The effect of static and dynamic spatially structured disturbances on a locally dispersing population

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Abstract

Previous models of locally dispersing populations have shown that in the presence of spatially structured fixed habitat heterogeneity, increasing local spatial autocorrelation in habitat generally has a beneficial effect on such populations, increasing equilibrium population density. It has also been shown that with large-scale disturbance events which simultaneously affect contiguous blocks of sites, increasing spatial autocorrelation in the disturbances has a harmful effect, decreasing equilibrium population density. Here, spatial population models are developed which include both of these spatially structured exogenous influences, to determine how they interact with each other and with the endogenously generated spatial structure produced by the population dynamics. The models show that when habitat is fragmented and disturbance occurs at large spatial scales, the population cannot persist no matter how large its birth rate, an effect not seen in previous simpler models of this type. The behavior of the model is also explored when the local autocorrelation of habitat heterogeneity and disturbance events are equal, i.e. the two effects occur at the same spatial scale. When this scale parameter is very small, habitat fragmentation prevents the population from persisting because sites attempting to reproduce will drop most of their offspring on unsuitable sites; when the parameter is very large, large-scale disturbance events drive the population to extinction. Population levels reach their maximum at intermediate values of the scale parameter, and the critical values in the model show that the population will persist most easily at these intermediate scales of spatial influences. The models are investigated via spatially explicit stochastic simulations, traditional (infinite-dispersal) and improved (local-dispersal) mean-field approximations, and pair approximations.

Keywords: Spatial population models; Heterogeneous habitat; Large-scale disturbance; Spatial autocorrelation; Pair approximation

1. Introduction

The effects of spatial structure and heterogeneity on population dynamics are well established, whether caused by external influences such as the distribution of resources, or arising from the behaviors and interactions of organisms. The availability and spatial distribution of suitable habitat have been shown to play a crucial role in population dynamics by many theoretical (Gamarra, 2005; Hiebeler, 2000, 2004; Hill and Caswell, 1999; Lande et al., 1999; Matlack and Monde, 2004; Neuhauser, 1998; Ovaskainen et al., 2002; Pearson and Dawson, 2005; With et al., 1999), observational (Kie et al., 2002; Roland and Taylor, 1997), and experimental studies (Collinge and Palmer, 2002; Dooley and Bowers, 1998; With et al., 1999). The importance of the spatial structure of disturbances acting on a population has also been demonstrated by several studies; some have shown that increasing the spatial scale of disturbance generally reduces population density (Caswell and Etter, 1993; Hiebeler, 2005b; Johst and Drechsler, 2003), although this result may be affected by landscape structure (Kallimanis et al., 2005) and by community structure and the scale of dispersal (Moloney and Levin, 1996). Intrinsically generated spatial clustering has been shown to play a key role in various types of epidemiological and population dynamics as well, for example, in the recent work by Bolker et al. (Bolker,
Recent work by Hiebeler (2000, 2004, 2005b) separately explored the effects of spatial autocorrelation in environmental heterogeneity and in disturbance events in lattice-based population models. It was shown that increasing local spatial clustering of suitable habitat on unchanging landscapes increases the equilibrium density of a locally dispersing population, because it reduces the chance that dispersing offspring will be deposited on an unsuitable site. As long as dispersal is entirely localized, the global density of suitable sites has very little effect on the population density, assuming there is enough habitat to sustain a population large enough to avoid significant stochastic fluctuations. Such heterogeneous landscapes may be thought of as static spatially autocorrelated disturbances, as the population cannot survive in the (permanently) unsuitable sites. On the other hand, increasing the local spatial autocorrelation in dynamic disturbance events, where multiple sites are simultaneously disturbed but then immediately able to be colonized again by occupied neighbors, reduces the equilibrium population density of a locally disturbing population. This is likely due to the resulting increase in temporal variability, which is known to reduce population growth rates (Case, 2000), and the fact that due to the localized dispersal, it takes time for the population growth to reach and recolonize the center of a disturbed area.

The primary question to be explored here is, how do these two factors interact? In particular, if environmental clustering and disturbance events have the same degree of spatial autocorrelation, which effect will have the dominant influence? The question is addressed using lattice models studied with spatially explicit simulations as well as moment-closure approximations. The latter includes two types of mean-field approximations (MFA) and pair approximation. MFA has been used to investigate the effects of habitat loss (Nee and May, 1992); but because it assumes all sites in the lattice are well mixed, the traditional (“infinite-dispersal”) MFA is not appropriate for investigating the effects of spatially autocorrelated influences in a population model. However, an improved (local-dispersal) mean-field approximation (IMFA) (Hiebeler, 1997, in press) is also used here to investigate the model. Ordinary pair approximation, which includes local clustering within pairs of adjacent sites, is also used. Pair approximation has proved useful with a variety of lattice models (e.g. Boots and Sasaki, 1999, 2000; Ellner, 2001; Filipe and Gibson, 2001; Harada and Iwasa, 1994; Hiebeler, 2005a, 2006; Kubo et al., 1996; Matsuda et al., 1992; Rand, 1999; Sato et al., 1994; van Baalen, 2000).

2. Simulation model

The model here is a generalization of the basic contact process in continuous time (Durrett and Levin, 1994; Liggett, 1985) with two additions: the presence of fixed spatially structured heterogeneous habitat, and disturbance at spatial scales larger than a single site. The model takes place on a regular lattice; a rectangular lattice where each site interacts with its four neighbors was used with all simulations, although the mathematical approximations allow for an arbitrary number of neighbors, such as six on a hexagonal lattice.

Following Hiebeler (2000, 2004), the population inhabits a landscape where sites are either suitable or unsuitable. For simplicity, unsuitable sites cannot be occupied, and the distribution of habitat is fixed over time. Landscapes are described by the habitat availability parameter \( p_s \), indicating the proportion of sites which are suitable, and the clustering parameter \( q_{ss} \), the probability that a randomly chosen neighbor of a randomly chosen suitable site is also suitable. (In general, \( q_{ss} \) will represent the probability that a randomly chosen neighbor of a site in state \( f \) is in state \( i \), where \( i, j \in \{s, u\} \), when discussing landscape parameters.) Together, \( p_s \) and \( q_{ss} \) describe both habitat availability/loss and fragmentation, and are constant over time because the landscape is static. The proportion of unsuitable sites is \( p_u = 1 - p_s \), and probabilities of joint state configurations for pairs of adjacent sites may be calculated as \( p[su] = p_d q_{su} \), \( p[us] = p_d (1 - q_{us}) \), and \( p[ud] = 1 - p_d (2 - q_{us}) \) (Hiebeler, 2000). When the population model is included, each site on the lattice may be in one of three states: empty suitable (0), unsuitable (1), and occupied suitable (2). Using \( P[i] \) to represent the proportion of sites in state \( i \), note that \( P[0] + P[2] = p_s \) and \( P[1] = 1 - p_s \).

In the population model, occupied sites attempt reproduction at rate \( \phi \) each; offspring are dropped on a randomly chosen neighboring site. If the chosen site is empty and suitable, it becomes occupied; otherwise (i.e. if the site is either occupied or unsuitable) the offspring is wasted. As in Hiebeler (2005b), disturbance here is viewed as an extra-systemic process, rather than representing intrinsic mortality. Disturbance events simultaneously affect \( b_1 \times b_2 \) rectangular blocks of sites (in either orientation with equal probability, to preserve isotropy in the lattice). To maintain an overall per-site disturbance rate of \( \mu \), these block disturbance events occur at rate \( \mu / (b_1 b_2) \). When an occupied site is disturbed, it becomes empty but remains suitable; empty and unsuitable sites are not affected by disturbance.

The simulation model is implemented as a discrete-event dynamical system representing a continuous-time Poisson process (Cassandras, 1993; Ross, 2002) with exponentially distributed times between events. By rescaling time, \( \mu = 1 \) may be assumed without loss of generality; this will be done at times to simplify the analysis. Equivalently, results may be stated in terms of the dimensionless parameter \( \phi / \mu \).

All simulations were performed on \( 400 \times 400 \) lattices, and begun with 50% of the suitable sites occupied. For this and prior related models, equilibrium results are generally not sensitive to initial conditions unless the habitat is highly fragmented and the initial population density is too
low; in that case, as further explained in the Discussion section below, there may be patches of suitable habitat which are initially empty, and which cannot be colonized due to the short-distance dispersal and the inability of the population to survive in unsuitable habitat. See also Hiebeler (in press) for an exploration of how using mixtures of short- and long-distance dispersal changes the dynamics and interactions of populations on heterogeneous landscapes. Every 40,000 events was considered to be a single time step. Beginning after 300 steps, on each time step a linear regression was fit to the population density during the previous 300 time steps. When the slope of this line had magnitude less than 0.001, the simulation was considered to have reached equilibrium. Simulations which have reached equilibrium on 100 × 100 lattices are shown in Fig. 1.

3. Mathematical models

Various mathematical approximations of the simulation model will now be developed. We begin with an equation describing the proportion of sites which are suitable and occupied, i.e. in state 2:

\[
\frac{dP[2]}{dt} = P[2]\phi Q_{0:2} - P[2]\mu,
\]

(1)

where \(Q_{ij}\) represents the conditional probability that a randomly chosen neighbor of a randomly chosen site in state \(j\) is in state \(i\), and so \(Q_{0:2}\) is the conditional probability that a neighbor of an occupied site is empty and suitable. The notation \(Q_{ij}\) will be used when discussing the population model on the landscape, to distinguish it from local probabilities \(q_{ij}\) involving only habitat types. Although the per-site rate of attempted reproduction is \(\phi\) in this model, the effective reproduction rate is reduced to \(\phi Q_{0:2}\) because only offspring which land on empty suitable sites are successful. Eq. (1) is not closed, because of the dependence on \(Q_{0:2}\), which changes over time.

3.1. Mean-field approximations

The simplest mathematical model of this system is an MFA, which assumes that all sites in the lattice are independent. This is equivalent to assuming that \(Q_{ij} = P[i]\), i.e. local conditional densities are the same as global densities. Substituting this into Eq. (1) gives \(dP[2]/dt = P[2](\phi P[0] - \mu)\). Because we assume the habitat distribution is fixed, \(dP[1]/dt = 0\) with \(P[1] = 1 - p_s\). The fact that the three state variables sum to one then gives \(P[0] = 1 - P[1] - P[2] = p_s - P[2]\), which may be substituted into the above differential equation. The nontrivial equilibrium of this system is \(P^*[2] = p_s - \mu/\phi\). At this equilibrium, the proportion of suitable sites occupied is \(s^* = P^*[2]/p_s = 1 - \mu/(\phi p_s)\). The trivial (extinction) equilibrium \(P^*[2] = 0\) is locally stable if \(\phi p_s < \mu\). The nontrivial equilibrium is only well defined (i.e. satisfies \(0 \leq P^*[2] \leq 1\)) when the trivial equilibrium is unstable. Because the ordinary MFA neglects all correlations among sites, it cannot perceive the local clustering \(q_{ss}\) of suitable habitat, although the global density of suitable habitat \(p_s\) appears in the results. This approximation also cannot include any information about the larger block disturbance events. This is an infinite-dispersal MFA (Hiebeler, 1997), because assuming complete independence of all sites is equivalent to assuming that offspring are dispersed at random to all sites in the lattice with equal probability, i.e. over arbitrarily large distances.

An IMFA which includes correlations in habitat type may also be developed. This approximation may be thought of as a continuous-time generalization of the local-dispersal MFA (Hiebeler, 1997). The probability that a neighbor of an occupied suitable site is suitable and empty may be broken into product of the probability that
the neighboring site is suitable and the conditional 
probability that the site is empty given that it is suitable. 
This gives \( Q_{02} = q_s P[0]/p_r \). Substituting this into Eq. (1) gives 
The model \( \frac{dP[0]}{dt} = P[0](\phi Q_{20} - \mu) \). This model has nontrivial equilibrium \( P[2] = p_s(1 - \mu/(\phi q_s)) \). At this equilibrium, proportion \( s^* = 1 - \mu/(\phi q_s) \) of the suitable sites are occupied, which now depends on \( q_s \) but not on \( p_r \). The trivial (extinction) equilibrium is now stable if \( q_s < \mu \). The local-dispersal MFA includes local spatial 
correlations in habitat types, which are important during 
reproduction attempts, but still assumes the population is 
well mixed among all suitable sites. This approximation 
still cannot include spatial information about block 
disturbance events, but is an improvement over the 
standard MFA.

### 3.2. Pair approximations

Although the MFA provide a baseline which the other 
methods may be compared to, they are unable to incorporate information 
about the spatial scale of disturbance events in the model. Pair approximations of the model were therefore also 
developed. Pair approximations have previously proven useful 
for investigating the effects of spatially structured habitat 
heterogeneities on populations (Hiebeler, 2000, 2004; Ives et al., 1998; Ovaskainen et al., 2002), and for studying the effects 
of simultaneous disturbance of multiple sites (Hiebeler, 2005b). 
In pair approximation models one writes differential equations 
for \( P[j] \), the probabilities that pairs of adjacent sites are in 
given configurations of states. Because there are three states per 
site, a pair of sites may have \( 3^2 = 9 \) configurations. But 
assuming rotational symmetry, a constant habitat distribution, 
and the fact that the nine probabilities must sum to one 
reduces the number of independent state variables to only three 
(Hiebeler, 2004). The pair approximation itself consists of the 
assumption that two nonadjacent sites separated by one other 
site are independent, conditioned on the state of the site 
between them. This assumption is used to approximate third-
order moments using second-order moments in differential 
equations for \( P[j] \) and obtain a closed system. See also Sato et al. (1994) for discussion of improved pair approximations 
which include some degree of additional clustering between 
nonadjacent sites, and Murrell et al. (2004) for general 
discussion of related moment-closure approximations.

Following Hiebeler (2005b), define \( \beta = 1 - b/(1/b_1 + 1/b_2) \) as the conditional probability that a particular 
neighbor of a chosen site is affected by a disturbance 
event, given that the chosen site is disturbed. Also, define \( z \) 
as the number of neighbors of each site on the lattice. The system of equations describing the model is then 

\[
\frac{dP[0]}{dt} = \frac{P[0]}{2}(z-1) + 2P[0](\mu - \mu) + p_s q_s \mu \beta, \\
\frac{dP[1]}{dt} = p_s(1 - q_s) - P[0](z-1) + \mu Q_{20} + \mu. 
\]

Because in the simulations a rectangular lattice was used 
without direct interaction between diagonal neighbors, we 
will assume \( z = 4 \) hereafter.

At the population extinction equilibrium, the values of 
the three state variables are determined by the landscape 
parameters with \( P[00] = p_s q_s, P[01] = p_s(1 - q_s), \) and 
\( P[02] = 0 \). Linearized stability analysis of this equilibrium 
shows that the equilibrium will be unstable, implying that 
the population will persist, if any of the roots of the 
characteristic polynomial 

\[
(\mu - \lambda)[(\mu + \lambda) \left( 3\mu + \frac{\phi}{4} - 2\mu + \lambda - \frac{3}{4}\phi q_s \right) + 2\mu(1 - \beta) \left( \mu(1 - \beta) - \frac{3}{4}\phi q_s \right) ]
\]

have positive real part. This occurs when 

\[
\frac{\phi}{\mu} > \frac{8 - 4\beta}{6q_s - 3\beta \beta - \beta} \quad \text{and} \quad q_s > \frac{\beta}{6 - 3\beta}. 
\]

The condition for \( \phi/\mu \) responds to the individual 
parameters in expected ways based on previous work, 
namely either decreasing \( q_s \) (and therefore increasing 
habitat fragmentation) or increasing \( \beta \) (increasing the 
spatial scale of disturbance events) requires a larger value of 
\( \phi/\mu \) for the population to persist (Hiebeler, 2004, 2005b). Defining \( f(\beta, q_s) = (8 - 4\beta)/(6q_s - 3\beta \beta) \), the 
first expression in (3), the partial derivatives with respect to the two parameters are 

\[
\frac{\partial f}{\partial \beta} = 8/\beta^2 \quad \text{and} \quad \frac{\partial f}{\partial q_s} = -(8 - 4\beta)/(6 - 3\beta)w^2 
\]

where \( w = 6q_s - 3\beta \beta - \beta \). These show that 
\( \partial f/\partial q_s \geq 0, \partial f/\partial \beta < 0 \), i.e. a change in spatial 
 autocorrelation of the suitable habitat has a larger effect 
than a change in the spatial autocorrelation of disturbance 
events does on the conditions required for population 
persistence. This is true for all values \( 0 < \beta, q_s < 1 \), although 
the result is really only meaningful when the second 
condition in (3) is satisfied.

The conditions given in (3) were derived in part from the inequality 

\[
\phi(6q_s - 3\beta q_s - \beta) > \mu(8 - 4\beta), 
\]

which if satisfied will cause the extinction equilibrium to be 
unstable. When the second inequality in (3) is violated, i.e. 

\[
q_s < \frac{\beta}{6 - 3\beta}, 
\]

the left-hand side of inequality (4) becomes negative. When \( \phi \) 
and \( \mu \) are brought to the same side, this condition then 
becomes \( \phi/\mu < (8 - 4\beta)/(6q_s - 3\beta \beta) \), where the right-hand 
side is negative. Mathematically, this means that \( \phi/\mu \) 
would need to be negative in order for the extinction 
equilibrium to be unstable; as this is not biologically
meaningful, when \( q_{ss} \) and \( \beta \) satisfy inequality (5), the population will not survive no matter how large \( \phi/\mu \) is. As \( q_{ss} \) approaches \( \beta/(6 - 3\beta) \) from above, the required value of \( \phi/\mu \) to give population persistence given by the first inequality in (3) approaches \( +\infty \).

Because one of the main questions of interest was how a population would respond to static and dynamic disturbance with the same degree of spatial autocorrelation, we consider the special cases where \( q_{ss} = \beta \) or \( q_{uw} = \beta \), where \( q_{uw} \) is the probability that the neighbor of an unsuitable site is also unsuitable. Under the assumption \( q_{ss} = \beta \), the second inequality in (3) will always be satisfied, and the condition for persistence of the population becomes simply \( \phi/\mu > G(\beta) \), where

\[
G(\beta) = f(\beta, \beta) = (8 - 4\beta)/(5\beta - 3\beta^2).
\]

To study the effect of constraining \( q_{uw} = \beta \), one may use the relations \( q_{ss} = p[s]/ps, p[ss] = 1 - p[uu] - 2p[us], p[uu] = p_s(1 - q_{ss})/(1 - p_s)(1 - q_{uw}) \), and \( p[us] = p[u]q_{uw} = (1 - p_s)q_{uw} \), all taken from or following those from Hiebeler (2000), to solve for

\[
q_{ss} = \frac{1 - (1 - p_s)(2 - q_{uw})}{p_s},
\]

which may then be substituted into (3). The results indicate that decreasing \( p_s \) while keeping \( q_{uw} \) constant decreases \( q_{ss} \), which in turn increases the minimum threshold value of \( \phi/\mu \) for the population to persist. Note that we require \( q_{uw} \geq 2 - 1/(1 - p_s) \) in order to satisfy \( 0 \leq q_{ss} \leq 1 \); if \( q_{uw} \) does not satisfy this inequality, then that particular combination of \( p_s \) and \( q_{uw} \) does not specify a valid landscape. In the special case where \( p_s = 0.5 \), then \( q_{ss} = q_{uw} \). Although \( q_{uw} \) specifies the local autocorrelation of static disturbance (rather than \( q_{ss} \) which indicates spatial autocorrelation of suitable habitat), the effects of \( q_{uw} \) were not directly explored further, as the landscape parameter \( q_{ss} \) more directly impacts the population, and all results obtained in terms of \( q_{ss} \) may be expressed in terms of \( q_{uw} \) via Eq. (7) above.

The nontrivial equilibrium for the pair approximation model may also be computed. From the three state variables in the model, the proportion of suitable sites occupied at equilibrium may be computed as \( s^* = P*[2]/p_s = 1 - (P*[00] + P*[01] + P*[02])/p_s \). Setting the derivatives of the differential equations (2) to zero, some manipulation shows that the nontrivial equilibrium value \( s^* \) is the root of the following polynomial:

\[
((1 - 2\beta) + \phi(2\beta - 3))(s^*)^2 + (2(5\beta - 4) + 6\phi q_{ss}(2 - \beta) + \phi(3 - 4\beta))s^* + (8(2 - \beta) + 6\phi q_{ss}(2 - \beta) + 2\phi\beta) = 0
\]

within the interval \([0,1]\) when there is such a root. Although this nontrivial equilibrium is easy to calculate, the expression does not yield any additional insight, but numerical results from the above expression are displayed in Figs. 2–4.

4. Results

To explore the possible behaviors of the system, various sweeps through the parameter space were performed, and results compared between all of the mathematical approximations and the spatially explicit simulations.

First, the proportion \( s^* \) of suitable sites occupied at equilibrium was measured as the clustering \( q_{ss} \) of suitable sites varied between 0 and 1. Other parameter values were \( p_s = 0.5 \) (50% of sites suitable), \( \phi = 10, \mu = 1 \), and \( b_1 = b_2 = 2 \) (giving \( \beta = 0.5 \)). For simulations, 20 independent replicated simulations were run on 400 \( \times \) 400 lattices for each value of \( q_{ss} \), and their results averaged to compute \( s^* \). The same landscape was used for all 20 replicates. Legend: MFA = ordinary mean-field approximation; IMFA = improved mean-field approximation; OPA = ordinary pair approximation; SIM = stochastic spatially explicit simulation.

Fig. 2. The proportion \( s^* \) of suitable sites occupied at equilibrium is shown as the clustering \( q_{ss} \) of suitable sites varies between 0 and 1. Other parameter values were \( p_s = 0.5 \) (50% of sites suitable), \( \phi = 10, \mu = 1 \), and \( b_1 = b_2 = 2 \) (giving \( \beta = 0.5 \)). For simulations, 20 independent replicated simulations were run on 400 \( \times \) 400 lattices for each value of \( q_{ss} \), and their results averaged to compute \( s^* \). The same landscape was used for all 20 replicates. Legend: MFA = ordinary mean-field approximation; IMFA = improved mean-field approximation; OPA = ordinary pair approximation; SIM = stochastic spatially explicit simulation.
0.5 and 0.95. A vertical line is drawn in Fig. 3 separating the results using these two different geometries. Note that the particular geometry of disturbance events only has an impact on the simulations; the pair approximation only perceives block sizes through $\beta$, and the MFA cannot include the correlated disturbance blocks. For the particular results shown in Fig. 3, the traditional MFA gives slightly more accurate predictions than the IMFA over much of the range of the parameter $\beta$. This is due to the fact that $q_{ss} > p_s$ in that figure; if $q_{ss}$ were smaller than $p_s$, the IMFA’s predictions would move down below the traditional version’s predictions and therefore be closer to simulation results (which would also shift down if $q_{ss}$ were decreased).

Fig. 4 displays equilibrium population density as $\beta$ is varied, but with the further assumption that spatial autocorrelation of the habitat distribution is equal to that of disturbances, i.e. $q_{ss} = \beta$. Because $p_s = 0.5$ in this figure, we also have $q_{ss} = \beta$.

Finally, Fig. 5 shows $G(\beta)$, the minimum value of $\phi/\mu$ required for population persistence under the assumption $q_{ss} = \beta$. Results are shown for pair approximations and simulations. The value of $G(\beta)$ was estimated from simulations as follows. Given particular values of the parameters $p_s$ and $q_{ss} = \beta$, the value $\phi = 1$ was initially chosen ($\mu = 1$ was assumed without loss of generality throughout this process). For a given value of $\phi$, eight replicate simulations were run, and if the population persisted in any of the eight runs, we recorded that the population could survive for that value of $\phi$. Note that with $\phi = 1$, the population does not persist, regardless of the values of $q_{ss}$ and $\beta$. The value of $\phi$ was then systematically increased until a value was reached for which the population could survive (in the sense of persisting for at least one out of eight runs). Once such a value for $\phi$ was found, the bisection algorithm was used to estimate the minimum value of $\phi$ for which the population would survive. Due to the stochastic nature of the simulations, different estimates for the critical value of $\phi$ may be produced if the entire process was repeated, but the methods above were deemed sufficient given the computational demands of the spatially explicit simulations. Figs. 4 and 5 together show that when the spatial scale of static
and dynamic disturbances are linked, an intermediate spatial scale of disturbances maximizes equilibrium population density and minimizes the required growth rate for the population to persist over time.

5. Discussion

Exogenous and endogenous spatial correlations have been shown to have important effects on the dynamics of populations and epidemics (e.g. Bolker, 1999, 2003). In particular, local spatial autocorrelation in fixed habitat heterogeneities has been shown to be helpful to locally dispersing populations, as it increases the probability that offspring dropped on the neighbor of a suitable parent site will land on another suitable site (Hiebeler, 2000, 2004). On the other hand, local spatial autocorrelation in dynamic disturbance events has been shown to have a detrimental effect on locally dispersing populations (Hiebeler, 2005b).

One limitation of pair approximations as used in the last two studies cited above (Hiebeler, 2004, 2005b) is that they fail to predict that the population cannot persist, no matter how large the reproduction rate, for some regions of the parameter space involving spatial influences. For example, on landscapes with spatially structured heterogeneous habitat distributions and only single-site mortality/disturbance, when \( q_{as} \) is small enough, suitable sites will be so isolated that almost all reproduction attempts will involve offspring being dropped on unsuitable sites. Patches of suitable sites will be very small and isolated from each other, and those patches will slowly but steadily become empty as their small local populations fluctuate to extinction, no matter how large the birth rate \( \phi \) is. However, in that model, for any value of \( q_{as} > 0 \), there is a critical value \( \phi_c \) such that if \( \phi > \phi_c \), pair approximation predicts that the population will survive (Hiebeler, 2004). For locally dispersing populations with block disturbance events on homogeneous landscapes, as the block sizes go to infinity, causing \( \beta \) to approach 1, simulations show that eventually any finite population will be eliminated by a large disturbance, no matter how large the growth rate \( \phi \) is. However, pair approximations predict that the equilibrium population density will approach \( 1 - 3/(\phi/\mu + 1) \) on a rectangular lattice as \( \beta \rightarrow 1 \) (Hiebeler, 2005b). As long as \( \phi/\mu > 2 \), this will give a positive equilibrium population density.

The combined model explored here includes fixed spatially structured heterogeneities as well as spatially correlated disturbance events. When both effects are included within a single model, pair approximation successfully predicts the existence of a region of the parameter space of \( q_{as} \) and \( \beta \) for which the population cannot survive, no matter how large the fecundity \( \phi \) is. The region of the parameter space satisfying inequality (5) may be referred to as a “negative zone”, as the reproductive rate would need to be negative in order to satisfy the mathematical conditions for persistence, and therefore there is no biologically feasible way for the population to persist. In the limit as \( \beta \rightarrow 1 \), this result indicates that any population on a landscape with \( q_{as} < \frac{1}{3} \) cannot persist regardless of its birth rate \( \phi \). One clear biological explanation for this is that the fragmentation of suitable habitat makes it much more likely that an entire patch of suitable sites will be simultaneously killed by a correlated disturbance event, an effect seen by Kallimanis et al. (2005). A numerical estimate of the boundary of the negative zone given by inequality (5) based on simulations was not computed due to the high computational demands of doing so. Particularly near the border of this region, simulations take extremely long to reach their equilibrium distribution. In a mathematical sense, in every simulation the population will eventually go extinct because it exists on a finite lattice, but the biologically important feature is the time until such extinction occurs. For parameter combinations which lead to what we refer to as “persistence” of the population, the time until stochastic fluctuation to extinction on e.g. a 400 \times 400 lattice as used here may be larger than the age of the universe (unless the nontrivial equilibrium level is very low). With such long timescales to extinction, evolutionary changes would begin to play a role before such stochastic fluctuations to extinction occurred. Although a systematic mapping of the boundaries of the negative zone via simulations was not conducted, some exploration did confirm that the zone existed in roughly the expected region of the parameter space.

Note that in their study Kallimanis et al. (2005) found that increasing spatial autocorrelation of habitat actually had a detrimental effect on populations when disturbance was spatially autocorrelated. At first this apparently disagrees with results from pair approximations here, e.g. the first inequality in (3) which shows that increasing \( q_{as} \) always makes it easier for a population to persist. The apparent disagreement is reconciled by observing that Kallimanis et al. (2005) saw this effect with 140 \times 140 block disturbances on 256 \times 256 lattices, giving \( \beta \approx 0.993 \), far beyond the range of values for which pair approximation is a valid technique. Also, the negative effect of increasing autocorrelation in habitat would almost certainly be reversed if the autocorrelation became strong enough, i.e. if \( q_{as} \) were to become large enough that contiguous patches of suitable habitat were much larger than the spatial scale of disturbance events.

Another feature of biological interest is the behavior of the model when \( q_{as} = \beta \), i.e. the fixed clustering of suitable habitat and the dynamic disturbance have the same spatial scale. Simulation results in Figs. 4 and 5 clearly show that the population persists at its highest levels for intermediate values of this combined spatial scale parameter, and that the critical value for the birth rate \( \phi \) is also lowest (i.e. the population can survive most easily) for intermediate values of the scale parameter. These results indicate that when the scale parameter is very small, the detrimental effect of the fragmentation of suitable habitat dominates the system. As the scale parameter becomes very large, the effect of
large-scale disturbances begins to dominate, despite the presence of large contiguous patches of suitable habitat, and the population again suffers. Pair approximations fail to predict the results as \( q_s = \beta \) becomes large, because in that parameter regime disturbances are having important effects at scales much larger than that pair approximations can capture. Other methods such as improved pair approximation which includes some correlations between nonadjacent sites (Sato et al., 1994) or other moment-closure approximations including structure beyond just pairs of sites (Hiebeler, 1997; Petermann and De Los Rios, 2004) may yield better predictions of the dynamics with large-scale disturbance events.

In natural environments with fragmented habitat, large-scale disturbance, or both, populations would likely evolve other spatiotemporal mechanisms to mitigate the effects of these two negative influences, such as dispersal at larger spatial scales, seed dormancy, or an ability to persist (perhaps with reduced fecundity or increased mortality) in unsuitable sites. Further generalizations of these models will explore these mechanisms.

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