ξ^2	V_s	ξ^2	V_s	ξ^2
0.64	779.0	27500.0	43400.0	2970.0	60.8	53.9	6270.0	70.3

Hierarchical Maps

				Map[b]			SAW[c]		DAP[c]	
P_1	P_2	P_3	ΣC	LC	ΣE	ξ^2	V_s	ξ^2	V_s	ξ^2
0.64	1.0	1.0	2.6	23100.0	1530.0	3640.0	16500.0	4100.0	10100.0	3480.0
1.0	0.64	1.0	27.4	24500.0	7670.0	3450.0	7360.0	3500.0	11900.0	6070.0
1.0	1.0	0.64	662.0	28000.0	44500.0	2890.0	149.0	142.0	6330.0	60.3
1.0	0.8	0.8	60.8	30200.0	27800.0	2520.0	14200.0	4450.0	10400.0	1580.0
0.8	0.8	1.0	3.4	29100.0	4910.0	2660.0	22800.0	3710.0	17200.0	5040.0
0.8	1.0	0.8	43.0	29200.0	25100.0	2710.0	22000.0	3730.0	14100.0	5930.0
0.86	0.86	0.86	14.0	29700.0	20100.0	2570.0	15600.0	4100.0	15400.0	5560.0

[a] The results are means of 5 replicate maps with dimension, M, of 216 x 216 (M^2 = 46,656 sites per map). The hierarchical maps are generated with $m_1 = m_2 = m_3 = 6$ ($6^3 = 216$). P, the fraction of suitable sites, is equal to 0.64 for all maps. For hierarchical maps, the fraction of suitable sites is calculated as $P = p_1 \times p_2 \times p_3$.

[b] The means characteristic of the maps are: P, the proportion of suitable sites; ΣC, the total number of clusters; LC, the number of sites in the largest cluster; Σ, the total amount of edge (the total number of non-habitat sites adjacent to each habitat site); and ξ^2, the correlation length (see text for details).

[c] SAW and DAP are results of simulations of a Self-Avoiding Walker and the Dispersal of an Annual Plant, respectively (see text for details of simulation methods). V_s is the number

Table 17.3. Samples from LUDA maps.[a]

Quadrangle	Sample	P	ΣC	LC	ΣC	ξ^2
Valdosta	a	0.57	221.0	16975.0	17372.0	3934.0
	b	0.42	279.0	7363.0	14238.0	4325.0
	c	0.66	53.0	27361.0	11444.0	2931.0
	d	0.59	237.0	15454.0	15876.0	5144.0
	e	0.52	258.0	12175.0	16294.0	8940.0
	mean	*0.412*	*135.0*	*5871.0*	*11163.0*	*3661.0*
Waycross	a	0.27	190.0	1493.0	11185.0	1690.0
	b	0.37	173.0	3028.0	12617.0	2478.0
	c	0.58	61.0	12543.0	10184.0	5510.0
	d	0.47	93.0	7664.0	11516.0	4416.0
	e	0.37	159.0	4625.0	11986.0	4213.0
	mean	*0.412*	*135.2*	*5870.0*	*11629.0*	*3661.0*
Macon	a	0.49	121.0	8909.0	11317.0	4904.0
	b	0.66	41.0	29357.0	8846.0	2680.0
	c	0.72	25.0	22611.0	8908.0	3399.0
	d	0.49	115.0	11592.0	14432.0	4285.0
	e	0.68	57.0	27480.0	9422.0	2914.0
	mean	*0.608*	*71.8*	*19990.0*	*10584.0*	*3636.0*
Athens	a	0.59	73.0	25444.0	12648.0	3450.0
	b	0.81	19.0	37000.0	7240.0	1650.0
	c	0.76	24.0	33935.0	8870.0	1960.0
	d	0.90	9.0	41630.0	5590.0	1400.0
	e	0.76	36.0	34700.0	8770.0	1930.0
	mean	*0.764*	*32.2*	*34541.0*	*8623.0*	*2078.0*
Greenville	a	0.69	94.0	29067.0	13528.0	2653.0
	b	0.88	17.0	40945.0	5888.0	1379.0
	c	0.75	40.0	33776.0	8902.0	1983.0

Table 17.3 (con't)

Quadrangle	Sample	P
	d	0.38
	e	0.76
	mean	*0.692*
Knoxville	a	0.92
	b	0.65
	c	0.81
	d	0.78
	e	0.94
	mean	*0.82*
Johnson City	a	0.53
	b	0.88
	c	0.76
	d	0.54
	e	0.66
	mean	*0.674*

[a]Five maps with dimension, M, of 216 by 2
from each LUDA quadrangle. The charac
suitable sites; ΣC, the total number of cluste
ΣE, the total amount of edge (the total num
site); and ξ^2, the correlation length (see te

Table 17.3 (con't)

Quadrangle	Sample	*P*	Σ*C*	*LC*	Σ*C*	ξ^2
	d	0.38	261.0	3942.0	14706.0	2053.0
	e	0.76	64.0	33947.0	10624.0	1978.0
	mean	*0.692*	*95.2*	*28335.0*	*10730.0*	*2009.0*
Knoxville	a	0.92	18.0	42525.0	4678.0	1322.0
	b	0.65	159.0	24736.0	9418.0	3357.0
	c	0.81	49.0	36123.0	6622.0	1733.0
	d	0.78	48.0	34795.0	7956.0	1936.0
	e	0.94	14.0	42716.0	3768.0	1252.0
	mean	*0.82*	*57.6*	*36179.0*	*6488.0*	*1920.0*
Johnson City	a	0.53	134.0	10717.0	13764.0	5972.0
	b	0.88	26.0	40308.0	6202.0	1427.0
	c	0.76	30.0	34502.0	7634.0	1921.0
	d	0.54	120.0	15200.0	10817.0	4787.0
	e	0.66	61.0	14286.0	10876.0	5627.0
	mean	*0.674*	*74.2*	*23001.0*	*9858.0*	*3946.0*

[a]Five maps with dimension, ***M***, of 216 by 216 (M^2 = 46,656 sites per map) were extracted from each LUDA quadrangle. The characteristics of the maps are: ***P***, the proportion of suitable sites; **Σ*C***, the total number of clusters; ***LC***, the number of sites in the largest cluster; **Σ*E***, the total amount of edge (the total number of non-habitat sites adjacent to each habitat site); and ξ^2, the correlation length (see text for details).

LC	Σ*C*	ξ^2
16975.0	17372.0	3934.0
7363.0	14238.0	4325.0
27361.0	11444.0	2931.0
15454.0	15876.0	5144.0
12175.0	16294.0	8940.0
5871.0	*11163.0*	*3661.0*
1493.0	11185.0	1690.0
3028.0	12617.0	2478.0
12543.0	10184.0	5510.0
7664.0	11516.0	4416.0
4625.0	11986.0	4213.0
5870.0	*11629.0*	*3661.0*
8909.0	11317.0	4904.0
29357.0	8846.0	2680.0
22611.0	8908.0	3399.0
11592.0	14432.0	4285.0
27480.0	9422.0	2914.0
19990.0	*10584.0*	*3636.0*
25444.0	12648.0	3450.0
37000.0	7240.0	1650.0
33935.0	8870.0	1960.0
41630.0	5590.0	1400.0
34700.0	8770.0	1930.0
34541.0	*8623.0*	*2078.0*
29067.0	13528.0	2653.0
40945.0	5888.0	1379.0
33776.0	8902.0	1983.0

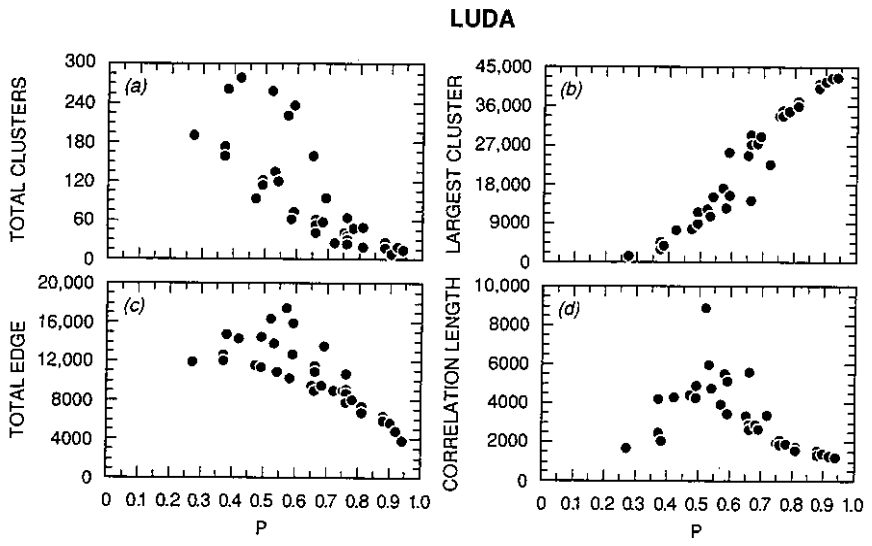


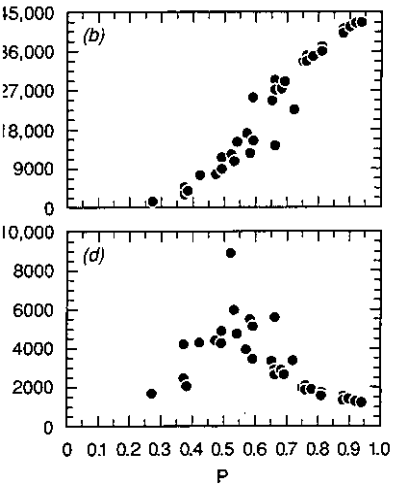
Figure 17.4. Patterns of forested areas for 35 LUDA maps plotted as a function of the percent of the map, P, that is forested: (a) total number of forest clusters; (b) the size of the largest cluster; (c) total amount of edge; and (d) the correlation length of forest patches.

of sites visited during the simulation by SAW, and the number of sites populated by DAP. ξ^2 is the correlation length of visited or populated sites for SAW and DAP, respectively.highest near 0.6, and declined with higher values of P. The pattern of change of the correlation length (Fig. 17.4d) was similar to that for random maps (Fig. 17.3a), although there was a great deal of variation among the LUDA maps. A comparison of the LUDA maps with P near 0.64 with the appropriate simple random and hierarchically random maps (Table 17.2) showed that the cumulative frequency distribution of cluster sizes of LUDA maps were significantly different from random, but quite similar to a hierarchical map with p_1, p_2, p_3 of 1.0, 0.64, 1.0, respectively.

Interaction Between Pattern and Process

The effects of changes in available habitat (e.g., changes in P for simple random maps) and the scale of habitat availability (e.g., hierarchical maps) are summarized in Tables 17.1 and 17.2, respectively. Previous results have shown probability of a site being altered by a population, h, has little effect on landscape abundance (the number of sites successfully colonized during a simulation), V_s, when $i = 1.0$, but dramatically decreases population abundance when $i < 1.0$. The reason is that alterations of local sites (h

DA



UDA maps plotted as a function of the
mber of forest clusters; (b) the size of the
the correlation length of forest patches.

/ SAW, and the number of sites
length of visited or populated sites
ıear 0.6, and declined with higher
he correlation length (Fig. 17.4d)
Fig. 17.3a), although there was a
DA maps. A comparison of the
: appropriate simple random and
.2) showed that the cumulative
f LUDA maps were significantly
to a hierarchical map with p_1, p_2,

and Process

tat (e.g., changes in P for simple
vailability (e.g., hierarchical maps)
respectively. Previous results have
by a population, h, has little effect
sites successfully colonized during
dramatically decreases population
that alterations of local sites (h

>0.0) effectively "disconnects" large patches of habitat, preventing the population from spreading across the landscape (Gardner et al. 1992).

For simple random maps, the landscape abundance, V_2, of SAW showed a 17-fold increase between P = 0.64 and 0.66 (Fig. 17.3b). The fact that this increase occurred well above the critical threshold (p_c = 0.5928) is an indication of the interaction effect of parameters P and i. Although V_s increased continually with increasing P, the correlation length showed a peak at P = 0.72, indicating that the sites occupied by SAW became more densely packed above P = 0.72, but fractured into many sub-populations below P = 0.72. This pattern was confirmed by the ratio of V_s to LC, which was 0.5 at P = 0.68, 0.29 at P = 0.72, and 0.42 at P = 0.76.

The DAP simulations showed a different pattern of landscape abundance on simple random maps. DAP was more abundant at smaller P, and rapidly increased in abundance at P = 0.62 (Fig. 17.3c). V_s and ξ^2 increased continuously with P, with a maximum increase for ξ^2 occurring between a P of 0.7 and 0.74.

The irregularity of the lines in Figure 17.3b and 17.3c for V_s and ξ^2 is due to the random initialization of populations at the beginning of each simulation. Although each point on the lines in Fig. 17.3b and 17.3c represents the mean of 5 iterations, if a population were randomly placed on a small cluster at the beginning of a simulation, the resulting growth would be dramatically different than if the population was initially placed on the large, percolating cluster. Hence, large variance between iterations will occur if random initialization results in 1 or more populations being placed on a small cluster. Because cluster size increases rapidly above the critical threshold, the probability of randomly initializing a small cluster diminishes as P increases.

Peak values of the correlation length occur when the population growth has just managed to reach the farthest extent possible. Randomly generated maps will produce habitat clusters that are larger than the map when P >0.5928 (i.e., infinite clusters; see Stauffer 1985; Feder 1988), and the border of the map will truncate the pattern. This effect is clearly illustrated in Fig. 17.3a, where the correlation length increases as P increases until the critical threshold is reached. Above this threshold, the extent of population growth is limited (i.e., truncated by finite map boundaries) and the cluster begins to fill in rather than expand. The growth of DAP showed a similar pattern (Fig. 17.3b), with a peak value for the correlation length occurring at P = 0.72. The continued increase in landscape abundance of DAP (solid line, Fig. 17.3b) indicates that above P = 0.72, growth is truncated by the map border and the population growth results in densely packed clusters. The effect of cluster truncation is a lower average mean squared distance between sites. Conversely, the landscape abundance of SAW (solid line, Fig. 17.3c) continues to increase as P increases, with no peak in the correlation length evident (dashed line, Fig. 17.3c). The different responses of these two

populations indicates that the spatial extent of the map is adequate for characterizing DAP until P = 0.72 and for SAW until at least P = 0.8.

Table 17.2 shows the effect of hierarchically structured maps on the patterns of abundance and correlation length for SAW. The abundance, V_s, of SAW ranged from 60.8 to 22,800 sites, while DAP ranged from 6,270 to 17,200. Both SAW and DAP showed smallest abundances on the simple random map. It is important to note that this result is not related to the size of LC because there is little difference in LC among the maps (Table 17.2). What does differ among maps is the scale at which the habitat pattern changes. When sites were fragmented at the finest scale (p_3 = 0.64), the lowest values of V_s occurred for SAW and DAP. Population abundances increased as fine-scale fragmentation diminished (e.g., p_1, p_2, p_3 = 1.0, 0.8, 0.8), with V_s highest when (p_1, p_2, p_3) was equal to (0.8, 0.8, 1.0) for both SAW and DAP.

Discussion

The unique response of individual species to fragmentation must be determined if patterns of abundance and extinction in response to human use of landscapes are to be predicted. Even simple differences among consumers show that the relationship between pattern (the amount and spatial arrangement of suitable habitat) and process (the growth and persistence of populations at landscape scales) can be complex. Previous results (Gardner et al. 1987; Gardner et al. 1992) demonstrated that the gradual loss of habitat (i.e., decreasing values of P, Fig. 17.3) produces critical thresholds in habitat connectivity that dramatically affect population abundance. Above the critical threshold (p_c = 0.5928) growth is a monotonic function of population-specific attributes. For instance, the simulated expansion of SAW above p_c is less than that of DAP because SAW has a high probability of resource depletion (h - 0.25 for DAP and 1.0 for SAW), preventing reestablishment of populations in previously inhabited sites. The effect of resource depletion becomes less important as habitat connectivity increases (P = 0.8, Table 17.1). Below the critical threshold, differences between species are small (Table 17.1) because the characteristically small size of habitat clusters limits population expansion.

The hierarchical maps allow the response of the SAW and DAP populations to scale-dependent changes to be systematically evaluated. The algorithm for generating hierarchically random maps (Fig. 17.2) can produce a variety of patterns while controlling the overall fraction of available habitat, P (Fig. 17.1). Hierarchically structured maps with P = 0.64 do not differ greatly in the size of the largest cluster, but show a 5-fold difference in the amount of edge and a 300-fold difference in the number of habitat clusters (Table 17.2).

The range of simulation re
that population abundance is n
as results from simple random
at which habitat fragmentatio
(i.e., map with p_1, p_2, p_3 =1.0,
levels of abundance for the SA
es between the two populati
patterns are similar, because t
(i = 0.8) are the same for bo

The correlation length, ξ^2, i
entire map, of the distances
connected. Highest values of ξ
when a single cluster extends
critical threshold are large but
the average distance between
above p_c as cluster size is trunc
densely packed (Fig. 17.3a). V
threshold because the map is

Peak values in the correlati
correlation length calculated
successfully colonized by the si
for determining when critical th
Maximum values of ξ^2 for SAW
17.1), while values of ξ^2 for D
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Values of ξ^2 for populations tha
values (Tables 17.2 and 17.3
dispersed than habitat.

The discontinuities produced
important implications for lan
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differences caused substantial s
differences among biota are li
implying that as landscapes are

The range of simulation results of SAW and DAP (Table 17.2) shows that population abundance is not predicted by the size of the largest cluster, as results from simple random maps might indicate, but rather by the scale at which habitat fragmentation occurs. Fragmentation at the finest scale (i.e., map with $p_1, p_2, p_3 = 1.0$, 1.0, and 0.8, Table 17.2) produces the lowest levels of abundance for the SAW and DAP populations. Although differences between the two populations do exist, it is not surprising that the patterns are similar, because the neighborhood rule and rate of expansion (i = 0.8) are the same for both populations.

The correlation length, ξ^2, is a measure of the average, taken across the entire map, of the distances over which habitats or populations are connected. Highest values of ξ^2 will occur at critical thresholds (Fig. 17.3) when a single cluster extends across the map. Because clusters at the critical threshold are large but very irregular (Stauffer 1985; Milne 1990), the average distance between sizes will be maximal. Values of ξ^2 decline above p_c as cluster size is truncated by the map boundary and sites become densely packed (Fig. 17.3a). Very low values of ξ^2 occur below the critical threshold because the map is composed of numerous, small clusters.

Peak values in the correlation length of population abundance (i.e., the correlation length calculated for those habitat sites which have been successfully colonized by the simulated population) provide a useful metric for determining when critical thresholds between pattern and process occur. Maximum values of ξ^2 for SAW occur on random maps at P = 0.72 (Table 17.1), while values of ξ^2 for DAP continue to increase with increasing P. The upper bound for the correlation length of habitat (Table 17.1) is 5530 at P = 0.6. The correlation length of population abundance for SAW and DAP approach the maximum possible value at P = 0.72 and P = 0.8. Values of ξ^2 for populations that are greater than the corresponding habitat values (Tables 17.2 and 17.3) indicate that the populations are more dispersed than habitat.

The discontinuities produced by thresholds in habitat connectivity have important implications for landscape studies. However, several important points must be kept in mind when interpreting these results: 1) thresholds in connectivity are dependent on the neighborhood rule (i.e., spread is limited to adjacent sites) used to define connectivity among sites. Because these rules may vary among species, and because different species are likely to respond uniquely to changes in landscape pattern, no single threshold will characterize the interaction between a variety of species and the landscape pattern. Populations capable of spreading to non-adjacent sites (i.e., long-range dispersal of seed) will show thresholds at values of P below that defined from nearest-neighbor rules of habitat connectivity; 2) the parameters used to simulate SAW and DAP were quite similar, yet slight differences caused substantial shifts in the observed thresholds. Therefore, differences among biota are likely to show broad ranges of thresholds, implying that as landscapes are progressively fragmented, successive shifts

in species composition can be expected; and 3) because all landscapes are finite, observed changes are not likely to be as sudden as those produced from theoretical studies of infinitely large systems. However, the identification of critical thresholds provides a quantification of the zone within which small changes in habitat connectivity will result in disproportionate changes in population abundances.

Fragmentation of natural landscapes is probably never random. The forested habitats analyzed from actual landscapes (i.e., the LUDA scenes) were quite different from random maps, but remarkably similar to hierarchically structured maps. However, there was still considerable variation among LUDA maps even when differences in P among maps were controlled. This range of patterns is not surprising because multiple factors, such as topography, climate, urban development, and other human land-uses, all contribute to producing these patterns. It is also noteworthy that although critical thresholds in habitat connectivity exist in real landscapes, the values of P at which connectivity occurs does not always occur at 0.5928, as it does for infinitely large random maps. Scale-dependent patterns within a landscape will influence the observed value of this threshold. Thus, our analyses of landscape pattern suggest that real landscapes exhibit scaled patterns that reflect a variety of causal factors.

The correlation length calculated for the LUDA maps provides a useful measure of habitat fragmentation (Table 17.3). For example, an examination of the four LUDA maps (Valdosta c, Macon b, Greenville a, and Johnson City e) which have a similar value of P near 0.66, shows that the pattern for Johnson City is quite different from the others. The largest cluster on the Johnson City map is considerably smaller while the correlation length is greater, indicating that, on average, the forested habits are more fragmented than the other landscapes at a similar value of P. Based on our simulations of SAW and DAP, we expect these differences in habitat patterns to produce large differences in the abundance of the biota.

The complex patterns of species response to the amount (Table 17.1) and scale (Table 17.2) of landscape fragmentation illustrate the importance of understanding relationships between pattern and process at landscape scales. It is clear that the data necessary to test the results of simple spatial models must be gathered at appropriate scales. An understanding of both the grain and extent of species interaction with the heterogeneity of landscapes is necessary to identify key processes and develop general principles for landscape management, the preservation of biodiversity, and habitat conservation.

Summary

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Acknowledgments

Special thanks are due to Sidey T
data possible. Frequent comment
in the manuscript by Roy Plotni
appreciated.

This research was funded by t
Health and Environmental Rese
Contract No. DE-AC05-84OR21
Inc.

Publication No. 3956, Envir
National Laboratory.

Summary

The effects of scale-dependent changes in landscapes are an important aspect of human interactions with ecosystems. Therefore, we investigated changes in habitat patterns by simulating two consumer populations on random and hierarchically random landscapes. The first consumer depleted resources as it randomly walked across the landscape, while the second consumer spread outward to suitable sites from an initial point. Simple model landscapes were generated by randomly selecting the habitat suitability of each site at a given probability, while hierarchically random maps were generated by a nested series of rules which changed the probabilities of site suitability with spatial scale. These two map types were compared to digitized land-use data.

Three effects were observed: 1) the reduction of available habitat always reduced population abundance and spread; 2) small changes in landscape pattern produced sudden changes in abundance which could be predicted from the interaction between landscape characteristics and population-specific life history parameters; and 3) the hierarchically structured landscapes affected abundances most when habitat fragmentation coincided with the scales at which the consumer populations utilized spatial resources.

The relationships among life history characteristics, landscape pattern, and the scale of disturbance must be jointly considered when predicting the broad-scale change in population abundance which may result from human-induced fragmentation of the landscape.

Acknowledgments

Special thanks are due to Sidey Timmons for making the analysis of LUDA data possible. Frequent comments and helpful suggestions for improvements in the manuscript by Roy Plotnick, Bill Hargrove, and Richard Flamm are appreciated.

This research was funded by the Ecological Research Division, Office of Health and Environmental Research, U.S. Department of Energy, under Contract No. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc.

Publication No. 3956, Environmental Sciences Division, Oak Ridge National Laboratory.