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A hierarchical neutral model for landscape analysis[1]

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Abstract

Empirical studies have revealed scaled structure on a variety of landscapes. Understanding processes that produce these structures requires neutral models with hierarchical structure. The present study presents a method for generating random maps possessing a variety of hierarchical structures. The properties of these scaled landscapes are analyzed and compared to patterns on totally random, unstructured landscapes. Hierarchical structure permits percolation (*i.e.*, continuous habitat spanning the landscape) under a greater variety of conditions than found on totally random landscapes. Habitat clusters on structured maps tend to have smaller perimeters. The clusters tend to be less clumped on sparsely occupied landscapes and more clumped in densely occupied conditions. Hierarchical structure changes the expected spatial properties of the landscape, indicating a strong need for this new generation of neutral models.

Introduction

Landscape ecology (Forman and Godron 1986; Turner 1989) investigates the interplay between spatial pattern and ecological processes. Neutral models (sensu Caswell 1976) based on percolation theory (Gefen *et al.* 1983; Stauffer 1985; Orbach 1986) have proven valuable for the analysis of landscape pattern (Gardner *et al.* 1987). These neutral models have found applications in the study of scales of animal movement (O'Neill *et al.* 1988) and in the prediction of disturbance spread (Turner *et al.* 1989). However, percolation models focus on maps that are unpatterned and unstructured. Since structure on the landscape affects ecological processes (Watt 1947), neutral models for the analysis of structured maps are needed.

Hierarchy theory (Allen and Starr 1982; O'Neill *et al.* 1986) predicts that complex systems, such as landscapes (O'Neill *et al.* 1989) will often develop hierarchical structure. This structure is reflected in multiple scales of spatial patterning (Urban *et al.* 1987). The prediction of hierarchical pattern is confirmed by a number of empirical studies. Anderson (1971) analyzed three Australian dry-land communities and found multiple scales of pattern in all three. Barnsley *et al.* (1986) found three distinct scales by fractal analysis of a coral reef. Krummel *et al.* (1987) examined the fractal dimension of a landuse map and found two distinct scales. O'Neill

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et al. (1991a) used a method devised by Levin and Buttel (1986) to detect multiple scales on four out of six sets of data on landcover. O'Neill *et al.* (1991b) examined plant data from Tennessee, New Mexico, and Washington and detected 3–5 scales in all locations.

These studies demonstrate the existence of hierarchical structure on landscapes but the causes for the scaled structure are unclear. Exploring the phenomenon requires neutral models that incorporate hierarchical structure. The new models can then be used to study the spatial properties of this type of landscape pattern.

A simple method for generating hierarchically structured random maps is provided by curdling algorithms derived from fractal geometry (Mandelbrot 1983). This approach has already proven useful in explaining landscape pattern (Lavorel *et al.*, manuscript). This paper introduces a new method for generating structured neutral models. The paper explores the spatial patterns generated by this new generation of models and demonstrates critical differences between hierarchically structured and totally random landscapes.

Methods

Let us consider the spatial pattern of oak stands on a landscape. We will regard the landscape as a square grid of 64 × 64 equally spaced sites with oak stands occupying 75% of the sites (*i.e.*, Pm = 0.75). We can generate a map with these properties by randomly assigning oak stands to 64 × 64 × 0.75 = 2560 sites. The expected properties of such a landscape can be determined by generating a number of random maps and calculating the mean properties.

On finite random maps, Pm predicts an important aspects of landscape structure. When Pm > 0.6 the largest cluster, *i.e.*, the largest contiguous grouping of oak stands, spans the entire map with high probability and the map is said to percolate (Gardner *et al.* 1987).

To introduce scaled structure, let us consider that the 64 × 64 landscape contains two soil types, A and B. The soil types occur in regular blocks of 8 × 8 sites. Thus, the landscape is divided into a total of 64 blocks of soil types. Soil type A is randomly distributed among these blocks, occupying a proportion, P_1. Soil type B occupies the remaining $(1 - P_1)$ blocks. Oak stands occupy a proportion, P_{2A}, of the sites on soil type A and a different proportion, P_{2B}, of the sites on soil type B. Notice that the total occupancy by oak stands is now:

$$Pm = (P_1 P_{2A}) + ((1 - P_1)P_{2B}) \qquad (1)$$

The new map possesses two scales of structure: the larger structure of the soil types, and the finer pattern of oak stands within each soil type. The expected patterns on these hierarchically structured landscapes can be calculated as the mean of a number of individual maps on which the soil types and oak stands are placed randomly.

For the present study we selected sets of triplet values (P_1, P_{2A}, and P_{2B}), and generated 20 maps for each set of values. Because of the importance of Pm = 0.6 on random maps, we chose values that produced Pm values (Eq. 1) over the interval $0.54 < Pm < 0.72$. We investigated 40 sets of values, systematically chosen to cover a broad range of values for P_1, P_{2A}, and P_{2B}.

The expected values for the hierarchically structured maps were compared to the expected values for totally random maps (n = 20) over the same interval, $0.54 < Pm < 0.72$.

Results

The hierarchically structured maps deviate significantly from totally random maps in their tendency to percolate. Figure 1 shows the percentage of random maps that percolate as a function of Pm (Eq. 1). As expected, random maps (open diamonds) show greater than 50% percolation for Pm > 0.6. The dots show the percentage percolation for the hierarchically structured maps. The deviations are striking. With structuring, it is possible to achieve 100% percolation at lower values of occupancy (ca. 56%), while at higher levels of occupancy (Pm > 68%), some structures only show 60% percolation.

Figure 1 demonstrates that hierarchically structured maps can show a much richer array of perco-

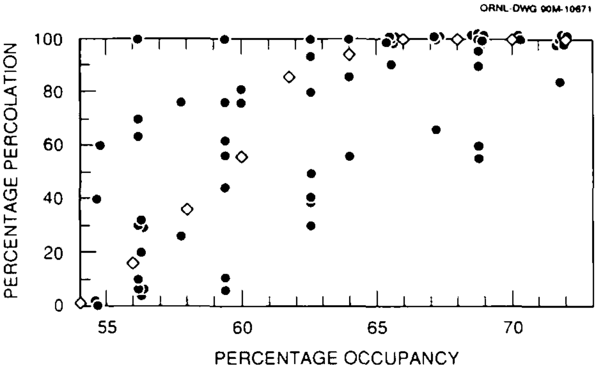

Fig. 1. Percentage percolation as a function of percentage occupancy. Open diamonds represent totally random maps and closed circles are hierarchically structured maps.

Table 1. Comparison of landscape structure at extreme values of P_{2B} = 1.0 (top half of table) and P_{2B} = 0.0 (bottom half of table)

		Pm = 0.625, P_1 = 0.5	
P_{2B}	1.00	0.875	0.75
% Percolation	40	50	80
# Clusters	213	191	122
Largest cluster	1362	1406	1798
Inner edge	61	869	1832
		Pm = 0.563, P_1 = 0.75	
P_{2B}	0.00	0.375	0.75
% Percolation	100	30	10
# Clusters	20	178	203
Largest cluster	2167	876	591
Inner edge	1888	1285	898

lation behavior. The criterion of 50% percolation can be met over a range of values of Pm from about 55% to about 68%. It is important to recognize that Pm alone is no longer an adequate descriptor of landscape properties. The hierarchical structure must also be considered.

Table 1 shows the spatial properties of landscapes at extreme values of P_{2B}. The upper half of the table compares three landscapes, all of which have P_1 = 0.5 and a value of Pm = 0.625 that exceeds the critical threshold for unstructured maps. However, at the extreme value of P_{2B} = 1.0, the percolation criterion is not satisfied. At P_{2B} = 1.0, the maps have an unexpectedly large number of clusters (213) and the largest cluster is relatively small (1362). These values indicate that the occupied sites are tightly clustered on "Soil Type B". The tightness of the clusters is also indicated by the very small number of inner edges (61). Thus, an extreme value of P_{2B} leads to the landscapes with a large number of relatively small, compact clusters. None of these clusters is large enough to span the map and permit percolation.

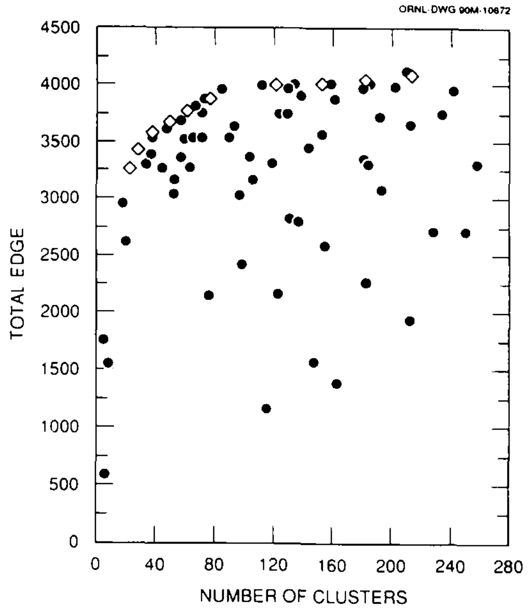

Fig. 2. Habitat edge as a function of the number of clusters on the landscape. Open diamonds represent totally random maps and closed circles are hierarchically structured maps.

The bottom half of Table 1 compares landscapes with P_1 = 0.75 and a Pm of 0.563 that is below the critical threshold for random maps. At the extreme value of P_{2B} = 0.0, 100% of the maps percolate. This is because there are an unusually small number of clusters (20) and the individual clusters are relatively large (2167). The large clusters are also very loosely structured as indicated by the inner edges of 1888. The clusters are diffuse and contain significant 'holes'. As a result, the largest cluster occupies sufficient space to span the map and cause percolation.

The ecotones between habitats are an important resource utilized by many wildlife species. Analysis of habitat edges has therefore been of concern to landscape ecology. The open diamonds on Fig. 2 indicate that the total edges on a random map increase to an asymptote. This random configuration

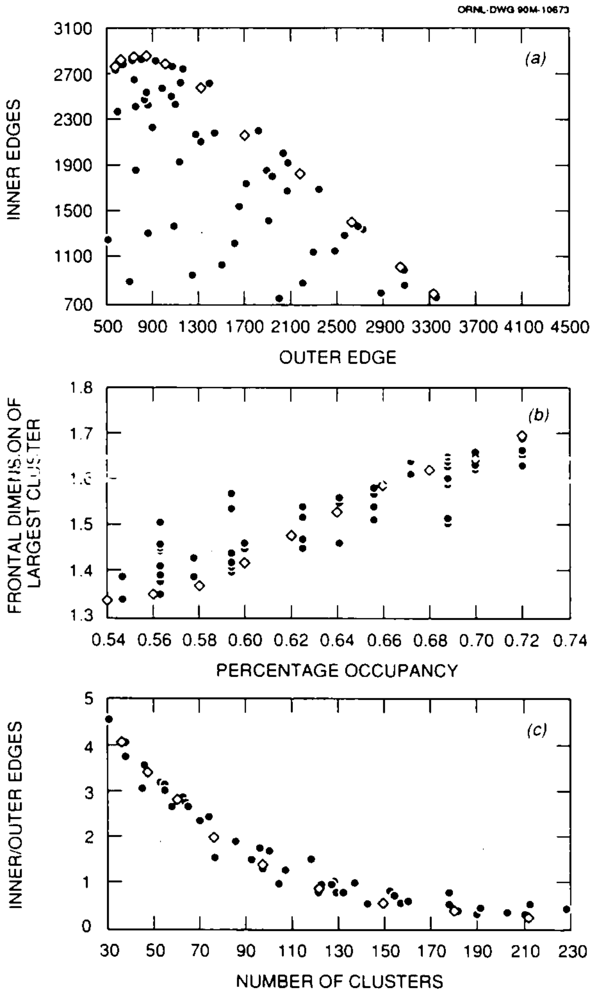

Fig. 3. Landscape properties on random (open diamond) and hierarchically structured (closed circle) maps.

a. Inner edges (surrounded or isolated within a cluster) versus outer edges.

b. Fractal dimension of the largest cluster as a function of percentage occupancy.

c. The ratio of inner to outer edges as a function of the number of clusters maps.

forms an envelope beneath which lie all of the hierarchically structured landscapes. The structured maps have less edge than the random maps.

Figure 3a compares the inner edges (totally surrounded or isolated within a cluster) and outer edges on the maps. As in Fig. 2, the random maps (open diamonds) form an envelope within which are found all of the structured maps. The structured maps are always more contagious or lumped than the random expectation.

Figures 2 and 3a suggest that the hierarchically structured landscapes tend to have 'tighter' clusters, *i.e.*, the clusters tend to have smoother boundaries (Fig. 2) and possess fewer 'holes' or internal openings (Fig. 3). Gardner *et al.* (1987) introduced the fractal dimension, $D = (\ln S - \ln 0.25)/\ln P$, as an index of the complexity of shape for a cluster of area S and perimeter P. Smaller values of D would be associated with 'tight' clusters and, therefore, one would expect small values of D on the structured maps.

Figure 3b shows that the expectation is only partially realized, at least for the largest cluster on the map. At percentage occupancies greater than 0.6, hierarchical structuring (closed circles) tends to coalesce the cluster, resulting in fractal dimensions less than the random expectation (open diamonds). Below 0.6, structuring produces a larger, more complex cluster with a higher fractal dimension than the random prediction.

Figures 1 to 3b emphasize the differences between random and hierarchical maps. But there are also striking similarities, for example, between the number of clusters and the ratio of inner to outer edges (Fig, 3c). Over a limited range of occupancies, pulling the occupied sites into fewer and fewer clusters increases the probability of enclosing 'islands' bounded by inner edges. With a large number of clusters, each cluster is small. There is little change of enclosing a non-habitat island and there is little or no inner edge.

There are a number of other properties that are predictable on structured landscapes. Basically, percolation occurs when the largest cluster spans the map from one side to the other. Therefore, no matter what the structure of the map, one would expect to see a relationship between the size of the largest cluster and the percentage of maps that percolate. Figure 4a shows the expected relationship. The random maps (open diamonds) and hierarchically structured maps (closed circles) are very similar, particularly for the largest cluster sizes.

A similar, but looser relationship would be expected between the number of clusters and percentage percolation (Fig. 4b). Over the range of occupancies used in this analysis ($0.54 < Pm < 0.72$) one would expect that maps with few clusters would also have larger clusters and would be more likely

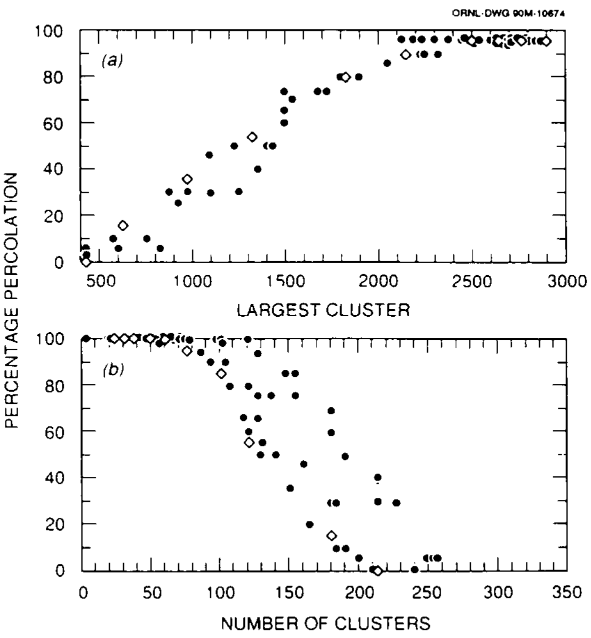

Fig. 4. Percentage percolation on random (open diamond) and hierarchically structured (closed circle) maps.

a. Percentage percolation as a function of the size of the largest cluster.

b. Percentage percolation as a function of the number of clusters on a map.

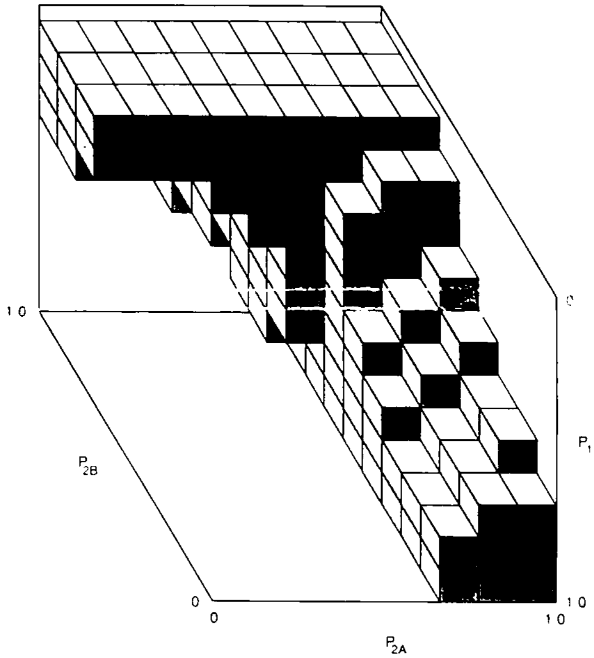

Fig. 5. Percolation on hierarchically structured landscapes as a function of the three occupancy parameters, P_1, P_{2A}, and P_{2B}. The solid blocks represent parameter combination that produce percolating clusters on more than 50% of the randomly generated maps.

to percolate. The relationship between random maps (open diamonds) and hierarchically structured maps (closed circles) is particularly close for maps with less than 70 clusters. For larger numbers of clusters, the structuring tends to form more coherent clusters and the structured maps are more likely to percolate on maps with larger numbers of clusters.

Many of the analyses (*e.g.*, Figs. 1 to 3b) leave the impression that the predictability characteristic of random maps has been lost by adding hierarchical structuring. In fact, the properties of the structured maps, such as the probability of having a percolating cluster, remain predictable, though significantly more complex.

Figure 5 shows the three-dimensional P_1, P_{2A}, P_{2B} space. The combinations of parameters that produce greater than 50% probability of percolation are shown as solid blocks. Although the sculpture formed by the blocks is complex, it is relatively easy to explain. For example, there are two sets of conditions in which either one or the other of the Soil types occupies almost all of the landscape and contains a percolating cluster.

When P_1 is large (*i.e.*, close to the 'floor' of the figure) most of the landscape is composed of Soil type A and landscape properties are dominated by P_{2A}, the percentage of occupied sites on soil type A. Thus, if P_1 is greater than 0.875 and P_{2A} is greater than 0.75, the landscape will percolate irrespective of the value of P_{2B}. These conditions form a solid (2 blocks high and three blocks wide) that extend from the front of the figure to the back along the lower right-hand edge.

There is a symmetric set of conditions as P_1 approaches 0.0. Now almost all of the landscape is in soil type B and properties are dominated by P_{2B}. The conditions, $P_1 < 0.125$ and $P_{2B} > 0.75$, form a solid (three blocks high and two blocks wide) that lies on the back 'ceiling' of the figure, running from left to right.

Finally, there is a set of conditions under which both P_{2A} and P_{2B} are large (*e.g.*, greater than 0.75). Now, both soil types contain a percolating cluster and it no longer matters how the landscape is divided into the two soil types. This set of conditions forms a solid (three blocks wide and deep) that occupies the furthest corner of the figure extending from 'floor' to 'ceiling'.

On the 'Z-shaped' backbone (Fig. 5), formed by these three sets of conditions, are additional parameter combinations that cause percolation. These represent conditions in which neither soil type A nor B contains a percolating cluster, but occupancy levels on each are high enough to form a percolating cluster that extends across the two soil types.

Discussion

Totally random maps provide useful neutral models for many landscape problems (Gardner *et al.* 1987). However, unstructured maps may not be sufficient to test hypotheses about processes on real landscapes that possess some degree of structure. The empirical studies reviewed in the introduction indicate that scaled or hierarchical structure may be common. The results of this study make it clear that totally random neutral models could produce a misleading impression of landscapes with scaled structure.

The most important point raised by this study is the potential influence of scale on landscape processes. Landscapes are complex and diverse. If one were to focus only on soil type A, for example, one might conclude that oak stands are sufficiently common to percolate. But for organisms that utilize more than a small block of the landscape, percolation depends on the overall properties of the landscape and pattern at higher scales. Thus, a landscape might provide adequate habitat at a fine scale and still not permit free movement for many species. For many landscape problems an explicit consideration of multiple scales may be needed to determine the persistence and stability of ecological processes.

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