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Neutral models for the analysis of broad-scale landscape pattern

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Abstract

The relationship between a landscape process and observed patterns can be rigorously tested only if the expected pattern in the absence of the process is known. We used methods derived from percolation theory to construct neutral landscape models, *i.e.*, models lacking effects due to topography, contagion, disturbance history, and related ecological processes. This paper analyzes the patterns generated by these models, and compares the results with observed landscape patterns. The analysis shows that number, size, and shape of patches changes as a function of p, the fraction of the landscape occupied by the habitat type of interest, and m, the linear dimension of the map. The adaptation of percolation theory to finite scales provides a baseline for statistical comparison with landscape data. When USGS land use data (LUDA) maps are compared to random maps produced by percolation models, significant differences in the number, size distribution, and the area/perimeter (fractal dimension) indices of patches were found. These results make it possible to define the appropriate scales at which disturbance and landscape processes interact to affect landscape patterns.

Introduction

Vegetation patterns are the result of complex interactions between climate, terrain, soil, water availability, biota (Whittaker 1975) and alterations resulting from wind and fire (Pickett and White 1985). Alterations in landscapes as a result of urbanization, agriculture, and forestry management have significant effects on the pattern of vegetation as established systems are removed and replaced with managed ones (e.g., Burgess and Sharpe 1981; Turner 1987a). The prediction of future landscape patterns requires an understanding of how processes vary in space, how they are influenced by disturbances, and how these processes will affect the landscape pattern (Forman and Godron 1986).

Fractal geometry (Mandelbrot 1983; Burrough 1983) has been used to characterize the shape and size of land cover types and relate these statistics to natural and human processes (Krummel *et al.* 1987; Milne in press a). These and other methods have generated hypotheses about the appropriate spatial scales for the study of ecological systems (e.g., Meentemeyer and Box in press). However, the usefulness of these methods and hypotheses as quantitative tools depends on our ability to statistically test results against a standard. One means of defining this standard is to develop an appropriate neutral model (Caswell 1976) that produces an expected pattern in the absence of specific landscape processes. Such patterns establish a base against which data and hypotheses can be rigorously tested to establish significant departures from the expected patterns. These differences can then be used to infer relationships between landscape processes and observed results.

Percolation theory as a neutral landscape model

Percolation theory was developed to describe physical properties of gels, polymers, and glassy materials and forms the basis for studies of the flow of liquids through material aggregates (Gefen *et al.* 1983; Orbach 1986). The first studies in percolation theory took place during the early 1940's, but the computer intensive nature of the geometrical and probabilistic concepts restricted the usefulness of percolation theory until large and fast computers became available. The analytical and computational methods developed from percolation theory (Stauffer 1985) provide a means of generating and analyzing patterns of two-dimensional arrays. Percolation arrays are similar to two-dimensional landscape maps and are appropriately 'neutral' to the physical and biological processes which shape landscape patterns because they are formed by simple random processes.

A two-dimensional percolating network within an array of size m by m is formed by randomly choosing the occupation of the m^2 sites with a probability of p. For large arrays pm^2 sites are occupied while $(1-p)m^2$ sites are empty. The number, size and shape of clusters of occupied sites changes as a function of p. A 'cluster' is formed by a group of occupied sites which have at least one common edge along the vertical and horizontal directions of a square lattice but not along the diagonals. Cluster characteristics have been found to change most rapidly near the critical probability, p_c (p_c = 0.5928 for a random square lattice, other values for differently shaped lattices or alternative network models, see Stauffer 1985). For very large lattices, the value of p_c is the probability at which the largest cluster will cross the grid continuously from one side to the other. This grid-spanning cluster is referred to as an infinite cluster because, for $p > p_c$, the cluster will span the infinite plane (Orbach 1986). On large grids ($m^2 > 10^6$), the shape of the largest cluster, as measured by the fractal dimension, has also been shown to be affected by p (Stauffer 1985) with clusters having a fractal dimension < 2 when $p < p_c$, but a dimension approaching 2 when $p > p_c$.

The simple nature and properties of percolation arrays make them useful for landscape studies. However, unlike most landscape analyses, percolation studies have relied on large arrays (e.g., m = 10^9; Stauffer 1985) which exhibit negligeable boundary effects. This study attempts to adapt some of the results of percolation theory to the finite scales of landscape maps and to use these results as a neutral model for analysis of landscape data.

Methods

Two-dimensional maps with m of 50, 100, 200 and 400 were randomly generated for different values of p. The number of replications (N) for each map size was set so that the total number of sites ($N * m^2$) evaluated for each value of p was at least 100,000. The total number and size distribution of clusters, the size and fractal dimension of the largest cluster, and the number of edges of all clusters were calculated and statistically summarized for all replicate combinations of m and p.

The fractal dimension is of interest because it is known that the shape of clusters changes as a function of p (Stauffer 1985). If clusters of finite maps can be shown to have consistent geometric characteristics over a range of map sizes (*i.e.,* self-similar) then the fractal dimension might allow us to translate results from one map scale to another (Milne in press b).

The method used to estimate the fractal dimension presents a number of practical considerations when applied to finite maps. Mandelbrot (1983) has shown that for two-dimensional objects the relationship between perimeter and area is described by:

$$S \simeq kP^d, \qquad (1)$$

where S = the area of the object, P is the perimeter, d is the fractal dimension, and k is a constant. The fractal dimension, d, in eq (1) will have the value of 2.0 for plane filling objects such as circles and

Table 1. Number of clusters[a] on a random map as a function of map size and probability of occurrence

Map size[b, c]	Probability of a site on the map being occupied (p)								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
50 (N = 40)									
mean	204	310	326	276	180	79	25	6.1	1.4
sd	13.1	9.9	12.3	14.1	16.0	12.4	5.5	2.3	0.6
cv%	6.4	3.2	3.8	5.1	8.8	16	22	37	43
100 (N = 10)									
mean	813	1224	1299	1096	691	279	87	19	2.3
sd	31.6	22.9	25.2	36.2	33.5	24.3	8.6	6.1	1.3
cv%	3.9	1.9	1.9	3.3	4.9	8.7	9.9	31	58
200 (N = 4)									
mean	3211	4903	5181	4300	2653	1021	318	65	4.8
sd	35.2	60.0	13.4	58.9	59.4	42	14.8	10.6	2.5
cv%	1.1	1.2	1.4	1.4	2.2	4.1	4.7	16	53
400 (N = 2)									
mean	12855	19455	20480	17003	10525	4141	1224	237	18.0
range	3	187	15	7	239	52	36	17	4

[a] Clusters are formed by occupied sites which are adjacent along the vertical and horizontal directions of a square grid, but not along the diagonals.

[b] Map size is the linear dimension, m, of a square map in arbitrary units. The square of the linear dimension, m^2, gives the total number of possible sites on the map.

[c] Mean, standard deviation and coefficient of variation (standard deviation/mean x 100) are given for 40, 10, and 4 replications (N) for map sizes 50, 100 and 200, respectively. The mean and range of two replications (N = 2) are reported for maps of linear dimension 400.

squares, and a value of 1.0 for a straight line.

Landscape studies usually involve maps with linear dimension (m) of less than 100 units. This results in maps with a limited number of clusters, a fractal dimension which may be seriously affected by the edges of the map, and the need to precisely estimate P and k of eq (1). Some practical choices for estimating P and k are: (1) the radius, r, of the cluster (P = r, k = 1); (2) the average diameter of the cluster (P = r and k = 2); and (3) or the total perimeter of the cluster (P = the perimeter and k = 0.25). Substituting these different values into eq (1), the fractal dimension for a solid cluster of 10^9 sites (expected d = 2.0) would be: (1) 2.056; (2) 1.988; and (3) 2.000. For reasonable ecological map lengths of m = 100 the estimates are: (1) 2.283; (2) 1.949; (3) 2.000. Thus, eq (1) is relatively insensitive to the choice of k and P when m is very large, but the smaller map size results in unacceptable errors for methods (1) and (2). Because method (3) is intuitively appealing for two dimensional objects and gives reliable estimates for small clusters, it will be used in this paper to estimate d, the fractal dimension.

The USGS digital land use and land cover data base (Fegas *et al.* 1983) provides landscape maps interpreted from NASA U2/R8-57 high-altitude aerial photo coverage obtained in 1973. The original aerial photographs were hand digitized into 37 land cover categories. Because the original USGS data set divides 1:250,000 quadrangles into 24 sections, a special computer program was written to remove section boundaries and convert the polygon data to grid format. This allowed an analysis of the entire quadrangle as one landscape with linear dimensions of 650 by 950 sites (each site or pixel has an area of 4.0 ha).

We selected three quadrangles with different fractions of forest cover: Florence, NC (p = 0.4); Montgomery, AL (p = 0.6); and Bluefield, WV (p = 0.8). Ten maps of size 100 by 100 were randomly sampled from each LUDA quadrangle. The number, size and fractal dimension of forest patches were determined for each sample, the

Table 2. The size (S) of the largest cluster[a] on a random map as a function of map size and probability of occurrence

Map size[b, c]	Probability of a pixel on the map being occupied (p)								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
50 (N = 40)									
mean	4.7	10.3	19.9	42.9	127	843	1691	1990	2247
sd	0.9	2.6	5.7	14.2	44.8	289	39.4	22.4	14.3
cv%	18	25	29	33	35	34	2.3	1.1	0.6
100 (N = 10)									
mean	5.6	12.4	24.2	59.8	239.4	3477	6826	7971	8990
sd	0.7	1.6	2.9	15	87	1063	54	39	21
cv%	13	13	12	26	36	30	0.8	0.5	0.2
200 (N = 4)									
mean	6.8	14.0	27.8	76	323	17844	27475	31939	35999
sd	0.5	1.4	5.0	26.9	76.1	1953	132	174	123
cv%	7.4	10	18	35	24	11	0.5	0.5	0.3
400 (N = 2)									
mean	8.0	18.0	39	87.5	501	64663	109923	127811	143995
range	0	0	2	37	213	616	207	29	86

[a] Clusters are formed by occupied sites which are adjacent along the vertical and horizontal directions of a square grid, but not along the diagonals.

[b] Map size is the linear dimension, m, of a square map in arbitrary units. The square of the linear dimension, m^2, gives the total number of possible sites on the map.

[c] Mean, standard deviation and coefficient of variation (standard deviation/mean x 100) are given for 40, 10, and 4 replications (N) for map sizes 50, 100 and 200, respectively. The mean and range of two replications (N = 2) are reported for maps of linear dimension 400.

results statistically summarized and compared with appropriate random maps.

Results

The number of clusters on a random map of size m varies as a function of p (Table 1). Although the proportion of the map that is occupied by a land cover type increases directly with p, the maximum number of clusters is found at p = 0.3. Below p = 0.3. the clusters are small and widely spaced. Above p = 0.3 the addition of new sites aggregates scattered clusters into fewer but larger patches (Table 2). The number of clusters per map declines above p = 0.3, decreasing more rapidly above the critical probability, p_c. The relative variability (cv% = coefficient of variation = [standard deviation/mean] * 100) of cluster number per map is also affected by p, increasing as the total number of clusters declines.

Table 1 indicates that if p is known, the number of clusters can be predicted with less than 5% error below p_c, but with an error greater than 10% above p_c. The reason for the increase in error above p_c is that the edges of the map truncates the larger clusters, producing a systematic bias. This effect diminishes with increasing map size. For instance, at p = 0.7 the extrapolation from m = 50 to m = 100 results in a 15% overestimation; from m = 100 to m = 200 a 9% overestimation; and from m = 200 to m = 400 a 4% overestimation of expected cluster number per map.

The size, S, of the largest cluster on the map varies with m and p (Table 2). S increases rapidly above p_c with cv%, showing a peak near p_c. For $p > p_c$ the effect of map size, m, on estimates of S is proportional to m^2. For instance, at p = 0.7 the value of S predicted from maps with m = 50 to maps with m = 100 has a prediction error less then 1%. However, the relationship between S and m^2 does not hold when $p < p_c$. Above p_c the largest cluster spans the map and will continue to do so as the map size increases (Orbach 1986). Below p_c the

Table 3. Fractal dimension of largest cluster[a] as a function of map size and probability of occurrence

Map size[b, c]	Probability of a pixel on the map being occupied (p)								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
50 (N = 40)									
mean	1.5	1.42	1.36	1.34	1.36	1.46	1.66	1.78	1.88
sd	0.08	0.11	0.07	0.06	0.06	0.05	0.03	0.03	0.02
cv%	5.1	7.5	5.2	4.2	4.1	3.5	1.9	1.4	1.0
100 (N = 10)									
mean	1.5	1.4	1.37	1.32	1.33	1.51	1.69	1.81	1.91
sd	0.09	0.1	0.04	0.05	0.02	0.03	0.01	0.02	0.01
cv%	5.9	6.9	3.2	4.1	1.5	2.1	0.5	0.8	0.7
200 (N = 4)									
mean	1.41	1.37	1.31	1.30	1.32	1.57	1.73	1.83	1.91
sd	0.01	0.07	0.01	0.06	0.03	0.02	0.01	0.004	0.003
cv%	0.9	5.1	1.1	4.6	2.5	1.4	0.8	0.2	0.2
400 (N = 2)									
mean	1.38	1.30	1.33	1.33	1.36	1.59	1.76	1.85	1.92
range	0	0.03	0.09	0.01	0.02	0.004	0.002	< 0.001	< 0.001

[a] Clusters are formed by occupied sites which are adjacent along the vertical and horizontal directions of a square grid, but not along the diagonals.

[b] Map size is the linear dimension, m, of a square map in arbitrary units. The square of the linear dimension, m^2, gives the total number of possible sites on the map.

[c] Mean, standard deviation and coefficient of variation (standard deviation/mean x 100) are given for 40, 10, and 4 replications (N) for map sizes 50, 100 and 200, respectively. The mean and range of two replications (N = 2) are reported for maps of linear dimension 400.

size of the largest cluster increases as a function of m (Stauffer 1985). Thus, estimates ‘of S for maps with $p < p_c$ is a sampling problem a large map examines a larger sample area and is more likely to include larger clusters.

The estimates of the fractal dimension of the largest cluster as a function of m and p are shown in Table 3. When p is small (0.1 to 0.3) the clusters are small (4 to 30, Table 2) and the fractal dimension is overestimated (biased) by the rectangular nature of the individual sites composing the cluster. As the clusters become larger the fractal dimension approaches 1.32 to $0.4 < p < 0.5$. Above p_c the value of d increases and approaches 2.0 as p approaches 1 .O.

The linear dimension of the map, m, has a small but noticeable effect on estimates of d. The larger edge/area ratio of small maps causes a higher estimated fractal dimension when $p < p_c$. This effect is not evident above p_c because the largest cluster will always be truncated by the map edge no matter how large the map becomes. Despite this effect, the estimates of d are quite stable with less than an 8% range in uncertainty associated with any given combination of m and-p.

The total number of edges for all clusters shows a peak value at p = 0.5 (Table 4). Figure 1 illustrates the change in inner and total edges as a function of p on a map with m = 100. Although the total number of edges changes slowly with p, inner edges decline rapidly as p is reduced below p_c. The reason is that cluster size is a function of p (Table 2), and as cluster size declines the gaps within a patch are opened and become a part of the external edge of the cluster. When p declines below 0.4 there are very few clusters with any inner edges.

A comparison of the cumulative frequency distribution (cfd) of cluster size for random maps was made with the cfd of actual landscape data from the LUDA maps (Fig. 2). Several differences between actual landscapes and simple random maps are evident. The number of forest patches sampled from the LUDA landscape data (352, 181, and 52 for values of p of 0.4, 0.6 and 0.8, respectively) differ

Table 4. The mean edge of all clusters[a] as a function of map size and probability of occurrence

Map size[b, c]	Probability of a pixel on the map being occupied (p)								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
50 (N = 40)									
mean	911	1620	2114	2428	2550	2470	2202	1734	1069
sd	55.2	43.0	41.1	44.2	37.7	37.8	44.6	54.7	46.6
cv%	6.1	2.7	1.9	1.8	1.5	1.5	2.0	3.2	4.3
100 (N = 10)									
mean	3640	6450	8441	9702	10116	9753	8618	6658	3956
sd	130	78.1	53.6	93.5	69.5	68.5	84.2	106	74
cv%	3.6	1.2	0.6	1.0	0.7	0.7	0.9	1.6	1.9
200 (N = 4)									
mean	14483	25808	33822	38641	40269	38554	33879	26076	15060
sd	211	237	211	219	185	29.2	168	362	378
cv%	1.5	0.9	0.6	0.6	0.5	0.08	0.5	1.4	2.5
400 (N = 2)									
mean	57810	102775	134476	153834	160193	153648	134969	103263	59065
range	45	626	452	132	110	796	526	198	418

[a] A cluster edge is defined as the number of sites which are not members of the same cluster. Clusters are formed by occupied sites which are adjacent along the vertical and horizontal directions of a square grid, but not along the diagonals.

[b] Map size is the linear dimension, m, of a square map in arbitrary units. The square of the linear dimension, m^2, gives the total number of possible sites on the map.

[c] Mean, standard deviation and coefficient of variation (standard deviation/mean x 100) are given for 40, 10, and 4 replications (N) for map sizes 50, 100 and 200, respectively. The mean and range of two replications (N = 2) are reported for maps of linear dimension 400.

considerably from the random maps (1096, 279, and 19 for values of p 0.4, 0.6, and 0.8, Table 1). The cumulative frequency distribution (cfd) for LUDA landscapes always lies below the cfd for the random maps, indicating a greater tendency for site aggregation in the actual landscape. Some of these differences can be attributed to the high proportion of single isolated sites on random maps (i.e., at S of 10^0 the cfd > 0.5, Fig. 2a and 2b, and cfd > 0.8, Fig. 2c). However, adjustment of the cfd of random maps by removal of these single isolated sites does not remove the significant differences between the LUDA landscapes and the random maps.

As the fraction of occupied sites increases above p_c, the random maps and LUDA landscapes become more similar. Both types of maps show fewer, larger clusters which tend to fill the entire 100 x 100 map. At p = 0.8 (Fig. 2c) the size of the largest clusters on random and LUDA maps are nearly the same. However, the shape of the cfd of Fig. 2c still shows that even at these high values of p, landscape processes continue to produce unique landscape attributes.

Discussion

The purpose of a neutral model is to generate the expected system behavior in the absence of specific processes which may affect that system (Caswell 1976). We have used percolation theory to develop neutral landscape models so that data can be objectively compared against random patterns. Because the difference between landscape data and model predictions is a measure of adequacy (i.e., goodness of fit), neutral models can be used to measure the improvement in predictability which may be achieved by modeling topographic, climatic, and disturbance effects.

The neutral models generated from percolation theory show that estimates of the expected number, size distribution and fractal dimension of clusters on a simple random map all vary as a function of m, the linear dimension of the map, and p, the fraction of available sites that are occupied by the landscape type of interest. These results provide important guidelines for comparative landscape studies.

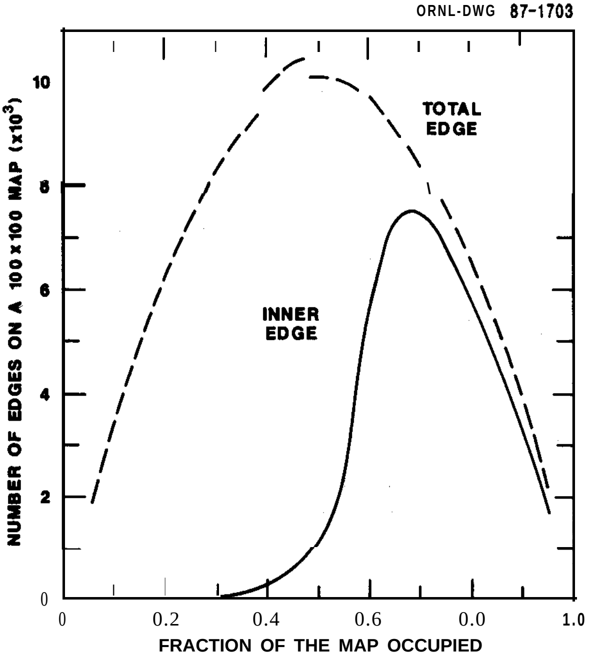

Fig. 1. The number of edges observed on a randomly generated map (linear dimension = 100) as a function of p, the fraction of sites occupies on the map. An edge is defined as the number of surfaces of a cluster that are adjacent to an unoccupied map site. Outer edges lie along the outside of a cluster while inner edges are adjacent to another land use type which is completely enclosed by the cluster. Total edges are sums of all inner and outer cluster edges.

If different land cover types are compared, differences in m and p must be understood before hypothesized effects can be tested. For some situations, knowing m and p may be sufficient to properly scale differences between maps. Consideration of m and p are also necessary for extrapolating the effect of disturbances measured at small scales to larger areas. Changes in spatial scale, however, should not be viewed as linear changes (Meentemeyer and Box 1987). For instance, a 10% reduction in land cover will have little noticeable effect on the number, size and shape of patches with p less than p_c but will have dramatic effects in areas where p is greater than p_c.

The analysis of simple random maps leads to several considerations involving the use of broad scale maps for studying landscape pattern and changes due to disturbance. (For our purposes a 'disturbance' is any process which breaks large patches into smaller ones (Burgess and Sharpe 1981)). Figure 3 illustrates these ideas by graphing p, the maximum observable fraction of land use type, as a function of m, the linear dimension of the map. No matter how rare the habitat, if m is sufficiently small some maps can be found where p = 1 .O (the 'undersized map', Fig. 3). As the area of the map is increased, the heterogeneity of the landscape reveals itself, and the fraction of the map occupied by that habitat drops below 1 .O. The fraction may remain high as long as the area chosen is uniform and the map size remains within the natural boundaries established by soils, geology, climate, etc. (the 'suitable resolution' zone, Fig. 3). Further increases in map size will increase the probability of encountering the limits of the range for that habitat type. When this happens the total fraction of the landscape occupied by that habitat will diminish (the 'transition zone' of Fig. 3). Finally, one arrives at map sizes at which the habitat of interest is rare (the 'oversized map', Fig. 3; see Allen and Starr 1982 for an example).

Disturbance effects will be most evident at scales where the disturbance forces the value of p for the landscape below p_c causing the curve to shift to the left (dashed line, Fig. 3). This change will necessitate using broader scale maps to minimize the relative coverage of patches newly created by the disturbance and thus maintain the original relationship of Fig. 3. Support for this hypothesis can be found in Shugart and West (1981) and Bormann and Likens (1979) who emphasized that vegetative changes form a dynamic equilibrium at sufficiently broad scales where the percent coverage of 'disturbed' areas is minimal. If the disturbance operates at a scale greater than the map then the results of simple random effects may be sufficient to predict the consequence of the disturbance. For example, if p > p_c then a random disturbance will increase habitat edge according to the relationships shown in Table 4 and Fig. 1, with a predictable increase in forest edge species.

Results of the analysis of percolation models indicate that important changes take place near p_c (= 0.5829 for random maps). The importance of p_c in landscape studies is obvious since contagion effects, pest disturbance, forest fires and pest out-

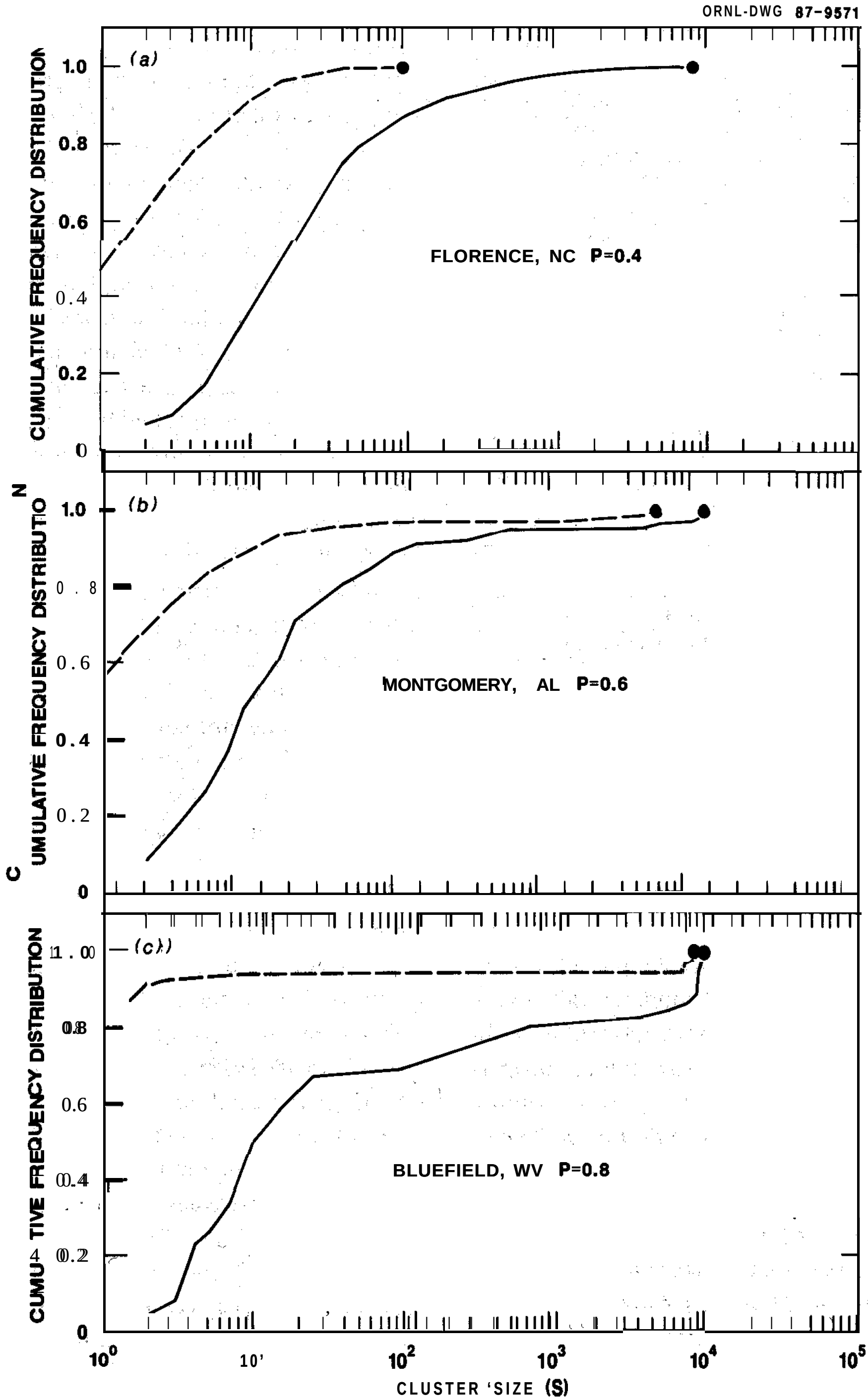

Fig. 2. Comparison of cumulative frequency distributions (cfd) of cluster size for 10 samples of random maps (dashed line) and 10 samples of the forested land type for each of three quadrangles of the USGS LUDA maps (solid line). The large circle at the end of the cfd line locates the largest cluster sampled. The value of p indicates the fraction of forested land sampled from these quadrangles: (2.a) Florence, NC, p = 0.4; (2.b) Montgomery, AL, p = 0.6; (2.c) Bluefield, WV, p = 0.8.

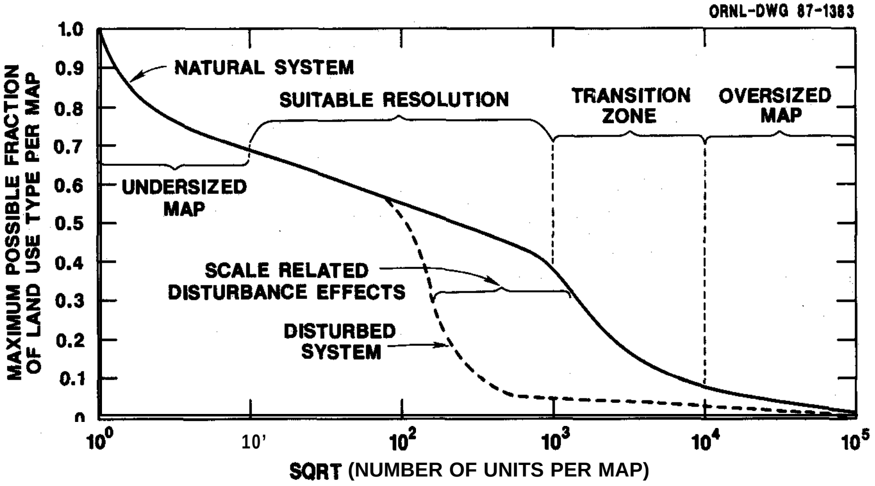

Fig. 3. Illustration of the hypothetical relationship between the size of the map, the suitable resolution for landscape studies, and the scale at which disturbance effects will be detected. See text for a description of this hypothesis.

breaks occur in habitats at or above p_c. This leads to the question of what is the critical value of p for actual landscapes. The relationship between landscape heterogeneity and spread of a disturbance is not yet clear (Turner 1987b) and the identification of p_c may elucidate this. The cumulative frequency distributions of forests patches measured from LUDA data (Fig. 2) shows that forests are more aggregated than clusters generated from simple random processes. This suggests that real landscapes may have a p_c lower than the theoretical value. A number of testable hypotheses could be generated by considering how cover type, topography, or patterns of disturbance would alter p_c.

Probabilistic considerations predict that random reductions in p will result in changes in the number, size, shape and character (inner *vs* outer edges) of land cover patches. Given that individual species display differential responses to these characteristics, it may be possible to generate expected spatial distributions of species abundance at the landscape scale. In addition, it may be possible to select optimum landscapes from scale and probabilistic arguments to maintain desirable frequencies of size, shape and edges of patches. Such considerations could lead toward a general theory of landscape ecology of immediate interest for application to management issues.

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