

Resource utilization scales and landscape pattern

R.V. O'Neill¹, B.T. Milne², M.G. Turner¹ and R.H. Gardner¹

¹*Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 378314038;*

²*Biology Department, University of New Mexico, Albuquerque, New Mexico 87131*

Keywords: percolation theory, probability theory, landscape ecology, scale, pattern

Abstract

The spatial patterning of resources constrains the movement of consumers on the landscape. Percolation theory predicts that an organism can move freely if its critical resource or habitat occupies 59.28% of the landscape. Sparse resources require an organism to operate on larger resource utilization scales. Multiple critical resources necessitate larger scales, while substitutable resources ease the scale requirements. Contagious spatial patterns require larger scales to permit movement between resource clusters. The study indicates a strong link between spatial pattern and ecological processes on a landscape.

Introduction

The spatial patterning of ecosystems influences many ecological phenomena (Naveh and Lieberman 1984; Forman and Godron 1986) such as the spread of disturbances (Turner 1987; Franklin and Forman 1987) and the movement and dispersal of animals (Fahrig and Merriam 1985; Freemark and Merriam 1986). Landscape ecology addresses the relationship between ecological patterns and the biotic processes affected by these patterns (Risser *et al.* 1984) but the implications for other areas of ecological research have only begun to be explored (Urban *et al.* 1987).

Spatial patterning on the landscape determines the distribution of resources that organisms must locate and utilize (Senft *et al.* 1987). This paper combines a result from percolation theory with consideration of how an organism moves on a heterogeneous landscape. The emphasis is on how the patterning of the landscape can alter the resource utilization scale of an organism.

Percolation theory

Percolation theory (Stauffer 1985; Orbach 1986) considers the random arrangement of items on a lattice, such as a landscape with land cover or vegetation specified at equidistant grid points. The grid points form clusters or sets of adjacent (either horizontally or vertically) points with the same land cover. A significant conclusion of percolation theory concerns the existence of percolating clusters, i.e., clusters that stretch from one side of the lattice to the other. The probability of a percolating cluster increases as the proportion of the grid points occupied by land use i , P_i , increases. As the lattice becomes large, the probability of a percolating cluster approaches a step function, changing from 0.0 to 1.0 over a very narrow range of P_i . On an infinite square lattice, a percolating cluster of land cover i will exist if i is randomly distributed and occupies at least 0.5928 of the lattice points (Orbach 1986).

The relevance of this result can be seen if we con-

sider an organism moving about on the landscape. If the organism must remain within land type *i*, e.g., forest, then forest must occupy 59.28% or more of a random landscape to enable the organism to move across the landscape and utilize the available resources. Some small, isolated pockets of resource may remain, but we can characterize the landscape as accessible to the organism in the sense that it can move freely across it. This observation provides a direct link between landscape pattern and an ecological consequence of scale.

Resource utilization scale

The analysis to this point assumes that the organism must locate a unit of resource at each grid point, *i.e.*, the organism is restricted to moving one grid point or one unit distance per unit time. Let us consider what happens if the organism can move more than a unit distance per unit time, *i.e.*, the organism can traverse *n* grid points per unit time. At what scale must the organism operate to utilize the resource on this landscape? Assume that the organism must find at least one resource unit as it moves *n* units on the landscape and the resource occupies a random proportion, *P*, of the landscape. The probability of finding exactly zero resources in *n* steps is $(1 - P)^n$. Then the probability, *R*, of finding at least one resource unit is 1.0 minus the probability of finding none:

$$R = 1 - (1 - P)^n \quad (1)$$

We know from percolation theory that if *R* = 0.5928, the organism can move across the landscape. Substituting this value for *R* into Equation (1) and rearranging, we find the following relationship between *n* and *P*:

$$n = -0.89845 / \ln (1-P) \quad (2)$$

Equation 2 gives the scale, *n*, required for an organism to move across a landscape on which a critical resource occupies *P* units. We will define *n* to be the resource utilization scale.

Table 1 gives values of the resource utilization scale for a variety of probabilities. For a sparse resource (small *P*), a large number of landscape

Table 1. Critical probabilities for percolation on a random, infinite landscape for various resource utilization scales. The first column represents the number of landscape units, *n*, searched by an organism in a unit time. Entries are the proportion of landscape units which must be occupied by resource *i* for an organism with search path, *n*, to be able to move across the landscape.

<i>n</i>	<i>P_i</i>
	0.592800
4	0.201174
9	0.095007
16	0.054606
25	0.035300
100	0.008944
400	0.002244
900	0.000998
1600	0.000561
2500	0.000359

units must be searched. Viewed in another way, an organism that can traverse large distances can use a resource which is sparsely distributed.

This approach to the scale of resource utilization on a landscape has some interesting ramifications. For example, at higher levels in a food chain, organisms will often operate at a larger *n*. With notable exceptions, such as ambush predators, first and second order carnivores will have to search larger areas on the landscape to locate prey. We would also expect that an organism with small *n* could only operate on landscapes with high *P* or be restricted to sections of the landscape where *P* was sufficiently high. This analysis helps explain why human disturbance of landscape scale (Urban *et al.* 1987) has serious impacts since organisms with large *n* may not be able to move over a sufficiently large area to utilize a sparse resource.

Multiple resources

The analysis can be expanded to include additional resource requirements. An organism requires multiple resources, such as both food and water, that independently occupy the landscape with probabilities, *P_i*. Because the organism must locate all of the resources in pathlength *n*, we must consider the product of the independent probabilities of locating

Table 2. Resource utilization scale, n' , for two critical resources. Table gives the number of grid points or steps an organism must traverse per unit time to insure that it will locate both resources as it moves across a landscape.

		P1								
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
P2	0.1	13.95	10.24	9.10	8.69	8.56	8.53	8.53	8.53	8.53
	0.2	10.24	6.59	5.34	4.72	4.37	4.17	4.08	4.04	4.03
	0.3	9.10	5.34	4.12	3.49	3.11	2.86	2.69	2.58	2.53
	0.4	8.69	4.72	3.49	2.88	2.50	2.23	2.04	1.90	1.80
	0.5	8.56	4.37	3.11	2.50	2.12	1.86	1.67	1.51	1.39
	0.6	8.53	4.17	2.86	2.23	1.86	1.60	1.41	1.26	1.12
	0.7	8.53	4.08	2.69	2.04	1.67	1.41	1.22	1.07	0.93
	0.8	8.53	4.04	2.58	1.90	1.51	1.26	1.07	0.91	0.77
	0.9	8.53	4.03	2.53	1.80	1.39	1.12	0.93	0.77	0.64

Table 3. Resource utilization scales, n'' , when an organism must locate either of two substitutable resources as it moves across the landscape.

		P1								
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
P2	0.1	4.26	2.73	1.94	1.46	1.12	0.88	0.69	0.52	0.37
	0.2	2.73	2.01	1.55	1.22	0.98	0.79	0.63	0.49	0.36
	0.3	1.94	1.55	1.26	1.03	0.86	0.70	0.57	0.46	0.34
	0.4	1.46	1.22	1.03	0.88	0.75	0.63	0.52	0.42	0.32
	0.5	1.12	0.98	0.86	0.75	0.65	0.56	0.47	0.39	0.30
	0.6	0.88	0.79	0.70	0.63	0.56	0.49	0.42	0.36	0.28
	0.7	0.69	0.63	0.58	0.52	0.47	0.42	0.37	0.32	0.26
	0.8	0.52	0.49	0.46	0.42	0.39	0.36	0.32	0.28	0.23
	0.9	0.37	0.36	0.34	0.32	0.30	0.28	0.26	0.23	0.20

zero resources. The multiple resource utilization scale, n' , becomes:

$$0.5928 = [P1]i (1 - (1 - P1)**n') \quad (3)$$

Values of n' for two resources are given in Table 2. An additional resource significantly increases the resource utilization scale. For example, with $P1 = 0.6$ we expect an organism with $n = 1.0$ to be able to move freely across the landscape (Table 1). But with the addition of a second critical resource, n' approaches 1.0 only as $P2$ approaches 1.0.

The organism can operate on smaller scales if there are substitutable resources (Tilman 1982) because only one of several possible resources must be located in a pathlength of n . For two resources, we can define a substitutable resource scale, n'' :

$$0.5928 = S1 + S2 - S1 S2 \quad (4)$$

where $S_i = (1 - (1 - P_i)**n'')$. Equation (4) can be solved for n'' to yield

$$n'' = -0.89845 / (\ln(1 - P1) + \ln(1 - P2)) \quad (5)$$

Similar expressions can be derived for more than two substitutable resources but the equations become quite complicated. In contrast to the multiple resource case (Equation 3 and Table 2), an additional substitutable resource decreases the minimal scale needed to utilize resources on a landscape (Table 3).

Scale and the efficiency of resource utilization

Few organisms are efficient enough to locate and utilize 100% of the resources available on a land-

scape. An inefficient dominant organism allows the survival of other organisms, operating at larger values of n . If the dominant randomly removes 90% of resource i , it leaves resources at 10% of the landscape locations. A subdominant organism can still utilize the landscape if it can use the resources at the larger scale predicted by Equation 2.

The large-scaled, subdominant organism would be considered rare in the sense that sampling any small area would be unlikely to locate an individual. However, the organism would not be rare in the sense that individuals would almost always be found in samples over sufficiently large areas.

Scale and habitat

A similar situation arises when we consider the suitability of a landscape to provide adequate habitat for an organism. Let us assume that a group of grid points will serve as adequate habitat if 50% or more of the landscape units are of type i , for example, forest.

Table 4 gives the probability that a group of m grid cells will contain more than 50% of a landscape type for various values of P_i . The table is constructed by looking up a table of the cumulative binomial distribution for $b = P = 0.5$. Notice that if there is a 50:50 chance of finding a suitable habitat unit at $m = 1$, then there is a 50:50 chance of finding suitable aggregates on that landscape. If the occupancy of sites at the unit scale is less than 0.5, then the probability of an aggregate being suitable decreases. The rate of decrease is greater, the rarer the habitat is at $m = 1$. If the habitat occupies more than 50% of the sites at $m = 1$, then any aggregate will be suitable.

The analysis indicates that animals operating at large scales (large m) should be generalists with respect to habitat requirements. At larger scales, very specific habitat aggregates ($P_i(m) < 0.5$) will be hard to find. Disturbances of landscape pattern will be serious, particularly disruptions that require the organisms to operate at larger scales to utilize resources.

Results for patterned landscapes

The results given above are limited by the assumption that resources are randomly distributed on the landscape. The results can be extended to landscapes that show significant contagion or pattern. To do this we introduce the adjacency matrix, Q . For two land cover types (e.g., resource P and non-resource $1 - P$) the matrix takes the form:

$$\begin{vmatrix} Q_{11} & Q_{12} \\ Q_{21} & Q_{22} \end{vmatrix}$$

where the elements Q_{ij} represent the probability of a unit of land cover i being adjacent to a unit of land cover j . The matrix is constrained such that each row sums to 1.0.

If directionality is ignored in constructing the adjacency matrix, the probability of being on land cover 1 and next to land cover 2 is equal to the probability of being on land cover 2 and next to land cover 1, *i.e.*,

$$P Q_{12} = (1 - P) Q_{21} \quad (6)$$

We will assume hereafter that the landscape is symmetric in the sense of Equation (6) and if we simplify notation to make $Q_{11} = Q$, the Q matrix becomes:

$$\begin{vmatrix} Q & 1 - Q \\ P(1 - Q)/(1 - P) & 1 - 2P + PQ/(1 - P) \end{vmatrix}$$

By analogy with Equation (1), the probability of encountering no resources in a pathlength of n is the probability of encountering a non-resource unit at the first step, $(1 - P)$ times the probability of being on a non-resource unit and standing next to a non-resource unit, *i.e.*, $Q_{22} = 1 - 2P + PQ/(1 - P)$ raised to the $(n - 1)$ power. Then, the probability of encountering at least one resource unit is:

$$R = 1 - (1 - P) (1 - 2P + PQ/(1 - P))^{(n-1)} \quad (7)$$

Once again, we can set $R = 0.5928$ and derive an expression for the resource utilization scale in terms of P , the proportion of landscape units occupied by the resource, and Q , the degree to which the

Table 4. Probability of finding suitable habitat on a landscape at various scales of resolution. Entries represent the probability of finding a suitable habitat (50% or more of the landscape units are of type i) for organisms that operate on various scales, m. Column headings, Pi, represent the proportion of landscape units of type i on the finest grain resolution, i.e., on the landscape at m = 1.

	Pi								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
m									
3	0.028	0.104	0.216	0.352	0.5	0.648	0.784	0.896	0.972
5	0.009	0.058	0.163	0.317	0.5	0.683	0.837	0.942	0.991
7	0.003	0.033	0.126	0.290	0.5	0.710	0.874	0.967	0.997
9	0.001	0.020	0.098	0.267	0.5	0.733	0.902	0.980	0.999
11	0.0	0.012	0.078	0.246	0.5	0.754	0.922	0.988	1.0
13	0.0	0.007	0.062	0.229	0.5	0.771	0.938	0.993	1.0
15	0.0	0.004	0.050	0.213	0.5	0.787	0.950	0.996	1.0
17	0.0	0.003	0.040	0.199	0.5	0.801	0.960	0.997	1.0
19	0.0	0.002	0.033	0.186	0.5	0.814	0.967	0.998	1.0

Table 5. Resource utilization scale, n^{'''}, for a resource occupying a proportion, P, of landscape sites and distributed with contagion, Q = - Q₁₁. Entries represent the scale at which an organism must operate in order for a landscape described by P and Q to percolate, i.e., for an organism to move freely across the landscape.

n	Q								
	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.1
0.5	2.94	1.92	1.58	1.40	1.30	1.22	1.17	1.13	1.09
0.4	6.62	3.71	2.74	2.25	1.96	1.76	1.62	1.51	1.42
0.3	13.4	7.04	4.94	3.88	3.25	2.82	2.52	2.29	2.11
0.2	27.7	14.2	9.66	7.41	6.06	5.16	4.51	4.03	3.65
0.1	72.0	36.3	24.4	18.4	14.9	12.5	10.8	9.52	8.53
0.01	881	441	294	221	177	148	127	111	98.3
0.001	8967	4484	2990	2242	1794	1495	1282	1121	999

resource is aggregated on the landscape:

$$n''' = (-0.89845 - 2\ln(1 - P) + \ln(1 - 2P + PQ)) / (\ln(1 - 2P + PQ) - \ln(1 - P)) \quad (8)$$

When P = 0.5928, n^{'''} = 1 irrespective of the value of Q. As Q approaches 1.0, i.e., the resource is clumped in one place on the landscape, the denominator approaches 0 and n^{'''} approaches infinity. As the resource becomes lumped into a single compact 'cluster, it becomes practically impossible to move throughout the landscape. As Q approaches 0.0, i.e., as the resource becomes completely across the landscape, P cannot be greater than 0.5. If p > 0.5 then at least a few of the resource units must necessarily be adjacent. When Q = P we have the situation in which the degree of contagion is exactly

what you would expect from a random landscape, i.e., there is no contagion. Under these circumstances, Equation (18) reduces to Equation (2).

Table 5 shows a range of values for n^{'''} for various values of P and Q. As we saw in the random landscape (Equation 2 and Table 1 resource) utilization scale increases rapidly as P decreases. In addition, as the degree of contagion of the resource increases, the scale must increase. The more clumped the resource, the larger the gaps between resource clusters.

Discussion

By considering the spatial distribution of resources,

we have derived the minimal scales for resource utilization. Not every grid point needs to contain the critical resource. The organism can move about as long as adjacent horizontal or vertical grid points contain the resource. The minimal requirement is that an organism be able to move in a zig-zag path of length n with a high probability of locating a resource.

Throughout this paper, we have accepted the results of percolation theory for an infinite lattice, *i.e.*, the critical probability is 0.5928. It is possible that a finite, patterned landscape will require a higher percentage occupancy to ensure a percolating cluster. On the other hand, linear corridors (Forman and Godron 1986) stretching across the landscape would permit percolation at lower values of P . Thus, a higher or lower value of R (Equations 1, 3, 5, 7) may be necessary to apply our results to a particular landscape.

If a resource is randomly distributed on the landscape, an organism must operate at a sufficiently large scale (Equation 2) to avoid being restricted to a portion of the total landscape. Still larger scales of operation will be required (Equation 3) for multiple critical resources. If several resources can be substituted for each other (Equation 4) the requirements of scale are eased. Because organisms differ in utilization scales, communities should show distinct patterns with dominants operating on small scales and subdominants operating at larger scales. Similar generalities result from considering that landscapes must contain a minimal percentage of specific vegetation cover to serve as suitable habitat for particular organisms.

An organism must adjust its resource utilization scale if a resource is distributed with contagion. In general, as the resource becomes highly clumped, it becomes clustered into only one portion of the landscape. The organism must then be able to operate at large scales to move from one resource patch to the next.

Thus, a consideration of resource patterning on the landscape leads directly to conclusions about the scale at which organisms must operate to utilize that resource. As the distribution and pattern of the resource change, so also the scale of utilization must change. This leads to a direct connection be-

tween pattern and the ecological processes involved in resource utilization. Although much additional research is needed, it is clear that a direct connection can be made between studies of landscape pattern and the ecological processes taking place on the landscape.

Acknowledgements

Research supported in part by the Office of Health and Environmental Research, Department of Energy under contract No. DE-AC05-84OR21400 to Martin Marietta Energy Systems, Inc. and in part by the Ecosystem Studies Program, National Science Foundation under grant No. BSR 8614981 to the University of New Mexico and Interagency Agreement No. BSR 8514981 to the Department of Energy. Support for M.G. Turner was provided by the Department of Energy's Alexander P. Hollaender Distinguished Postdoctoral Fellowship, administered by Oak Ridge Associated Universities. Publication No. 3161 of the Environmental Sciences Division, Oak Ridge National laboratory.

References cited

- Allen, T.F.H. and T.B. Starr. 1982. *Hierarchy: Perspectives for ecological complexity*. University of Chicago Press, Chicago, IL.
- Fahrig, L. and Merriam, H.G. 1985. Habitat patch connectivity and population survival. *Ecology* 66: 1762–1768.
- Forman, R.T.T. and Godron, M. 1986. *Landscape Ecology*. Wiley, New York, NY.
- Franklin, J.F. and Forman, R.T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landsc. Ecol.* 1: 5–18.
- Freemark, K.E. and Merriam, H.G. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biol. Cons.* 31: 95–105.
- Gardner, R.H., Milne, B.T., Turner, M.G. and O'Neill, R.V. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landsc. Ecol.* 1: 19–28.
- Naveh, Z. and Lieberman, A.S. 1984. *Landscape Ecology: Theory and Application*. Springer-Verlag, New York, NY.
- Orbach, R. 1986. Dynamics of fractal networks. *Science* 231: 814–819.
- Risser, P.G., Karr, J.R. and Forman, R.T.T. 1984. *Landscape Ecology: Directions and Approaches*. Illinois Natural History Survey, Champaign, Illinois. Special Publication 2.

- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* 37: 789-799.
- Stauffer, D. 1985. *Introduction to Percolation Theory*. Taylor and Francis, London.
- Tilman, D. 1982. Resource competition and community struc-

- ture. Princeton University Press, Princeton, NJ.
- Turner, M.G. (ed.) 1987. *Landscape heterogeneity and disturbance*. Springer-Verlag, New York, NY.
- Urban, D.L., O'Neill, R.V. and Shugart, H.H. 1987. Landscape ecology: A hierarchical perspective. *Bioscience* 37: 119-127.