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Epidemiology theory and disturbance spread on landscapes*

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Abstract

Epidemiology models, modified to include landscape pattern, are used to examine the relative importance of landscape geometry and disturbance dynamics in determining the spatial extent of a disturbance, such as a fire. The models indicate that, except for very small values for the probability of spread, a disturbance tends to propagate to all susceptible sites that can be reached. Therefore, spatial pattern, rather than disturbance dynamics, will ordinarily determine the total extent of a single disturbance event. The models also indicate that a single disturbance will seldom become endemic, *i.e.*, always present on the landscape. However, increasing disturbance frequency can lead to a landscape in which the proportion of susceptible, disturbed, and recovering sites are relatively constant.

Introduction

The role of disturbance has been an important topic in ecology during the past decade (*e.g.*, White 1979, Romme and Knight 1982, Mooney and Godron 1983, Pickett and White 1985, Turner 1987), but many questions remain regarding the dynamics of disturbance at the landscape scale. What factors enhance or retard disturbances spreading across a landscape? How do landscape geometry (*e.g.*, size, shape, and arrangement of susceptible habitats) and disturbance dynamics (*e.g.*, frequency and intensity) interact to control the total area affected by a disturbance? What conditions might produce an equilibrium landscape mosaic? In this paper we use epidemiology theory to address these questions.

Epidemiology models are designed to predict the spread of disease through a population (Bailey 1975). The analogy to an ecological disturbance, such as a forest fire, spreading across the landscape is obvious. However, the models must be modified to include aspects of spatial pattern of interest in landscape ecology.

The basic epidemiology model considers a well-mixed population in which each individual has an equal probability of being infected. To make the model suitable for landscape studies, the theory must be extended to two dimensions (Bailey 1965). Considerable work has been done on this problem, using simple versions of the model (Mollison 1977, Kuulasmaa 1982, Cardy 1983, Faddy 1986). Some studies have considered more complex spatial

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models but have emphasized population phenomena such as family groups (Ball 1985) or immigration of new susceptibles from an external reservoir (Smith 1985). The studies most relevant to landscape disturbances emphasize the difference between spatial and non-spatial models. Spatial models demonstrate, for example, that equilibrium populations of infected individuals are always smaller than would be expected from the well-mixed model (Mollison and Kuulasmaa 1985).

Landscape ecology is particularly concerned with spatial pattern on the landscape. Previous landscape investigations, using percolation theory (Gardner *et al.* 1987, in press), have demonstrated its utility at handling random spatial patterns. Epidemiologists have also utilized percolation theory to introduce spatial considerations into the models (Smythe and Wierman 1978, Cardy and Grassberger 1985).

A fundamental result of percolation theory is that a two-dimensional square lattice, with a percentage, p, of the cells randomly occupied, becomes disconnected below a critical value, p_c = 0.5928. In the context of a landscape disturbance, such as forest fire, the percentage, p, represents the fraction of the landscape occupied by burnable forest stands (Turner *et al.* 1989a). Above the critical value, a fire starting at any point on the landscape can spread across the landscape. Below p_c, the landscape is dissected into many discrete patches, and natural barriers prevent the fire from spreading throughout the landscape.

For simplicity, we assume that space and time are appropriately scaled, *i.e.*, the disturbance can only move a unit in space during a unit of time. In some cases, such as wind-dispersed embers, the disturbance may jump over narrow barriers. We will deal with this special case of jump dispersal in a later section of the paper.

Using simple models, it has been demonstrated that critical percolation thresholds exist for epidemiological processes (Grassberger 1983, Kuulasmaa and Zachary 1984, Mollison 1986) and that simple epidemics die out at a critical threshold of occupancy on a landscape (Cox and Durrett 1988). A few studies have considered simple models of forest fires on percolating landscapes (McKay and Jan 1984, von Diessen and Blumen 1986, Ohtsuki and Keyes 1986).

The purpose of the present study is to modify the epidemiology model to incorporate spatial pattern and to explore the potential of the model to (1) estimate the extent of a disturbance, (2) examine equilibrium conditions for a disturbed landscape, and (3) study the interplay between spatial pattern and disturbance processes.

The epidemiology model

The simple epidemiology model (Bailey 1975) considers a population composed of three groups: x susceptibles, y infected, and z recovered individuals. Recovered individuals are considered to be immune and no longer susceptible to infection. In the context of a fire disturbance, x represents the unburned forest in hectares or map pixels, y represents the forest actually burning, and z represents burned forest that is no longer susceptible to burning. The model takes the form:

$$\begin{aligned} dx/dt &= -\, a\, xy \\ dy/dt &= a\, xy - b\, y \\ dz/dt &= b\, y \end{aligned} \qquad (1)$$

where a represents the rate of disturbance spread or the probability of a fire spreading to other sites, and b is the rate of disturbance extinction, *i.e.*, the inverse of the length of time a site burns.

Equations (1) assume a well-mixed population in which all susceptibles have the same chance of exposure to an infection. Therefore, not only is it assumed that the population is uniformly distributed in space, it is assumed that the individuals move around freely.

To modify the equations for landscape studies, we need the probability that a disturbance will spread to an adjacent site multiplied by the probability that the adjacent site is susceptible to disturbance. In previous studies, we have used the parameter, i, to represent the probability of a disturbance spreading to an adjacent site (Turner *et al.* 1989a, 1991, Gardner *et al.* in press) and contagion, q, to represent the probability that a susceptible site will be found adjacent to a disturbance

(O'Neill *et al.* 1988, Turner 1990, Turner *et al.* 1991). The revised equations become

$$\begin{aligned} dx/dt &= -\,iq\,xy \\ dy/dt &= iq\,xy - b\,y \\ dz/dt &= b\,y. \end{aligned} \tag{2}$$

The parameter, q, permits us to deal with some aspects of spatial pattern. Assume that we can represent a landscape as a square lattice of N cells with a fraction, p, of the cells susceptible to disturbance, *i.e.*, x at time zero, $x(0) = pN$. The remainder of the landscape is not susceptible, *i.e.*, $z(0) = (1-p)N$. If the susceptible sites are randomly distributed in space, then the probability that a randomly chosen point is adjacent to a susceptible site is just $q = p$. If $q > p$, then the landscape is patchy with susceptible sites occurring together in clusters. If $q < p$, then the susceptibles are dispersed. Thus, the parameter q represents the degree to which the landscape is patterned, *i.e.*, the extent to which the landscape deviates from a random distribution.

For a particular number of susceptible sites, it may be of interest to know the maximum and minimum values of contagion. Contagion reaches its maximum value when all of the susceptible sites, $x = pN$, occur together as a single patch. On a square lattice, each susceptible pixel has 4 edges for a total of 4pN edges. If the singular contagious patch is square, $4\,(pN)^{0.5}$ of the total 4pN edges occur on the perimeter of the square. Each perimeter edge represents an adjacency (x−z) between a susceptible and nonsusceptible site. Therefore, maximum contagion occurs when $4pN - 4(pN)^{0.5}$ edges are (x−x) adjacencies within the square patch, and

$$\begin{aligned} \mathrm{Max}\,(q) &= (4pN-4(pN)^{0.5})/4pN = \\ &(pN-(pN)^{0.5})/pN. \end{aligned} \tag{3}$$

To determine the minimum value of q, we assume that if $p < 0.5$, it is possible to arrange the x sites so that contagion is zero, *e.g.*, a checkerboard pattern. Above $p = 0.5$, each susceptible site added to the landscape generates 4 x−x adjacencies. So the minimum value of q is given by,

$$\begin{aligned} &\mathrm{Min}\,(q,\ p<0.5) = 0.0, \\ &\mathrm{Min}\,(q,\ p>0.5) = 4\,(pN-0.5N)/(4pN) = \\ &(p-0.5)/p. \end{aligned} \tag{4}$$

It should be clearly understood that the model developed above (Eqs 2−4) deals with landscape level processes. We are considering the spread of a disturbance, such as fire, across blocks of two-dimensional space representing, for example, forest stands. In our analyses, we will not be considering the spread of a pathogen among individuals of a population. As a result, our assumptions and definitions deviate significantly from the extensive body of literature in epidemiology. The most important distinction is whether individuals or units of space are the variables of interest.

Predicting the spatial extent of a single disturbance

One of the most useful features of the landscape model (Eqs 2) is the ability to estimate the total extent of a single disturbance. Once initiated, the disturbance spread accelerates only as long as $dy/dt > 0$. When $dy/dt = 0$, the rate of disturbance spread begins to decrease. At this threshold point,

$$dy/dt = 0 = iq\,xy - by. \tag{5}$$

Equation (5) implies that there exists a threshold value of unburned sites, $x = k = b/iq$, that defines the turning point in the disturbance spread. If the initial value of $x(0) = pN$ is less than or equal to the threshold k, the disturbance does not spread. If the initial number of susceptible sites is greater than the threshold value, *i.e.*, $x(0) = k + m$, then the total extent of the disturbance will be 2m. There will be m sites disturbed up to the point that $dy/dt = 0$ and an equal number of sites disturbed until $y(t) = 0$.

Then, working from $x(0) = k + m = pN$ and $k = b/iq$, the model predicts the total extent of the disturbance as

$$2m = 2pN - 2b/iq \tag{6}$$

Inspection of Eq. (6) reveals that 2m may be larger than the total number of susceptible sites, pN. In this case, the theory predicts that all susceptible sites will be disturbed.

The effect of pattern on disturbance extent

From the viewpoint of landscape ecology, the important thing to note about Eq. (6) is the interplay between the dynamics of the disturbance, represented by b and i, and the pattern of the landscape, represented by p and q. The conditions under which Eq. (6) predicts that all susceptible sites will be disturbed (*i.e.*, substitute $2m = pN$) can be stated in several ways, but a useful form is:

$$i > 2b/qpN, \qquad (7)$$

which emphasizes the sensitivity of the prediction to disturbance spread, i. As the probability of spread increases beyond the critical value given in Eq. (7), all susceptible sites will be disturbed if they can be reached. Consider the case where the disturbance extinction rate $b = 1$, $p = q = 0.7$ and the landscape size $N = 100 \times 100 = 10{,}000$. Under these circumstances, any value of $i > 0.0004$ will cause the disturbance to spread to all sites that it can reach. Any further increase in intensity may increase the rate at which the disturbance spreads but will have little effect on the total extent of the disturbance. The extent of the disturbance will be determined by the spatial pattern of susceptible sites on the landscape, rather than the dynamics of the disturbance itself.

The effect of spatial pattern on the spread of disturbance can be illustrated by simulated disturbances on landscapes of 100 × 100 cells. Using an existing model for disturbance spread (Turner *et al.* 1989a), a single disturbance was initiated at a randomly chosen susceptible site. The disturbance can spread to any of the four adjacent cells with probability i, given that the adjacent site is susceptible to disturbance. The simulation ends when the disturbance is extinguished, *i.e.*, $y(t) = 0$.

The results in Table 1 are based on 10 replicate simulations with parameters set so that $2m > pN$ for $p > 0.83$ and $2m < pN$ for smaller values of p. Percolation theory predicts that the well-mixed model (Eq. 6) will only be accurate at $p > p_c = 0.5928$. Below the critical threshold, the landscape is fragmented and the well-mixed model will predict that the disturbance will spread to sites that cannot, in fact, be reached. The table reveals that simulations begin to deviate from the 2m prediction (Eq. 6) at significantly higher values of p. For the parameter values in Table 1, the well-mixed model and simulations begin to diverge at $p = 0.72$. If we use the criterion that a threshold occurs where simulation and model differ by a factor of 2, then the threshold is at $p = 0.70$.

Table 1. Simulations relating landscape pattern to the spread of disturbance. Simulated values are based on 10 replicates of a 100 × 100 landscape with parameter values were chosen so that $2m < pN$ for $p < 0.833$. The ratio of simulated to predicted (Column 4) and should be 1.0 if Eq. (6) accurately predicts the extent of the simulated disturbance, *i.e.*, if spatial pattern does not influence disturbance extent.

	Extent of Disturbance		
Susceptible Sites (pN)	Predicted (Eq. 6)	Simulated	Simulated/Predicted
10,000	10,000	9,974	0.997
9,000	9,000	8,906	0.989
8,000	7,666	7,651	0.998
7,400	6,466	6,077	0.940
7,300	6,266	5,326	0.850
7,200	6,066	3,652	0.602
7,100	5,866	3,411	0.581
7,000	5,666	2,876	0.508
6,900	5,466	1,104	0.202
6,800	5,266	1,103	0.209
6,600	4,866	451	0.093
6,400	4,466	192	0.043
6,200	4,066	120	0.029
6,000	3,666	84	0.023
5,500	2,666	30	0.010
5,000	1,666	15	0.009

The results in Table 1 suggest that the pattern of susceptible patches plays an important role in disturbance spread that is not reflected in the simple epidemiology model. The relative importance of landscape pattern and disturbance dynamics depends on the value of p and on the ratio 2b/iq in Eq. (6). At small values of the ratio, the disturbance reaches all available sites. However, landscape pattern limits the disturbance spread to the cluster on which the disturbance began. As p becomes smaller, the likelihood increases that the disturbance will (1) be halted by the increasing number of edges with non-susceptible sites, (2) be unable to pass a bottleneck in the increasing complex shape of the cluster, or (3) trap itself in a corner.

The effect of landscape contagion, q, are greatest at small values of p. Table 2 shows the size of the largest cluster of susceptible sites on landscapes

Table 2. Largest cluster of susceptible sites on 100 × 100 simulated landscapes. Results for various values of landscape occupancy, p, without contagion and with $q = 0.9$ are the mean of 10 replicate landscapes.

p	No contagion	q = 0.9
0.80	7996	7998
0.75	7440	7408
0.70	6836	6575
0.65	5796	5192
0.60	2941	4431
0.55	576	3214
0.50	190	1395
0.45	105	934
0.42	77	499

with no contagion and with relatively high contagion, $q = 0.9$. The effect of contagion begins to become important at $p_c = 0.5928$ and becomes increasingly important as p becomes smaller. At small values of p, the landscape with contagion contains clusters that are significantly larger than the purely random landscape.

Landscapes with recovery

On natural landscapes, the vegetation recovers from the effects of single disturbances. The spatial pattern seen on the landscape results, in part, from the complex interactions of repetitive disturbance and recovery events. To examine the long-term behavior of a disturbed landscape, it is necessary to modify Eq. (2) to include recovery. We introduce the probability, c, that a randomly selected disturbed site will recover during a unit of time, *i.e.*, a unit of z becomes a unit of x. The equations now become:

$$\begin{aligned} dx/dt &= -iq\,xy + c\,z \\ dy/dt &= iq\,xy - b\,y \\ dz/dt &= b\,y - c\,z. \end{aligned} \tag{8}$$

Equation (8) admits an equilibrium solution and allow us to examine the circumstances under which a single disturbance may become endemic, *i.e.*, always present on the landscape. Setting Eqs (8) to zero, solving the second equation for x(eq), and remembering that $x + y + z = N$, we find

$$\begin{aligned} x(eq) &= b/iq \\ y(eq) &= c\,(iqN - b)/iq\,(b + c) \\ z(eq) &= b\,(iqN - b)/iq\,(b + c). \end{aligned} \tag{9}$$

However, the disturbance can only continue to spread across the landscape as long as the susceptible habitat remains connected, *i.e.*, if x(eq) remains greater than or equal to p_c N. We will use this information in the first equation to set

$$i = b/(0.5928Nq). \tag{10}$$

Under this constraint, we find:

$$\begin{aligned} x(eq) &= 0.5928\ N \\ y(eq) &= 0.4072\ cn/(b + c) \\ z(eq) &= 0.4072\ bN/(b + c) \end{aligned} \tag{11}$$

Equations (11) will always yield feasible equilibria, permitting an endemic disturbance. However, it must be recognized that the constraint represented by Eq. (10) is severe. For example, if $b = 1.0$, $N = 100 \times 100 = 10{,}000$, and $q = 0.7$, then i must be equal to or less than 0.00024. If the probability of spread becomes greater than this value, x(t) becomes less than p_c N and the disturbance can no longer spread throughout the landscape. Eventually, the disturbance becomes isolated in a small portion of the landscape and burns itself out.

It is interesting to notice the effect of the pattern parameter, q, on this result. At $p_c = 0.5928$ and $N = 10{,}000$, contagion can take on values, $0.156 < q < 0.987$ (Eqs 3 and 4). This range of feasible values of q permits some flexibility in i. With $b = 1.0$ and $N = 10{,}000$, the Min (q) = 0.156 allows $i = 0.0022$. The Max (q) = 0.987 constrains i to be less than 0.0003. Thus, the inclusion of spatial pattern in the form of contagion permits the values of i to vary by a factor of 7. If the susceptible sites are dispersed (minimal q) the disturbance can continue at larger values of spread. But as q increases to a maximum, the susceptible sites tend to be clumpted. The disturbance attacks all sites in the clump and dies out. However, even with the modification introduced by contagion, the probability of spread of a single disturbance must be very small to remain endemic on the landscape.

Landscapes with multiple disturbances

Equations (8) only consider the fate of a single disturbance event. To consider more realistic disturbance regimes, we must include the possibility of multiple disturbances, *e.g.*, repeated lightning strikes beginning fires. We will introduce this factor with the parameter f, representing the probability that a randomly selected susceptible site will be disturbed during a unit of time. The equations now become:

$$\begin{aligned} dx/dt &= -\,iq\,xy + c\,z - f\,x \\ dy/dt &= iq\,xy + f\,x - b\,y \\ dz/dt &= b\,y - c\,z. \end{aligned} \qquad (12)$$

The resulting equilibrium solutions are complex and most simply stated as:

$$\begin{aligned} x(eq) &= by/(iq\,y+f) \\ z(eq) &= by/c \\ y(eq) &= (U + (U^2+V)^{0.5})/W \end{aligned} \qquad (13)$$

where: $U = iqN - b - fR$,
$V = 4iqfNR$,
$W = 2iqR$,
$R = 1 + b/c$.

The radical $(U^2+V)^{0.5}$ is always larger than U. Therefore, the root of the equation with $-(U^2+V)^{0.5}$ is always negative and of no interest. If U is positive, then y, the number of sites being disturbed, is relatively large. If U is negative, then y is relatively small.

Equations (13) always give feasible solutions. The condition for x to be positive is $y + z < N$, or

$$R\,[(iqN-b-fR)+((iqN-b-fR)^2+4iqfNR)^{0.5}]/2iqR < N$$

which reduces to $0 < iqbN$ and is always satisfied for non-zero values of the parameters.

It is interesting to examine Eqs (13) for insights into the proportion of the landscape that will be susceptible sites (*i.e.*, x(eq)) and the proportion that will be in recovery stages (*i.e.*, z(eq)). For many situations, z(eq) can be considered as sites in various successional stages. The stable ratio

$$x(eq)/z(eq) = c \;/\; iqy + f. \qquad (14)$$

implies that faster recovery rates will increase the number of mature, susceptible sites, while greater disturbance intensity, greater contagion and greater disturbance frequency will all favor a landscape dominated by successional stands.

It is also interesting to examine Eqs (13) for conditions under which y(eq) is small. This represents conditions where the disturbances are small in extent but consistently present on the landscape. The minimum value of y(eq) occurs when U is negative, V is small, and W is large. For $V = 4iqfNR$ to be small, while $W = 2iqR$ is large, the value of f must be small. Then, if f is small, b must be relatively large. To ensure that U is negative, requires $b > (iqcN - fc)/(c+f)$. It is also necessary that x(eq) remain above $p_c\,N$ for the disturbance to be endemic. This requires that $y(eq) + z(eq) < N - p_c\,N$, or $p_cqN + 1.4558fR < b$ and once again we see that f must be relatively small and b must be relatively large.

Limiting assumptions

The current study was designed as a theoretical investigation of the interplay between landscape pattern and disturbance dynamics. The equations should not be considered a simulation model that would accurately predict dynamics on a specific landscape. Nevertheless, the theory contains a series of assumptions that could limit the applicability of the conclusions. Without repeating the entire analysis, it is possible to consider these assumptions, suggest ways that the assumptions could be eased, and discuss how the conclusions might be effected.

The present analysis assumes that disturbance can spread only to immediately adjacent cells, *i.e.*, the adjacency x–x is necessary. Many disturbances exhibit 'jump dispersal' that moves across barriers. The simplest way to handle such a disturbance is to rescale the landscape data so that the size of x is sufficiently large so that a disturbance moved across one unit of x in one unit of time considering all methods of dispersal. This would require that the size of x be larger than any of the small barriers. The net effect would be to increase both p and q and significantly decrease the importance of small-scale spatial pattern in determining the extent and persistence of a disturbance. The impact of this change of scale on the percolation threshold, p_c, has been considered in O'Neill *et al.* (1988).

An alternative approach to 'jump dispersal' might consider disturbance spread across additional adjacencies. Consider a disturbance that can 'jump' a single non-susceptible pixel. Then the disturbance can spread across 3 of the four possible configurations: x–x–x with occurrance probability q^2, x–x–z with occurrance probability $q(1-q)$, and x–z–x with probability $(1-q)q$. Only the configuration x–z–z contains a double barrier that would be effective. The effective adjacency, q^*, then becomes the sum of the probabilities of finding any of the three configurations that permit transmission:

$$q^* = q^2 + q(1-q) + (1-q)q = q(2-q) \quad (15)$$

Then, q^* can be substituted into any of the equations (Eqs 1–14) to examine the importance of 'jump dispersal'. Once again, the general effect is to decrease the importance of small scale pattern in determining disturbance extent and persistence.

Another potentially limiting assumption can be found in Eqs (8). The recovery process, *e.g.*, succession, may occur far more slowly than the process of disturbance spread, *i.e.*, $c << i$. This difference in scale may lead to real problems (O'Neill *et al.* 1986). This assumption can be lifted by considering a number of successional stages, z_j, $j = 1, 2, \ldots, n$, such that c_j is of the same magnitude as disturbance spread, i. However, it should be noted that this change does not alter Eq (10) or the conclusions based on Eq (10). In general, the change only reinforces the conclusion that endemic disturbances are difficult to achieve on patterned landscapes.

Conclusions

Examination of epidemiology models, modified to account for spatial pattern, has suggested a number of ways that pattern and process interact. For all but the smallest values of disturbance spread, the disturbance moves to all reachable sites. The reachable sites are a function of landscape pattern and the extent of the disturbance is determined by spatial pattern that limits access to susceptible sites.

Contagion is a simple way to represent landscape pattern. It represents the degree to which the susceptible sites are clumped or dispersed. High levels of contagion tend to increase the extent of a single disturbance, particularly when the number of susceptible sites is small and the probability of disturbance spread is large. Low levels of contagion tend to increase the probability that a single disturbance can become endemic on a landscape.

The model provides insight into factors that determine the relative proportions of susceptible, disturbed, and successional sites when a landscape is exposed to repeated disturbance. Under these circumstances, landscape composition is determined by a balance between spatial pattern and factors characterizing disturbance spread and recovery.

Landscape geometry clearly influences the spatial extent of disturbances. Thus, our results have implications for the analysis of disturbed landscapes. Ecologists have tended to focus on disturbance dynamics and have given little attention to spatial effects. Our results suggest that new experimental designs ought to address both the spatial pattern of susceptible habitat and the dynamics of the disturbance. In this way, ecologists will gain a more complete understanding of the causes and consequences of ecological disturbances.

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