

POPULATIONS ON FRAGMENTED LANDSCAPES WITH SPATIALLY STRUCTURED HETEROGENEITIES: LANDSCAPE GENERATION AND LOCAL DISPERSAL

DAVID HIEBELER¹

Center for Applied Math, 657 Rhodes Hall, Cornell University, Ithaca, New York 14853 USA

Abstract. The goal of this investigation was to study the effects of spatially structured habitat heterogeneities on locally dispersing single-species populations. In this investigation, the environmental heterogeneities were not randomly distributed, but rather were clustered by specifying probabilities of small local configurations of the landscape, as in local structure or pair approximations. This allows the study of landscapes with the same amount of habitat loss but different levels of fragmentation or clustering. I describe a simple algorithm for generating such structured landscapes. Spatially explicit simulations of population models on these landscapes were performed using stochastic cellular automata and compared to predictions from mean-field and pair approximations, for which detailed derivations are presented.

For populations with local dispersal, I show that the spatial correlations of habitat types completely determine equilibrium population density on suitable sites and that the amount of suitable habitat has no effect, precisely the opposite of what the mean-field approximation predicts. When habitat types are randomly distributed on the landscape, the two approximations do almost equally well, and thus the additional complexity of the pair approximation is not justified. However, when habitat types are not randomly distributed, the mean-field approximation gives qualitatively incorrect predictions for population response to varying habitat heterogeneity. Thus, pair approximations combine some of the best features of spatially explicit and implicit models and serve as a useful supplement to those methods for understanding spatially structured ecological systems, especially where environmental heterogeneities are spatially correlated.

Key words: *cellular automata; dispersal; fragmented landscapes; habitat fragmentation; habitat heterogeneity; habitat loss and fragmentation, separating effects; local-structure approximations; mean-field approximations; pair approximations; population models; stochastic spatial models; structured landscapes, algorithm.*

INTRODUCTION

The effects of landscape heterogeneity resulting from the loss and fragmentation of habitats upon biological populations is a problem of great concern to ecologists (Diffendorfer et al. 1995, Bjørnstad et al. 1998), conservation biologists (Fahrig and Merriam 1994, McCullough 1996) and agricultural managers (Topping and Sunderland 1994). There has been growing interest in theoretical studies of habitat fragmentation, and in particular the importance of the spatial configuration of habitat (Adler and Nuernberger 1994, Hanski 1994a, b, Ives et al. 1998). For example, Cantrell and Cosner (1991:320) used reaction-diffusion equations to show that “it is not only the amount of favorable habitat but also its arrangement that determines the overall suitability of the environment.”

Currently, investigations into questions about spatial issues in ecology, and landscape heterogeneity in particular, usually fall into three categories. The first category, spatially implicit models, is the most common

theoretical approach. These models, which include mean-field approximations and spatially implicit meta-population models (Lande 1987, Gilpin and Hanski 1991, Nee and May 1992, May and Nowak 1994, Tilman 1994, Hanski and Gilpin 1997), remove almost all of the detailed spatial structure, and essentially assume that spatial correlations neither exist nor play an important role. The second category, spatially explicit models, is explored via computer simulations (Doak et al. 1992, Dunning et al. 1995, Pulliam and Dunning 1995, Turner et al. 1995, With and Crist 1995, Bascompte and Solé 1996), which are based on detailed maps of the distribution of populations or habitat types. This approach is becoming more popular due to the rapid growth of available computing power. The third category, statistical approaches, is most commonly used in field studies (e.g., Mladenoff et al. 1995, Thomlinson 1995) to describe patterns seen in nature.

Recently, progress has been made toward bridging the gap between spatially implicit and explicit population models by developing analytic models that incorporate a small amount of local spatial structure. Researchers have applied the simplest of these techniques, known as “pair approximations,” to a variety of lattice-

Manuscript received 5 February 1999; accepted 24 April 1999;
final version received 27 May 1999.

¹ E-mail: hiebeler@cam.cornell.edu

based spatial models (Matsuda et al. 1992, Harada and Iwasa 1994, Sato et al. 1994, Harada et al. 1995, Kubo et al. 1996, Levin and Durrett 1996, Hiebeler 1997, Ives et al. 1998). Whereas mean-field approximations assume that no correlations develop between sites in the lattice over time so that one can write down a set of differential or difference equations for the frequencies or probabilities of each state on the lattice, pair approximations involve equations describing the probabilities of all possible state configurations of 2×1 blocks of sites (or another equivalent set of parameters, as explained in the next section). More general versions of these techniques, known as "local-structure theory," have been applied to single-species stochastic spatial population models using even larger blocks of sites, such as 4×1 and 2×2 , thus incorporating even more detailed spatial information (Hiebeler 1997). Alternatives to the lattice-based approach are models often called "incidence-function metapopulation models," based on a description of the sizes and distances between various habitat patches (Adler and Nuernberger 1994, Hanski 1994a, b), and models incorporating spatial correlations that are continuous in space and time (Bolker and Pacala 1997).

In this study, I adapted the techniques of pair approximations to predict the behavior of spatially explicit models that are discrete in time and space, to characterize heterogeneous landscapes with spatial correlations in habitat types, and to generate artificial landscapes with spatially structured heterogeneities. This landscape-generation algorithm allows one to specify the proportion of sites on the landscape that are of various habitat types, and also to specify a parameter indicating the degree of clustering of habitat types. This method can be used to generate structured landscapes for theoretical studies such as the one presented here, and also to design structured landscapes for experimental manipulations in the field (e.g., Bowers et al. 1996, Bjørnstad et al. 1998, Collinge and Forman 1998, Dooley and Bowers 1998).

After many landscape lattices were generated, the behavior of a locally dispersing population on these landscapes was studied. A local-dispersal model was chosen because many natural populations exhibit very localized dispersal (e.g., Price et al. 1994, Topping and Sunderland 1994, Kendrick and Walker 1995, Le Corff 1996), and it is feasible to mathematically analyze this type of dispersal. The behavior of the population model was investigated through spatially explicit simulation models, spatially implicit mean-field approximations, and finally via pair approximations, which incorporated the spatial structure of the environmental heterogeneity as well as local spatial correlations of the population on the landscape. This allows one to separately study the effects of habitat loss and of fragmentation on the population, without the complete spatially explicit description of the landscape others have claimed necessary (e.g., Bascompte and Solé 1996). Note that the

pair-approximation model developed here does not neatly fall into any of the categories of spatial models described in Hanski and Simberloff (1997) such as spatially implicit or explicit, but rather incorporates some aspects of both of these categories. Because developing spatial models in discrete time can require a large amount of bookkeeping (particularly for the pair approximation), detailed developments of the models used here are included.

By using the extreme case of local dispersal and local correlations of habitat types on the landscape, I demonstrate that spatially implicit models (such as mean-field approximations), currently the most common analytic technique for studying spatial models, can give predictions that are qualitatively incorrect when habitat types are not randomly spatially distributed. Nonrandom habitat patterns are probably the norm rather than the exception in nature (e.g., Smith et al. 1993). Thus, the qualitative results from modeling studies based on mean-field approximations (e.g., Lande 1987, Nee and May 1992) may change drastically when landscape structure is taken into account.

THE LANDSCAPES

The landscapes used in this investigation consisted of rectangular lattices of sites, or patches. Each site was characterized by a value indicating its habitat type. For simplicity, only two habitat types were used, labeled "type 0" and "type 1." To completely specify the landscape, one must know the state (habitat type) of every site in the lattice, i.e., one must have a map of the landscape. This is the spatially explicit description. However, there are also more coarse characterizations of the landscape. The simplest is the spatially implicit measure p_0 , the proportion of sites in the lattice that are of type 0. From this, $p_1 = 1 - p_0$, the proportion of sites of type 1, may then also be computed. This is a spatially implicit description because it gives no information at all about the actual spatial arrangement of habitat types. See Table 1 for definitions of many of the terms and symbols used in this study.

A slightly more refined description of the landscape, which incorporates a small amount of information regarding spatial structure, is that which specifies the frequencies or probabilities of all possible 2×1 blocks of sites. Throughout this paper, I will assume complete spatial symmetry, in particular rotational symmetry, i.e., $p[i\ j] = p[j\ i]$, for i and j equal to 0 or 1. There are four 2×1 block probabilities: $p[00]$, $p[01]$, $p[10]$, and $p[11]$, but by spatial symmetry, $p[01] = p[10]$. Also, the four probabilities must sum to 1:

$$p[00] + 2p[01] + p[11] = 1 \quad (1)$$

so in fact there are only two free parameters. For example, one can choose $p[00]$ and $p[01]$ as the two parameters. A convenient way to specify the two free parameters is via the global probability p_0 of seeing a site of type 0, and the conditional probability q_{00} that

TABLE 1. Definitions of terms and symbols.

Term or symbol	Definition
Spatially implicit model	A model that describes the proportions of the landscape that are in various states (such as empty, occupied, or unsuitable), without any information about the locations of such sites
Spatially explicit model	A model based on a complete map of sites, which records the exact locations of each type of site (such as empty, occupied, or unsuitable)
Mean-field approximation	A method for developing a spatially implicit model of the system of interest, by assuming that no spatial corrections develop over time, i.e., that “space doesn’t matter”
Pair approximation	An approximation method that incorporates local spatial correlations between adjacent sites on a lattice
p_0	The amount of suitable habitat on the landscape
q_{00}	The clustering of suitable habitat on the landscape
$p[i]$	The probability that a randomly chosen site on the landscape is of habitat type i
$p[ij]$	The probability that a randomly chosen 2×1 block on the landscape is an $[ij]$ block of habitat types
$P[i]$	The probability that a randomly chosen site on the lattice in the populations model is in state i ($0 = \text{empty}$, $1 = \text{unsuitable}$, $2 = \text{occupied}$)
$P[ij]$	The probability that a randomly chosen 2×1 block on the lattice in the population model is an $[ij]$ block
γ	In the pair approximation model, the probability that an empty site does <i>not</i> get colonized by any of three neighbors whose state is unknown (defined in Eq. 15)
ϕ	Fecundity (note that this parameter also incorporates aspects of dispersal and establishment). In this study, $\phi = 0.5$
μ_i	Population mortality during a time step on a site of habitat type i . In this study, $\mu_0 = 0.3$ and $\mu_1 = 1$
ρ	Normalized population density, i.e., the proportion of suitable sites that are occupied by the population

a randomly chosen neighbor of a type-0 site will also be of type 0, or $p[00]0^*$ in the notation of Hiebeler (1997), where “*” is a placeholder indicating that we are not specifying the value of that site. Thus, we see that the 2×1 characterization of the lattice specifies not only the proportion of sites that are of type 0, but also a measure of the spatial correlation or clustering of the types of adjacent sites. Note that when the spatial distributions of the two habitat types is random, then $q_{00} = p_0$, i.e., the conditional probability that a neighbor of a type-0 site is also of type 0 is simply p_0 .

Given the 2×1 block probabilities $p[00]$ and $p[01]$, one can translate to the global probability and clustering conditional probability as follows:

$$p_0 = p[00] + p[01] \quad (2)$$

$$q_{00} = p[00]/p_0. \quad (3)$$

Note that Eq. 2 is a special case of the general relation

$$p[i] = \sum_j p[ij] \quad (4)$$

which can be used to obtain any single-site global probability from the distribution of 2×1 block probabilities.

Similarly, one can translate in the opposite direction:

$$p[00] = p_0 q_{00} \quad (5)$$

$$p[01] = p_0(1 - q_{00}). \quad (6)$$

From Eq. 1, one can then calculate

$$p[11] = 1 - p[00] - 2p[01] = 1 + p_0(q_{00} - 2). \quad (7)$$

Note that Eq. 7 requires $0 \leq 1 + p_0(q_{00} - 2) \leq 1$ in order to define a valid probability. When solved for q_{00} , this constraint becomes

$$q_{00} \geq 2 - 1/p_0. \quad (8)$$

The intuitive explanation of this constraint is that when a large proportion of the habitat is of type 0 (p_0 is large), then it is fairly likely that a type-0 site will have some neighbors that are also of type 0 (q_{00} cannot be too small). Note that when $p_0 < 0.5$, the constraint vanishes, and any value of q_{00} is possible.

Given a landscape image, one can measure p_0 and q_{00} (or equivalently, the 2×1 block probabilities $p[ij]$) in order to give a simplified description of the landscape that captures some of the spatial structure. On the other hand, given values for p_0 and q_{00} , one can construct a landscape that has the given characterization. This is more difficult than constructing a random landscape with a specified proportion p_0 of type-0 sites, but can be achieved through the following procedure:

1) Given p_0 and q_{00} , compute the desired 2×1 block probabilities $p[ij]$ using Eqs. 5–7.

2) Generate a random lattice that has the correct proportion p_0 of sites of type 0, e.g., by setting each site’s state to 0 independently with probability p_0 . Then, measure the 2×1 block probabilities in the lattice by looking at the four neighbors of each site. Denote the measured block probabilities by $\hat{p}[ij]$. On the initial randomly generated lattice where the states of sites are independently chosen, one will find $\hat{p}[00] = p_0^2$,

$\hat{p}[11] = p_1^2$, and $\hat{p}[01] = p_0 p_1$, with slight deviations from these values possible due to the randomness of the algorithm and finite size of the lattice.

3) Next, select a site at random in the lattice. Compute the 2×1 block probabilities that would result on the lattice from changing the site's state (from 0 to 1, or 1 to 0). If making this change will move the lattice's 2×1 probabilities closer to the desired probabilities, change the state of the site; otherwise, leave the site in its current state. To calculate the difference D between the measured and desired block probabilities, use the following expression, which is simply the mathematical norm $\|p - \hat{p}\|_1$:

$$D = |p[00] - \hat{p}[00]| + 2 |p[01] - \hat{p}[01]| + |p[11] - \hat{p}[11]|.$$

4) Choose another site at random (with replacement) and try again, i.e., return to step 3. Continue selecting sites and possibly changing their values in this way, until the difference D between the lattice's measured 2×1 probabilities and the desired probabilities is less than a specified tolerance, or until some specified maximum number of iterations has been performed.

This procedure will generate a landscape with the desired 2×1 block probabilities. However, as will be seen later (*Discussion*, below), the landscape may contain features at larger spatial scales as well. Note that the measured value of p_0 in the landscape may deviate from its initial correct value as the values of sites are changed. However, when the algorithm converges on a landscape with a small deviation D in the 2×1 block probabilities, then the measured values of p_0 and q_{00} will also converge to values very close to their desired values; this follows from Eqs. 2 and 3. The algorithm converges very quickly when the difference between p_0 and q_{00} is not very large; if the difference is large, more iterations are usually required. In very extreme cases, the algorithm may fail to converge, as will be discussed later (*Results*, below).

This method could be loosely described as an asynchronous analog of the method described in Mangel and Adler (1994), but that avoids the complex rescalings necessary in their method. Other methods for generating landscapes with spatially structured heterogeneities include those that distribute habitat types in regular or random patterns but at multiple scales (Lavoire et al. 1994, Neuhauser 1998), algorithms that generate fractal patterns (With et al. 1997), and methods that distribute habitat patches in regular or clustered ways across a landscape based on the distances between patches (Deutschman et al. 1993, Adler and Nuernberger 1994).

Fig. 1 displays several landscapes generated using the algorithm presented here, all of which have $p_0 = 0.3$, i.e., 30% of the sites are of type 0 (white) and 70% are of type 1 (black). The various landscapes were generated using different values of the clustering parameter

q_{00} . The landscape in the upper right part of the figure has $q_{00} = p_0 = 0.3$, i.e., randomly distributed habitat types. For larger values of q_{00} , the habitat types are more clustered, forming large homogeneous areas in the landscape. For smaller values of q_{00} , the two types of habitat are more mixed, in patterns that avoid placing too many sites of the same type next to each other. If we think of the black sites as disturbed habitat, we see that the 2×1 probability characterization, particularly when using the p_0 and q_{00} parameterization, allows one to separately characterize the loss and fragmentation of habitat on a landscape. Fig. 2 shows a single large composite landscape with all possible values of p_0 and q_{00} .

THE POPULATION MODEL

The goal of this investigation was to study the effects of spatially structured heterogeneities on locally dispersing single-species populations on the landscape. The population model used was a discrete-time version of the basic contact process (Durrett and Levin 1994, Hiebeler 1997), modified slightly to respond to the habitat types of the landscape. This is a patch-occupancy model, where each site on the lattice contains a binary state variable, indicating whether the species is present or absent at that site (in addition to the binary state variable indicating the habitat type of the site). During each time step, two things happen:

1. *Fecundity/Dispersal/Establishment.*—First, every occupied site sends propagules to each of its four adjacent neighbors, independently each with probability ϕ . Thus, the number of propagules produced in one time step by an occupied site follows a binomial ($n = 4$, $p = \phi$) distribution (so for example with $\phi = 0.5$, an occupied site produces an average of two propagules per time step). If one or more propagules lands on an empty site, that site becomes occupied. This step also implements a nonlinear density dependence through competition for space, because if multiple propagules land on an empty site all but one are wasted, as are all propagules that land on an occupied site. For simplicity ϕ is simply referred to as a "fecundity parameter" hereafter, even though it incorporates aspects of dispersal and establishment as well.

2. *Mortality.*—Next, mortality occurs. Each site in the lattice undergoes mortality (i.e., the population at that site is removed—the site's habitat type is not changed) independently with probability μ_i on sites of type i (for $i = 0, 1$). For simplicity, in this study I always fixed $\mu_1 = 1$, i.e., habitat type 1 was completely unsuitable. Note that the habitat types of sites do not change over time; that is, the environmental heterogeneity is fixed.

This spatially explicit model was then studied via computer simulations, using stochastic cellular automata (see, e.g., Caswell and Etter 1993) on a 180×180 lattice with wraparound boundaries (i.e., on a torus). Since exploration of the simulation model showed

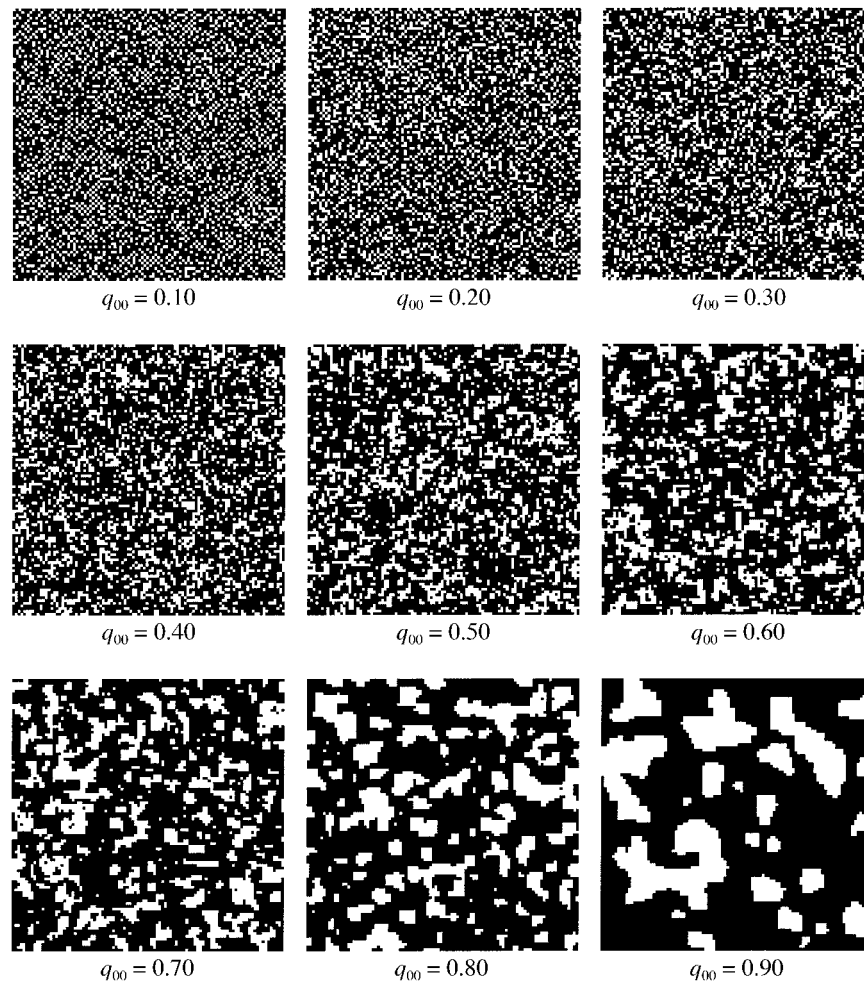


FIG. 1. Several artificially generated landscapes are shown, each of which has 30% of the sites of type 0 (white) and 70% of type 1 (black). The clustering parameter q_{00} (see *The landscapes*) was varied from 0.10 (very few sites of the same type next to each other) to 0.90 (a large degree of clustering; adjacent sites are often of the same type). The landscape in the upper right has $p_0 = q_{00} = 0.30$; the habitat types are randomly distributed in this case. These landscapes are 100×100 for clarity; 180×180 lattices were used for the actual simulations.

that the initial population density had no significant effects on equilibrium density, the simulations were always begun with 50% of the suitable sites occupied, chosen at random. On each time step, the proportion of suitable (type-0) sites that were occupied, known as the “normalized patch occupancy probability” ρ_t , was measured. The simulation was run until the least-squares regression line of ρ_t vs. time over the last 100 time steps had a slope < 0.001 , an indication that the population density had converged to equilibrium. At that time, the value of ρ_t averaged over the final 10 time steps was recorded as the equilibrium value of ρ for the simulation. Fig. 3 shows a sample configuration of the lattice after reaching equilibrium.

APPROXIMATIONS

Mean field approximation

One can write down spatially implicit mean-field equations to approximate the population model on the

heterogeneous landscape, although the mean-field approximation fails in two ways: it does not account for the spatial clustering of habitat types on the landscape, nor the clustering of the population within patches of suitable landscape. Since type-1 sites are unsuitable (because $\mu_1 = 1$), any given site on the lattice may be in one of three states: 0 (empty, suitable type-0 site), 1 (unsuitable type-1 site), or 2 (occupied, suitable type-0 site). The local-dispersal mean-field approximation (Hiebeler 1997) assumes that no spatial correlations develop over time between sites in the lattice, but otherwise retains the details of the spatially explicit model. This is equivalent to running the detailed spatial simulation, but randomly shuffling the sites on the lattice between each time step to remove any spatial correlations. Under this model, one can write down a set of nonlinear difference equations to describe the probabilities of a given site being in each state on the next time step, $P_{t+1}[i]$ for $i = 0, 1, 2$, given their probabilities

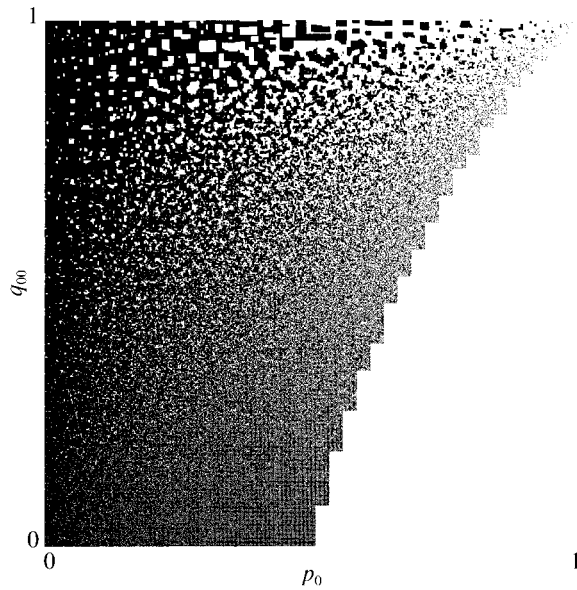


FIG. 2. A composite landscape with varying values of the amount of suitable habitat p_0 (horizontal axis) and its clustering q_{00} (vertical axis). This allows one to see the patterns of habitat distribution that result from various combinations of the two landscape parameters. For example, the region across the top of the figure has highly clustered patterns, but with varying amounts of suitable habitat available from left to right. The large white area in the lower right represents invalid landscapes, that is, values of the parameters p_0 and q_{00} which do not satisfy Inequality 8.

at the current time. (For clarity, capital P will be used to denote probabilities involving the population model, while lower case p will denote probabilities involving only the landscape heterogeneities as in *The landscapes* section, above.) However, $P_{t+1}[1] = P_t[1] = p_1 = 1 - p_0$ (unsuitable sites remain fixed through time), and the three values must sum to one, i.e., $P_t[0] + P_t[1] + P_t[2] = 1$, which may be solved for

$$P_t[0] = 1 - P_t[1] - P_t[2] = p_0 - P_t[2]. \quad (9)$$

Therefore, only one independent equation is really needed:

$$\begin{aligned} P_{t+1}[2] &= P_t[0]P(0 \rightarrow 2) + P_t[2]P(2 \rightarrow 2) \\ &= P_t[0](1 - (1 - P_t[2]\phi)^4)(1 - \mu_0) \\ &\quad + P_t[2](1 - \mu_0) \\ &= (p_0 - P_t[2])(1 - (1 - P_t[2]\phi)^4)(1 - \mu_0) \\ &\quad + P_t[2](1 - \mu_0) \end{aligned} \quad (10)$$

where $P(2 \rightarrow 2) = 1 - \mu_0$ is the probability that an occupied site remains occupied until the next time step (i.e., survives the mortality phase), and $P(0 \rightarrow 2) = (1 - (1 - P_t[2]\phi)^4)(1 - \mu_0)$ is the probability that an empty site is colonized by at least one of its four neighbors and then survives mortality. The latter equation follows from the mean-field assumption of indepen-

dence of sites, i.e., the assumption that any given neighbor of the empty site under consideration is occupied with probability $P_t[2]$. This implies that the empty site will receive a propagule from that neighbor with probability $P_t[2]\phi$, and thus will have probability $(1 - P_t[2]\phi)^4$ of not being colonized by any of its four neighbors.

The proportion of suitable sites that are occupied, i.e., the normalized patch-occupancy probability, may then be calculated as

$$\rho_t = \frac{\text{no. of occupied sites}}{\text{no. of suitable sites}} = \frac{P_t[2]}{P_t[0] + P_t[2]}. \quad (11)$$

Eq. 10 is nonlinear, but may easily be solved numerically to find its fixed point $P^*[2]$. Once the fixed point has been found, the equilibrium value of ρ , denoted ρ^* may then be calculated using Eqs. 9 and 11 as $\rho^* = P^*[2]/p_0$. Note that q_{00} , the clustering parameter of the landscape, does not appear anywhere in the mean-field equations, because of the spatially implicit nature of this approximation.

Finally, note that the spatially implicit mean-field approximation developed here is a local-dispersal approximation, which simply assumes that the sites of the lattice are randomly shuffled between each time step. Another, more common technique for deriving spatially implicit approximations is the infinite-dispersal approximation, which assumes that propagules disperse randomly across the landscape. That is the technique used for example by Tilman (1994), since it is the most straightforward technique for continuous-time models. The infinite-dispersal mean-field approximation would differ only slightly from the local-dispersal approximation developed here. Both approxi-

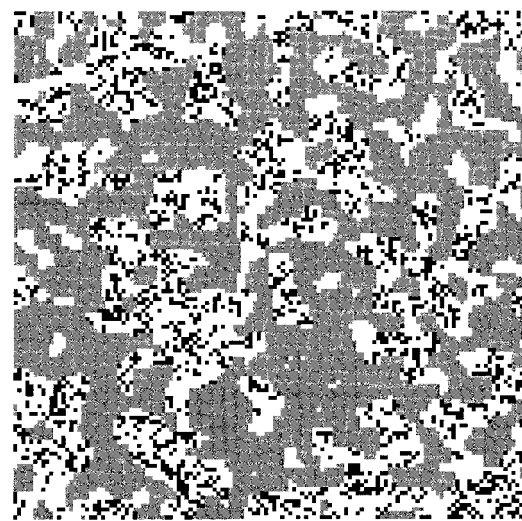


FIG. 3. The configuration of the lattice after reaching equilibrium, with $\phi = 0.5$, $\mu_0 = 0.5$, $\mu_1 = 1$, $p_0 = 0.5$, and $q_{00} = 0.90$. White represents empty type-0 (suitable) sites, gray represents type-1 (unsuitable) sites, and black represents occupied type-0 sites.

mations would have the same qualitative behavior (Hiebeler 1997), and the linear terms would in fact be the same; thus stability analyses of the linearized systems (e.g., Edelstein-Keshet 1988:41–44) would be identical.

Pair approximation

Because the spatial configuration of habitat types on the landscape plays a significant role in the dynamics of the population (as will be seen in *Results*, below), a more appropriate analytic technique for predicting the behavior of the spatially explicit simulation model is the pair approximation, also known as the 2×1 local-structure approximation. In this approach, one writes down a set of equations describing $P_i[ij]$, the frequencies or probabilities of the 2×1 blocks $[ij]$, for i and j taking values 0, 1, and 2, where these three values represent empty, unsuitable, and occupied sites, respectively, as in the previous subsection. Although there are technically nine such probabilities, various symmetry assumptions and constraints reduce the number of independent probabilities to only three. The three pair-approximation equations, derived in Appendix 1, are as follows:

$$P_{t+1}[00] = P_t[00]\{\gamma^2(1 - \mu_0)^2 + 2\gamma\mu_0(1 - \mu_0)\} + 2P_t[02]\gamma\mu_0(1 - \phi)(1 - \mu_0) + \mu_0^2 p_0 q_{00} \tag{12}$$

$$P_{t+1}[01] = P_t[01]\gamma(1 - \mu_0) + \mu_0 p_0(1 - q_{00}) \tag{13}$$

$$P_{t+2}[02] = P_t[00]\{\gamma(1 - 2\mu_0)(1 - \mu_0) - \gamma^2(1 - \mu_0)^2\} + P_t[02]\gamma(1 - 2\mu_0)(1 - \mu_0)(1 - \phi) + \mu_0(1 - \mu_0)p_0 q_{00}. \tag{14}$$

where

$$\gamma = \left(1 - \frac{\phi P_t[02]}{P_t[0]}\right)^3 = \left(1 - \frac{\phi P_t[02]}{P_t[00] + P_t[01] + P_t[02]}\right)^3. \tag{15}$$

The other probabilities $P_{t+1}[11]$, $P_{t+1}[12]$, and $P_{t+1}[22]$ may be computed as shown in Eqs. A.1, A.8, and A.9 in Appendix A. Note that the three Eqs. 12–14 are equivalent to the set of equations involving many thousands of terms that one would obtain by following the techniques described in Hiebeler (1997); but by rearranging and grouping the terms, one can instead write down a more compact set of equations as above. Also note that the above equations capture some of the spatial correlations that exist in the habitat distribution on the landscape, the distribution of the population on the landscape, and even spatial correlations between the two. Also, although developed independently, this approach is very similar to that followed by Ives et al. (1998), although in their model they also considered

diagonally adjacent sites for habitat heterogeneity and population dispersal. See Appendix A for further explanation of differences between the pair approximation developed here and that in Ives et al. (1998).

These equations may again easily be solved numerically to find the equilibrium (fixed point). Next, note that Eq. 4 is just as valid with population-model probabilities as it was with landscape probabilities:

$$P_t[i] = \sum_j P_t[ij]. \tag{16}$$

Thus, one can use Eq. 16 to compute the probabilities $P_t[0]$ and $P_t[2]$, and then compute the equilibrium value ρ^* using Eq. 11 as before.

RESULTS

Now that the two methods for approximating the population dynamics on structured heterogeneous landscapes have been developed, they can be compared to the behavior of the actual spatially explicit simulations. The population model on heterogeneous landscapes was investigated for landscapes with various values of the parameters p_0 (the proportion of sites that are of types 0) and q_{00} (the clustering parameter), with mortality parameters $\mu_0 = 0.3$, $\mu_1 = 1$ (type-1 sites unsuitable), and fecundity $\phi = 0.5$. Fig. 4A shows the equilibrium normalized patch-occupancy probability ρ^* as predicted by the mean-field approximation. As explained earlier (see *Approximations*), in the mean-field approximation ρ^* depends only on the amount of habitat available p_0 (on the horizontal axis), and not on the clustering parameter q_{00} (vertical axis).

Fig. 4B shows the equilibrium normalized patch-occupancy probability as predicted by the pair approximation. Observe that the pair approximation predicts that ρ^* depends only on the landscape clustering parameter q_{00} and not at all on the amount of habitat available p_0 , i.e., entirely the opposite qualitative behavior of the mean-field approximation. This result can be derived analytically from Eqs. 12–14, as shown in Appendix B. Intuitively, this result follows from the fact that occupied patches (which are by necessity suitable—i.e., habitat type 0) only disperse propagules to the four adjacent sites; thus, the conditional probability that a neighboring site is also suitable (which is precisely q_{00}) is all that really matters.

Fig. 4C shows the equilibrium normalized patch-occupancy probability as measured from the actual simulations. One can see that the results qualitatively match the pair-approximation predictions much more closely than the mean-field approximations, i.e., ρ^* depends primarily on the clustering parameter q_{00} and very little on the habitat availability p_0 . For large enough values of q_{00} , the population essentially perceives the landscape as being undamaged at a local level—there may be a reduced amount of habitat available, but what remains can be utilized as effectively as habitat patches on an undamaged landscape. In the limit

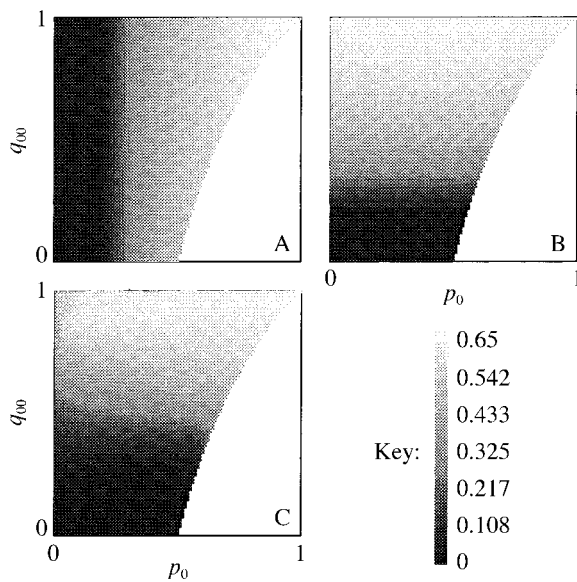


FIG. 4. Equilibrium normalized patch occupancy ρ^* (the proportion of suitable sites that are occupied) as a function of the proportion of suitable habitat p_0 (horizontal axis) and the habitat clustering parameter q_{00} (vertical axis). The white area in the lower-right portion of each picture represents invalid landscapes, that is, values of the parameters p_0 and q_{00} which do not satisfy Inequality 8. (A) Predictions from the mean-field approximation. Observe that ρ^* depends only on the amount of habitat available, p_0 , and not its spatial arrangement q_{00} . (B) Predictions from the pair approximation. Observe that ρ^* depends only on the habitat-clustering parameter q_{00} , and not on the amount of habitat available, p_0 . (C) Measurements from simulations. For each combination of landscape parameters, five replicate simulations were performed on independent 180×180 unit landscapes with the given parameters as described in *The population model*, and their results averaged. Observe that ρ^* depends primarily on the habitat-clustering parameter q_{00} , and only very slightly on the amount of habitat available, p_0 , as was also predicted by the pair approximation.

as $q_{00} \rightarrow 1$, the behavior of the system will approach that of a population on an undamaged (perfect) landscape. As q_{00} becomes smaller, the proportion of suitable sites that are occupied at equilibrium diminishes. This is because habitat fragmentation is playing a larger role—with smaller values of q_{00} , suitable sites are more often bordered by unsuitable sites. Thus, propagules from occupied sites are often wasted by being dropped on unsuitable sites.

The small region in the upper-left area of Fig. 4C where the population does more poorly than expected from q_{00} alone is due to problems generating the landscapes. The landscape-generation algorithm has trouble producing landscapes only when there is such a large difference between p_0 and q_{00} , i.e., when there is very little habitat available ($p_0 < 0.05$) but very high clustering ($q_{00} > 0.8$). In this situation the algorithm actually produced landscapes with slightly less clustering than was desired, which then reduced the normalized

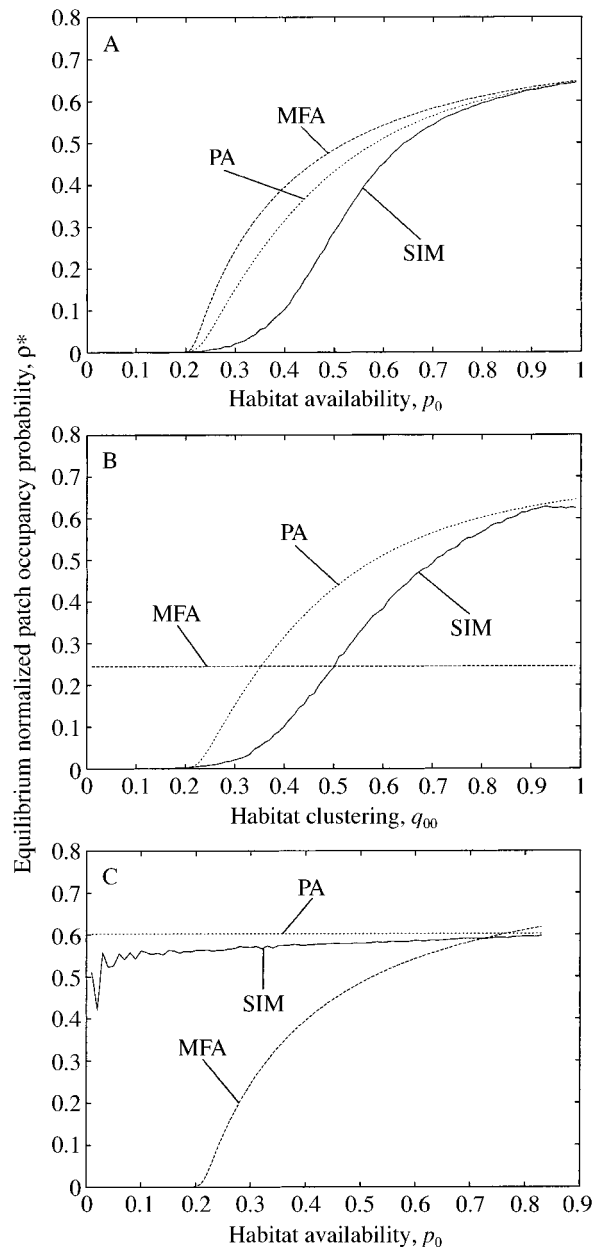


FIG. 5. Equilibrium normalized patch occupancy, ρ^* (the proportion of suitable sites that are occupied), as measured from simulations (SIM), and predicted by the mean-field approximation (MFA) and pair approximation (PA), is plotted against the chosen landscape parameter. The distribution of habitat types is: (A) random, i.e., $p_0 = q_{00}$; (B) fixed amount of habitat available ($p_0 = 0.3$) with varying clustering q_{00} ; and (C) fixed clustering ($q_{00} = 0.8$) with varying amount p_0 of habitat available. Simulations were performed as in Fig. 4C.

population density accordingly. For the vast majority of the parameter space, the landscape-generation algorithm converges rapidly and produces landscapes with the desired structure.

Finally, Fig. 5 shows the results from simulations as

well as predictions from the mean-field approximation and pair approximation, for three types of landscapes: landscapes with randomly distributed habitat types (i.e., $p_0 = q_{00}$) and varying amounts of habitat available; landscapes with a fixed amount of habitat available ($p_0 = 0.3$) with varying degrees of clustering; and landscapes with a fixed amount of clustering ($q_{00} = 0.8$) and varying amounts of habitat available. The randomly structured landscapes allow a comparison of the two approximations when the spatial distribution of habitat types matches the assumption of independence made by the mean-field approximation. As shown in Fig. 5A, on randomly structured landscapes, the pair approximation does not do significantly better than the mean-field approximation; for example, both methods accurately predict the critical value of $p_0 \approx 0.2$ above which the population will persist. Thus, the extra complexity of the pair-approximation model is not warranted in situations where habitat types are randomly distributed across the landscape. However, such situations are probably somewhat rare, as habitat types in nature are often clustered (e.g., Smith et al. 1993). As Fig. 5B and C show, when landscape structure is varied in a nonrandom way, the mean-field approximation gives qualitatively incorrect behavior. Thus, the results of theoretical studies based on mean-field approximations (e.g., Lande 1987, Nee and May 1992), would likely not be applicable to situations where habitat types are not randomly distributed. Also, note that even for randomly distributed heterogeneities, both methods of approximation (dashed lines) overestimate the normalized patch-occupancy probability ρ as measured from the simulations (solid line).

DISCUSSION

I have explored the behavior of a simple discrete stochastic single-species population model with local dispersal on heterogeneous landscapes via spatially explicit simulations, spatially implicit analytic approximations (i.e., the mean-field approximation), and pair approximations that incorporate a small amount of spatial structure. The techniques of pair approximations have proven useful for characterizing spatial correlations in heterogeneous landscapes, as well as for generating new landscape maps with specified amounts of two habitat types and their clustering. These generated landscapes may be used for spatially explicit theoretical studies that require a complete landscape map, as well as for analytic approximations based on pair approximations as shown here. The pair-approximation model directly incorporates information about spatial correlations of habitat types, the population, and even correlations between the two. Finally, note that the landscapes generated here can also be applied to the experimental design of field studies that manipulate habitat in nonrandom ways (e.g., Collinge and Forman 1998, Dooley and Bowers 1998).

It is also apparent from this investigation that the classification of metapopulation or patch-occupancy models as either spatially implicit or explicit (Hanski and Simberloff 1997) is in fact not simply a dichotomy. Instead there is room between the two extremes for models that incorporate varying degrees of spatial structure, such as the simple local correlations used here, or possibly even more spatial information (Hiebler 1997).

For the specific model studied here, I have shown that with local dispersal and the characterization of habitat as either suitable or unsuitable, only the habitat clustering affects equilibrium normalized population density, while the actual amount of habitat available has no effect (assuming there is enough habitat available to avoid strong finite-size effects). Many natural populations do exhibit very localized dispersal, although in such situations there may be very rare long-distance dispersal events (e.g., Kendrick and Walker 1995). The population behavior may begin to show some dependence on p_0 (the amount of suitable habitat), depending on the frequency of such long-distance dispersal events (*unpublished manuscript*). Similarly, the behavior of the population may show some dependence on p_0 if it were able to survive in the unsuitable habitat, perhaps with reduced fecundity and increased mortality. However, the latter change would complicate the pair approximation somewhat, requiring the addition of a new state representing occupied type-1 habitat sites, and seven independent equations would be needed rather than just three.

The model may be modified in other ways as well. In particular, neither the landscape-generation model nor the population model depend strongly on the geometry of the lattice. For example, the exact same techniques can be used to generate clustered landscapes on hexagonal lattices where each site has six neighbors, provided one measures the 2×1 block probabilities by looking at all six neighbors of each site. Also, the pair approximation of the population model on a hexagonal lattice would be the same (assuming an occupied site sends propagules to each of its six neighbors with probability ϕ), except that the exponent in Eq. 15 defining γ would be 5 rather than 3. Equations 12–14 would be unchanged on a hexagonal lattice, as would all of the conclusions I have drawn from the model. The model may also be reformulated in continuous time with the same results, and in fact the simulation and approximation models are all much simpler in continuous time.

Although the concepts of pair approximations have only been applied in this paper to a single-species population model on structured heterogeneous landscapes, the potential applications are much broader. Of course pair approximations are useful for bringing more realism to theoretical studies that often assume a random distribution of populations or habitat types on a landscape. Basic theoretical investigations of dispersal

(e.g., Waser 1985, 1987), which involve propagules moving around in a lattice until finding an empty site, were developed based on the importance of the proportion of empty sites. However, in fact they really only depend on the conditional probability of seeing an empty site when moving to the neighbor of the site currently under consideration. Similarly, many of the results of percolation theory (Plotnick and Gardner 1993, Bascompte and Solé 1996), such as the distribution of patch sizes or number of patches, while traditionally formulated based on the probability of a site being suitable (p_0), should in fact be expressed in terms of q_{00} (the clustering parameter) since patches are simply collections of connected, adjacent, suitable sites. In short, people have been thinking quite often about local spatial correlations of the kind used here, even though it was often not explicitly recognized. This is because people have generally operated only within the context of random distributions, i.e., situations where $p_0 = q_{00}$, and then have thought in terms of p_0 for their studies. Recognizing the important role of q_{00} allows one to begin moving away from this oversimplified assumption that there is no spatial structure in the world.

Although the mean-field approximation failed to capture the qualitative behavior of the population model on structured heterogeneous landscapes, it fared reasonably well when the approximation's inherent assumption of randomly distributed habitat was met. In situations where this is a reasonable assumption, the extra effort of the pair approximation would not be justified, unless one were specifically interested in studying the spatial correlations of the population itself, which the mean-field approximation cannot do. We see from Fig. 5A that on landscapes with randomly distributed habitat, both approximation techniques overestimate the normalized equilibrium population density as measured from the explicit simulations. This is usually the case for any kind of analytic approximation that is spatially implicit or only spatially explicit to a small degree, since it does not take into account the full degree of clustering seen in the simulations. Underestimating the degree of clustering causes the approximations to overestimate recruitment, because in the simulations more propagules are being wasted by falling on occupied sites than the approximation methods would predict, and thus recruitment to empty suitable patches is reduced. The pair approximation does slightly better than the mean-field approximation even on random landscapes, since at least it does incorporate some amount of population clustering.

Another factor that may lead to inaccuracies in the approximation methods for some landscapes is the emergence of spatial structure at much larger scales than the 2×1 scale used to characterize or even generate them in this study. On some landscapes, for example the one shown in Fig. 3, there are several regions

consisting of small groups of roughly 4–10 suitable sites, surrounded by an unsuitable boundary. Such regions are small enough to be prone to local extinctions, and they cannot be recolonized because of the assumption $\mu_1 = 1$, i.e., complete unsuitability of type-1 sites on the landscape. Yet these configurations occur at a scale too large to be accurately predicted by the 2×1 pair approximation, an effect that likely contributes to this method's overestimation of ρ . Incorporating landscape effects and the spatial structure of populations at multiple spatial scales into a single analytic approximation method remains one of the greatest difficulties of spatial models.

When studying a spatial system in ecology, the choice of methodology strongly depends on the system. For a system that exhibits local dispersal on a heterogeneous landscape where habitat types are not randomly distributed, the pair approximation is a practical theoretical technique. If dispersal occurs at a very large scale relative to habitat heterogeneity, or if habitat types are randomly distributed on the landscape, then a spatially implicit mean-field approximation would be more appropriate. In situations where dispersal occurs at intermediate scales, spatially explicit simulations may be required, or another modeling technique (Adler and Nuernberger 1994, Hanski 1994a, b), although it may also be possible to extend the pair approximations to handle this case as well.

Finally, the techniques of pair approximations used here capture some of the spatial structure of spatially explicit models. These approximations are often slightly too complex for complete analytic solution (though in continuous time, analytic solutions are often more feasible); however, they can generally be implemented and solved numerically almost as efficiently as spatially implicit models such as mean-field approximations or spatially implicit metapopulations. Thus, they combine some of the attractive features from both spatially implicit and explicit methods, and may be useful for better understanding a variety of spatial issues in ecology such as dispersal and environmental heterogeneity.

ACKNOWLEDGMENTS

This work was conducted with financial support from a graduate fellowship funded by NSF training grant BIR-9113307, "The Dynamics of Heterogeneous Ecological and Evolutionary Systems," and by U.S. Environmental Protection Agency STAR graduate fellowship U-915235-01-0, both administered by Cornell University with invaluable help from Dolores Pendell. I am grateful to Jianmei Wang, David Winkler, Ben Bolker, Mark Lewis, Fred Adler, Laura Stenzler, Becca Safran, Stephen Ellner, and an anonymous reviewer for comments on early drafts of the manuscript.

LITERATURE CITED

- Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* **45**:41–75.
- Bascompte, J., and R. V. Solé. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology* **65**:465–473.

- Bjørnstad, O. N., H. P. Andreassen, and R. A. Ims. 1998. Effects of habitat patchiness and connectivity on the spatial ecology of the root vole *Microtus oeconomus*. *Journal of Animal Ecology* **67**:127–140.
- Bolker, B., S. W. Pacala. 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theoretical Population Biology* **52**: 179–197.
- Bowers, M. A., S. F. Matter, J. L. Dooley, Jr., J. L. Dauten, and J. A. Simpkins. 1996. Controlled experiments of habitat fragmentation: a simple computer simulation and a test using small mammals. *Oecologia* **108**:182–191.
- Cantrell, R. S., and C. Cosner. 1991. The effects of spatial heterogeneity in population dynamics. *Journal of Mathematical Biology* **29**:315–338.
- Caswell, H., and R. J. Etter. 1993. Ecological interactions in patchy environments: from patch occupancy models to cellular automata. Pages 93–109 in T. Powell, S. Levin, and J. Steele, editors, *Patch dynamics*. Springer-Verlag, New York, New York, USA.
- Collinge, S. K., and R. T. T. Forman. 1998. A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. *Oikos* **82**:66–84.
- Deutschman, D. H., G. A. Bradshaw, W. M. Childress, K. L. Daly, D. Grünbaum, M. Pascual, N. H. Schumaker, and J. Wu. 1993. Mechanisms of patch formation. Pages 184–209 in T. Powell, S. Levin, and J. Steele, editors, *Patch dynamics*. Springer-Verlag, New York, New York, USA.
- Diffendorfer, J. E., M. S. Gaines, and R. D. Holt. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology* **76**:827–839.
- Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theoretical Population Biology* **41**:315–336.
- Dooley, J. L., Jr., and M. A. Bowers. 1998. Demographic responses to habitat fragmentation: experimental tests at the landscape and patch scale. *Ecology* **79**:969–980.
- Dunning, J. B., Jr., B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* **5**:3–11.
- Durrett, R., and S. A. Levin. 1994. Stochastic spatial models: a user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London* **B 343**:329–350.
- Edelstein-Keshet, L. 1988. *Mathematical models in biology*. McGraw-Hill, New York, New York, USA.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50–59.
- Gilpin, M. E., and I. Hanski, editors. 1991. *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, San Diego, California, USA.
- Hanski, I. 1994a. Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* **9**:131–135.
- Hanski, I. 1994b. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**:151–162.
- Hanski, I., and M. E. Gilpin, editors. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in I. Hanski and M. E. Gilpin, editors, *Metapopulation dynamics: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Harada, Y., H. Ezoe, Y. Iwasa, H. Matsuda, and K. Sato. 1995. Population persistence and spatially limited social interaction. *Theoretical Population Biology* **48**:65–91.
- Harada, Y., and Y. Iwasa. 1994. Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Researches on Population Ecology* **36**:237–249.
- Hiebeler, D. E. 1997. Stochastic spatial models: from simulations to mean field and local structure approximations. *Journal of Theoretical Biology* **187**:307–319.
- Ives, A. R., M. G. Turner, and S. M. Pearson. 1998. Local explanations of landscape patterns: Can analytical approaches approximate simulation models of spatial processes? *Ecosystems* **1**:35–51.
- Kendrick, G. A., and D. I. Walker. 1995. Dispersal of propagules of *Sargassum* spp. (Sargassaceae: Phaeophyta): observations of local patterns of dispersal and consequences for recruitment and population structure. *Journal of Experimental Marine Biology and Ecology* **192**:273–288.
- Kubo, T., Y. Iwasa, and N. Furumoto. 1996. Forest spatial dynamics with gap expansion: total gap area and gap size distribution. *Journal of Theoretical Biology* **180**:229–246.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**:624–635.
- Lavorel, S., R. V. O'Neill, and R. H. Gardner. 1994. Spatio-temporal dispersal strategies and annual plant species coexistence in a structured landscape. *Oikos* **71**:75–88.
- Le Corff, J. 1996. Establishment of chasmogamous and cleistogamous seedlings of an ant-dispersed understory herb, *Calathea micans* (Marantaceae). *American Journal of Botany* **83**:155–161.
- Levin, S. A., and R. Durrett. 1996. From individuals to epidemics. *Philosophical Transactions of the Royal Society of London* **B 351**:1615–1621.
- Mangel, M., and F. R. Adler. 1994. Construction of multi-dimensional clustered patterns. *Ecology* **75**:1289–1298.
- Matsuda, H., N. Ogita, A. Sasaki, and K. Sato. 1992. Statistical mechanics of population. *Progress of Theoretical Physics* **88**:1035–1049.
- May, R. M., and M. A. Nowak. 1994. Superinfection, metapopulation dynamics, and the evolution of diversity. *Journal of Theoretical Biology* **170**:95–114.
- McCullough, D. R., editor. 1996. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C., USA.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* **9**:279–294.
- Nee, S., and R. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* **61**:37–40.
- Neuhauser, C. 1998. Habitat destruction and competitive coexistence in spatially explicit models with local interactions. *Journal of Theoretical Biology* **193**:445–463.
- Plotnick, R. E., and R. H. Gardner. 1993. Lattices and landscapes. Pages 129–157 in R. H. Gardner, editor, *Predicting spatial effects in ecological systems*. American Mathematical Society, Providence, Rhode Island, USA.
- Price, M. V., P. A. Kelly, and R. L. Goldingay. 1994. Distances moved by Stephens' kangaroo rat (*Dipodomys stephensi* Merriam) and implications for conservation. *Journal of Mammalogy* **75**:929–939.
- Pulliam, H. R., and J. B. Dunning, Jr. 1995. Spatially explicit population models. *Ecological Applications* **5**:2.
- Sato, K., H. Matsuda, and A. Sasaki. 1994. Pathogen invasion and host extinction in lattice structured populations. *Journal of Mathematical Biology* **32**:251–268.
- Smith, B. E., P. L. Marks, and S. Gardescu. 1993. Two hundred years of forest cover changes in Tompkins County, New York. *Bulletin of the Torrey Botanical Club* **120**:229–247.
- Thomlinson, J. R. 1995. Landscape characteristics associated

with active and abandoned Red-cockaded Woodpecker clusters in east Texas. *Wilson Bulletin* **107**:603–614.
 Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.
 Topping, C. J., and K. D. Sunderland. 1994. A spatial population dynamics model for *Lepthyphantes tenuis* (Araneae: Linyphiidae) with some simulations of the spatial and temporal effects of farming operations and land-use. *Agriculture, Ecosystems & Environment* **48**:203–217.
 Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, and J. Liu. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* **5**:12–16.

Waser, P. M. 1985. Does competition drive dispersal? *Ecology* **66**:1170–1175.
 Waser, P. M. 1987. A model predicting dispersal distance distributions. Pages 251–256 in B. D. Chepko-Sade and Z. T. Halpin, editors. *Mammalian dispersal patterns*. University of Chicago Press, Chicago, Illinois, USA.
 With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* **76**:2446–2459.
 With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* **78**:151–169.

APPENDIX A

DERIVATION OF THE PAIR-APPROXIMATION EQUATIONS

First, there are nine probabilities P_{ij} for $i, j = 0, 1, 2$ in the pair approximation model. Assuming symmetry (i.e., $P_{ij} = P_{ji}$), this is reduced to six probabilities: $P_{[00]}$, $P_{[01]}$, $P_{[02]}$, $P_{[11]}$, $P_{[12]}$, and $P_{[22]}$. Next, there are three constraints that should be recognized:

$$P_{t+1}[11] = P_t[11] = p[11] = 1 + p_0(q_{00} - 2) \tag{A.1}$$

$$\sum_{i=0}^2 \sum_{j=0}^2 P_t[ij] = 1 \tag{A.2}$$

$$P_{t+1}[1] = P_t[1] = p_1 = 1 - p_0 \\ = P_{t+1}[01] + P_{t+1}[11] + P_{t+1}[21]. \tag{A.3}$$

Eq. A.1 follows from Eq. 7, which is applicable because $P_t[11] = p[11]$, since the population cannot exist on sites with habitat type 1. Eq. A.3 follows from Eq. 16.

Under the assumptions of the pair approximation, the probability that a given site adjacent to an empty site is occupied (in state 2) at time t is $P_t[02|0^*] = P_t[02]/P_t[0]$, where the probability of seeing a single empty site $P_t[0]$ is calculated using Eq. 16. The probability that an empty site is colonized by a given neighbor whose state is not explicitly known is then $\phi P_t[02]/P_t[0]$. Thus the probability that a given empty site does *not* get colonized by any of three neighbors whose states are not known is given by $\gamma = (1 - \phi P_t[02]/P_t[0])^3$, which will be useful shortly.

Consider now Eq. 14, which specifies $P_{t+1}[02]$ in terms of probabilities $P_t[ij]$ at the current time. There are four types of blocks that could produce a [02] block at the next time; they are [00], [02], [20], and [22]. (Any block with a site in state 1 cannot produce a [02] block, because the landscape is fixed.) Thus,

$$P_{t+1}[02] = P_t[00]P([00] \rightarrow [02]) \\ + P_t[02]P([02] \rightarrow [02]) \\ + P_t[20]P([20] \rightarrow [02]) \\ + P_t[22]P([22] \rightarrow [02]). \tag{A.4}$$

The first term represents the contribution to $P_{t+1}[02]$ from $P_t[00]$. Thus we need to compute $P([00] \rightarrow [02])$, the probability that a [00] block at time t becomes a [02] block at time $t + 1$. In order for this to happen, two events must occur: (a) the left site in the [00] block must remain in state 0 (empty), and (b) the right site must change its state to 2 (occupied). The left site may remain in state 0 in one of two ways: (a1) it may not be colonized, or (a2) it may be colonized but then become empty in the mortality phase of the same time step. Because the left site could only be colonized by three of its neighbors (since we know its neighbor to the right is empty and thus cannot colonize the left site), the probability that it will not be colonized, i.e., the probability of event (a1),

is simply γ . Then, since the left site will be colonized with probability $1 - \gamma$, we multiply by the mortality probability μ_0 to see that the probability of event (a2) is $(1 - \gamma)\mu_0$. Events (a1) and (a2) are disjoint, so by adding their probabilities, one obtains the probability of event (a), i.e., the event that the left site remains in state 0. Now consider event (b): in order for the right site in the [00] block to change its state to 2, it must be colonized (with probability $1 - \gamma$), and survive mortality (with probability $1 - \mu_0$); multiplying these two independent probabilities gives the probability of event (b). Finally, events (a) and (b) are independent, so their probabilities may be multiplied to obtain $P([00] \rightarrow [02]) = (\gamma + (1 - \gamma)\mu_0)(1 - \gamma)(1 - \mu_0)$.

The next term in Eq. A.4 is $P_t[02]P([02] \rightarrow [02])$. We proceed as before: for a [02] block at time t to remain a [02] block at time $t + 1$, two events must occur: (a) the left site must remain in state 0, and (b) the right site must remain in state 2. Event (a) may occur in one of two disjoint ways: (a1) the site is not colonized, or (a2) it is colonized and then immediately dies. This time, the left site may be colonized by at least one of its three unknown neighbors, with probability $1 - \gamma$, or by its occupied neighbor to the right, with probability ϕ . Thus the probability that the left site is not colonized, event (a1), is $\gamma(1 - \phi)$. The probability that the left site is colonized is then $1 - \gamma(1 - \phi)$, giving the probability of event (a2) as $(1 - \gamma(1 - \phi))\mu_0$. Again, the probabilities of events (a1) and (a2) sum to give the probability of event (a). The probability of event (b) is simply $1 - \mu_0$, the probability that the right site survives mortality and hence remains in state 2. Again, multiplying the probabilities of events (a) and (b) gives $P([02] \rightarrow [02]) = (\gamma(1 - \phi) + (1 - \gamma(1 - \phi))\mu_0)(1 - \mu_0)$.

One may proceed in this fashion to fill in the coefficients of all of the $P_t[ij]$ terms in Eq. A.4, as well as coefficients in similar equations for $P_{t+1}[00]$ and $P_{t+1}[01]$. The results are the following three equations:

$$P_{t+1}[00] = P_t[00](\gamma + (1 - \gamma)\mu_0)^2 \\ + 2P_t[02](\gamma(1 - \phi) + (1 - \gamma(1 - \phi))\mu_0)\mu_0 \\ + P_t[22]\mu_0^2 \tag{A.5}$$

$$P_{t+1}[01] = P_t[01](\gamma + (1 - \gamma)\mu_0) + P_t[21]\mu_0 \tag{A.6}$$

$$P_{t+1}[02] = P_t[00](\gamma + (1 - \gamma)\mu_0)(1 - \gamma)(1 - \mu_0) \\ + P_t[02](\gamma(1 - \phi) \\ + (1 - \gamma(1 - \phi))\mu_0)(1 - \mu_0) \\ + P_t[20]\mu_0(1 - \gamma(1 - \phi))(1 - \mu_0) \\ + P_t[22]\mu_0(1 - \mu_0). \tag{A.7}$$

In Eq. A.5, the coefficients of the $P_t[02]$ and $P_t[20]$ terms

are the same; thus under the symmetry assumption $P_i[02] = P_i[20]$ they may be combined—hence the factor of 2 on the $P_i[02]$ term in that equation. The $P_i[02]$ and $P_i[20]$ terms were written separately in Eq. A.7 for clarity, since they had different coefficients.

We may then use Eqs. A.1 and A.3 to obtain

$$\begin{aligned} P_{t+1}[12] &= P_{t+1}[1] - P_{t+1}[10] - P_{t+1}[11] \\ &= (1 - p_0) - P_{t+1}[01] - p[11] \\ &= p_0(1 - q_{00}) - P_{t+1}[01] \end{aligned} \quad (\text{A.8})$$

and Eqs. A.1, A.2, and A.8 to get

$$\begin{aligned} P_{t+1}[22] &= 1 - P_{t+1}[00] - P_{t+1}[11] \\ &\quad - 2P_{t+1}[01] - 2P_{t+1}[02] - 2P_{t+1}[12] \\ &= 1 - P_{t+1}[00] - 2P_{t+1}[02] - p_{11} \\ &\quad - 2p_0(1 - q_{00}) \\ &= p_0q_{00} - P_{t+1}[00] - 2P_{t+1}[02]. \end{aligned} \quad (\text{A.9})$$

Finally, one can use Eqs. A.8 and A.9 to rewrite Eqs. A.5–A.7 in terms of only $P_i[00]$, $P_i[01]$, and $P_i[02]$ (as well as the parameters ϕ , μ_0 , p_0 , and q_{00}). The results are Eqs. 12–14.

Note that Ives et al. (1998) follow a similar approach to develop a pair-approximation model of a population on a

structured heterogeneous landscape. In their model, however, diagonally adjacent sites are considered adjacent for both dispersal and characterizations of landscape heterogeneities. However, their pair-approximation model contains only two equations, rather than the three used here. This is because they made the further simplifying assumption that the conditional probability that a randomly chosen neighbor of an occupied suitable site will be suitable (this probability is $(P[02] + P[22])/P[2]$ in the notation used in this paper) simply equals the conditional probability that a randomly chosen neighbor of a suitable site is also suitable (i.e., q_{00}). This assumption basically neglects the clustering of the population, or spatial correlations between the population and landscape. This assumption, in my notation, becomes $(P[02] + P[22])/P[2] = q_{00}$, which together with Eqs. 16, A.8, and A.9 leads to the relation

$$P[01] = \frac{1 - q_{00}}{q_{00}}(P[00] + P[02]).$$

This may then be used to eliminate $P[01]$ from the definition of γ in Eq. 15, and thus eliminate $P[01]$ entirely from Eqs. 12 and 14. The resulting two modified Eqs. 12 and 14 then serve as the complete pair-approximation model. The analytic model of Ives et al. (1998) is further slightly simplified because it does not consider the possibility that colonization and extinction can both occur at a single site during a single time step.

APPENDIX B

PROOF THAT ρ^* IN THE PAIR APPROXIMATION DOES NOT DEPEND ON p_0

Using Eqs. A.8 and A.9 together with Eq. 16, one can obtain

$$\begin{aligned} P_i[2] &= P_i[02] + P_i[12] + P_i[22] \\ &= p_i[02] + p_0(1 - q_{00}) - P_i[01] + p_0q_{00} \\ &\quad - P_i[00] - 2P_i[02] \\ &= p_0 - P_i[00] - P_i[01] - P_i[02] \\ P_i[0] &= P_i[00] + P_i[01] + P_i[02]. \end{aligned}$$

Using these in Eq. 11 and simplifying, we obtain

$$\rho_i = 1 - \frac{P_i[00] + P_i[01] + P_i[02]}{p_0}. \quad (\text{B.1})$$

Next, consider the rescaled variables $P'_i[00] = P_i[00]/p_0$, $P'_i[01] = P_i[01]/p_0$, and $P'_i[02] = P_i[02]/p_0$. If we rewrite Eqs. 12–14 using these rescaled variables, they become:

$$\begin{aligned} P'_{t+1}[00] &= P'_t[00]\{\gamma^2(1 - \mu_0)^2 + 2\gamma\mu_0(1 - \mu_0)\} \\ &\quad + 2P'_t[02]\gamma\mu_0(1 - \phi)(1 - \mu_0) + \mu_0^2q_{00} \\ P'_{t+1}[01] &= P'_t[01]\gamma(1 - \mu_0) + \mu_0(1 - q_{00}) \\ P'_{t+2}[02] &= P'_t[00]\{\gamma(1 - 2\mu_0)(1 - \mu_0) - \gamma^2(1 - \mu_0)^2\} \\ &\quad + P'_t[02]\gamma(1 - 2\mu_0)(1 - \mu_0)(1 - \phi) \\ &\quad + \mu_0(1 - \mu_0)q_{00} \end{aligned}$$

where

$$\begin{aligned} \gamma &= \left(1 - \frac{\phi P_t[02]}{P_t[00] + P_t[01] + P_t[02]}\right)^3 \\ &= \left(1 - \frac{\phi P'_t[02]}{P'_t[00] + P'_t[01] + P'_t[02]}\right)^3. \end{aligned}$$

That is, we see that $P'_i[00]$, $P'_i[01]$, and $P'_i[02]$ do not depend on p_0 . Finally, since by Eq. B.1, $\rho_i = 1 - (P'_i[00] + P'_i[01] + P'_i[02])$, we see that ρ , also does not depend on p_0 . Thus, the behavior of the pair-approximation model does not depend on the amount of suitable habitat available, but only its clustering parameter q_{00} , i.e., exactly the opposite behavior of the mean-field approximation.

APPENDIX C

The computer source code (written in C) used to generate these landscapes is available in ESA's Electronic Data Archives: *Ecological Archives* E081-019.