CONF-8812141--1

DE90 014211

A Percolation Model of Ecological Flows[1]

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[1] Research supported by the Ecological Research Division of the Office of Health and Environmental Research, U. S. Department of Energy under contract No. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. and by an Alexander Hollaender Distinguished Postdoctoral Fellowship to M. G. Turner.

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INTRODUCTION

The boundary zone between adjacent communities has long been recognized as a functionally important component of ecosystems (Odum 1959). The diversity and abundance of species (Noss 1983), the flow and accumulation of material and energy (Ranney et al. 1981), and the propagation of disturbances (Turner et al. 1989, Picket and White 1985) may all be affected by landscape boundaries. However, the spatial arrangement of different habitats and their boundaries has received little direct study (Krummel et al. 1987, Wiens et al. 1985). It is not surprising, therefore, that Hansen et al. (1987) have noted "...the extent to which landscape boundaries influence ecological flows is not well known and recent treatments of the topic remain speculative."

The difficulty in studying landscape boundaries has been due, in part, to the variety of responses of organisms to ecotones. Therefore, definitive tests of relationships between ecological processes and the pattern of landscape boundaries will be greatly assisted by developing a standard against which comparisons can be made. Neutral models (Caswell 1976) can define this standard by producing the "expected pattern" for testing predictions against observations. The advantages of a neutral model for testing the spatial distribution of plants against the "expected" Poisson distribution have been well established (Greig-Smith 1952, 1964), but a general approach for relating ecological processes and landscape patterns must still be defined. The desirable features of a neutral model for studying landscape boundaries are (1) the model should be simple, with few parameters needed to describe the system; (2) the model should be general in scope and easily applied to a variety of problems; and (3) the model should produce results that can be extrapolated across spatial and temporal scales.

We have explored the use of percolation theory to generate neutral models for landscape studies (Gardner et al. 1987). The analytical and computational methods of percolation theory (Stauffer 1985) are quite general and can be easily applied to a variety of two-dimensional arrays. Because two-dimensional percolation arrays (1) are similar to landscape maps and can be generated by specifying a few parameters, (2) can be used as the basis for simulating a variety of ecological processes, and (3) are appropriately neutral to the physical and biological processes which often shape landscape patterns, they provide useful means of forming neutral models for relating pattern and process.

The purpose of this chapter is to illustrate how neutral models that are developed from percolation theory can be used to address the problem "How do ecological system boundaries influence biotic diversity and the flow of energy, information and materials?" (Holland 1988).

Percolation Methods for the Study of Landscape Boundaries

A two-dimensional percolating network within an array of size $\underline{\mathbf{m}}$ by $\underline{\mathbf{m}}$ is formed by randomly choosing the state of each of the $\underline{\mathbf{m}}^2$ sites by a probability of $\underline{\mathbf{p}}$. Figure 1 shows three example maps of size $\underline{\mathbf{m}} = 20$, with values of $\underline{\mathbf{p}}$ of 0.4, 0.6 and 0.8. The dark pixels or 'occupied sites' in Figure 1 can be thought of as locations of a habitat of interest (e.g., habitats susceptible to disturbance or capable of sustaining populations of rare species). For large arrays, $\underline{\mathbf{pm}}^2$ sites are occupied while $\underline{\mathbf{(1-p)m}}^2$ sites are empty. A 'cluster' is arbitrarily defined as a group of occupied sites which have at least one common edge along the vertical or horizontal directions of an array but not along the diagonals. The number, size, and shape of clusters will change as a function of $\underline{\mathbf{p}}$, with rapid changes occurring near the critical probability, $\underline{\mathbf{p}}_c$, when the largest cluster manages to extend, or percolate, from one edge of the grid to the other.

The value of $\mathbf{p}_c$ for extremely large arrays has been experimentally determined to be 0.5928 (Stauffer 1985). The shape of the largest cluster, as measured by the fractal dimension, has also been shown to be affected by $\mathbf{p}$ (Stauffer 1985): clusters are simple when $\mathbf{p} < \mathbf{p}_c$ but more complex when $\mathbf{p} > \mathbf{p}_c$.

Analysis of arrays generated by percolation theory has provided a means of applying these methods to ecological systems (Gardner et al. 1987). Results show that when $\mathbf{p}$ is low, finite arrays exhibit habitats arranged as many small, isolated clusters. As $\mathbf{p}$ increases, the average size of the clusters also increases (Fig. 1). When $\mathbf{p}$ exceeds the critical threshold, adjacent clusters coalesce into a large cluster which spans the map or "percolates" from edge to edge (Fig. 1b). The relationship between the number of inner and outer edges of clusters can be used to characterize the degree of habitat fragmentation. Inner edges, or gaps within a habitat patch, are frequent when $\mathbf{p}$ is high, but decline rapidly as $\mathbf{p}$ is reduced below $\mathbf{p}_c$, the critical threshold (Fig. 2). The reason for the sudden change near $\mathbf{p}_c$ is that cluster size declines as a function of $\mathbf{p}$ (Stauffer 1985) and gaps within a patch are opened and become a part of the external edge of the cluster (Gardner et al. 1987). When $\mathbf{p}$ declines below 0.4, there are very few clusters with any inner edges. Percolation studies of diffusion in two-dimensions have shown that movement is affected by the size and shape of clusters (Gefen and Aharony, 1983), with anomalous dynamics occurring near the critical threshold, $\mathbf{p}_c$ (Stauffer 1985). These anomalous patterns occur because the structure of the system shifts from diffusive flow in a disconnected system (below $\mathbf{p}_c$) to convective low in a connected network (above $\mathbf{p}_c$, see Ohtsuki and Keyes 1988).

Interaction of Landscape Boundaries with Disturbances

We have used percolation methods to simulate the interaction of a disturbance with the spatial pattern of a susceptible habitat (Turner et al. 1989). The habitat is generated at random on a map (i.e. percolation array) and the disturbance is specified by two parameters which define the frequency, $\underline{f}$, and spread, $\underline{i}$. Frequency, $\underline{f}$, is the probability that a disturbance will be initiated in a unit of susceptible habitat at the beginning of the simulation (e.g., the probability of lightning striking a hectare of pine forest during a particular time period). Disturbance spread, $\underline{i}$, is the probability that the disturbance, once initiated, will affect adjacent sites of the same habitat. A simulation concludes when the disturbance is no longer able to spread to adjacent sites.

The result of a series of simulations of disturbance spread where the disturbance destroys each site (e.g., fire) have shown qualitatively different effects when the proportion, $\underline{p}$, of the landscape occupied by susceptible habitat is above or below $\underline{p}_c$ (Turner et al. 1988, Turner et al. 1989). The effects of disturbance frequency are most important below $\underline{p}_c$ because clusters tend to be fragmented and the disturbance is constrained by the size and shape of the habitat clusters. For example, when $\underline{p} = 0.4$, an increase in disturbance frequency causes a substantial increase in the proportion of habitat affected, even when the probability of disturbance spread is low. The influence of $\underline{i}$, the probability of the disturbance spreading to adjacent sites, is most important above $\underline{p}_c$ because the habitat is more continuous and a relatively rare disturbance can propagate across the landscape. If the probability of spread is sufficiently high (e.g., $\underline{i} = 0.75$), more than 90% of the habitat can be affected by a low frequency of disturbance. When the habitat susceptible to disturbance is rare (e.g., $p = 0.4$), less than 20% of the habitat is disturbed, even when the probability of spread of the disturbance reaches 1.0. When the susceptible habitat is common (e.g., $p = 0.8$), even low values of i produce extensive disturbance effects (Turner et al. 1989).

Habitat boundaries are also affected by the interaction of i and p, with the total amount of edge declining as habitat is removed by the disturbance. High values of i (e.g., $i \geq 0.75$) interact with the connectance of the habitats ($p > p_c$) to cause extensive loss of habitat (e.g., $p = 1.0$; Fig. 3), but the probability of disturbance spread has relatively minor effects on landscape boundaries when the habitat is fragmented (e.g., $p = 0.4$ in Fig 3). Inner edges, or gaps within habitat patches, dominate undisturbed landscapes ($i = 0.0$) when $p > p_c$, but as habitat is destroyed with increasing levels of disturbance the internal gaps are opened and the landscape becomes dominated by outer edges (e.g., $i = 0.75$, $p = 0.6$ in Fig. 3). The complex interaction between disturbance and landscape pattern illustrated in Fig. 3 defines the region in parameter space near $p = 0.6$ and $i = 0.5$ where sudden changes in boundaries are likely to be observed.

Boundary effects on ecological flows

Simple modifications of the disturbance model allow this approach to be used to investigate the flow of populations of different species through the landscape. If we were to substitute directly the flow of species for the spread of disturbance, the existing model would assume: (1) that populations colonize adjacent sites at each time step with probability i; (2) each colonized site becomes unsuitable for continued persistence of the population at each time step; and (3) sites cannot be recolonized during the course of the simulation. To adapt the model for species colonization, we relaxed these assumptions by: (1) defining a probability, e, per unit time for local extirpation of the population (the expected residence time of a population at a site will be $1/e$); (2) defining a probability, h, of the habitat becoming unsuitable for recolonization after a local population has been extirpated (values of $h < 1.0$ implies that resources are diminished by colonization of the site); and (3) allowing sites to be recolonized if the site remains unaltered. When $h = 1.0$ and $e = 1.0$ the "species" version of the percolation model behaves as the previous "disturbance" model.

Simulations of the movement and persistence of populations with a variety of different parameters were performed to examine the interaction between different species and the spatial pattern of landscape boundaries (Table 1): Some populations rapidly spread to adjacent sites ($i = 1.0$) and cause all occupied habitats to be altered ($h = 1.0$) while other populations spread slowly ($i = 0.2$), remain at each site for longer a time ($1/e = 15$) and have little or no impact on occupied sites ($i \leq 0.2$). The percent of the simulations in which the population reaches the edge of the map (**%edge**), the number of time steps to spread across the map (t), and the percent of sites altered or occupied (**%site**) were recorded as a function of i, e, and h (Table 1).

The number of time steps, t, necessary for a simulated population to reach the edge of the map is inversely related to i (compare populations 7, 13 and 19 in Table 1) but directly related to e, the probability of local extinction (compare populations 11, 12 and 13 in Table 1). The percent of the simulations that reached the edge of the map (**%edge**) is also inversely related to e because values of $e < 1.0$ allow a single population several time steps to reach adjacent sites (values of e are irrelevant when $i = 1.0$). When i is small (populations

14-19), low values of e are necessary for a simulated population to reach the edge of the map (populations 16 and 19). The probability of a site being altered by a population has little effect when $i = 1.0$, but dramatically decreases the probability of survival when $i < 1.0$. The reason is that alterations of a site ($h > 0.0$) can disconnect the percolating cluster and prevent the species from moving across the map (note populations 8 vs 11). Table 1 illustrates that population specific attributes result in the existence of different thresholds at which critical phenomena will be observed. For instance, alterations in e and h result in remarkably different levels of success for populations 14 through 19.

Scaling Relationships

Studies of the relationships between pattern of landscape boundaries and ecological processes will be most useful if site specific information can be extrapolated to broad geographic regions. Previous studies in percolation theory provide a basis for generating rules for extrapolating measurements across broad spatial scales. For instance, the theory for determining scaling relationships near the critical threshold, p_c, is well established for infinite percolation networks (see Ohtsuki and Keyes 1988, Voss et al. 1982, Margolina et al. 1984). These authors have shown that the time, t, required to move across a two-dimensional percolation network scales approximately as $t \quad m^d$, where m is the linear dimension (extent) of the map and d is the fractal exponent relating space to time [see arguments presented by Stauffer (1987) justifying this use of a fractal dimension]. The exponent, d, can be experimentally determined for any percolation model by simulating movement from the center of a map of size m, and measuring the time, t, necessary for the organisms to reach the map edge and then calculating d as $[\ln(t) / \ln(m)]$.

A series of Monte Carlo simulations of the disturbance model (Turner et al. 1989) was performed to determine scaling relationships for maps which differ in grain (the size of the individual site) and extent (m). Results show that d varies as a function of p, the fraction of occupied sites, and i, the probability of spread of the disturbance (Fig. 4). The adjustment necessary to obtain the exact relationship for finite systems is: $t = 1/k_g\ (m/2)^d$, where k_g is the grain size of the map (linear dimension of an individual site) and m is the linear dimension of map. The division of m by 2 is necessary because the simulations were started in the center of the map. As an example, suppose that a 100 by 100 grid is placed over a landscape map with the scale of each grid unit equal to 10 m; the grain of the map, k_g, is equal to the length of each grid unit and the total extent of the map, m, is then 1000 m (100 X 10 m). Thus, for this example the time, t, to reach the map boundary will scale as $1/10\ (1000/2)d$.

Figure 4 indicates that critical phenomena occur as a function of the product of p and i. When $(p * i) = 1.0$, then $d = 1.0$, and results scale as a direct function of the extent of the map. When $(p * i) < p_c$, then the landscape pattern prevents disturbance from spreading (note the break in the curve for values of $p * i$ near 0.6). Because uncertainties are largest near the critical threshold, the disturbance parameter, i, is best estimated when $(p * i)$ is greater than p_c. If $d = 1.0$ then $(p * i)$ must also equal 1.0, but when $d > 1.0$ and p is known, then values of i can be estimated independently of the grain and extent of the map. Similar methods can be devised for extrapolating predictions on the spread of species (e.g., **%site**, Table 1) as a function of the grain and extent of the map.

DISCUSSION

Understanding the relationships between landscape boundaries and ecological processes is necessary for advancing ecological theory (Hansen et al. 1988), managing preserves (Noss 1983, Quinn and Harrison 1988), and understanding the spread of disturbance (Turner et al. 1989). The simulation of interactions between disturbance and landscape pattern shows that sudden changes in the number and shape of boundaries may occur (i.e., $\underline{p} = 0.6$ and $\underline{i} = 0.5$, Fig. 3). Although our results are based on arbitrarily selected parameter values, the existence of critical phenomena are a general property of flow through heterogeneous media (Stauffer 1985). Therefore, differences in the characteristics of flow (i.e., different types of species or disturbances, Table 1) do not affect the generality of the results, but rather define the temporal and spatial scales at which critical phenomena may be observed. For instance, species that are able to distribute their progeny over a large region will not be affected by landscape heterogeneity below the scale set by the average dispersal distance (Gardner et al. in press), but will show critical changes in flows at very broad spatial scales.

The existence of critical thresholds is dependent on both the spatial pattern and the process of flow. Because the rate of flow can change suddenly at the critical threshold, it is difficult to extrapolate fine-grained observations to broader spatial areas. However, methods developed from percolation theory provide a quantitative basis for measuring and extrapolating results across spatial scales. We have illustrated the utility of this approach for extrapolation as a simple function of the grain and extent of the map (Fig. 4). Because this extrapolation process is based on empirical information, it provides a convenient means for comparing processes at many spatial scales. It has been shown that the general properties of random landscapes compare favorably with simulations based on actual landscape data (Gardner et al. 1987, Gardner et al. in press), indicating that these methods can also be applied to structured (i.e., nonrandom) systems.

Further developments in spatial modeling will be useful for understanding the process of flow and the role of ecotones. The results presented here have concentrated on impenetrable boundaries, but organisms respond to edges in a variety of ways. The effect of gradients that exist at boundaries, the variety of factors which affect growth and survival of competing species, and the spatial arrangement of multiple resources should be further explored. For instance, the effect of connectivity between similar habitat types can be examined by varying connectivity as a function of landscape characteristics and the behavior of organisms (see Fahrig and Paloheimo 1988, O'Neill et al. 1988). Simulations of this type may be important for identifying the potential response of organisms to changing landscape patterns.

The effect that relative distance (Meentemeyer and Box 1987) has on the spread of disturbance and species abundance should also be considered. Because relative distance metrics transform actual distances based on the unique spatial relationships of the system (e.g., for species that are dispersed by water, sites connected by streams are relatively closer than land-locked sites), it may be possible to use geographical and econometric methods to address the question "At what scale should diversity be measured and managed?" (Noss, 1983).

The availability of a general predictive theory for spatial systems is a prerequisite for interpreting the effect of landscape boundaries (and changes in landscape boundaries) on ecological systems. The numerical tools provided by percolation theory and the integration of these tools with data available from geographic information systems provides an exciting new area for investigating the effects of pattern and process. Because human activities are causing new environmental problems at local, regional and global scales, the need to understand, predict, and manage these problems is more urgent than ever.

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Table 1. Ten simulations each of a series of hypothetical populations. Each simulation was performed on a 100 by 100 percolation map with p (the fraction of suitable sites) of 0.6. Simulations were concluded when the population went extinct at all sites (no organisms left on the map) or movement has reached the map edge.

Population Number	Percolation parameters[a]			Simulation results[a]		
	i	e	h	%edge	t	%site
1	1.0	1.0	1.0	90	74.3	13.6
2	1.0	1.0	0.5	50	71.8	8.7
3	1.0	0.5	0.5	80	72.0	10.5
4	1.0	0.07	0.5	90	76.4	13.9
5	1.0	1.0	0.0	90	79.3	5.9
6	1.0	0.5	0.0	60	74.8	6.4
7	1.0	0.07	0.0	70	76.7	10.7
8	0.6	1.0	0.5	0	---	0.1
9	0.6	0.5	0.5	0	---	0.7
10	0.6	0.07	0.5	70	128.9	10.6
11	0.6	1.0	0.0	60	172.5	3.3
12	0.6	0.5	0.0	80	156.1	5.6
13	0.6	0.07	0.0	100	122.8	11.9

Table 1, continued

14	0.2	1.0	0.2	0	---	0.0
15	0.2	0.5	0.2	0	---	0.0
16	0.2	0.07	0.2	20	467.0	6.7
17	0.2	1.0	0.0	0	---	0.0
18	0.2	0.5	0.0	0	---	0.0
19	0.2	0.07	0.0	70	377.1	8.5

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[a] Parameters: i is the probability of colonizing adjacent sites; e is the probability of local population extinction; and h is the probability of a site being altered (i.e., resource depleted) by the population. Results: **%edge** is the percent of simulations that reached the edge of the map; t is the mean number of time steps to reach the edge; and **%site** is the mean percent of sites occupied or altered at the end of the simulation.

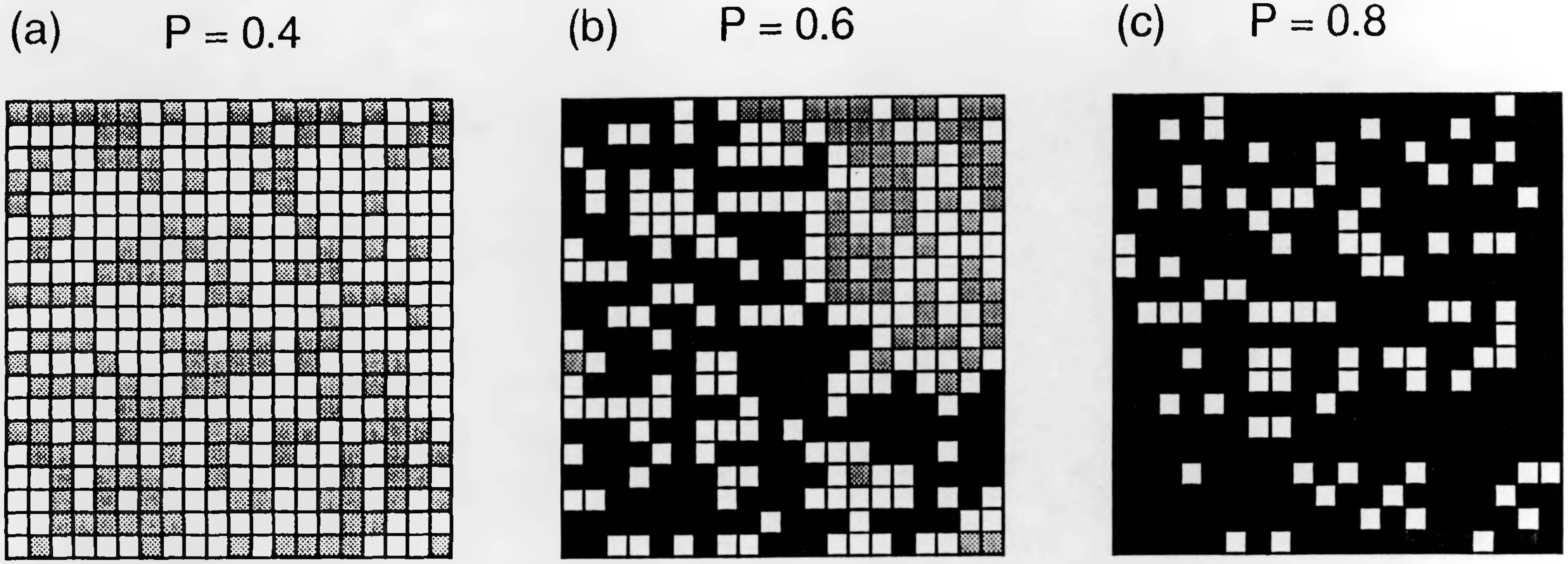
FIGURE LEGENDS

Figure 1: Example percolation maps of a 20 by 20 array. P is the fraction of the array occupied by grey or black sites. The percolating cluster is shown in black, and remaining occupied sites in grey.

Figure 2: The number of edges observed on a randomly generated map (linear dimension = 100) as a function of p, the fraction of sites occupied on the map. Edges are a unitless number found by counting the number of surfaces of occupied sites that are adjacent to an unoccupied 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 edges.

Figure 3: Habitat edge as a function of p, the fraction of habitat susceptible to disturbance, and the probability of disturbance spread. Each bar in the histogram represents the total edge on randomly generated maps (linear dimension = 100). The darker vs lighter portion of each bar indicates the amount of inner vs outer edge, respectively.

Figure 4: Changes in the critical exponent, d, for scaling predictions when p, the fraction of susceptible sites, and i, the probability of disturbance spread, are subject to variability. The scaling formula is: $t = 1/k_g\ (m/2)^d$, where k_g is the grain size of the map (linear dimension of each site) and m is the linear dimension of map.



No. of clusters: 49
Size of largest: 18

No. of clusters: 17
Size of largest: 163

No. of clusters: 1
Size of largest: 320

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Fig 1

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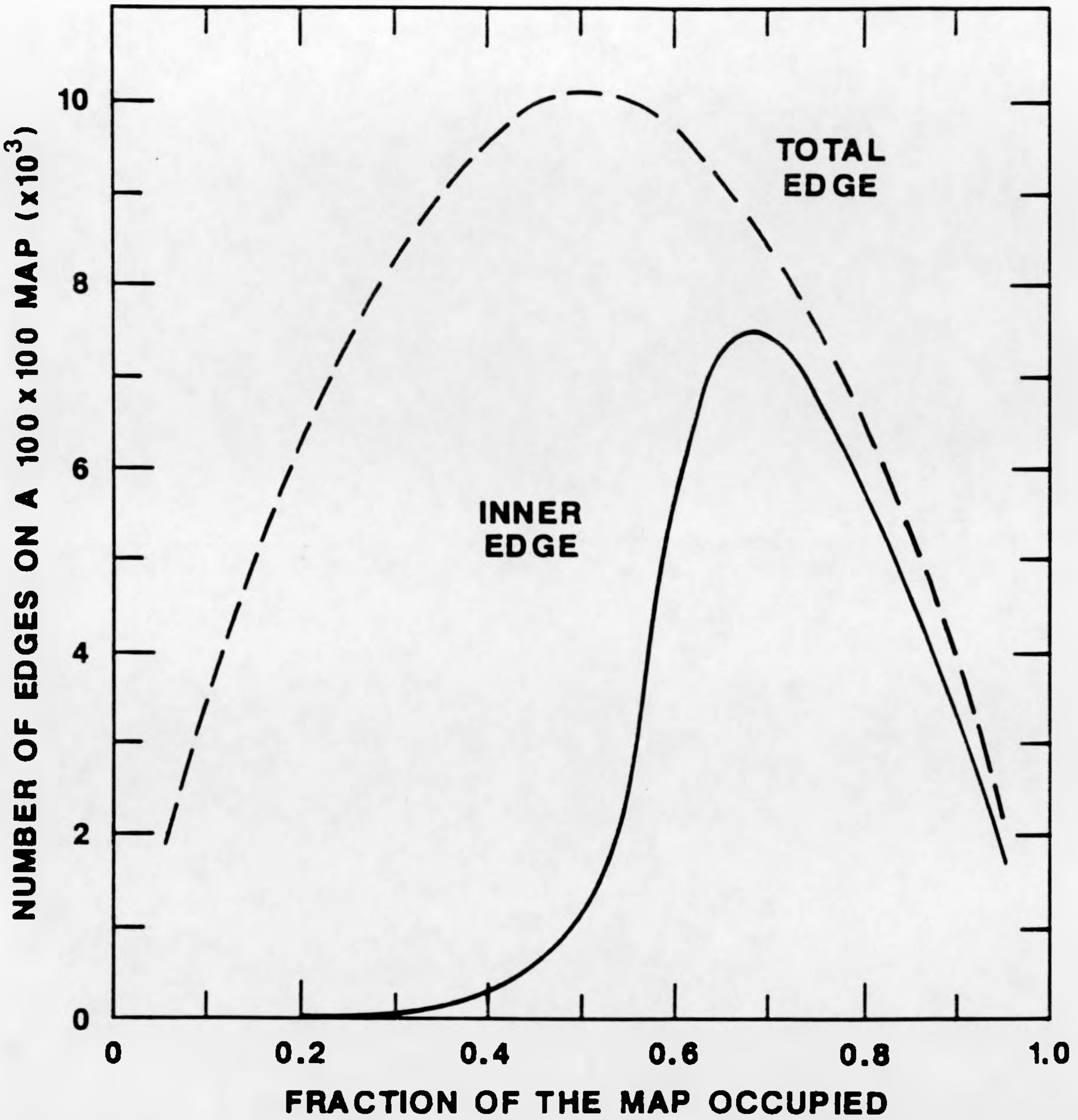

Gardner et al
Fig 2

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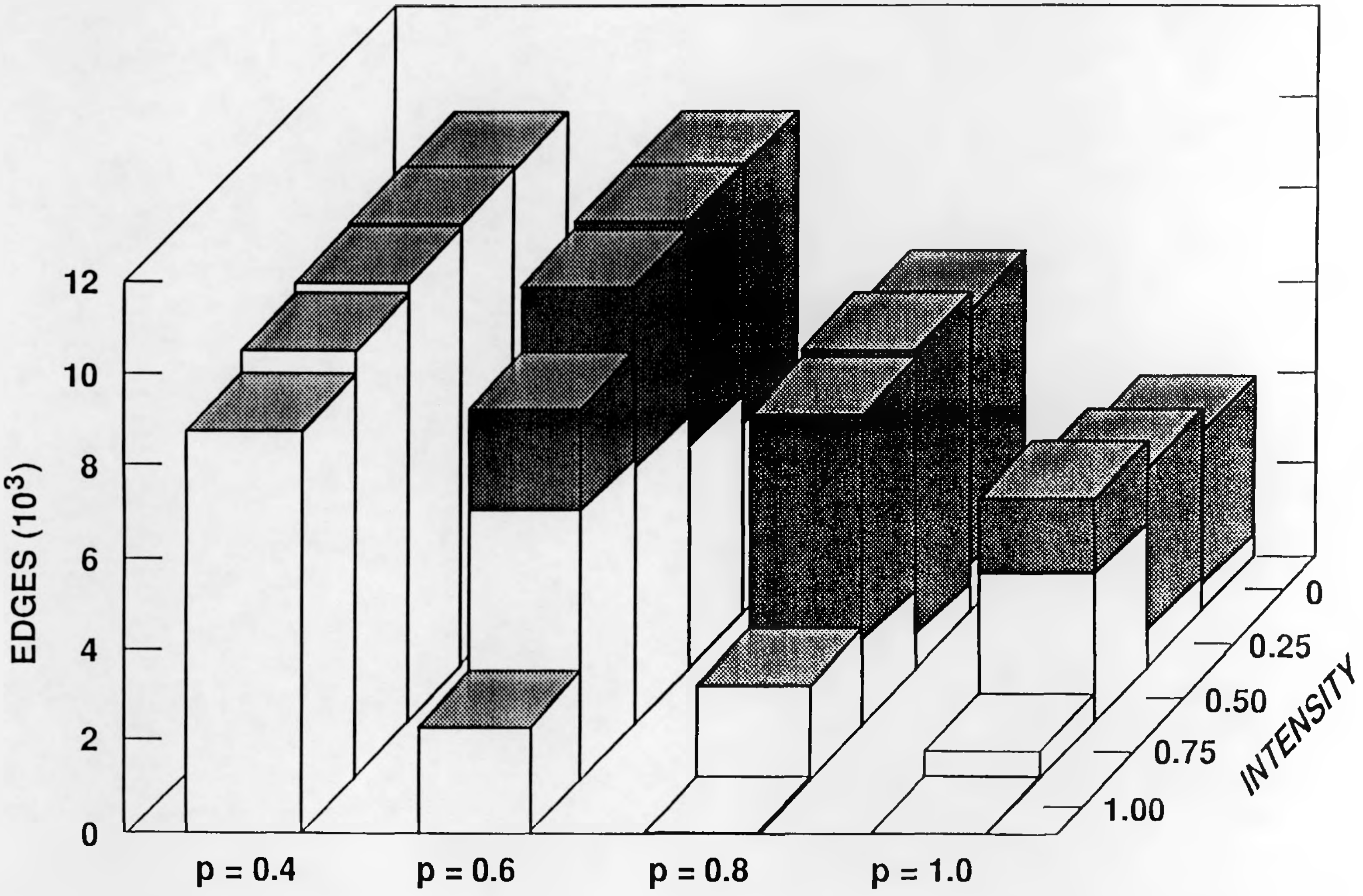

Goodman et al
Fig 3

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CRITICAL EXPONENT

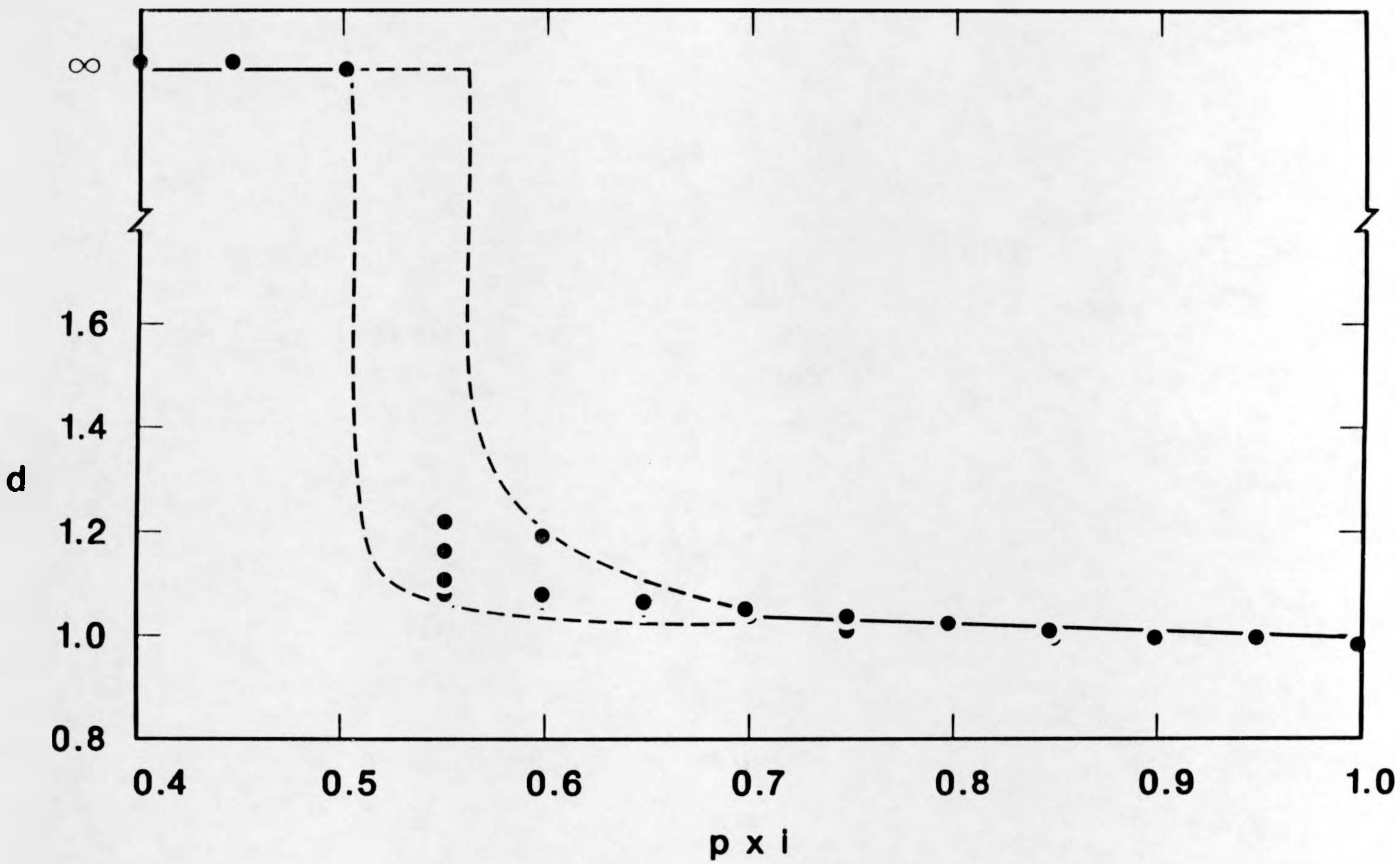

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Fig 4