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Effects of changing spatial scale on the analysis of landscape pattern

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Abstract

The purpose of this study was to observe the effects of changing the grain (the first level of spatial resolution possible with a given data set) and extent (the total area of the study) of landscape data on observed spatial patterns and to identify some general rules for comparing measures obtained at different scales. Simple random maps, maps with contagion *(i.e.,* clusters of the same land cover type), and actual landscape data from USGS land use (LUDA) data maps were used in the analyses. Landscape patterns were compared using indices measuring diversity (*H*), dominance (*D*) and contagion (*C*). Rare land cover types were lost as grain became coarser. This loss could be predicted analytically for random maps with two land cover types, and it was observed in actual landscapes as grain was increased experimentally. However, the rate of loss was influenced by the spatial pattern. Land cover types that were clumped disappeared slowly or were retained with increasing grain, whereas cover types that were dispersed were lost rapidly. The diversity index decreased linearly with increasing grain size, but dominance and contagion did not show a linear relationship. The indices *D* and C increased with increasing extent, but Hexhibited a variable response. The indices were sensitive to the number (*m*) of cover types observed in the data set and the fraction of the landscape occupied by each cover type (P_k); both m and P_k varied with grain and extent. Qualitative and quantitative changes in measurements across spatial scales will differ depending on how scale is defined. Characterizing the relationships between ecological measurements and the grain or extent of the data may make it possible to predict or correct for the loss of information with changes in spatial scale.

Introduction

The range of spatial and temporal scales at which ecological problems are posed has expanded dramatically in recent years, and the need to consider scale in ecological analyses has often been noted (e.g., Allen and Starr 1982; Delcourt *et al.* 1983; O'Neill *et al.* 1986; Addicott *et al.* 1987; Getis and Franklin 1987; Meentemeyer and Box 1987; Morris 1987). Parameters and processes important at one scale are frequently not important or predictive at another scale, and information is often lost as spatial data are considered at coarser scales of resolution (Henderson-Sellers *et al.* 1985; Meentemeyer and Box 1987). Ecological problems often require the extrapolation of fine-scale measurements for the analysis of broad-scale phenomena. Therefore, the development of methods that will preserve information across scales or quantify the loss of information with changing scales has become a critical task. Such methods are necessary before ecological insights can be extrapolated between.

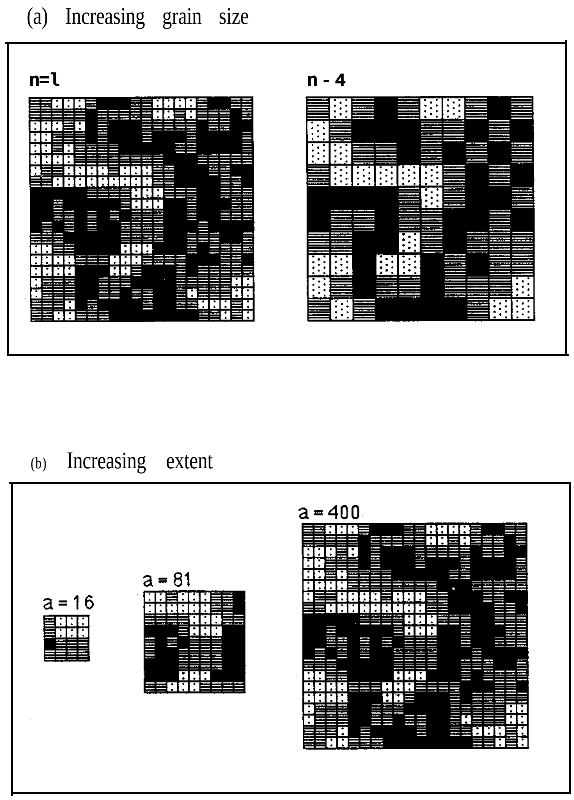

Fig. I. Schematic illustration of (a) increasing grain size and (b) increasing extent in a landscape data set. The number of cells aggregated to form a new data unit are indicated by *n*; total area is indicated by a; see Methods for complete explanation.

spatial and temporal scales.

The spatial scale of ecological data encompasses both grain and extent. Grain refers to the resolution of the data, *i.e.,* the area represented by each data unit. For example, a fine-grain map might organize information into l-ha units, whereas a map with an order of magnitude coarser resolution would have information organized into 10-ha units. Extent refers to the overall size of the study area. For example, maps of $100 km^2$ and $100,000 km^2$ differ in extent by a factor of 1000. In studies of landscape structure or function (e.g., Naveh and Lieberman 1984; Forman and Godron 1986; Turner 1987a), information may be available at a variety of levels of resolution, data must often be compared across large geographic regions, and it may be necessary to extrapolate information from local to regional scales. Applications of geographic information systerns (GIS) also frequently require the integration of data obtained at different spatial scales. The effects of grain and extent are thus of particular concern, and the response of ecological attributes measured on the landscape to changes in spatial scale is not known. It has been demonstrated (Gardner *et al.* 1987) that the number, size and shape of patches in randomly simulated landscapes varies with extent, as indicated by the linear dimension of the landscape. It has also been suggested (Allen *et al.* 1987) that information can be transferred across scales if both grain and extent are specified.

The purpose of this study was to observe the effects of changing the grain and extent of landscape data on observed spatial patterns and to identify some general rules for comparing measures obtained at different scales. The effects of changing grain size on the proportion of a landscape occupied by a particular land cover type were first predicted analytically then tested against randomly generated landscapes. The grain and extent of real and simulated landscapes were also experimentally varied and indices of diversity, dominance and contagion were used to compare resulting landscape patterns.

Methods

Landscape data

The USGS digital land use and land cover data base (Fegas *et al.* 1983), which provides landscape maps interpreted from NASA U2/R8–57 high altitude aerial photo coverage obtained in 1973, was used for the analyses. 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 created a single quadrangle for each landscape with linear dimensions of 650 by 950 pixels (each pixel or site has an area of 4.0 ha). The largest square (measuring 618 by 618 pixels) in the map that was free of edge effects was used for the analysis.

Table 1. Proportion of land cover type k that will be observed as a function of resolution in a random two-phase landscape. The coarse scales of resolution assume that an aggregate of n sites will be assigned to k if the majority of the sites are of type k.

Grain size (n)	$P_k(n)$				
1	0.10	0.30	0.50	0.70	0.90
3	0.028	0.216	0.500	0.784	0.912
7	0.003	0.126	0.500	0.874	0.997
11	0.0	0.078	0.500	0.922	1.0
15	0.0	0.050	0.500	0.950	1.0
19	0.0	0.033	0.500	0.967	1.0

Changing scale: Grain and extent

The grain of the landscape data was changed by aggregating groups of n adjacent pixels into a single data unit. The land cover type of the majority of pixels in an aggregate was assigned to the new data unit (shown schematically in Fig. la). If two land covers in an aggregate occurred in equal proportions (e.g., two pixels each of agriculture and forest), the assignment of a landscape type was done at random. Grain was varied through 19 separate aggregations such that an exact number of aggregates fit into the central portion of the map and no artifacts resulted from omitting a few rows or columns. The finest aggregation was 2 x 2 (*n* = *4* original pixels forming each aggregate) and the coarsest aggregation was 50 *x* 50 (*n* = 2500 original pixels per aggregate data unit). This method of aggregation simulates cases in which only coarse resolution data about land cover are available.

The extent *(a)* of the landscape map was altered without affecting the grain size using a nested quadrat design (shown schematically in Fig. lb). Pattern analysis began using a group of pixels (*a* = *40)* located in the center of the map. The area was then gradually increased until the entire map was covered (*a* = 381,924).

Analysis of landscape pattern

The fraction of the landscape occupied by each cover type was calculated from the LUDA data, and several indices (O'Neill *et al.* 1988) based on information theory (Shannon and Weaver 1962) were used to describe the pattern of each landscape map. The first index, H, is a measure of diversity:

$$H = -\sum_{k=1}^{m} (P_k) \log(P_k), \qquad (1)$$

where P_k is the proportion of the landscape in cover type k, and m is the number of land cover types observed. The larger the value of H, the more diverse the landscape.

The second index, D, is a measure of dominance, calculated as the deviation from the maximum possible diversity:

$$D = H_{max} + \sum_{k=1}^{m} (P_k) \log(P_k), \qquad (2)$$

where *m* = number of land use types observed on the map, P_k is the proportion of the landscape in land use *k*, and H_{max} = log (m), the maximum diversity when all land uses are present in equal proportions. Inclusion of H_{max} in Eq. 2 normalizes the index for differences in numbers of land cover types between different landscapes. Large values of D indicate a landscape that is dominated by one or a few land uses, and low values indicate a landscape that has many land uses represented in approximately equal proportions. However, the index is not useful in a completely homogeneous landscape (*i.e.*, *m* = 1) because D then equals zero.

The third index, C, measures contagion, or the adjacency of land cover types. The index is calculated from an adjacency matrix, Q, in which $Q_{i,j}$ is the proportion of cells of type *i* that are adjacent (diagonals are excluded) to cells of typej, such that:

$$C = K_{max} + \sum_{i=1}^{m} \sum_{j=1}^{m} (Q_{i,j}) \log(Q_{i,j}), \qquad (3)$$

where K_{max} = 2 m log(m) and is the absolute value of the summation of $(Q_{i,j})\log(Q_{i,j})$ when all possible adjacensies between land cover types occur with equal probabilities. K_{max} normalizes landscapes with differing values of m and causes C to be

Table 2. Number of land cover types retained at each level of aggregation for seven landscapes.

Grain size (n)	Landscape scene							Mean
	Knoxville	Athens	Natchez	Macon	Greenville	Goodland	Waycross	
1	7	6	7	7	6	7	6	6.6
4	7	6	7	7	6	6	6	6.4
16	7	6	1	7	6	5	6	6.3
25	7	6	7	6	5	4	5	5.1
50	6	6	6	6	5	4	4	5.3
80	5	6	6	6	5	3	4	5.0
100	5	6	6	6	5	3	4	5.0
160	4	6	6	5	5	3	4	4.1
200	4	6	6	4	5	3	4	4.6
320	4	5	6	4	4	3	4	4.3
400	3	5	6	4	5	2	4	4.1
500	3	4	5	4	4	2	4	3.1
625	3	4	5	4	4	2	4	3.1
800	3	4	5	4	4	2	4	3.1
1000	3	3	3	4	4	2	4	3.3
1250	3	3	3	4	4	2	4	3.3
2000	3	3	3	4	4	2	3	3.1
2500	3	2	3	4	4	2	3	3.0

Table 3. Proportion of land cover type k observed as a function of grain size in random multiphase landscapes. The coarse scales of resolution assume that an aggregate of n sites will be assigned to k if the majority of the sites are of type k.

Grain size (n)	A. Initial proportions taken from Goodland, KS $P_k(n)$			
1	0.001	0.004	0.29	0.10
4	0.0	0.001	0.205	0.195
16	0.0	0.0	0.044	0.956
50	0.0	0.0	0.015	0.985
80	0.0	0.0	0.001	0.999
loo	0.0	0.0	0.0	1.0

Grain size (n)	B. Initial proportions taken from West Palm Beach, FL $P_k(n)$						
1	0.051	0.053	0.062	0.082	0.182	0.259	0.310
4	0.031	0.033	0.040	0.058	0.114	0.288	0.316
16	0.002	0.003	0.005	0.011	0.125	0.333;	0.520
25	0.001	0.001	0.001	0.003	0.095	0.328	0.512
50	0.0	0.0	0.0	0.0	0.052	0.296	0.652
80	0.0	0.0	0.0	0.0	0.022	0.211	0.707
100	0.0	0.0	0.0	0.0	0.018	0.252	0.130

Table 4. Contagion values $Q_{j,k}$ for which there will be no change in P_k with aggregation.

P_k	$Q_{k,j}$ 0.10	0.30	0.50	0.70	0.90
0.1	0.011	0.033	0.055	0.077	0.100
0.2	0.025	0.075	0.125	0.175	0.225
0.3	0.043	0.128	0.214	0.300	0.386
0.4	0.066	0.200	0.333	0.460	0.600
0.5	0.100	0.300	0.500	0.700	0.900
0.6	0.150	0.450	0.750	*	*
0.7	0.230	0.700	*	*	*
0.8	0.400	*	*	*	*
0.9	0.900	*	*	*	*

* There is no feasible value (*i.e.*, $Q_{j,k} < 1.0$)

zero when $m = 1$ or all possible adjacencies occur with equal probability. When $m \geq 2$, large values of C will indicate a landscape with a clumped pattern of land cover types.

Results

Effects of changing grain

1. Analytical solution for P_k *at different scales in random landscapes*

Consider alandscape with two randomly distributed land cover types **($m = 2$),** each of which occupies a proportion P_k of the landscape. The probability of having r sites of cover type k in an aggregate of n cells is given by the binomial distribution:

$$b\ (r;\ n,\ P_k) = (n!/r!\ (n-r)!)\ P_k^r\ (1-P_k)\ (n-r) \quad (4)$$

An aggregate is assigned to type k using the majority rule if at least 50% of the cells are of type k. The proportion of aggregates that will contain 50% or more sites of type k can be determined by using a table of the cumulative binomial distribution for $P = b = 0.50$.

The proportion $P_k(n)$ of data units formed by aggregating n cells that will be assigned to cover type k in a two phase landscape (cover type k and all non-k; $m = 2$) is shown in Table 1. If $P_k(1)$ on the random landscape is exactly 0.5, this proportion will be maintained at all levels of aggregation (Table 1). If $P_k(1)$ is even slightly less than 0.5, land type k will be lost at coarser resolutions; the smaller the initial P_k, the faster the disappearance of land type k. If $P_k(1)$ is greater than 0.5, cover type k will dominate the landscape at coarser resolutions until it covers the entire landscape. These results (Table 1) apply only if k is independently and randomly distributed on the landscape. Although this condition will seldom be satisfied exactly, the general pattern holds for a variety of actual landscapes (Table 2). At increasingly coarser scales of resolution, cover types with a small $P_k(1)$ disappear.

Random landscapes with the same proportions of cover types observed in the LUDA maps for Goodland, Kansas (dominated by agriculture and rangeland) and West Palm Beach, Florida (having a more even distribution of cover types) were generated to further test the relationship between P_k and grain (Table 3). Although the rare land cover types do indeed disappear, when the fractions of the landscape occupied by two cover types are similar in size and there is no extreme dominance by either (e.g., P_k's of 0.259 and 0.310 in West Palm Beach, Table 3) both values increase while rare cover types are lost. Thus, P_k values do not necessarily change unidirectionally in landscapes occupied by numerous cover types. However, with continued aggregation, the land cover type with the greatest P_k will eventually dominate the landscape.

2. Analytical solution for P_k *at different scales in landscapes with contagion*

The results for a simple random landscape can be extended by analyzing a landscape on which cover type k is distributed with contagion. Contagion simulates the tendency of land cover types to form clusters or patches rather than to occur at random. The probability that two adjacent sites are of type k, $Q_{k,k}$ can be calculated by moving through the landscape along transects and observing the frequency at which land cover types are adjacent to each other. The proportion of the landscape occupied by cover type k when two cells are aggregated, $P_k(2)$, is then given by:

$$P_k(2) = P_k(1)\ Q_{k,k} + 0.5\ [P_k(1)\ Q_{k,j} + P_j(1)\ Q_{j,k}] \quad (5)$$

Table 5. Regression of three landscape indices with grain (log aggregate size) for seven landscape scenes. Values are the slopes and (r^2).

Scene	Landscape parameter		
	Diversity (*H*)	Dominance (*D*)	Contagion (*C*)
Goodland, KS	-0.047 (0.98)	-0.144 (0.80)	-1.737 (0.77)
Natchez, MS	-0.055 (0.96)	-0.090 (0.48)	-1.666 (0.46)
Knoxville, TN	-0.068 (0.98)	-0.112 (0.75)	-2.775 (0.76)
Greenville, SC	-0.036 (0.94)	-0.037 (0.50)	-0.808 (0.43)
Waycross, GA	-0.034 (0.92)	-0.053 (0.50)	-0.915 (0.37)
Macon, GA	-0.038 (0.94)	-0.076 (0.66)	-2.038 (0.68)
Athens, GA	-0.090 (0.94)	-0.066 (0.32)	-1.517 (0.46)
Random Goodland, KS	-0.052 (0.53)	-0.116 (0.62)	-0.576 (0.68)
Random West Palm, FL	-0.235 (0.99)	-0.67 (0.23)	-1.57 (0.45)

where $P_j(1) = 1.0-P_k(1)$, representing the landscape sites occupied by something other than k. Cover type k will be assigned to an aggregate if both pixels are of type k. In addition, half of the k pixels adjacent to j and half of the j pixels adjacent to k will also be assigned to type k. Thus, of the sites that were type k at $n = 1$, $P_k(1)Q_{k,k}$ are retained at $n = 2$, 0.5 $P_k(1)Q_{k,j}$ are reclassified as j, and 0.5 $P_j(1)Q_{j,k}$ are reclassified from j to k. The balance between sites reclassified from j to k and *vice versa* determines whether $P_k(2)$ is greater or less than $P_k(1)$. The net change, A, in P_k is thus:

$$\Delta = 0.5\ [P_j(1)Q_{j,k}-P_k(1)Q_{k,j}]. \qquad (6)$$

Consider now the special case in which j is not contagiously distributed, *i.e.*, $P_j(1) = Q_{j,j}$. Recall that $P_j(1) = 1-P_k(1)$ and $Q_{j,k} = 1-Q_{j,j} = 1-P_j(1) = 1-(1-P_k(1)) = P_k(1)$. Equation 3 then becomes:

$$\Delta = 0.5\ P_k(1)\ [Q_{k,k}-P_k(1)] \qquad (7)$$

Cover type k will occupy an increasing proportion of sites at coarser resolution if $P_k(1)$ is contagiously distributed, *i.e.*, $Q_{k,k} > P_k(1)$ and $P_k(2) > P_k(1)$. Type k will occupy less of the landscape at coarser resolution if $P_k(1)$ is dispersed, *i.e.*, $Q_{k,k} < P_k(1)$ and $P_k(2)$ c $P_k(1)$. The proportion of k will not change with aggregation if the landscape is symmetric, *i.e.*, if $P_k(1) = Q_{k,k}$ and $P_k(2) = P_k(1)$. This result can be generalized because $P_k(2)$ will tend to be larger than expected for a random distribution if $P_k(1)$ is contagiously distributed for any value of $Q_{j,j}$. Thus, the rate at which rare land cover types decreases with decreasing resolution depends on their spatial arrangement. If a rare land cover type is highly aggregated, it tends not to disappear or to diminish slowly; if it is well-dispersed in small patches, it disappears rapidly.

If the landscape is symmetric, the probability of adjacency of j to k is equal to the probability of adjacency of k to j, *i.e.*,

$$P_k(1)Q_{k,j} = P_j(1)Q_{j,k}. \qquad (8)$$

This symmetry occurs if the elements of the Q matrix are calculated irrespective of a specific direction, *i.e.*, $Q_{i,j}$ represents the probability of i being adjacent to j in any direction, horizontally, vertically, or diagonally. No change will occur in P_k as grain increases under the conditions shown in Table 4. Cover type k will increase with aggregation if the value of $Q_{j,k}$ is larger than the entry in the table, and P_k will decrease if the value of $Q_{j,k}$ is less than the table entry. For the situations indicated by an asterisk, $P_k(2)$ will decrease for any feasible value of $Q_{j,k}$, *i.e.*, any value less than or equal to 1.0.

The value of $P_k(n)$ for coarser scales of resolution can be determined analytically by considering the set of adjacency probabilities that would result in an aggregate being classified as k. For example:

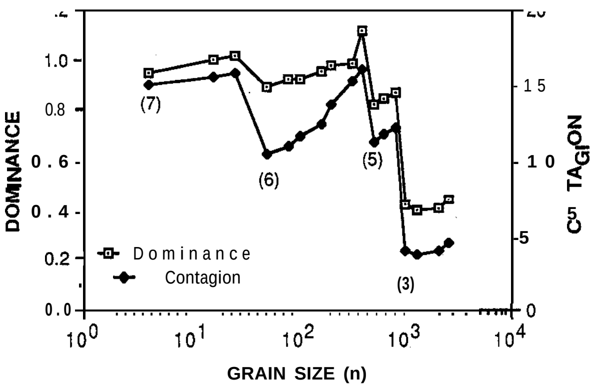

Fig. 2. Landscape indices as a function of increasing grain size as indicated by log(n) using the Natchez, Mississippi, quadrangle. Note the sensitivity of the dominance and contagion indices to the number of cover types present, m, indicated in parentheses. Other landscape scenes also showed this stair-step pattern.

$$P_k(3) = P_k(1)\,[Q_{k,k}Q_{k,k} + Q_{k,k}Q_{k,j} + Q_{k,j}Q_{j,k}] + P_j(1)\,Q_{j,k}Q_{k,k} \quad (9)$$

However, the algebraic manipulations become quite laborious as n increases.

3. Effects on landscape indices

Regressions of the landscape indices against log (n) (Table 5) were calculated to examine the relationship of the indices to different grain sizes. Milne *et al. (unpublished ms.)* demonstrated that a simple linear relationship existed between diversity, H, and log (scale) with consistent negative slopes and r^2 values that exceed 0.9. In contrast, the r^2 values for the regressions of D and C range from 0.32 to 0.80. The range of values for the slopes is also larger for D and C, indicating less consistency among landscapes. The linear relationship between diversity and grain does not assure a similarly simple relationship between grain and other landscape indices.

The dominance and contagion indices both depend on a maximum value, which is determined by m, the number of land cover types present. The number of land cover types observed decreases as resolution becomes increasingly more coarse and rare cover types disappear (Table 2). Indices D and C are sensitive to loss of cover types, and break points occur when the indices are plotted against grain (Fig. 2). C and D increase with grain size until another cover type is lost, at which point the indices decline sharply. The net change in the indices over all aggregations is negative (Table 5). The sensitivity to m suggests that knowledge of the number of cover types at each scale may permit extrapolation of dominance and contagion from one level of resolution to another. Direct, linear extrapolation appears possible if m does not change with particular grain sizes; as m changes, the slope and intercept of the extrapolation function vary.

Effects of changing extent

The number of land cover types present *(m)* increases with increasing extent (Table 6), as expected. The observed P_k values of the land cover types vary with changes in extent (Table 7), asymptotically approaching the final values observed on the entire map. We further expected that the landscape indices would remain constant as extent increased until a natural boundary (e.g., mountains, rivers, etc.) was crossed. The variance in the indices would increase rapidly in cases where these boundaries occur because the spatial patterning across the region would no longer be similar. This expectation held for diversity; a linear relationship was not observed between diversity and extent, as measured by regression of H against log *(a)* (Table 8). The slopes are small and often change sign. The r^2 values indicate that the linear trend through the data explains little of the total variance. The regressions D with extent show small positive slopes, but the r^2 values range from 0.019 to 0.926, indicating that a linear relationship exists for some landscapes but is not consistent across landscape scenes. Regressions of C show greater consistency, with relatively steep slopes and larger r^2 values. The slopes, however, still range from 0.0669 to 3.253 and the r^2 values are all below 0.90.

The indices are also sensitive to the number of land uses present (Fig. 3). Dominance and contagion appear to decrease with increasing extent until another cover type is included, at which point there is a large increase. The overall change in the

Table 6. Number of land cover types observed with increasing extent for seven landscapes.

Extent (a)	Landscape scene							Mean
	Knoxville	Athens	Natchez	Macon	Greenville	Goodland	Waycross	
40	2	1	2	4	2	2	2	2.1
126	4	2	2	4	3	2	2	2.7
360	4	3	3	4	5	2	2	3.3
1000	6	3	3	4	5	2	2	3.6
2146	6	4	3	5	5	2	2	3.9
2924	6	4	4	5	5	2	4	4.3
4452	6	4	5	5	5	3	5	4.1
6300	6	4	5	5	6	3	5	4.9
9000	6	5	6	6	6	4	6	5.6
14,440	6	5	6	6	6	4	6	5.6
20,340	6	5	6	6	6	4	6	5.6
49,000	6	5	6	6	6	5	6	5.1
100,902	6	5	6	6	6	7	6	6.0
150,430	6	6	6	6	6	7	6	6.1
225,000	7	6	6	7	6	7	6	6.4
305,026	7	6	7	7	6	7	6	6.6
361,000	7	6	7	7	6	7	6	6.6

Table 7. Proportion of land cover type k (P_k) observed as a function of extent in two sample landscapes.

A. Goodland, KS

Extent (a)	P_1	P_2	P_3	P_4	P_5	P_6	P_7
entire map	0.005	0.118	0.216	0.001	0.0001	0.0001	0.0003
40	0.0	0.450	0.550	0.0	0.0	0.0	0.0
126	0.0	0.122	0.211	0.0	0.0	0.0	0.0
360	0.0	0.144	0.255	0.0	0.0	0.0	0.0
1000	0.0	0.115	0.285	0.0	0.0	0.0	0.0
2146	0.0	0.141	0.259	0.0	0.0	0.0	0.0
2924	0.0	0.159	0.241	0.0	0.0	0.0	0.0
4452	0.0	0.194	0.206	0.0	0.0	0.0	0.0
6300	0.002	0.814	0.186	0.0	0.0	0.0	0.0
9000	0.002	0.800	0.199	0.0	0.0	0.0	0.0
14,440	0.002	0.800	0.196	0.0	0.0	0.0	0.001
20,340	0.003	0.805	0.190	0.0	0.0	0.0	0.001
49,000	0.008	0.119	0.212	0.0	0.0001	0.0	0.001
100,902	0.005	0.113	0.221	0.0001	0.0001	0.0001	0.001

B. Greenville, SC

Extent (a)	P_1	P_2	P_3	P_4	P_5	P_6	P_7
entire map	0.066	0.308	0.0	0.599	0.021	0.001	0.005
40	0.0	0.115	0.0	0.825	0.0	0.0	0.0
126	0.040	0.115	0.0	0.186	0.0	0.0	0.0
360	0.012	0.236	0.0	0.675	0.006	0.0	0.011
1000	0.057	0.202	0.0	0.583	0.140	0.0	0.018

Table 7. Continued.

2146	0.051	0.266	0.0	0.434	0.118	0.0	0.064
2924	0.051	0.262	0.0	0.432	0.186	0.0	0.069
4452	0.044	0.303	0.0	0.417	0.165	0.0	0.011
6300	0.037	0.332	0.0	0.431	0.137	0.001	0.062
9000	0.031	0.369	0.0	0.424	0.114	0.001	0.056
14,440	0.031	0.390	0.0	0.424	0.114	0.001	0.040
20,340	0.033	0.316	0.0	0.425	0.136	0.001	0.029
49,000	0.050	0.413	0.0	0.429	0.093	0.001	0.013
100,902	0.068	0.389	0.0	0.482	0.053	0.001	0.009

dominance and contagion indices is generally positive.

Discussion

The effect of changing grain can be compared with the effect of changing extent by comparing Tables 5 and 8. In general, it appears that indices of dominance and contagion decrease as grain size increases, but these indices increase as extent increases. Changing the meaning of ‘scale’ from grain to extent can have important qualitative and quantitative effects on how measurements change across scales. We hypothesized that dominance and

Table 8. Regression of three landscape indices with extent (log area). Values are the slopes and (r^2).

Scene	Landscape parameter		
	Diversity (H)	Dominance (D)	Contagion (C)
Goodland, KS	0.008 (0.19)	0.197 (0.88)	3.253 (0.78)
Natchez, MS	0.127 (0.78)	-0.015 (0.02)	1.535 (0.72)
Knoxville, TN	-0.058 (0.38)	0.111 (0.87)	0.938 (0.47)
Greenville, SC	0.023 (0.10)	0.067 (0.70)	0.067 (0.67)
Waycross, GA	0.044 (0.84)	0.081 (0.50)	1.519 (0.57)
Macon, GA	-0.006 (0.06)	0.077 (0.93)	1.373 (0.66)
Athens, GA	0.041 (0.42)	0.081 (0.57)	1.569 (0.83)

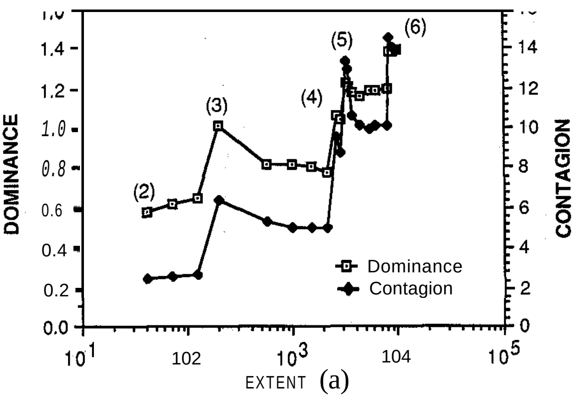

Fig. 3. Landscape indices as a function of increasing extent as indicated by log (area) in the Natchez, Mississippi, quadrangle. Note the sensitivity of the dominance and contagion indices to the number of cover types present, m, indicated in parentheses. Other landscape scenes also showed this stair-step pattern.

contagion would increase as resolution was decreased. This effect was observed as long as m (the number of land cover types) did not change, but the overall effect of losing cover types dominated. Similarly, the number of land uses tends to increase as extent increases, and dominance appears to increase as m increases.

Meentemeyer and Box (1987) proposed that increasing the extent of a study area would tend to increase the range of values for a landscape variable. Our results support this hypothesis, as the P_k values vary considerably as extent increases. Meentemeyer and Box further suggested that apparent detail is lost with increased area (subject to the density of patchiness), and decreased area involves newly apparent detail. Our results also support this statement, as the apparent proportion of the landscape in different cover types changes with grain. The grain size at which a land cover type k disappears depends on P_k of the original data, *i.e., $P_k(1)$*. The smaller the initial probability, the sooner type k is lost as aggregation proceeds. However, the changes in each land cover type are not necessarily unidirectional through all aggregations. Furthermore, the spatial arrangement of the land cover also influences the rate at which it disappears. Rare cover types with patchy arrangements disappear more rapidly with decreasing resolution than contagious ones. Patch density and the appropriate scale of analysis may thus be inversely related (Meentemeyer and Box 1987).

The quantification of spatial pattern is necessary to link the effects of landscape heterogeneity with ecological function and to use remotely sensed data to measure change in large spatial units. Patch size and distribution (e.g., Gardner *et al.* 1987), fractal dimension (e.g., Krummel *et al.* 1987), edges (e.g., Turner 1987b), diversity (e.g., Romme 1982; Romme and Knight 1982), and indices of dominance or contagion can all be used to quantify landscape pattern. Our results demonstrate that the spatial scale at which these patterns are quantified influences the result, and measurements made at different scales may not be comparable. Furthermore, qualitative and quantitative changes in measurements across spatial scales will differ according to how scale is defined. Thus, the definition and methods of changing scale must always be explicitly stated. It is important to define the scale of ecological data in terms of both grain, S_g, and extent, S_e. The identification of properties that do not change or change predictably across scales would simplify the extrapolation of measurements from fine scales to broad scales. However, although it may be possible to identify simple relationships between landscape parameters measured at different scales (e.g., diversity, Table 4), the exact. relationship varies across landscapes and does not permit extrapolation from one region to another.

Our results verify that information is lost in coarser grained spatial data. In general, information about the less frequent land cover types is most easily lost, but the rate of loss depends upon their spatial arrangement. It is possible to predict the loss of information if the contagion of cover types is known. These results may have important implications for comparing information obtained at different grain sizes. If cover type k is randomly distributed, knowledge of P_k may permit extrapolation of' P_k to other scales of resolution. This may allow direct comparison between landscape data-of different grain sizes. The ability to extrapolate will break down when P_k reaches 0.00 or 1.00, however, because these values can be reached through aggregation from many starting points. It is not then possible to extrapolate to finer scales. Characterizing the relationships between ecological measurements and the grain and extent of the data may make it possible to predict or correct for the loss of information with changes in spatial scale. More importantly, the ability to predict how ecological variables change with scale may open the door to extrapolating information to larger scales and to comparing data measured in different regions.

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