Spatially Correlated Disturbances in a Locally Dispersing Population Model*

David Hiebeler
Dept. of Mathematics and Statistics
333 Neville Hall
University of Maine
Orono, ME 04469-5752 USA
hiebeler@math.umaine.edu

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Abstract

The basic contact process in continuous time is studied, where instead of single occupied sites becoming empty independently, larger-scale disturbance events simultaneously remove the population from contiguous blocks of sites. Stochastic spatial simulations and pair approximations were used to investigate the model. Increasing the spatial scale of disturbance events increases spatial clustering of the population and variability in growth rates within localized regions, reduces the effective overall population density, and increases the critical reproductive rate necessary for the population to persist. Pair approximations yield a closed-form analytic expression for equilibrium population density and the critical value necessary for persistence.

1 Introduction

There has recently been renewed interest in the effects of spatial structure on a variety of models in population biology, fueled both by the continual growth in inexpensive computer power for performing spatially explicit simulations, as well as the application of moment-closure, pair approximation, and related techniques for building mathematical models which include some amount of local spatial correlations. These models have been applied to gap formation in forests (Kubo et al., 1996), patch-occupancy models with variable disturbance sizes (Caswell and Etter, 1993; Moloney and Levin, 1996), epidemiological models (Boots and Sasaki, 1999), local versus global dispersal on homogeneous landscapes (Harada, 1999; Harada and Iwasa, 1994) as well as heterogeneous

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landscapes (Hiebeler, 2000, submitted), populations with multiple spatial scales of interactions (Ellner, 2001), and competition in spatially structured populations (Bolker and Pacala, 1999), among many others.

For many of the models used to investigate these phenomena, spatially implicit (“mean field”) mathematical approximations, which were used for many years but which neglect spatial correlations, are either inaccurate or outright misleading about the behaviors of the models.

This paper revisits the topic of a simple spatial population model, the basic contact process with spatially localized dispersal to nearest-neighbor sites, but with larger-scale disturbance events, as explored by Caswell and Etter (1993) and Moloney and Levin (1996).

2 The Model

The population model used is a modified version of the basic contact process in continuous time, where each site on the lattice may be either empty or occupied. Each occupied site produces propagules at a fixed rate $\phi$; each propagule is then deposited on one of the site’s $z$ neighbors, chosen at random. On a rectangular lattice, $z = 4$ (assuming diagonally adjacent sites are not considered neighbors); on a hexagonal lattice, $z = 6$. The rectangular lattice was used for this study.

In the standard contact process, each occupied site becomes empty at rate $\lambda$. This process can be thought of as intrinsic mortality, or external disturbance, or a combination of both. If this process is thought of as external disturbance, then each site, whether occupied or empty, is disturbed (i.e. becomes empty) at rate $\lambda$. Of course, in practice this has no effect on sites which were already empty.

In the version of the model studied here, disturbance events consist of rectangular blocks of contiguous sites simultaneously becoming empty. The blocks used have dimensions $b_1$ and $b_2$. A disturbance block thus consists of $b_1 b_2$ sites in total. Each time a block of sites is disturbed, the block will be $b_1 \times b_2$, or $b_2 \times b_1$, each with probability 0.5, to maintain rotational symmetry on the lattice. Block disturbance events happen at rate $\lambda/(b_1 b_2)$, so that the overall per-site disturbance rate is still simply $\lambda$.

Without loss of generality, either $\phi = 1$ or $\lambda = 1$ may be assumed by rescaling the time variable, because only the ratio $\phi/\lambda$ affects qualitative dynamics of the system.

When implemented as a spatial stochastic simulation model, the process is simulated as a Poisson process where times between events are independent and follow exponential distributions. The spatially implicit (mean-field) approximation of the equilibrium density of this model is $1 - \mu/\phi$. Simulations are therefore performed starting with an initial density of $1 - \mu/\phi$ or 0.1, whichever is larger, to avoid stochastic population extinction due solely to small initial conditions.

Although this is a continuous-time model, when being simulated on an $N \times N$ lattice, as in Hiebeler (submitted) a “step” is defined as $N^2$ events, where an event is either a “birth” (propagule production) or “disturbance” (a block
of sites have their states set to empty). During a single step, each site in the lattice is updated on average approximately one time, although due to the stochastic nature of the model, the actual number of times any particular site is updated will follow a Poisson distribution with mean approximately equal to 1. Because disturbance events affect multiple sites, in fact the average number of updates per site during a time step will be larger than one; this is of no concern, since time steps were defined only as a convenience for testing convergence to equilibrium.

To determine when the system has reached equilibrium, the population density is recorded after every step. Beginning at step 300, a regression line is fit to the data over the most recent 100 steps. If the slope of this regression line is less than 0.001, the system is considered to have reached equilibrium.

Figure 1 shows two configurations of the lattice after reaching equilibrium, with disturbance block sizes of $1 \times 1$ with $\mu = 0.4$, and $5 \times 5$ with $\mu = 0.19$, both with $\phi = 1$. These parameters yield approximately equal equilibrium population densities, although very different spatial arrangements of occupied sites.

### 3 Pair Approximation

If we use 0 to represent empty sites, and 1 to represent occupied sites, pair approximation can be used to describe this model with a system of two differ-
ential equations, as follows. One can describe the state of the system using the probabilities that a pair of adjacent sites are in one of four state configurations: 00, 01, 10, and 11. These four probabilities must sum to one, and assuming rotational symmetry imposes the constraint $P[01] = P[10]$ (we also assume $P[ij] = P[ji]$, so in fact only two probabilities are needed, e.g. $P[00]$ and $P[01]$. Marginal probabilities of single-site states can be computed by summing over block probabilities,

$$P[i] = P[i0] + P[i1] \quad \text{for } i \in \{0, 1\}. \quad (1)$$

The pair approximation used here is that given information about a target site’s nearest neighbor, the target site’s state is independent of the next-nearest neighbors, i.e.

$$P[**c|ab] = P[*c|*b] = P[bc]/P[b], \quad (2)$$

where “*” is a placeholder to show the relative positions of the sites. That is, the probability that the third site is in state $c$ does not depend on the first site being in state $a$, given the information that the second site is in state $b$.

If a given site, referred to as the target site, is disturbed, let $\beta$ be the probability that a particular one of its neighbors, say the neighbor to the right, is also disturbed. If the target site was part of a $b_1 \times b_2$ block disturbance event (where dimensions are given as rows $\times$ columns), then because the target site is equally likely to be in any position within the disturbance block, the probability that its right neighbor was also disturbed is simply $1 - 1/b_2$, the fraction of sites in the disturbance block which are not on the right edge of the block. If on the other hand the target site was part of a $b_2 \times b_1$ disturbance event, then the probability that its right neighbor was also disturbed is $1 - 1/b_1$. Because both types of disturbance blocks occur with equal frequency 0.5, the overall probability that a particular neighbor of a disturbed site is also disturbed is

$$\beta = 0.5(1 - 1/b_1) + 0.5(1 - 1/b_2) = 1 - 0.5(1/b_1 + 1/b_2). \quad (3)$$

To derive the differential equations for $P[00]$ and $P[01]$, we need the rates of two types of disturbance events that can affect a pair of adjacent sites. Consider a horizontal pair of sites in state $[ij]$. The rate of the left site being disturbed but the right site not disturbed is the rate of the left site being disturbed, times the probability that its neighbor is not disturbed:

$$r_1 = \text{Rate}([ij] \to [0j]) = \mu(1 - \beta). \quad (4)$$

Similarly, the rate of both sites being simultaneously disturbed is

$$r_2 = \text{Rate}([ij] \to [00]) = \mu\beta. \quad (5)$$

Using these two rates, the system of differential equations describing the
system is

\[
\frac{dP[00]}{dt} = -2P[00] \left( \frac{(z-1)Q_{1|0} \phi}{z} \right) + 2P[01](r_1 + r_2) + P[11]r_2
\]

\[
\frac{dP[01]}{dt} = P[00] \left( \frac{(z-1)Q_{1|0} \phi}{z} - P[01] \right) \left[ r_1 + r_2 + \frac{\phi}{z} + \frac{(z-1)Q_{1|0} \phi}{z} \right] + P[11]r_1
\]

where

\[Q_{1|0} = P[01]/P[0]\]

is the pair approximation of the probability that a given neighbor of an empty site is occupied. See e.g. Levin and Durrett (1996) or Hiebeler (submitted) for derivations of similar pair approximation equations; the system here is very similar, with the primary difference that for this model a [11] block of sites can change to state [00] if both sites are simultaneously disturbed. In continuous-time models with single-site disturbances, this state transition is impossible. Also, note that a [01] block can become a [00] block if the right site is disturbed but the left one is not, or if both sites are disturbed.

Using the fact that \(P[11] = 1 - P[00] - 2P[01]\), these equations can be rewritten as

\[
\frac{dP[00]}{dt} = -P[00] \left( \frac{2(z-1)Q_{1|0} \phi}{z} + r_2 \right) + 2P[01]r_1 + r_2 \tag{6}
\]

\[
\frac{dP[01]}{dt} = P[00] \left( \frac{(z-1)Q_{1|0} \phi}{z} - P[01] \right) \left[ r_1 + r_2 + \frac{\phi}{z} + \frac{(z-1)Q_{1|0} \phi}{z} \right] + P[11]r_1 \tag{7}
\]

The pair approximation extension process in equation (2) can also be applied repeatedly to estimate the probabilities of longer blocks of sites, by covering the longer block with \(2 \times 1\) blocks:

\[
P[s_1s_2s_3 \ldots s_k] = \frac{\prod_{i=1}^{k-1} P[s_is_{i+1}]}{\prod_{i=2}^{k-1} P[s_i]}
\]

Probabilities of blocks of sites with only some sites’ values specified may then be obtained by summing as in equation (1). In particular, to compute the probability that the first and last sites in a \(1 \times k\) block of sites are in state 1, written as \(P_k[11]\), one can use

\[
P_k[11] = P[1 \ast \ldots \ast 1] = \sum_{k-2 \text{ sites}} P[1s_1s_2 \ldots s_{k-1}].
\]

The conditional probability that a site \(k\) units away from an occupied site is also occupied, denoted by \(Q_k[1|1]\), can then be computed, recognizing that there must be \(k - 1\) sites between the two sites under consideration and thus \(k + 1\) sites including the two occupied sites: \(Q_k[1|1] = P_{k+1}[11]/P[1]\).
Finally, the correlation coefficient between two sites separated by distance $k$, as estimated by the pair approximation, is given by

$$\rho_k = \frac{Q_k[1][1] - P[1]}{1 - P[1]}.$$  

(8)

4 Results

The trivial (extinction) equilibrium for the pair approximation model in equations (6) and (7) is $P^*[00] = 1$, $P^*[01] = 0$, when all sites are empty. As derived in the appendix, there is also a nontrivial equilibrium if and only if

$$\frac{\phi}{\mu} > \frac{2 - \beta}{2 - \beta - 2/z}.$$  

(9)

This nontrivial equilibrium has a population density of

$$P^*[1] = 1 - \frac{2(z - 1)}{\beta z + \frac{\phi}{\mu} z(2 - \beta) - 2\left(\frac{\phi}{\mu} + 1\right)}.$$  

(10)

Equilibrium values of $P^*[1]$, the proportion of sites occupied, are shown in figure 2 for both simulations and pair approximations, with fixed reproductive rate $\phi = 1$ and varying mortality rate $\mu$. It can be clearly seen that increasing the size of disturbances reduces equilibrium population density. With larger-scale disturbance events, it takes time for the locally-dispersing population to recolonize a disturbed patch by growing in from the edges (as also observed by Caswell and Etter, 1993). This increases temporal variability in the growth rate, which reduces the overall effective population growth rate (Case, 2000). Figure 2 also shows that pair approximations consistently overestimate $P^*[1]$; this is typical of pair approximations (Levin and Durrett, 1996). This discrepancy increases as the size of disturbance blocks becomes larger. The larger-scale disturbances create correlations over larger spatial scales than the pair approximation can accurately capture. This effect can be considered in the extreme — with $n \times n$ blocks, as $n \to \infty$ then according to equation (3), $\beta \to 1$, and inequality (9) and equation (10) still predict that the population will survive as long as $\phi/\mu > z/(z - 2)$. However, actual simulations show that as the size of disturbance blocks grows, the population goes extinct (in the limit as $n \to \infty$, using simulations the entire population will be disturbed at once).

Figure 3 shows the equilibrium values of $P[01]$, the probability that in a pair of sites, the left site is empty and the right site is occupied, as a function of $\mu$ with $\phi = 1$. Again, pair approximations overestimate the probabilities, and as in figure 2, the discrepancy is greatest near the critical value at which the population just goes extinct.

Figure 4 shows equilibrium population density for varying values of $\mu$, with $n \times 1$ disturbances, i.e. larger-scale one-dimensional disturbances. Although such disturbances also affect large contiguous blocks of sites, because the disturbances
are only one site “thick,” the population can recolonize the disturbed region quickly from adjacent sites. For example, although not shown in the figures, with $\phi = 1$ and $\mu = 0.4$, the population easily persists with an equilibrium density of approximately 0.34 with $16 \times 1$ disturbances, but quickly goes extinct with $4 \times 4$ disturbances. In the pair approximation, with $n \times 1$ disturbance blocks as $n \to \infty$, $\beta \to 0.5$, and the population is predicted to survive if $\phi/\mu > 3z/(3z-4)$.

The error in the pair approximation as compared to simulations is greatest at the critical value of $\mu$ between population persistence and extinction, as can be seen in figures 2 and 4. This is due to the fact that in these types of spatial population models, near the critical value, there are correlations even between sites quite far apart in the lattice. Figure 5 shows the correlations between pairs of sites at varying distances as measured from simulations and predicted by equation (8), after the population has reached equilibrium. In simulations, when correlations over the lattice were measured, only the states of a target site and other sites separated by an $(x, y)$ displacement of $(\pm d, 0)$ and $(0, \pm d)$ were used, i.e. correlations were only computed between pairs of sites separated along a single dimension of the lattice. All sites in the lattice were used to compute the correlation in simulations. The figure displays results for the model with $2 \times 2$ disturbance events, with two values of $\phi/\mu$. The model with $\phi/\mu$ near the critical value clearly shows that in simulations, correlations decay much more slowly with distance between sites, but pair approximations do not accurately
Figure 3: Equilibrium probability that a pair of sites has the left site empty and the right site occupied, with $\phi = 1$ as disturbance rate $\mu$ is varied, for varying sizes of $n \times n$ disturbance events.

reflect this phenomenon.

5 Conclusions

Many recent papers have shown that the spatial structure of one or more populations and/or their habitat can change the qualitative outcome of population dynamics. Caswell and Etter (1993) found that variable-size disturbance events affected dynamics in a two-species model of competition; however, their study was based on simulations, which are less general than an analytical model, and spatially implicit mean-field approximations, which are unable to incorporate the effects of events simultaneously affecting multiple sites.

The model studied here shows that the spatial scale and geometry of disturbance effects have a quantifiable impact on spatial correlations in a basic population model with local dispersal, and thus strongly affect basic population dynamics. Pair approximations predict the impact of such correlated disturbances, although the technique becomes less accurate as the spatial scale of disturbance events increases, and near the critical value for survival of the population. A mathematical model incorporating more detailed spatial correlation information (Hiebeler, 1997) would presumably improve the predictions; it may also be possible to build a pair approximation model tracking correlations at multiple scales (Ellner, 2001) to improve the predictions.
Figure 4: Equilibrium proportion of sites occupied with $\phi = 1$ as disturbance rate $\mu$ is varied, for varying sizes of disturbance events. Here, disturbance events affect $n \times 1$ blocks of sites, for varying values of $n$.

In natural systems, as explored by Caswell and Etter (1993), disturbances may be happening at many different scales. Although not explored here, the pair approximation model used here can include this effect by simply using the probabilities of different disturbance geometries when calculating the rates $r_1$ and $r_2$. For example, adapting Caswell and Etter (1993), if the probability that a disturbance event affects a $j \times j$ block of sites is $g_j$, then equations (4) and (5) can be modified as

$$r_1 = \mu \sum_{j=1}^{\infty} g_j (1 - \beta_j)$$
$$r_2 = \mu \sum_{j=1}^{\infty} g_j \beta_j$$

where $\beta_j = 1 - 1/j$ is the value of $\beta$ following equation (3) when considering $j \times j$ disturbance events.

Moloney and Levin (1996), using spatially explicit simulations, found that the temporal autocorrelation structure of disturbance affected species landscape-scale population dynamics and species diversity. They also found that the size and spatial autocorrelation of disturbance events had a minor effect on population dynamics, and speculate that it may be due to the details of dispersal in their model; this speculation is most likely correct. Their model contained a
Figure 5: The correlation coefficient $\rho$ between pairs of sites is plotted against the distance separating the sites, as measured from simulations and predicted by pair approximations, after the population reaches equilibrium. The model in both graphs used $2 \times 2$ disturbances with $\phi = 1$, and (a) $\mu = 0.3$ (far from the critical value, with equilibrium density $\approx 0.53$), and (b) $\mu = 0.5$ (near the critical value, equilibrium density $\approx 0.02$). Correlations decay much more slowly with distance near the critical value, which pair approximations do not recognize.
mixture of no dispersal (offspring stay at the site of their birth), local dispersal to neighboring sites, and long-distance dispersal (i.e. equal dispersal to all sites on the lattice). Of the three types of dispersal in their model, only local dispersal to neighboring sites will be affected by the size of disturbance events. Among the three species in their model, the species which had the highest proportion of local dispersal only allocated 12% of its reproduction to local dispersal, the rest of the offspring either not dispersing or dispersing long-distance. Experimentation with a related model with spatially correlated environmental heterogeneities (Hiebeler, submitted) indicates that a mixed dispersal strategy with such a low proportion of local dispersal will be relatively insensitive to spatial correlations among adjacent sites. Finally, the spatial autocorrelations between disturbances in the model of Moloney and Levin (1996) were over distances too large to strongly affect a locally dispersing population (and again, would have no effect on the long-distance dispersing component of the population dynamics).

The model investigated here generally agrees with results of earlier models, within an analytically tractable mathematical framework, and is another approach to studying the effects of spatial correlations among populations and their environment.

6 Acknowledgements

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References


Appendix: Derivation of Nontrivial Equilibrium

If the system of equations (6) and (7) reaches a nontrivial equilibrium, it will satisfy

\[ \phi Q_{0|1} = \mu, \]  

where \( Q_{0|1} \) is the conditional probability that the neighbor of an occupied site is in state 0, which using the pair approximation is given by

\[ Q_{0|1} = \frac{P[01]}{P[1]} \]  

(12)

Equation (11) simply says that at equilibrium, the disturbance rate per occupied site equals the corrected reproduction rate taking into account the fact that a reproduction attempt is successful only if the offspring lands on an empty site adjacent to the (occupied) parent’s site. Using the fact that

\[ P[1] = 1 - P[0] = 1 - P[00] - P[01], \]  

(13)

together with equation (12), equation (11) can be solved for \( P^*[01] \) in terms of \( P^*[00] \):

\[ P^*[01] = \frac{\mu(1 - P^*[00])}{\phi + \mu}. \]  

(14)
This may then be substituted into equation (6) and that equation set equal to zero to find the equilibrium value \( P^*[00] \). The result is a quadratic equation

\[
f(P[00]) = (P^*[00])^2 \phi \left( \frac{2(z-1)\mu}{z} - r_2 - \frac{2\mu r_1}{\phi + \mu} \right)
+ P[00] \left( -\frac{2(z-1)\phi \mu}{z} + r_2(\phi - \mu) - \frac{2\mu^2 r_1}{\phi + \mu} + \frac{2\mu r_1 \phi}{\phi + \mu} \right) + \mu \left( \frac{2\mu r_1}{\phi + \mu} + r_2 \right) = 0
\]

We know \( f(1) = 0 \) because \( P[00] = 1 \) is an equilibrium. Also, \( f(0) = \mu(2\mu r_1/(\phi + \mu) + r_2) > 0 \). These imply that \( f(x) \) will have a second root \( x^* \) satisfying \( 0 < x^* < 1 \), representing a nontrivial equilibrium, if and only if \( f'(1) > 0 \). This happens precisely when \( \phi/\mu > (2 - \beta)/(2 - \beta - 2/z) \). When this inequality is satisfied, one root of \( f(x) \) is \( x = 1 \); the other root gives the nontrivial equilibrium value \( P^*[00] \). That, together with equations (13) and (14) yield the nontrivial population density given in equation (10).