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Author(s): Monica G. Turner, Robert H. Gardner, Virginia H. Dale, Robert V. O'Neill

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# Predicting the spread of disturbance across heterogeneous landscapes

Monica G. Turner, Robert H. Gardner, Virginia H. Dale and Robert V. O'Neill

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The expected pattern of disturbance propagation across a landscape was studied by using simple landscape models derived from percolation theory. The spread of disturbance was simulated as a function of the proportion of the landscape occupied by the disturbance-prone habitat and the frequency (probability of initiation) and intensity (probability of spread) of the habitat-specific disturbance. Disturbance effects were estimated from the proportion of habitat affected by the disturbance and changes in landscape structure (i.e., spatial patterns). Landscape structure was measured by the number of habitat clusters, the size and shape of the largest cluster, and the amount of edge in the landscape. Susceptible habitats that occupied less than 50% of the landscape were sensitive to disturbance frequency but showed little response to changes in disturbance intensity. Susceptible habitat that occupied more than 60% of the landscape were sensitive to disturbance intensity and less sensitive to disturbance frequency. These dominant habitats were also very easily fragmented by disturbances of moderate intensity and low frequency. Implications of these results for the management of disturbance-prone landscapes are discussed. The propagation of disturbance in heterogeneous landscapes depends on the structure of the landscape as well as the disturbance intensity and frequency.

*M. G. Turner, R. H. Gardner, V. H. Dale and R. V. O'Neill, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA.*

## Introduction

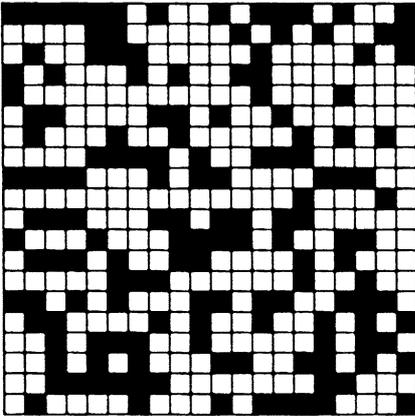
The effects of spatial heterogeneity on ecological processes at broad spatial scales are of current interest in ecological research (Risser et al. 1984, Wiens et al. 1985, Forman and Godron 1986, Risser 1987, Sala et al. 1988, Fahrig and Paloheimo 1988). The spread (i.e., propagation) of a disturbance across a landscape is an important example of a functional characteristic that is influenced by spatial heterogeneity (e.g., Romme 1982, Romme and Knight 1982, Turner 1987). Disturbance can be defined as “any relatively discrete event in time that disrupt ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (Pickett and White 1985). The general role of ecological disturbances has received considerable attention (e.g., White 1979, Barret and Ro-

senberg 1981, Mooney and Godron 1983, Sousa 1984, Pickett and White 1985, Rykiel 1985, Turner 1987), but few studies have been done on the relationship between landscape pattern and disturbance. Landscape heterogeneity may enhance (e.g., Turner and Bratton 1987, Franklin and Forman 1987) or retard (e.g., Knight 1987) the spread of disturbance, and disturbances may generate new landscape patterns (e.g., Pickett and White 1985, Remillard et al. 1987, Krummel et al. 1987). However, a general theory to predict the effects of spatial heterogeneity on disturbance propagation has not yet emerged. This paper presents a conceptual framework for studying the effect of landscape pattern on the spread of disturbance. Generalizations are then developed from simulation experiments based on percolation theory.

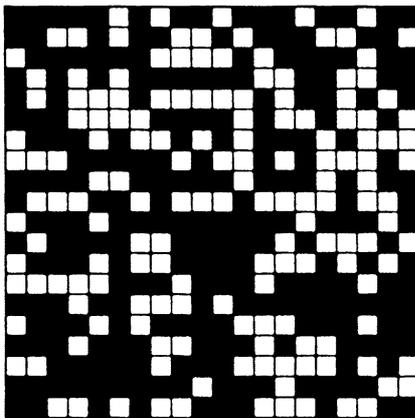
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$P = 0.4$



$P = 0.6$



$P = 0.8$

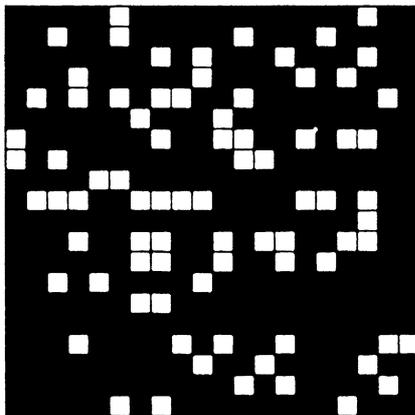


Fig. 1. Sample percolation maps with the probability of occurrence of disturbance-susceptible habitat,  $p$ , being 0.4, 0.6, and 0.8. The arrays depicted are  $20 \times 20$  portions of the  $100 \times 100$  arrays used in this study. The dark areas are habitats susceptible to the disturbance, and the white regions are not susceptible.

### Conceptual framework

It is useful to distinguish two types of disturbances: (1) those that spread *within* the same cover type (e.g., the spread of a species-specific parasite through a forest); and (2) those that cross ecosystem boundaries and spread *between* different cover types (e.g., fire spreading from a field to a forest). Whether landscape heterogeneity enhances or retards the spread of disturbance may depend on which of these two modes of propagation is dominant. If the disturbance is likely to propagate *within* a community, high landscape heterogeneity should retard the spread of the disturbance. If the disturbance is likely to move *between* communities, increased landscape heterogeneity should enhance the spread of disturbance. Furthermore, the rate of disturbance propagation should be directly proportional to landscape heterogeneity for disturbances that spread *between* communities, but inversely proportional for disturbances that spread *within* the same community.

The movement of disturbances across landscapes can be studied within the framework of percolation theory (Stauffer 1985, Orbach 1986, Gardner et al. 1987). Percolation theoretic methods provide a means of generating and analyzing patterns of two-dimensional arrays, which are similar to maps of landscape patterns. These random maps can be used to generate an expected pattern in the absence of specific processes and thereby identify landscape-dependent departures from expected patterns. A two-dimensional percolating network within an  $m$  by  $m$  array is formed by randomly choosing the occupation of the  $m^2$  sites with probability  $p$ . For large arrays,  $pm^2$  sites are occupied while  $(1-p)m^2$  sites are empty (Fig. 1). A cluster is formed by a group of occupied sites that have at least one common edge along the vertical and horizontal directions of a square lattice but not along the diagonals. The number, size, and shape of clusters of occupied sites change as a function of  $p$ . Cluster characteristics change most rapidly near the critical probability,  $p_c$ , which is the probability at which the largest cluster "percolates" or connects the grid continuously from one side to the other ( $p_c = 0.5928$  for very large arrays). On large grids, the shape of the largest cluster, as measured by the fractal dimension (Mandelbrot 1977, 1983), has also been shown to be affected by  $p$ . Percolation maps at finite scales ( $m = 50$  to 400), similar to the spatial scales common in landscape analyses, have been characterized in terms of cluster size, fractal dimension, and edges (Gardner et al. 1987).

The simple nature and properties of percolation arrays make them particularly useful for landscape studies. A landscape can be characterized in terms of habitat that is susceptible to a particular disturbance (e.g., pine forests susceptible to bark beetle infestations) and habitat that is not susceptible to the disturbance (e.g., hardwood forests, grasslands). The spatial arrangement of the disturbance-susceptible habitat can be randomly generated at probability  $p$  on an appropriately scaled

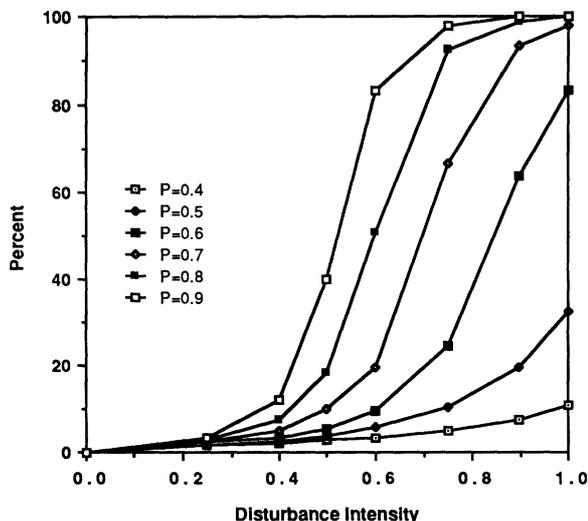


Fig. 2. Mean ( $n = 10$ ) percent of susceptible habitat affected by disturbance of different intensities in landscapes with different initial probabilities of occurrence ( $p$ ) of susceptible habitat.

percolation map, and the propagation of disturbances that spread within the susceptible habitat may then be studied.

Ecological disturbance regimes can be described by a variety of characteristics, including spatial distribution, frequency, return interval, rotation period, predictability, area, intensity, severity, and synergism (e.g., White and Pickett 1985, Rykiel 1985). This study focuses on two disturbance characteristics, intensity and frequency, as they interact with landscape pattern. We define disturbance frequency as the probability that a new disturbance will be initiated in a unit of susceptible habitat during the time period represented by the simulation. Intensity is defined as the probability that the disturbance, once initiated, will spread to adjacent sites of the same habitat. We predict the spread of a disturbance across a landscape as a function of (1) the proportion of the landscape occupied by the disturbance-prone cover type, (2) disturbance intensity, and (3) disturbance frequency.

### Methods

Two-dimensional landscape maps ( $100 \times 100$ ) were randomly generated for the disturbance-susceptible habitat at different values of  $p$ . The probability,  $p$ , for maps this large represents the proportion of a landscape occupied by a susceptible habitat. The remainder of the landscape is considered unsuitable for propagation of the simulated disturbance. Thus, the maps are composed of 10,000 cells, each of which is randomly designated as suitable or unsuitable for a disturbance. A disturbance that could propagate through the habitat was character-

ized by frequency and intensity. Disturbance frequency,  $f$ , is the probability that a new 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 storm event or time period). Disturbance intensity,  $i$ , is defined as the probability that the disturbance, once initiated, will spread to adjacent sites of the same habitat (e.g., the probability of fire or a pathogen spreading to an adjacent site of susceptible forest). In the first set of simulations, disturbance frequency was set at  $f = 0.01$  and was not varied; the actual number of discrete disturbances per simulation is given by  $fpm^2$ . Ten replicates were simulated for each paired combination of distur-

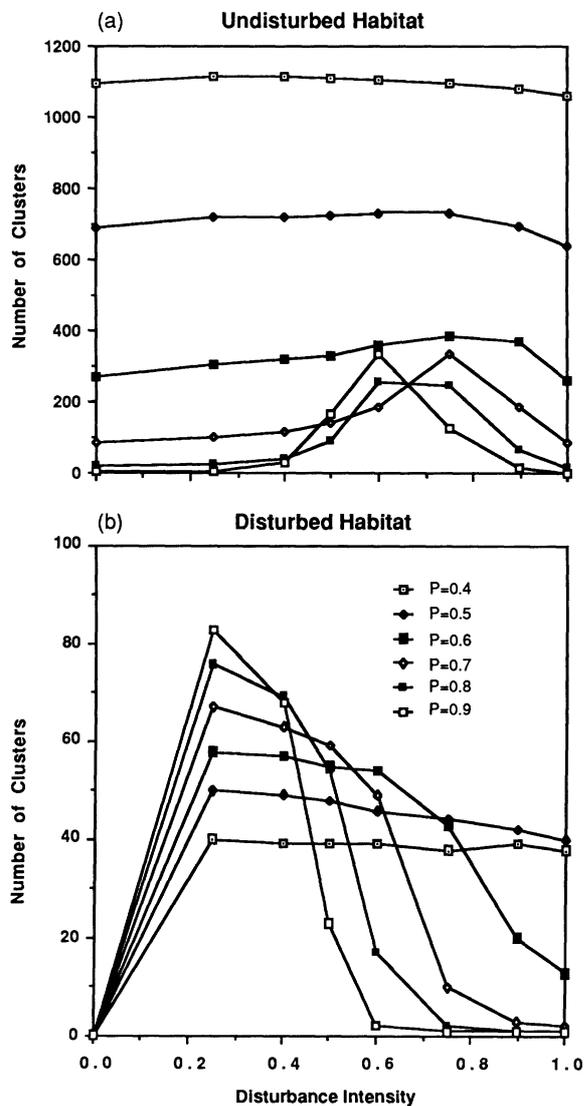


Fig. 3. Mean ( $n = 10$ ) number of clusters remaining of undisturbed habitat (a) and disturbed habitat (b) after simulating the propagation of disturbances of varying intensities ( $i$ ) through landscapes with different initial probabilities of occurrence ( $p$ ) of susceptible habitat.

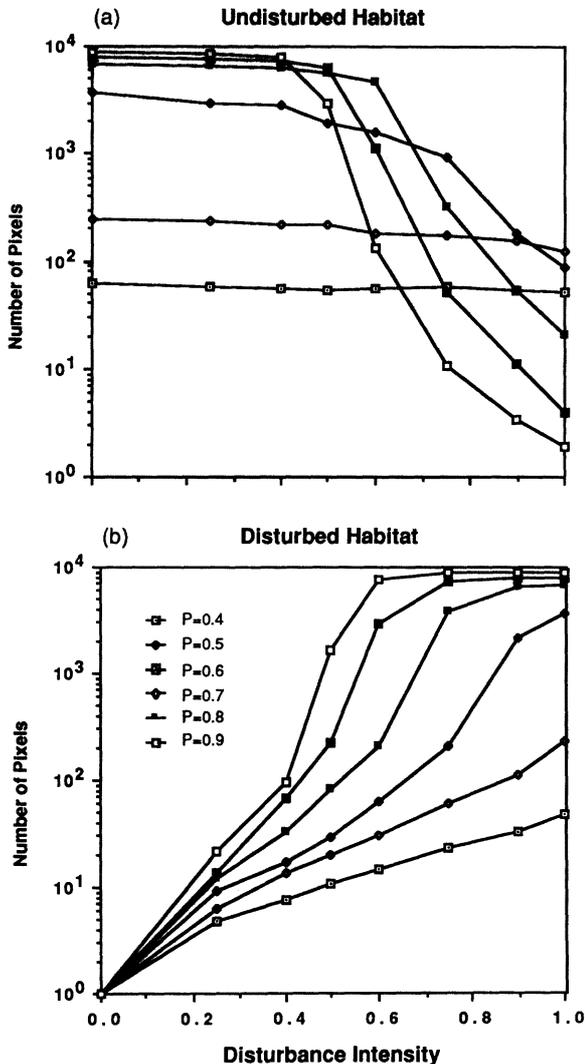


Fig. 4. Mean ( $n = 10$ ) size of the largest remaining cluster of undisturbed habitat (a) and disturbed habitat (b) after simulating the propagation of disturbances of varying intensities ( $i$ ) through landscapes with different initial probabilities of occurrence ( $p$ ) of susceptible habitat.

ance intensity ( $i = 0.25, 0.4, 0.5, 0.6, 0.75, 0.9$ , and  $1.0$ ) and  $p$  ( $p = 0.4, 0.5, 0.6, 0.7, 0.8$ , and  $0.9$ ). In the second set of simulations, disturbance frequency was simulated at three levels ( $f = 0.01, 0.10$ , and  $0.50$ ). For each frequency level, ten replicates were simulated for paired combinations of disturbance intensity ( $i = 0.25, 0.50, 0.75$ ) and  $p$  ( $p = 0.4$  and  $0.8$ ).

The number of clusters, the size and shape of the largest cluster, and the amount of edge in the landscape were calculated for each landscape before disturbances began. Landscape disturbance was then simulated as follows. Sites were randomly disturbed at a given frequency until exactly  $fpm^2$  disturbances were initiated. Each disturbed cell was changed to a state that was no longer vulnerable to disturbance. The disturbance was

then randomly propagated with an intensity,  $i$ , to an adjacent disturbance-prone cell. The process was repeated until the disturbance could not spread any farther. The disturbed landscape was then analyzed, and the number, sizes and shapes of clusters of the disturbed habitat and of the remaining undisturbed habitat were summarized.

## Results

### Disturbance intensity

The proportion of the available habitat that was disturbed varied with both  $i$  and  $p$  (Fig. 2). A greater proportion of habitat was affected at the same disturbance intensity for high values of  $p$  than for low values. The percent of available habitat affected by a disturbance increased rapidly above the percolation threshold,  $p_c$ , when the largest cluster could span the entire map. When the habitat susceptible to disturbance was rare (e.g.,  $p = 0.4$ ), less than 20% of the habitat was disturbed, even when the intensity of the disturbance reached 1.0. When the susceptible habitat was common (e.g.,  $p = 0.8$ ), a relatively low disturbance intensity led to the widespread propagation of the disturbance.

The number of clusters of undisturbed habitat also varied with  $p$  and  $i$  (Fig. 3). For cover types below the percolation threshold (e.g.,  $p = 0.4$  and  $0.5$ ), the amount of undisturbed habitat remained relatively high, showing little change in the number of clusters as disturbance intensity increased (Fig. 3a). Above the percolation threshold (e.g.,  $p > 0.6$ ), the number of remaining clusters increased with moderate disturbance intensities and then declined (Fig. 3a). For example, for  $p$

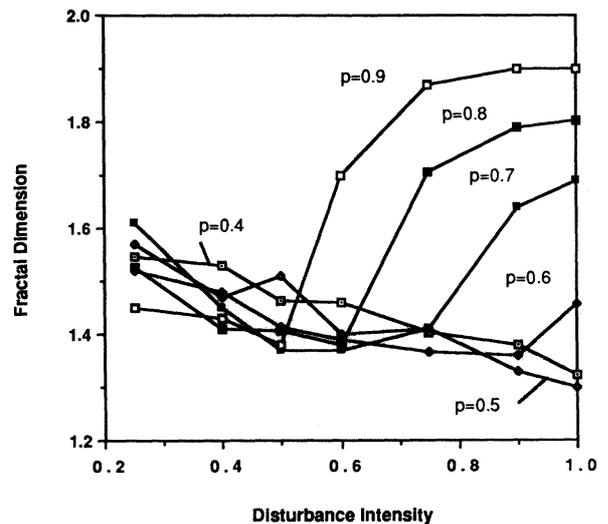


Fig. 5. Mean ( $n = 10$ ) fractal dimension of the largest cluster of disturbed habitat as a function of disturbance intensity ( $i$ ) in landscapes with different initial probabilities of occurrence ( $p$ ) of susceptible habitat.

Tab. 1. Mean number ( $n = 10$ ) of inner and outer edges in undisturbed and disturbed habitat by  $p$  and disturbances intensity ( $i$ ). Simulated landscapes are  $100 \times 100$  arrays.

Disturbance intensity ( $i$ )	Undisturbed habitat		Disturbed habitat	
	Inner edge	Outer edge	Inner edge	Outer edge
			$p = 0.4$	
0.00	176	9533	0	0
0.25	153	9491	0	205
0.50	151	9403	0	286
0.75	153	9193	6	438
1.00	131	8735	46	812
			$p = 0.6$	
0.00	5731	3998	0	0
0.25	5080	4670	0	354
0.50	4042	5500	9	650
0.75	2193	5856	421	1806
1.00	148	2175	5240	2157
			$p = 0.8$	
0.00	5961	662	0	0
0.25	6172	713	0	558
0.50	5219	1489	202	1745
0.75	29	1970	5514	755
1.00	0	71	5992	583

= 0.9 the peak in the number of clusters occurs between  $i = 0.5$  and  $i = 0.75$ .

The number of clusters of disturbed habitat also differed for habitats below and above  $p_c$  (Fig. 3b). Below  $p_c$ , the number of disturbed clusters showed little change with disturbance intensity. Above  $p_c$ , low disturbance intensity created many clusters; the number of disturbed clusters then declined as  $i$  increased (Fig. 3b). This decline was most rapid in landscapes with high values of  $p$ .

The size of the largest cluster was also influenced by  $i$  and  $p$ , with qualitative differences above and below  $p_c$  (Fig. 4a). Largest cluster size was not affected by disturbances of any intensity below  $p_c$ . Above  $p_c$ , the size of the largest undisturbed cluster decreased rapidly when  $i > 0.5$  (Fig. 4a). The decline was sharpest for the highest values of  $p$ . The size of the largest disturbed cluster increased with both  $i$  and  $p$  (Fig. 4b). The maximum cluster size was approached asymptotically with increasing disturbance intensity at high  $p$ , whereas cluster size appeared to increase linearly at low values of  $p$ .

The largest disturbed cluster tended to be simple in shape, as measured by the fractal dimension, when the disturbance-susceptible habitat was rare (Fig. 5). The fractal dimension of the disturbed cluster also tended to decrease (indicating less complexity) as  $i$  increased in these rare habitats. In contrast, the shape of the largest cluster of disturbed habitat tended to become complex when disturbance intensity was moderate to high ( $i \geq 0.6$ ) and the disturbance-susceptible habitat was common ( $p > 0.6$ ) (Fig. 5).

Prior to disturbance, the relative amount of outer edge (e.g., perimeter) and inner edge (e.g., interior gaps) is a function of  $p$  (Gardner et al. 1987). For  $p < p_c$ , outer edges dominate; for  $p > p_c$ , inner edges

dominate. Disturbances of low intensity ( $i \leq 0.5$ ) tend to decrease the number of inner edges in an undisturbed habitat that is rare or moderately common ( $p < 0.8$ ), but they increase the inner edges for  $p \geq 0.8$  (Tab. 1). Disturbances of high intensity ( $i > 0.5$ ) cause both the inner and outer edges of undisturbed habitats to decline for all values of  $p$ . Clusters of disturbed habitat resulting from low-intensity disturbance contain more outer edges than inner edges for all values of  $p$ . Clusters of disturbed habitat resulting from high-intensity disturbance respond differently in landscapes with different  $p$  values (Tab. 1). For  $p < p_c$ , outer edges continue to exceed inner edges, even with  $i = 1.0$ . For  $p > p_c$ , however, inner edges exceed outer edges.

The reversal in the relative importance of inner and outer edges (Fig. 6) at certain combinations of  $p$  and  $i$  indicates qualitative changes in the habitat. For  $p < p_c$ , outer edges exceed inner edges in both the undisturbed and disturbed habitats. For  $p \geq p_c$ , a qualitative change is observed. The undisturbed habitat initially has more inner edges, but a disturbance of moderate to high intensity ( $i \geq 0.5$ ) causes outer edges to dominate. When this switch occurs, the habitat changes from being highly connected with interior patches of other habitats to being fragmented. The disturbed habitat, in contrast, begins as small isolated patches at low disturbance intensities ( $i < 0.5$ ), but the disturbed patches coalesce to form connected patches with internal holes at higher disturbance intensities. The disturbance intensity required to effect this shift decreases as  $p$  increases.

#### Disturbance frequency

The proportion of habitat affected by disturbance was influenced by disturbance frequency but varied for

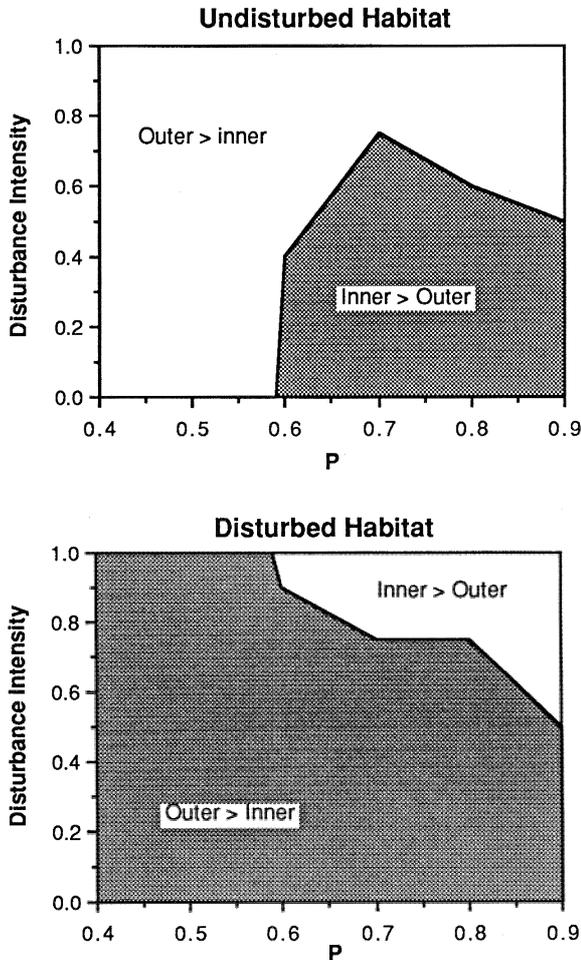


Fig. 6. The combination of disturbance intensity ( $i$ ) and initial probability of occurrence of susceptible habitat ( $p$ ) at which there is a reversal in the relative importance of inner and outer edges in undisturbed and disturbed habitats. Reversals indicate a qualitative change in the landscape structure.

landscapes above and below  $p_c$  (Fig. 7). For example, when  $p = 0.4$ , an increase in frequency causes a substantial increase in the proportion of habitat affected, even when intensity is low (Fig. 7a). When  $p = 0.8$ , increasing frequency increases the amount of habitat affected only when intensity is low (Fig. 7b). If intensity is sufficiently high (e.g.,  $i = 0.75$ ), more than 90% of the habitat can be affected by disturbance of very low frequency.

The number of clusters of both disturbed and undisturbed habitats is influenced more by disturbance frequency than by disturbance intensity for  $p < p_c$  (Fig. 8). High disturbance frequencies result in an increase of disturbed clusters, even when intensity is low. The number of undisturbed clusters is not affected by low frequency disturbances, but decreases sharply with high frequency. For  $p > p_c$ , the numbers of clusters of dis-

turbed and undisturbed habitats peak when both frequency and intensity are at intermediate levels (e.g.,  $f = 0.1$ ,  $i = 0.25$ ,  $0.50$ ). The number of clusters declines as  $f$  and  $i$  increase.

When  $p = 0.4$ , the size of the largest undisturbed cluster is not altered by disturbances of low frequency but decreases with disturbances of high frequency (Fig. 9). When  $p = 0.8$ , cluster size decreases with both intensity and frequency. The size of the largest disturbed cluster increases with disturbance frequency when  $p = 0.4$ , but increases with disturbance intensity when  $p = 0.8$ .

## Discussion

The simulation results indicate that the propagation of disturbance and the associated effects on landscape pat-

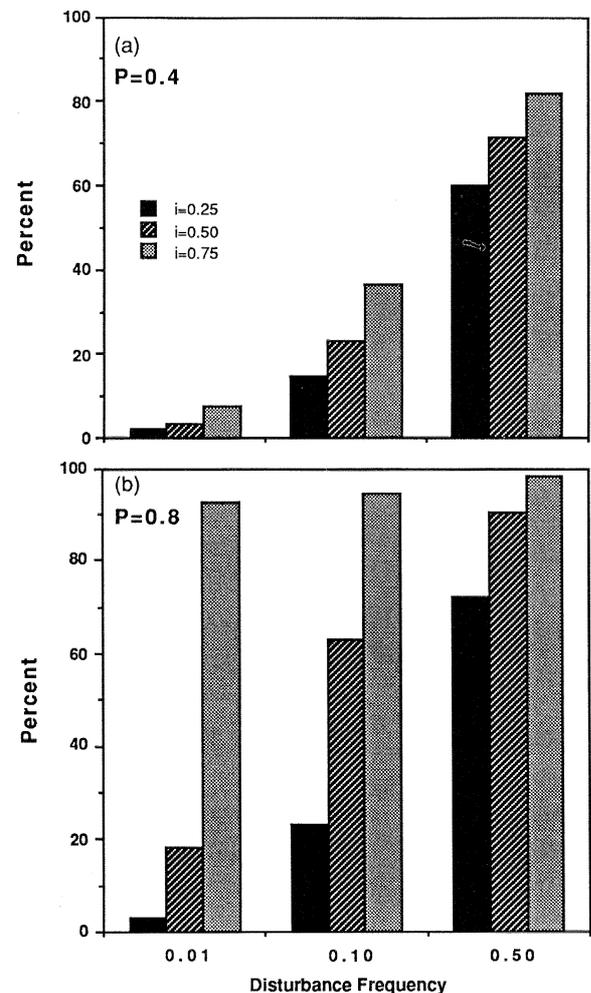


Fig. 7. The percent of habitat disturbed as a function of both disturbance intensity and disturbance frequency for initial probabilities ( $p$ ) of occurrence of susceptible habitat of  $p < p_c$  (a) and  $p > p_c$  (b).

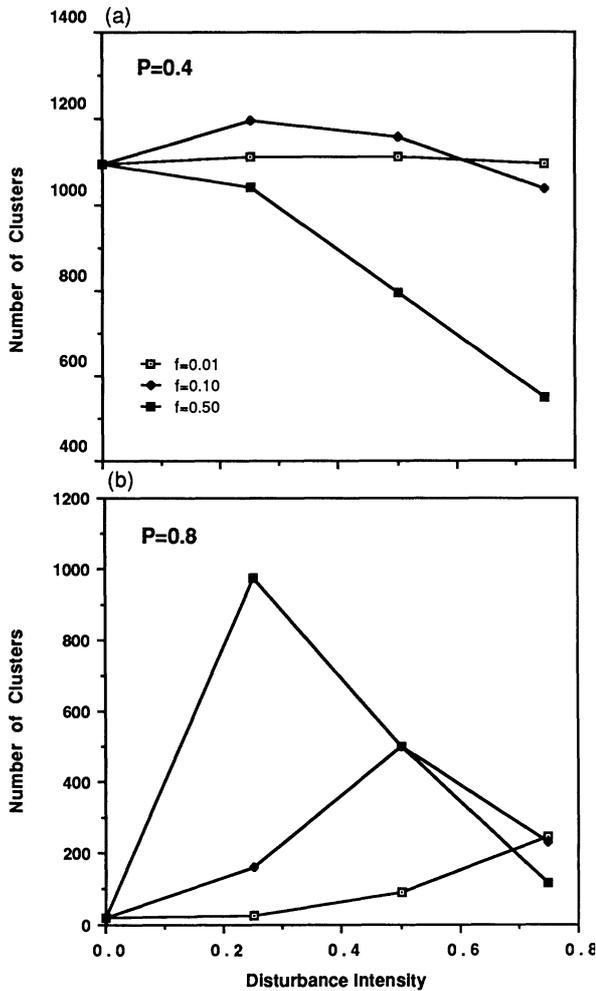


Fig. 8. Number of clusters of undisturbed habitat for low and high frequency disturbances for initial probabilities ( $p$ ) of occurrence of susceptible habitat of  $p < p_c$  (a) and  $p > p_c$  (b).

tern are qualitatively different when the proportion ( $p$ ) of the landscape occupied by disturbance-susceptible habitat is above or below the percolation threshold ( $p_c$ ). Both the distribution and spatial arrangement of the susceptible habitats help explain these differences. Habitats occupying less than  $p_c$  tend to be fragmented, with numerous small patches and low connectivity (Gardner et al. 1987). The propagation of a disturbance is constrained by this fragmented spatial pattern, and the sizes and numbers of clusters are not substantially affected by disturbance intensity ( $i$ ), the probability of spread. Habitats occupying more than  $p_c$  tend to be highly connected, forming continuous clusters (Gardner et al. 1987). Disturbance can spread through the landscape even when frequency is relatively low.

The persistence of rare habitats ( $p < p_c$ ) that are susceptible to disturbance appears to depend upon disturbance frequency ( $f$ ) (Tab. 2). The long-term viability of remnant forest stands or other dispersed patches of

rare communities (e.g., cedar barrens, granite outcrops) in a landscape may therefore depend on the number of disturbances rather than on their intensity. A locally intense disturbance may eliminate a cluster of habitat, but have little effect on the persistence of that habitat in the landscape. In contrast, a large number of disturbances of low intensity over a large region could reduce or eliminate the habitat.

Habitats that are common may be easily fragmented by disturbances of only low to moderate intensity. Intermediate levels of disturbance intensity and frequency created greater patchiness in landscapes that were dominated by a disturbance-prone habitat (Tab. 2). The interaction among  $p$ ,  $i$ , and  $f$  may thus affect the landscape in ways that are counterintuitive. Large tracts of forest, for example, may be fragmented by disturbances of relatively low frequency (e.g., Franklin and Forman 1987). Structural changes associated with this fragmen-

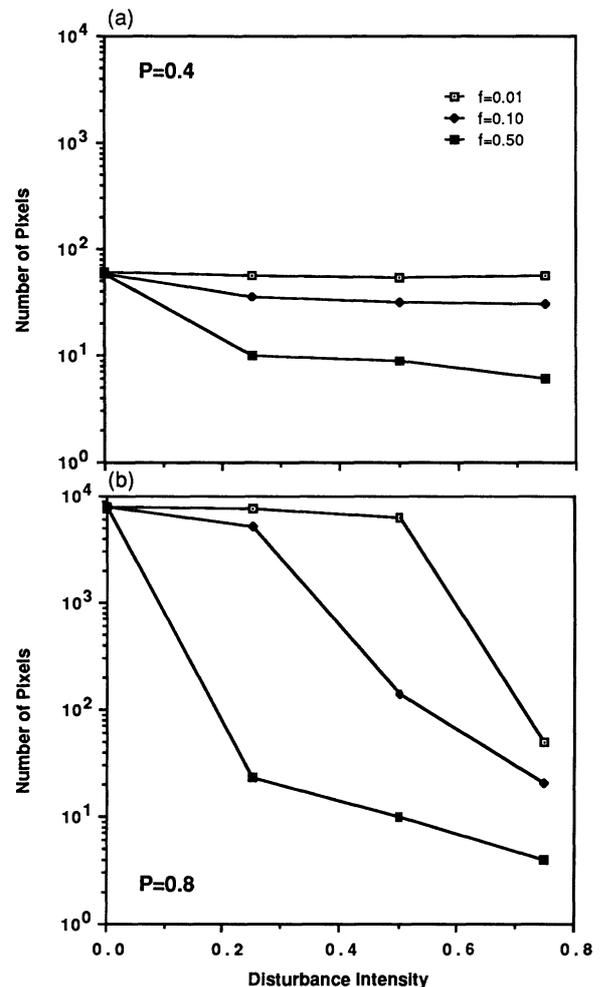


Fig. 9. Size of the largest cluster of undisturbed habitat for low and high frequency disturbances for initial probabilities ( $p$ ) of occurrence of susceptible habitat of  $p < p_c$  (a) and  $p > p_c$  (b).

Tab. 2. Summary of landscape structure in response to the spread of a disturbance.

Susceptible habitat	Parameter		Response	
	intensity	frequency	Area of habitat affected	Comments
Rare	Low	Low	<5%	Little structural change
Rare	Low	High	55–75%	Number of clusters decreases in undisturbed habitat but increases in disturbed habitat; size of largest cluster decreases in undisturbed habitat but increases in disturbed habitat
Rare	High	Low	<5%	Little structural change
Rare	High	High	75–95%	Number of clusters declines sharply in undisturbed habitat but increases sharply in disturbed habitat; size of largest cluster decreases in undisturbed habitat and increases in disturbed habitat
Common	Low	Low	<5%	Little structural change, but edges increase slightly
Common	Low	High	>50%	Undisturbed habitat is fragmented into a large number of clusters; edges increase
Common	Moderate	Low	<50%	Number of clusters of disturbed and undisturbed habitat increase; size of largest cluster of undisturbed habitat declines slightly; edges increase
Common	Moderate	High	>80%	Structure of the disturbed habitat approaches initial structure of the undisturbed habitat
Common	High	Low	>95%	Initial structure of the undisturbed habitat becomes the structure of the disturbed habitat
Common	High	High	>95%	Initial structure of the undisturbed habitat becomes the structure of the disturbed habitat

tation, such as the increased number of edges, have important implications for the susceptibility to other disturbances (e.g., windthrow) and for the distribution and abundance of species.

The results of these disturbance simulations have implications for the management of disturbance-prone landscapes. If a habitat type is rare, management should focus on the frequency of disturbance initiation. Disturbances with low frequencies will have little impact, even at high intensities of disturbance propagation, because there is insufficient landscape connectivity (Tab. 2). Therefore, new disturbances will tend to be contained by the landscape structure. In contrast, high frequencies of disturbance initiation can substantially change landscape structure (Tab. 2). If a habitat type is common, management must consider both frequency and intensity. The effects of disturbance can be predicted at the extreme ends of the ranges of frequency and intensity (Tab. 2). Disturbances of low intensity and low frequency will have little effect, whereas disturbances of high intensity will cause substantial changes. At intermediate levels of intensity, however, responses can be quite complicated and more difficult to predict. A common habitat type can be easily fragmented and qualitatively changed by disturbances of low to moderate intensity and low to high frequency.

Relationships between pattern and process can be inferred from significant departures from an expected pattern generated in the absence of specific ecological process. This type of expected pattern has been termed

a “neutral model” (Caswell 1976). We have used percolation theory as a neutral model to suggest that knowledge of a few parameters describing the heterogeneity of the landscape and the propagation of disturbance may provide useful information for estimating the expected landscape effects. However, the structure of habitats within real landscapes differs from a random distribution, and contagion between cells of the same habitat is greater than expected at random (Gardner et al. 1987). Similarly,  $p$ ,  $i$ , and  $f$  were all varied independently in our simulations, whereas these variables are likely to be correlated in real landscapes. For example, some disturbances (e.g., fire) exhibit an inverse relationship between intensity and frequency, whereas anthropogenic disturbances (e.g., land clearing for urbanization; clear-cutting) tend toward both high intensities and high frequencies. Our neutral model can be compared to data from actual landscapes to test for the importance of such relationships. Disturbance effects on real landscapes might be observed at lower intensities than in the random landscapes, because greater connectivity is observed in actual landscapes. A combined approach of modeling and empirical study could lead to a predictive theory of the spread of ecological disturbances.

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## References

- Barrett, G. W. and Rosenberg, R. (eds) 1981. Stress effects on natural ecosystems. – Wiley, New York.
- Caswell, H. 1976. Community structure: a neutral model analysis. – *Ecol. Monogr.* 46: 327–354.
- Fahrig, L. and Paloheimo, J. 1988. Effect of spatial arrangement of habitat patches on local population size. – *Ecology* 69: 468–475.
- Forman, R. T. T. and Godron, M. 1986. Landscape ecology. – Wiley, New York.
- Franklin, J. F. and Forman, R. T. T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. – *Landscape Ecol.* 1: 5–18.
- Gardner, R. H., Milne, B. T., Turner, M. G. and O'Neill, R. V. 1987. Natural models for the analysis of broad-scale landscape pattern. – *Landscape Ecol.* 1: 19–28.
- Knight, D. H. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. – In: Turner, M. G. (ed.), *Landscape heterogeneity and disturbance*. Springer, New York, pp. 59–83.
- Krummel, J. R., Gardner, R. H., Sugihara, G., O'Neill, R. V. and Coleman, P. R. 1987. Landscape patterns in a disturbed environment. – *Oikos* 48: 321–324.
- Mandelbrot, B. B. 1977. *Fractals: form, chance, and dimension*. – Freeman, San Francisco.
- 1983. *The fractal geometry of nature*. – Freeman, New York.
- Mooney, H. A. and Godron, M. (eds) 1983. *Disturbance and ecosystems*. – Springer, New York.
- Orbach, R. 1986. Dynamics of fractal networks. – *Science* 231: 814–819.
- Pickett, S. T. A. and White, P. S. (eds) 1985. *The ecology of natural disturbance and patch dynamics*. – Academic Press, New York.
- Remillard, M. M., Gruending, G. K. and Bogucki, D. J. 1987. Disturbance by beaver (*Castor canadensis* Kuhl) and increased landscape heterogeneity. – In: Turner, M. G. (ed.), *Landscape heterogeneity and disturbance*. Springer, New York, pp. 103–122.
- Risser, P. G. 1987. Landscape ecology: state-of-the-art. – In: Turner, M. G. (ed.), *Landscape heterogeneity and disturbance*. Springer, New York, pp. 3–14.
- , Karr, J. R. and Forman, R. T. T. 1984. *Landscape ecology: directions and approaches*. – Special Publ. No. 2. Illinois Natural History Survey, Champaign, IL.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. – *Ecol. Monogr.* 52: 199–221.
- and Knight, D. H. 1982. Landscape diversity: the concept applied to Yellowstone Park. – *BioScience* 32: 664–670.
- Rykiel, E. J., Jr. 1985. Towards a definition of ecological disturbance. – *Aus. J. Ecol.* 10: 361–365.
- Sala, O. E., Parton, W. J., Joyce, L. A. and Lauenroth, W. K. 1988. Primary production of the central region of the United States. – *Ecology* 69: 40–45.
- Sousa, W. P. 1984. The role of disturbance in natural communities. – *Ann. Rev. Ecol. Syst.* 15: 353–391.
- Stauffer, D. 1985. *Introduction to percolation theory*. – Taylor and Francis, London.
- Turner, M. G. (ed.) 1987. *Landscape heterogeneity and disturbance*. – Springer, New York.
- and Bratton, S. P. 1987. Fire, grazing and the landscape heterogeneity of a Georgia barrier island. – In: Turner, M. G. (ed.), *Landscape heterogeneity and disturbance*. Springer, New York, pp. 85–101.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. – *Bot. Rev.* 45: 229–299.
- and Pickett, S. T. A. 1985. Natural disturbance and patch dynamics: an introduction. – In: Pickett, S. T. A. and White, P. S. (eds), *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, pp. 3–13.
- Wiens, J. A., Crawford, C. S. and Gosz, J. R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. – *Oikos* 45: 421–427.