

Stochastic models in population biology and their deterministic analogs

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We introduce a class of stochastic population models based on “patch dynamics.” The size of the patch may be varied, and this allows one to quantify the departures of these stochastic models from various mean-field theories, which are generally valid as the patch size becomes very large. These models may be used to formulate a broad range of biological processes in both spatial and nonspatial contexts. Here, we concentrate on two-species competition. We present both a mathematical analysis of the patch model, in which we derive the precise form of the competition mean-field equations (and their first-order corrections in the nonspatial case), and simulation results. These mean-field equations differ, in some important ways, from those which are normally written down on phenomenological grounds. Our general conclusion is that mean-field theory is more robust for spatial models than for a single isolated patch. This is due to the dilution of stochastic effects in a spatial setting resulting from repeated rescue events mediated by interpatch diffusion. However, discrete effects due to modest patch sizes lead to striking deviations from mean-field theory even in a spatial setting.

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I. INTRODUCTION

Traditional theoretical ecology, in which the time evolution of population densities is described by differential equations, has a long history [1–3]. For a single species the simplest form of the governing equation is assumed to take the form $dN/dt = \Phi(N)N$, where $\Phi(N)$ describes the growth of the population. A common choice when modeling this growth is to take $\Phi(N) = r(1 - N/K)$, where r and K are two constants. By analogy, when describing the interaction of two species, it is natural to postulate that the populations of the two species, N_1 and N_2 , change according to $dN_1/dt = f(N_1, N_2)$ and $dN_2/dt = g(N_1, N_2)$. The functions f and g are chosen according to whether the interactions are purely competitive, predator-prey like, or include other effects such as cooperation. We will refer to descriptions of this kind as population based; they are arrived at without the need for a detailed knowledge of the interaction between individuals and rely instead on assuming that the terms which arise in the governing equations represent the net effects of individual interactions in some generic way. Equations of this kind play such a central role in population biology, that many subsequent elaborations of the theory have taken them as the starting point: spatial variation is introduced by adding a drift term $\nabla^2 N_\alpha$ ($\alpha = 1, 2$) to the right-hand side of the α th equation, and the models are sometimes interpreted as referring to individuals by assuming that the functions f and g also describe interactions at the level of the individual.

In the last decade or so, an alternative approach to that of classical theoretical ecology described above has been developed. This involves abandoning the traditional population-level description in favor of an individual-based description in which explicit rules governing the interaction of individuals with each other and with the environment are given. The popularity of these individual-based models (IBM's) is undoubtedly due to the continuing increase in the availability of

powerful computers, but they also have other attractive features, such as the ability to directly model individual attributes. At this point we should stress that we will assume that the individuals of a given species in our models are identical, and thus the term IBM should not be confused with agent-based models which are often designed to study the ecological effects of behavioral and physiological variation among individuals. A better term might be individual-level model (ILM), but the term IBM has wide usage, and so we will use it here. In this paper we will be concerned with theoretical issues which relate to the connection between models defined at the individual level and those at the population level. Thus, the individuals in our models will be identical within a given species. The relation between population-level and individual-level descriptions has been a focus of discussion within the theoretical ecology community for some time [4,5]. Some regard the nature of the population-based models as obvious and either write them down without comment or derive mean-field equations by making an assumption of homogeneous mixing of the populations [6,7]. However, there is also some recognition that the situation may be more complicated than this [8,9] and that the transition to a partial differential equation required for a spatial description, from the ordinary differential equation obtained by using mean-field theory, may not be as simple as just adding the term $\nabla^2 N_\alpha$ [10–12].

From a statistical physics perspective it is natural to expect that fluctuations may play an important role in these systems and lead to important differences between microscopic (IBM) and macroscopic (population-level) descriptions. A formal analysis of such issues has been presented for simple birth and death processes [13] and annihilation reactions [14] using the language of field theory and the renormalization group. Here, we take a different approach, using van Kampen's system size expansion, in order to probe the connection between more complex IBM's and mean-field theories. This has some advantages; for instance, it is not

necessary using this technique to first construct a corresponding field theory and then extract the mean-field equations and the Gaussian fluctuations about them to model the macroscopic behavior. There is also less of an emphasis of the role of phase transitions, which are not usually of prime interest in ecological models.

We would like to stress from the outset that our use of “mean-field theory” or “mean-field model” is in the spirit of statistical mechanics. By “mean field” we mean the neglect of correlations between degrees of freedom, allowing one to write the mean of the product of two stochastic variables as the product of their means. Thus, a spatial model in which statistical correlations are neglected is still a “mean-field model” within this usage. This is in contrast to some papers in population biology in which “mean-field” is reserved exclusively to describe nonspatial models.

In this paper, the models which we study will be defined only at the level of direct interaction among individuals and in terms of local properties such as birth, death, and migration rates. The population-based properties of the model will then be derived within a well-defined approximation scheme. We will show that, beginning with reasonable models at the individual level, the corresponding population-level models are similar in structure to those that we would naively write down, but have important differences. For instance, small-scale diffusion may not simply translate into $\nabla^2 N_\alpha$ terms and the parameters defined at the individual-based level may not map directly into their equivalents at the population level.

The individual interactions may be naturally introduced using a “patch model.” From a biological perspective, a patch can be thought of as a small spatial region within which interactions between individuals occur. The patch is assumed to be sufficiently small that there are no spatial effects. In other words, there is complete mixing, and all individuals have the same chance of potentially interacting with each other. In the nonspatial version of the model this simply amounts to stating that the probability of any individual dying in unit time should be proportional to the density of individuals existing at that time, and for processes which involve two individuals, the probability involved should be that found when drawing two of these types of individuals at random from a patch which contains all the individuals in the system. Not all constituents of the patch will correspond to individuals; some will correspond to empty sites in the spatial version of the model. A more detailed specification is given in Sec. II. Patch models such as this have been used in many areas of science [15] and often go under the name of “urn models.” Two early examples were the Ehrenfest urn, which was used to discuss the foundations of statistical mechanics, and the Pólya urn, which was originally devised to describe contagious diseases [16]. In both cases the problem of interest can be mapped onto an urn which contains balls of different colors—say, black and white—which are drawn randomly one at a time. In the case of the Ehrenfest urn, each time a ball is drawn it is replaced by one of the other color. For the Pólya urn, the chosen ball is replaced together with an extra ball of the same color. The relation to the modeling of contagious diseases should be clear: each occurrence of a particular color increases the probability of further occurrences. Since the introduction of

these particular urn models, the notion has been generalized considerably. For example, both models fall into the class of urn models which have the properties that if a white ball is drawn, it is replaced together with a white balls and b black ones, and if a black ball is drawn, it is replaced together with c white balls and d black ones. A further generalization is to consider r different colors, with the drawn ball of color i being replaced together with a_{ij} balls of color j ($i, j = 1, \dots, r$) [17]. It is also clear that two, or more, balls can be drawn together or, as we will have occasion to assume in this paper, two balls could be drawn for a fraction μ of the time and one ball for a fraction $(1-\mu)$ of the time.

Urn models are concrete realizations of stochastic processes with probabilities which depend only on the instantaneous state of the system—that is, Markov processes. They have proved useful in several areas of the biological sciences. Perhaps the most obvious application is in population genetics, implicitly in the early work of Fisher and Wright [18] and explicitly in later developments [19–25]. However, they have also been used in a number of other areas such as the study of radioactive particles in animals [26–28], the study of patterns of vegetation [29], models of interaction between species [30–32], and metapopulation models [33]. The last three applications are closest to the ones discussed in this paper, but differ in that the balls represent forest or grassland in the first case, species in the second case and colonies in the third case, rather than individuals as in the present paper.

Since urn, or patch, models are representations of Markov processes, the continuous time version of their dynamics may be described using a master equation. The use of master equations is familiar to physicists, but they are still not widely appreciated in the biological community (but see above references and Refs. [34–36], for instance). Once the process has been formulated in this way, we may use standard techniques to take the mean-field limit and so obtain the corresponding population-based equation. Much of this paper will be taken up with a comparison of results obtained from the full model (averaged over many realizations) and the mean-field results. Our approach will be particularly useful in distinguishing situations where mean-field theory is a good approximation to the full theory and situations where it is not. We will mainly concentrate on competitive interactions in systems with one or two species, but our method applies equally well to predator-prey or epidemic models and multispecies communities.

The outline of the paper is as follows. We first motivate and define the rules for the nonspatial patch models in Sec. II, starting with a single-species model and then generalizing to a two-species competition model. The full stochastic nature of the models is described using master equations, and the associated mean-field models are derived. In the following section we go one step beyond mean-field theory and derive the dynamics of the Gaussian fluctuations about the mean-field solutions. This is equivalent to not only following the mean position of the probability distributions over time, but also describing their broadening. In Sec. IV we present numerical simulations of the fully stochastic nonspatial models, for both one and two species. We compare our results to numerical integration of both the mean-field equations and

the improved models with Gaussian fluctuations included. We find that the agreement between mean-field theory and simulations is excellent for larger patches, as is to be expected, but that the breakdown of mean-field theory occurs precipitously below critical patch sizes which are still fairly large. We proceed in Sec. V to generalize our patch model formulation to spatially explicit population dynamics of two species competition. From the master equation we derive the spatial mean-field equations. We note important differences between these equations and “intuitive” versions which have appeared in the literature. These mean-field equations are tested against simulations of the fully stochastic models in Sec. VI. In this introductory paper we are unable to give a comprehensive analysis of the two species model. Instead we present two interesting scenarios and note the successes and failures of the mean-field equations, which are strongly dependent on patch size and the presence or absence of interspecific competition. We end the paper with our conclusions along with a discussion of future directions. Two appendixes contain technical details. The first concerns the system size expansion for two species and the second the formalism for spatial systems.

II. BASIC FORMALISM AND THE NONSPATIAL MODEL

In this section we will introduce the essential features of our approach by formulating an individual based stochastic model of competition between two species. We will then show that in the limit of large population sizes, the time evolution of this model reduces to the well known differential equations describing the population growth of two competing species.

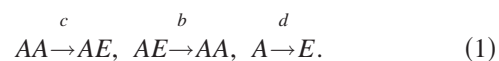
The two species will be labeled A and B . To motivate the approach we will adopt, suppose that we model the interactions of A and B individuals in an area of land by subdividing it into N plots of equal area. The plot sizes are chosen so that each one either contains one A individual, or one B individual, or neither an A nor a B . We will call the latter an empty site and label it by E . In a spatial version of the model we would give rules for how A , B , and E interact, specify birth and death rates for A and B , and allow them to move to nearest-neighbor sites. In later sections we will describe such a model, but we will begin, for simplicity, by ignoring the spatial aspects. We do this by imagining that we pluck all the A , B , and E from their particular sites and put them into a single large patch, with no record of their original spatial locations. Any memory of which individuals were nearest neighbors is now lost, and any two individuals picked at random are just as likely to interact as any other two similar individuals picked at random. In fact the time evolution of the spatial model which would read, pick a site at random, then pick a nearest neighbor of this site and implement the interaction rule for the two chosen individuals, now reads, pick two individuals from the patch and implement the reaction rule for the two chosen individuals.

There are other, slightly different, ways of arriving at the above picture. For example, instead of dividing up the area of land into sites containing either one individual or no individuals, it could be divided up into a number of smaller

patches, each of which contains several individuals. In this way of thinking, each small patch contains several A , B , and E types, which interact with each other in the same way as for the large patch described above and which move by exchange interactions with neighboring patches. While this defines a slightly different spatial model, the nonspatial version of the model is the same: all the individuals from the various patches are collected together into a single large patch. Moreover, even the spatial version of the model is in some sense a “coarse-grained” version of the original model—several sites in that model when viewed on a coarser scale can be reinterpreted as a site in the latter model. These features will be explored in more detail when we discuss the spatial aspects of these models in Sec. V. For the remainder of this section we will consider only the nonspatial model.

Suppose to begin with we consider the simpler case of a single species—that is, a patch containing only A and E individuals. We shall postulate that the population dynamics of the system can be essentially described by three processes: birth, death, and competition. The first and third processes will involve two individuals, $AE \rightarrow AA$ (birth) and $AA \rightarrow AE$ (competition), but the second process involves only one individual, $A \rightarrow E$ (death). These seem natural choices since, while death can be modeled as constant, independent of the density of individuals, the reduction in the numbers of A due to competition and the growth in numbers of A due to births will be density dependent. In other words, there will be a tendency for AA to go to AE because of overcrowding, and for AE to go to AA due to the presence of resources (space) to sustain a new individual.

The time evolution of the model can now be described. At each time step we sample the patch. On a fraction μ of these occasions we randomly choose two individuals and allow them to interact and for $(1 - \mu)$ of the draws we choose only one individual randomly. If in the former case we draw two E “individuals” or in the latter case one E “individual,” we simply put them back into the patch. For all other choices, an interaction may occur, leading to the replacement of a different set of individuals to those drawn. For each of these processes we will introduce rate constants b , c and d as follows:



We now only need to know the probabilities of drawing various combinations from the patch. Simple combinatorics gives

$$\text{probability of picking } AA = \mu \frac{n(n-1)}{N(N-1)},$$

$$\text{probability of picking } AE = 2\mu \frac{n(N-n)}{N(N-1)},$$

$$\text{probability of picking } A = (1 - \mu) \frac{n}{N}, \quad (2)$$

where the factor of 2 in the second term comes from the fact that the choices AE and EA are identical. These results enable us to write down expressions for the transition probabil-

ity, per unit time step, of the system of individuals going from a state with n A individuals to a state with n' A individuals. We denote this quantity by $T(n'|n)$. Since only transitions from n to $n \pm 1$ may take place during one time step, the only nonzero $T(n'|n)$ are

$$\begin{aligned} T(n-1|n) &= \mu c \frac{n(n-1)}{N(N-1)} + (1-\mu)d \frac{n}{N}, \\ T(n+1|n) &= 2\mu b \frac{n(N-n)}{N(N-1)}. \end{aligned} \quad (3)$$

The process defined by Eqs. (3) is a one-step Markov process and so we can immediately write down a master equation describing how the probability of having n individuals present in the patch, $P(n, t)$, changes with time [37]. The rate of change of this quantity with time is simply the sum of transitions from the states with $n+1$ and $n-1$ A individuals to the state with n A individuals, minus the sum of transitions from the state with n A individuals to the state with $n+1$ and $n-1$ A individuals:

$$\begin{aligned} \frac{dP(n, t)}{dt} &= T(n|n+1)P(n+1, t) + T(n|n-1)P(n-1, t) \\ &\quad - T(n-1|n)P(n, t) - T(n+1|n)P(n, t). \end{aligned} \quad (4)$$

This set of coupled equations has to be solved subject to an initial condition, typically $P(n, 0) = \delta_{n, n_0}$ —that is, a condition stating that there are known to be n_0 individuals in the patch at $t=0$. Care should also be taken with the boundary values $n=0$ and $n=N$, since not all of the transitions are present in these cases. From Eqs. (3) we see that $T(-1|0)$ and $T(N+1|N)$ are formally zero. As long as we define $T(0|-1) = T(N|N+1) = 0$, we may use the general form (4) even for $n=0$ and $n=N$.

The master equation (4) gives a complete description of the time evolution of the nonspatial model. In the next section we will discuss the model predictions in more detail. Here we simply wish to make contact with the mean-field (i.e., the deterministic) version of the model, obtained by taking the $N \rightarrow \infty$ limit. This is most easily accomplished by multiplying the master equation (4) by n and summing over all values of n . By shifting the variable in two of the sums on n by $+1$ and -1 , the following rate equation is obtained:

$$\frac{d\langle n \rangle}{dt} = \sum_{n=0}^N T(n+1|n)P(n, t) - \sum_{n=0}^N T(n-1|n)P(n, t), \quad (5)$$

where angular brackets signify averages over the possible states of the system. Defining

$$\tilde{c} = \frac{\mu c}{N-1}, \quad \tilde{b} = \frac{\mu b}{N-1}, \quad \tilde{d} = \frac{(1-\mu)d}{N}, \quad (6)$$

and using Eqs. (3), Eq. (5) becomes

$$\frac{d\langle n \rangle}{dt} = 2\tilde{b} \left\langle \frac{n}{N} \left(1 - \frac{n}{N} \right) \right\rangle - \tilde{c} \left\langle \frac{n}{N} \left(\frac{n}{N} - \frac{1}{N} \right) \right\rangle - \tilde{d} \left\langle \frac{n}{N} \right\rangle. \quad (7)$$

So far no approximation has been made in the derivation of Eq. (7). However, we now take the limit $N \rightarrow \infty$. In addition to eliminating the $1/N$ factor in the second term on the right-hand side of Eq. (7), it allows us to replace $\langle n^2 \rangle$ by $\langle n \rangle^2$. This gives

$$\frac{d\phi}{dt} = 2\tilde{b}\phi(1-\phi) - \tilde{c}\phi^2 - \tilde{d}\phi, \quad \text{where } \phi \equiv \frac{\langle n \rangle}{N}. \quad (8)$$

Here $\phi(t)$ is the density of individuals in a given area. It is more conventional to write this in the form

$$\frac{dN_A}{dt} = N_A(r - aN_A), \quad \text{where } N_A(t) = \langle n \rangle = N\phi(t), \quad (9)$$

and where

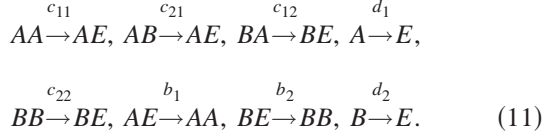
$$r = 2\tilde{b} - \tilde{d}, \quad a = \frac{2\tilde{b} + \tilde{c}}{N}. \quad (10)$$

Equation (9) is the mean-field equation of the model and is the familiar logistic equation, usually written down as a phenomenological description of the population growth of a single species with intraspecific competition. Here it is derived as the $N \rightarrow \infty$ limit of our stochastic model and thus provides a reasonable description of our system when the potential size (number of A plus number of E types) of the system is relatively large. Of course, this limit is purely formal. In practice what we mean that if N is of the order 10^4 ; for instance, then this approximation is good if we are only interested in accuracies of up to 0.01% (if the next-order corrections are of order $1/N$) or 1% (if the next-order corrections are of order $1/\sqrt{N}$). This approximation obviously cannot describe chance extinctions, which occur when n is small, nor does it predict a mean time to extinction for the A population. In regimes where these effects are important, it provides a poor description of the system, but this will inevitably be true of any purely deterministic description.

The necessity of introducing the “empty site” individuals E should be clear from the above derivation. In order to be able to define a population density which changes with time we need a null population which can be displaced if the A species is successful and increase if the A population falters. It is also very natural to have a ceiling on the growth of A individuals ($N_A \leq N$) representing a limit on the available resources. If no E 's were introduced in the two-species case, the two population sizes would not be independent and would simply add up to N . The A population would obey Eq. (9) and $N_B = N - N_A$. This is clear if we simply imagine repeating the above derivation for a two species system by replacing E by B . Although the interaction rules would be altered by this replacement, it would still be the case that $N_A + N_B = N$. So it is vital to have “empty space” for individuals to exploit in order to obtain a realistic population dynamics.

We have discussed the single-species case in some detail since the construction of the master equation in the two-species case (and, in fact, in the S -species case for arbitrary

S) follows similar lines. We still draw two individuals μ of the time and one individual $(1-\mu)$ of the time, but the processes and their rate constants are now



The rate constants $c_{\alpha\alpha}$, $\alpha=1,2$, represent intraspecific competition and $c_{\alpha\beta}$, $\alpha \neq \beta$, interspecific competition. Analogous probabilities to Eqs. (2) of choosing particular combinations of A , B , and E are

$$\begin{aligned} & AA: \mu \frac{n(n-1)}{N(N-1)}, AE: 2\mu \frac{n(N-n-m)}{N(N-1)}, A: (1-\mu) \frac{n}{N}, \\ & BB: \mu \frac{m(m-1)}{N(N-1)}, BE: 2\mu \frac{m(N-n-m)}{N(N-1)}, B: (1-\mu) \frac{m}{N}, \\ & AB: 2\mu \frac{n}{N} \frac{m}{N-1}. \end{aligned} \quad (12)$$

Transition probabilities now have initial and final states specified by two integers. The transition probability per unit time from the state (n, m) to the state (n', m') will be denoted by $T(n', m' | n, m)$. The nonzero transition probabilities are

$$\begin{aligned} T(n-1, m | n, m) &= \mu c_{11} \frac{n(n-1)}{N(N-1)} + (1-\mu) d_1 \frac{n}{N} \\ &\quad + 2\mu c_{12} \frac{mn}{N(N-1)}, \\ T(n, m-1 | n, m) &= \mu c_{22} \frac{m(m-1)}{N(N-1)} + (1-\mu) d_2 \frac{m}{N} \\ &\quad + 2\mu c_{21} \frac{mn}{N(N-1)}, \\ T(n+1, m | n, m) &= 2\mu b_1 \frac{n(N-n-m)}{N(N-1)}, \\ T(n, m+1 | n, m) &= 2\mu b_2 \frac{m(N-n-m)}{N(N-1)}. \end{aligned} \quad (13)$$

The master equation is an obvious generalization of Eq. (4):

$$\begin{aligned} \frac{dP(n, m, t)}{dt} &= T(n, m | n+1, m)P(n+1, m, t) \\ &\quad + T(n, m | n-1, m)P(n-1, m, t) \\ &\quad + T(n, m | n, m+1)P(n, m+1, t) \\ &\quad + T(n, m | n, m-1)P(n, m-1, t) \\ &\quad - \{T(n-1, m | n, m) + T(n+1, m | n, m) \\ &\quad + T(n, m-1 | n, m) + T(n, m+1 | n, m)\}P(n, m, t). \end{aligned} \quad (14)$$

This equation simply expresses the increase in $P(n, m, t)$ due to the four possible transitions into the state (n, m) described by $T(n, m | n \pm 1, m \pm 1)$ and the decrease due to transitions out of this state described by $T(n \pm 1, m \pm 1 | n, m)$. The boundary and initial conditions are obvious analogs of those in the one-species case. The generalizations of Eq. (5) are quite simple, since none of the transition probabilities involving changes only in m enter into the equation for $d\langle n \rangle / dt$ and none of the transition probabilities involving changes only in n enter into the equation for $d\langle m \rangle / dt$:

$$\begin{aligned} \frac{d\langle n \rangle}{dt} &= \sum_{n,m=0}^N T(n+1, m | n, m)P(n, m, t) \\ &\quad - \sum_{n,m=0}^N T(n-1, m | n, m)P(n, m, t), \\ \frac{d\langle m \rangle}{dt} &= \sum_{n,m=0}^N T(n, m+1 | n, m)P(n, m, t) \\ &\quad - \sum_{n,m=0}^N T(n, m-1 | n, m)P(n, m, t). \end{aligned} \quad (15)$$

We can now substitute the forms for Eqs. (13) into this equation and take the mean-field limit $N \rightarrow \infty$. This allows us to factor $\langle mn \rangle$ into $\langle m \rangle \langle n \rangle$, as well as $\langle n^2 \rangle$ into $\langle n \rangle^2$ and $\langle m^2 \rangle$ into $\langle m \rangle^2$ as before. The final result for the rate of change of population densities is the competition equations

$$\begin{aligned} \frac{dN_A}{dt} &= N_A(r_1 - a_{11}N_A - a_{12}N_B) \text{ where } N_A = \langle n \rangle, \\ \frac{dN_B}{dt} &= N_B(r_2 - a_{21}N_A - a_{22}N_B) \text{ where } N_B = \langle m \rangle, \end{aligned} \quad (16)$$

familiar from population biology textbooks. The parameters in Eqs. (16) are related to the parameters of the stochastic model by

$$\begin{aligned} r_\alpha &= \frac{2\mu b_\alpha}{N-1} - \frac{(1-\mu)d_\alpha}{N}, \quad a_{\alpha\alpha} = \frac{\mu(2b_\alpha + c_{\alpha\alpha})}{N(N-1)}, \\ a_{\alpha\beta} &= \frac{2\mu(b_\alpha + c_{\alpha\beta})}{N(N-1)} \quad (\alpha \neq \beta). \end{aligned} \quad (17)$$

As we will see in Sec. V, essentially the same kind of reasoning as that given above can be applied in the spatial version of the model. Before discussing this, however, we will investigate the large- N limit of Eqs. (4) and (14) a little more carefully, obtaining corrections to mean-field theory and comparing these to simulations.

III. BEYOND MEAN-FIELD THEORY FOR THE NONSPATIAL MODEL

In the last section we gave arguments to show that the mean-field versions of the stochastic models we had intro-

duced were indeed the deterministic models conventionally used to describe these systems. In this section we will apply an elegant method due to van Kampen [37], which not only allows us to obtain these results in a more systematic way, but also gives a method of finding stochastic corrections to this deterministic result for large N . We will only work to next-to-leading order in this paper. This will give a Gaussian broadening to $P(n, t)$, or $P(n, m, t)$, with the peak of the distribution moving according to the relevant deterministic equation. We will then compare these results with numerical simulations of the full stochastic process. The large- N expansion is very clearly explained by van Kampen in his book [37], so we will content ourselves with giving a brief outline of the method as applied to the one-species case. The two-species calculation follows very similar lines.

We saw in the last section that, in the limit $N \rightarrow \infty$, the variable n became deterministic and equal to $N\phi(t)$. In this limit the function $P(n, t)$ will be a δ function. For large, but finite N , we would expect $P(n, t)$ to have a finite width of order $NN^{-1/2} = N^{1/2}$. Now n is once again a stochastic variable, and it is natural to bring out the large- N structure of the theory by transforming to a new stochastic variable ξ by writing

$$n = N\phi(t) + N^{1/2}\xi. \quad (18)$$

We will not need to assume that the function $\phi(t)$ satisfies any particular differential equation; if we simply choose it to follow the peak of the distribution as it evolves in time, then the equation it satisfies will emerge. A new probability distribution function Π is defined by $P(n, t) = \Pi(\xi, t)$, which implies that

$$\dot{P} = \frac{\partial \Pi}{\partial t} - N^{1/2} \frac{d\phi}{dt} \frac{\partial \Pi}{\partial \xi}. \quad (19)$$

When using this formalism it is useful to rewrite the master equation (4) using step operators which act on an arbitrary function of n according to $\mathcal{E}f(n) = f(n+1)$ and $\mathcal{E}^{-1}f(n) = f(n-1)$. This gives

$$\begin{aligned} \frac{dP(n, t)}{dt} &= (\mathcal{E} - 1)[T(n-1|n)P(n, t)] + (\mathcal{E}^{-1} - 1) \\ &\times [T(n+1|n)P(n, t)]. \end{aligned} \quad (20)$$

This form of the master equation is useful because the step operators have a simple expansion involving powers of the operator $N^{-1/2}\partial/\partial\xi$, which simplifies the identification of differing orders in $N^{-1/2}$. We shall assume the initial condition on the equation to be $P(n, 0) = \delta_{n, n_0}$.

Applying the method and identifying powers of $N^{1/2}$ yields the macroscopic equation

$$\frac{d\phi}{dt} = \alpha_{1,0}(\phi) \quad (21)$$

to leading order and a Fokker-Planck equation

$$\frac{\partial \Pi}{\partial t} = -\alpha'_{1,0}(\phi) \frac{\partial}{\partial \xi} [\xi \Pi] + \frac{1}{2} \alpha_{2,0}(\phi) \frac{\partial^2 \Pi}{\partial \xi^2} \quad (22)$$

describing a linear stochastic process to next order. Here the functions $\alpha_{1,0}(\phi)$ and $\alpha_{2,0}(\phi)$ (we have used van Kampen's notation) are given by

$$\begin{aligned} \alpha_{1,0}(\phi) &= 2\tilde{b}\phi(1-\phi) - \phi(\tilde{d} + \tilde{c}\phi), \\ \alpha_{2,0}(\phi) &= 2\tilde{b}\phi(1-\phi) + \phi(\tilde{d} + \tilde{c}\phi). \end{aligned} \quad (23)$$

Since the Fokker-Planck equation (22) describes a linear process, its solution is a Gaussian. This means that the probability distribution $\Pi(\xi, t)$ is completely specified by the first two moments $\langle \xi \rangle_t$ and $\langle \xi^2 \rangle_t$. Multiplying Eq. (22) by ξ and ξ^2 and integrating over all ξ one finds

$$\begin{aligned} \partial_t \langle \xi \rangle_t &= \alpha'_{1,0}(\phi) \langle \xi \rangle_t, \\ \partial_t \langle \xi^2 \rangle_t &= 2\alpha'_{1,0}(\phi) \langle \xi^2 \rangle_t + \alpha_{2,0}(\phi). \end{aligned} \quad (24)$$

The procedure is to solve Eq. (21) and obtain ϕ as a function of t . This function is then substituted into Eqs. (24) and these equations solved for $\langle \xi \rangle_t$ and $\langle \xi^2 \rangle_t$. In the case of the first moment this may be performed quite generally to give

$$\langle \xi \rangle_t = \langle \xi \rangle_0 \exp \left\{ \int_0^t d\tau \alpha'_{1,0}(\phi(\tau)) \right\}. \quad (25)$$

Choosing our initial condition to be

$$\phi(0) = \frac{n_0}{N}, \quad (26)$$

the initial fluctuations vanish and $\langle \xi \rangle_0 = 0$. Thus $\langle \xi \rangle_t = 0$ for all t .

This summarizes the method. We therefore start by solving Eq. (21), subject to Eq. (26). Defining

$$\rho \equiv 2\tilde{b} - \tilde{d}, \quad \sigma \equiv 2\tilde{b} + \tilde{c}, \quad (27)$$

for convenience, the general solution for $\rho \neq 0$ is

$$\phi(t) = \frac{\rho}{\sigma - A e^{-\rho t}}, \quad \rho \neq 0, \quad (28)$$

where the constant A is determined by the initial condition

$$A = \sigma - \frac{\rho}{\phi(0)} \quad [\phi(0) \neq 0]. \quad (29)$$

If $\phi(0) = 0$, then $\phi(t) = 0$ for all t . If $\rho = 0$, a degenerate form of the solution exists and is given by

$$\phi(t) = \frac{\phi(0)}{1 + \sigma \phi(0)t} \quad (\rho = 0). \quad (30)$$

This solution can now be substituted into the equation for $\langle \xi^2 \rangle_t$ given in Eq. (24). An integrating factor for this equation is $e^{2\rho t} / \phi^4(t)$, which yields upon use of the initial condition $\langle \xi^2 \rangle_0 = 0$ when $\rho \neq 0$:

$$\begin{aligned}
\langle \xi^2 \rangle_t = & \frac{1}{[\sigma - A e^{-\rho t}]^4} \{ 2\sigma^2 \tilde{b}(\tilde{c} + \tilde{d})[1 - e^{-2\rho t}] \\
& - \sigma A [4\tilde{b}^2 + 10\tilde{b}(\tilde{c} + \tilde{d}) + \tilde{c}\tilde{d}] e^{-\rho t} [1 - e^{-\rho t}] \\
& + 2A^2 \rho [4\tilde{b}^2 + 4\tilde{b}(\tilde{c} + \tilde{d}) + \tilde{c}\tilde{d}] t e^{-2\rho t} \\
& - A^3 (2\tilde{b} + \tilde{d}) e^{-2\rho t} [1 - e^{-\rho t}] \}. \quad (31)
\end{aligned}$$

Of course, care has to be taken when applying this approximation. If the distribution has significant interaction with the boundaries at $n=0$ or $n=N$, the Gaussian approximation will break down. So, for example, if $\rho > 0$, the peak of the distribution will move from n_0 eventually coming to rest at $N\rho/\sigma$. While this is happening the probability distribution broadens, eventually reaching its stationary value at

$$\lim_{t \rightarrow \infty} \langle \xi^2 \rangle_t = \frac{2\tilde{b}(\tilde{c} + \tilde{d})}{(2\tilde{b} + \tilde{c})^2}. \quad (32)$$

On the other hand, if $\rho \leq 0$, the peak of the distribution will eventually tend to zero, and so the Gaussian approximation will break down at some finite time.

The case of two species follows in an exactly analogous manner: one writes $n = N\phi(t) + N^{1/2}\xi$ and $m = N\psi(t) + N^{1/2}\eta$ and defines a new probability distribution Π via $P(n, m, t) = \Pi(\xi, \eta, t)$. The macroscopic equations obeyed by $\phi(t)$ and $\psi(t)$ are again found to be identical to those given in Sec. II, and Π is again found to satisfy a Fokker-Planck equation describing a linear process and is therefore a multivariate Gaussian distribution. Details are given in Appendix A, where one sees that analytic expressions for the analogs of $\langle \xi^2 \rangle_t$ cannot be obtained, in part at least, because the macroscopic equations cannot be solved in closed form. However, we have solved them numerically, and we now go on to compare the large N results in both the one-species and two-species cases with simulations of the original stochastic process.

IV. SIMULATIONS OF NONSPATIAL MODELS

In order to better understand the range of validity of mean-field theory and its Gaussian corrections, we have performed numerical simulations of the nonspatial model described above. The simulation of stochastic models of population dynamics has progressed in line with the availability of high-speed computers over the last two decades. During the beginning of this period, books on the stochastic dynamics of fluctuations in biological systems only mentioned simulations fleetingly [38]; about a decade ago they had assumed a more central role [39] and are now regarded as essential in the understanding of these systems [40,41]. We refer the reader to these last two references for more details on how these simulations are carried out in practice.

In our numerical algorithm an ensemble of patches is iterated forward in time. To achieve reasonable statistics we generally take the size of the ensemble to be several thousand realizations. In each small time step a single individual or a pair are selected from each patch in turn and with the

TABLE I. Parameter values for Figs. 1 and 2.

	Samples	N	μ	b	d	c
Fig. 1	10 000	100	0.5	0.5	0.5	0.5
Fig. 2	50 000	10	0.5	0.5	0.5	0.5

appropriate probabilities transitions are made and the new individuals replaced.

We periodically average over the ensemble to measure both the mean densities of individuals and the variance in the densities. Concurrent with the stochastic simulation we also integrate forward the mean-field equations and the equations for the Gaussian variances [Eqs. (24) and (A5)–(A9)] to allow a direct comparison. Forward integration of the differential equations is performed using a second-order Runge-Kutta scheme.

We will present some examples of our numerical work which illustrate the main effects that we have found. We have not performed an exhaustive numerical analysis due to the large parameter space of the competition models. The examples we give here are fairly typical of a wide range of parameter space and are chosen to illustrate a variety of effects. Our results may be summarized by the statement that as long as the size of the patch is large and the system is not close to extinction (such that discrete effects play a strong role), then the mean-field equations and the large- N correction yield a remarkably accurate description of the system dynamics. However, there is a fairly sharp transition signaling the failure of mean-field theory as the patch size is reduced below a critical value. For smaller patches, the quantitative precision of the mean-field theory fails badly. This inaccuracy gives way to qualitative errors if one runs the system close to extinction. In this case the probability distribution of the populations is poorly approximated by a Gaussian function and one is compelled to abandon mean-field theory and its Gaussian corrections. It is significant that the critical patch size depends sensitively on whether the patch contains one or two species and whether there is interspecific competition. To clarify these statements we now lead the reader through some illustrative examples. An exhaustive list of parameter values is given in Tables I and II.

In Fig. 1 we give an example of a moderately large patch ($N=100$) containing a single species. The mean density soon settles down to a (quasi-)steady-state value as does the variance in the population density. Mean-field theory and the large- N corrections give very good agreement. In Fig. 2 we show results for an identical situation but with the patch size reduced from 100 to 10. In this case the quasi steady state is meaningless since extinction events are frequent and the mean density (measured over the ensemble of patches) steadily decays to zero [38,42]. Note that the variance also decays to zero, since as time proceeds more and more realizations go extinct and the probability distribution of population densities is dominated by a δ function peak at zero. This illustrates the effect of discrete individuals for small systems.

We now consider competition between two species in a single patch. We only consider large patches, where, naively,

TABLE II. Parameter values for Figs. 3–5.

	Samples	N	μ	b_1	b_2	d_1	d_2	c_{11}	c_{22}	c_{12}	c_{21}
Fig. 3	1000	400	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.0	0.0
Fig. 4	1000	200	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.0	0.0
Fig. 5	1000	400	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.0	0.1

discrete individual effects may be neglected. In Fig. 3 we study the simplest case in which the A and B individuals have identical birth, death, and intraspecific competition rates. There is no explicit interspecific competition (i.e., $c_{12} = c_{21} = 0$), although the finiteness of the patch leads to indirect competition between all individuals [see Eqs. (16) and (17)]. The patch is taken to be very large with a capacity of 400 individuals. We find satisfactory agreement between simula-

tions and the mean-field theory and its large- N corrections. It is somewhat surprising that on reducing the patch size from 400 to 200 (Fig. 4) the variance in the system increases steadily, far exceeding the large- N corrections. Returning to the large 400-capacity patch and now introducing a small amount of interspecific competition (Fig. 5) we again find that the large- N corrections fail to capture the growing fluctuations in the system. We conclude from this and other simulations that mean-field theory and its Gaussian corrections can work well, but only for patches above a critical size. This critical size is itself strongly dependent on the number of species, various growth parameters, and the presence or not of explicit interspecific competition.

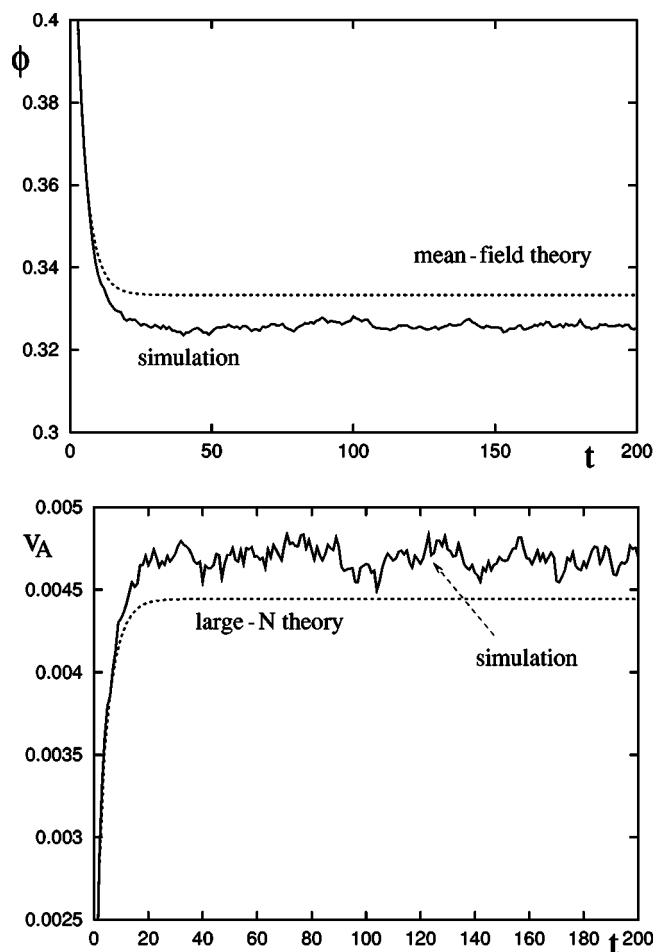


FIG. 1. A comparison of theory to simulation for a single patch containing a single species. The upper panel shows the time evolution of the population density $\phi(t) = \langle n \rangle / N$, where n is the number of individuals and N is the size of the patch. The lower panel shows the time evolution of the variance, $v(t) = (\langle n^2 \rangle - \langle n \rangle^2) / N^2$, of the population. The subscript A refers to the fact that the individuals belong to species A . In this case the patch size has the relatively large value of 100 and we see that theory and simulation are in good agreement. See Table I for specific parameter values used in Figs. 1 and 2.

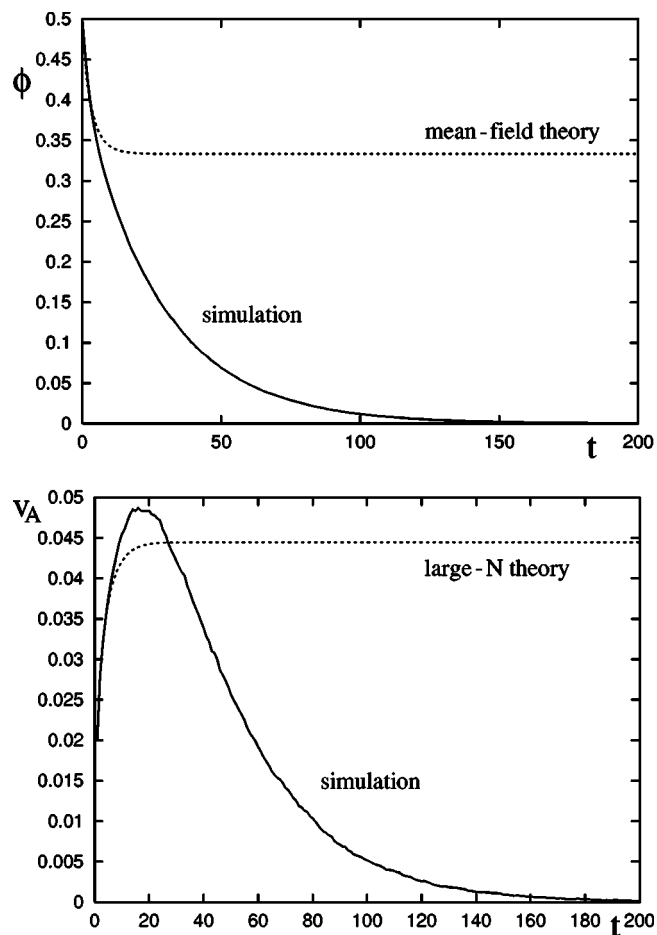


FIG. 2. The same as Fig. 1 but with the patch size reduced to 10. In this case the mean population density falls to zero due to fluctuation induced extinctions. The true variance first exceeds the large N prediction and then falls steeply below due to the growing number of realizations which have become extinct.

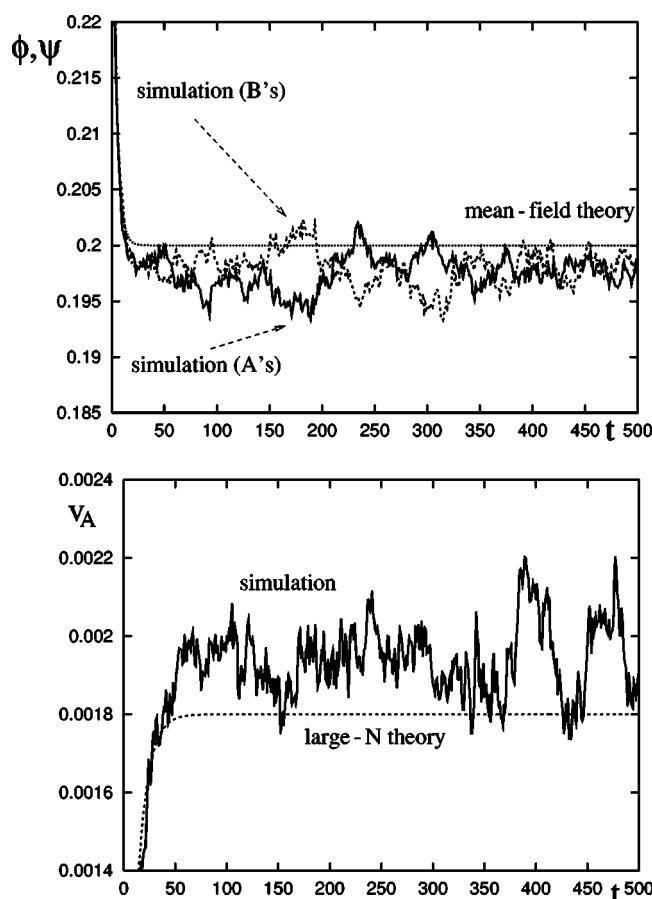


FIG. 3. Comparison of theory to simulation for a patch containing two species *A* and *B*. Initially each species has a density of one-quarter of the total patch capacity. The upper panel shows the time evolution of the densities of *A* and *B* [$\phi(t)$ and $\psi(t)$, respectively], while the lower panel shows the time evolution of the variance of *A* compared with the large-*N* theory. In this case the *A* and *B* individuals have identical birth, death, and competition parameters, and the interspecific competition is set to zero. The patch size has the large value of 400. See Table II for specific parameter values used in Figs. 3–5.

V. SPATIAL MODELS

We have already discussed the spatial versions of the model in Sec. II. In one version of the model, the area under consideration is divided into a large number of patches, each containing a small number of individuals, which are then identified with the sites of a regular two-dimensional lattice (usually a square lattice). Competition takes place between individuals of a particular patch, and the birth rate is similarly only dependent on the population density of the parental patch, but individuals are allowed to migrate to nearest-neighbor patches, if space is available (that is, if an empty space *E* exists at the neighboring site). In terms of this picture, the lattice consists of an array of patches, which interact through migration of individuals from one patch to a nearest-neighbor patch. In the other version of the model introduced in Sec. II, each patch contains only one individual; thus the sites of the lattice represent individuals rather than patches. In this case competition and birth processes, as well as mi-

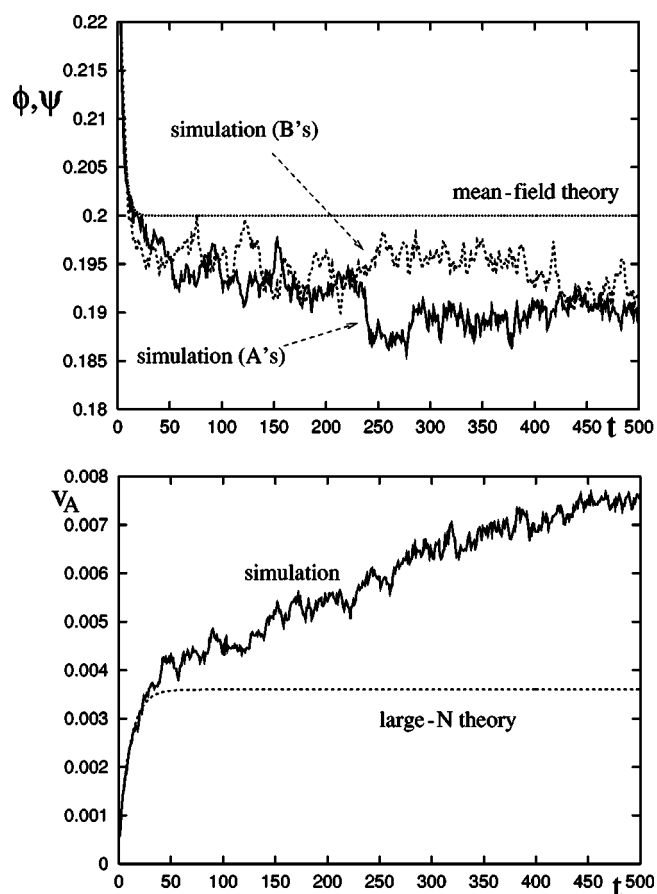


FIG. 4. The same as Fig. 3 but with a patch size of 200. Note that although the mean-field theory still works fairly well, the large-*N* prediction for the variance is very poor. Even for such a large patch, the fluctuations are increasing steadily with time.

gration, depend on the occupancy of nearest-neighbor sites. In both versions of the model, the death rate is constant.

It is clear that many other variants are possible. In general, the first model will be more applicable to situations where individuals move on length scales which are much larger than the communities they live in and the second model more applicable when all these processes occur on scales which are of the same order. However, we will see that in the exploration of the nature of the mean-field limit and the importance of stochastic effects, which is what interests us in this paper, these differences play a secondary role. In the next two sections we will follow the same program as was carried through for the nonspatial case: describing the stochastic process which defines the model, obtaining the mean-field limit, and finally comparing the mean-field equations with simulations of the full model. Much of the mathematical detail will be relegated to Appendix B; unfortunately, while many of the ideas are simple generalizations of those introduced earlier, the mathematical notation becomes (of necessity) rather complex and detracts from the points which we wish to emphasize.

The simplest spatial process to describe is that of a single species in the first version of the model. The processes in this case may be broken down into three classes.

(i) For a fraction q_1 of the events we randomly pick a site *i* and then randomly draw two individuals from within the

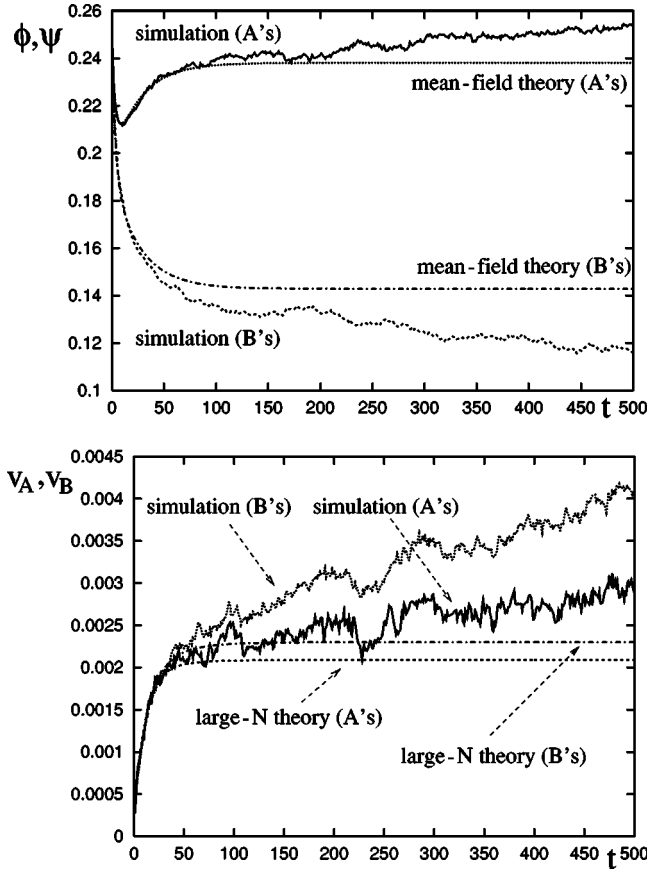
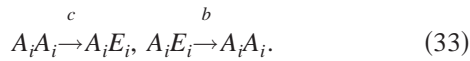
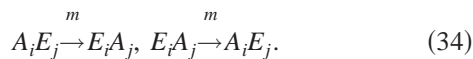


FIG. 5. A similar scenario to Fig. 3, with the addition of weak interspecific interactions (one-fifth of the strength of the intraspecific interactions, with A outcompeting B). Here, the patch size is 400, and the densities are fairly well approximated by mean-field theory, although we see a slow decline in the B population. However, the fluctuations are again increasing with time and are not well described by the large- N theory for large times.

patch at that site. If two E individuals are drawn, they are simply replaced; otherwise, the following interactions may occur [cf. Eq. (1)]:



(ii) For a fraction q_2 of the events we randomly pick a site i and then randomly pick another site j which is a nearest neighbor of i . One individual is drawn from the patch at i and another from the patch at j . If these two individuals are of the same type (two A 's or two E 's), no action is taken; otherwise, migration with a rate constant m may occur:



(iii) For a fraction $1 - q_1 - q_2$ of the events we randomly pick a site i and then randomly draw a individual from within the patch at that site. If an E individual is drawn, no action is taken; otherwise, death may occur at a constant rate d :



The probabilities of choosing these various processes are in the case of (i) and (iii) simply modifications of Eqs. (2). The

modifications that are required are that all n should be written as n_i to denote the number of A 's in the patch at site i , μ should be replaced by q_1 , $(1 - \mu)$ by $(1 - q_1 - q_2)$, and all terms multiplied by Ω^{-1} , where Ω is the number of sites in the lattice. We assume that the number of individuals in each patch is the same for all sites and is denoted by N . If the sites i and j have already been chosen, the probabilities for the processes (ii) are

$$\text{probability of picking } A_i E_j = q_2 \frac{n_i (N - n_j)}{N},$$

$$\text{probability of picking } E_i A_j = q_2 \frac{n_j (N - n_i)}{N}. \quad (36)$$

The transition probabilities, master equation, and the derivation of the population-level equation corresponding to this model, are discussed in Appendix B. The lattice version of this latter equation is given by Eq. (B8). On taking the continuum limit, defined by Eq. (B9), it becomes

$$\frac{\partial \phi}{\partial \tau} = \tilde{m} \nabla^2 \phi + 2\tilde{b} \phi (1 - \phi) - \tilde{c} \phi^2 - \tilde{d} \phi, \quad (37)$$

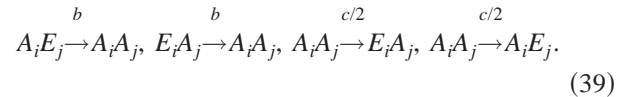
where $\phi(\mathbf{x}, \tau)$ is the continuum version of $\langle n_i(\tau) \rangle / N$ in the limit $N \rightarrow \infty$ and where τ is a rescaled time. This equation is exactly the result (8) obtained in the nonspatial case, but with the addition of a $\nabla^2 \phi$ drift term. We can write Eq. (37) in a more standard form by defining a diffusion constant $D_A \equiv \tilde{m}$ and making the identification (10). This gives

$$\frac{\partial N_A}{\partial \tau} = D_A \nabla^2 N_A + N_A (r - a N_A), \quad (38)$$

where, as before, $N_A \equiv N \phi$.

The discussion of the second version of the spatial model follows similar lines. Now there is only one individual per site, and therefore n_i can only take on only two values: 0 and 1. In addition, birth and competition processes, as well as migration, depend on the occupancy of nearest-neighbor sites. Therefore there are only two classes of processes.

(i) For a fraction μ of the events we randomly pick a site i and then randomly pick another site j which is a nearest neighbor of i . If these sites are both E 's, no action is taken; otherwise, migration with a rate constant m may occur according to Eq. (34) or birth and competition may take place with rate constants b and $c/2$, respectively:



The factor of 1/2 has been introduced into the rate constant for competition in order to be consistent with the nonspatial case and the first version of the spatial case.

(ii) For a fraction $1 - \mu$ of the events we randomly pick a site i . If the site contains an E individual, no action is taken. Otherwise, death may occur at a constant rate d given by Eq. (35).

Since there is only one individual per each site, the probabilities of picking $A_i E_j$ or $E_i A_j$ are simply Eq. (36) with $N=1$ and q_2 replaced by μ . Similarly, the probability of picking A_i is as in the first version, but again with $N=1$ and with $(1-q_1-q_2)$ replaced by $(1-\mu)$. The only new feature is

$$\text{probability of picking } A_i A_j = \mu n_i n_j. \quad (40)$$

Just as before, we have assumed that the sites i and j were already chosen, so that the above probabilities only represent the choices of types of individuals at these chosen sites (or patches) and also the choice of the number of individuals in an event (one or two). In the first model, we denoted the number of sites in the lattice by Ω . This was independent of N , the number of individuals in a patch. It was this latter quantity that we allowed to become infinitely large, in order to deduce the population-level description. In this second version, there is only one individual per site, and so it is the number of lattice sites (now denoted by N) which we take to be infinitely large. More details of this approach are given in Appendix B, where it is shown that, in the large- N limit, the population-level description is again given by Eq. (37) — albeit with slightly different definitions of the parameters. This is not a surprise; we would expect there to be a large number of IBM's which differ in detail, but which have the correct qualitative features, and give the same population-level description.

The partial differential equation (38) is simply the ordinary differential equation for the nonspatial case (8), but with a term $\nabla^2 N_A$ added. So the corresponding spatial description is indeed obtained by using the simplest prescription. However, this will not turn out to be the case when more than one species are present. It is this scenario which is of most interest to us in this paper; we have described the one species case in some detail, largely because it is technically simpler and therefore the crucial steps in the argument clearer. The many species case may differ at the population level, but the the setting up of the IBM's and the derivation of the population-level equations are a straightforward generalization of the one-species case.

Let us once again begin with the first version of the model where birth, competition, and death processes are purely local (they take place in a single patch at a specific site on the lattice) and only the process of migration involves nearest-neighbor patches. All of the transitions are variants of those in models previously considered in this paper. Specifically the three classes of processes are the following.

(i) For a fraction q_1 of the events we randomly pick a site i and then randomly draw two individuals from within the patch at that site. If two E individuals are drawn, they are simply replaced; otherwise, the interactions are given by the 6 two individual interactions in Eqs. (11) with a site index i added on to the A , B , and E individuals.

(ii) For a fraction q_2 of the events we randomly pick a site i and then randomly pick another site j which is a nearest neighbor of i . One individual is drawn from the patch at i and another from the patch at j . If neither of these two individuals are E 's (no space) or both are E 's (no migration possible), then no action is taken; otherwise, migration with rate constants m_1 or m_2 may occur:

$$A_i E_j \xrightarrow{m_1} E_i A_j, \quad E_i A_j \xrightarrow{m_1} A_i E_j, \quad B_i E_j \xrightarrow{m_2} E_i B_j, \quad E_i B_j \xrightarrow{m_2} B_i E_j. \quad (41)$$

(iii) For a fraction $1-q_1-q_2$ of the events we randomly pick a site i and then randomly draw a individual from within the patch at that site. If an E individual is drawn, no action is taken; otherwise, death may occur at constant rates d_1 or d_2 :

$$A_i \xrightarrow{d_1} E_i, \quad B_i \xrightarrow{d_2} E_i. \quad (42)$$

The probabilities of choosing these various processes are in the case of (i) and (iii) simply modifications of (12). The modifications that are required are exactly those we described in the similar version of the one species case: the n 's and m 's should be written as n_i and m_i respectively, μ should be replaced by q_1 , $(1-\mu)$ by $(1-q_1-q_2)$, and all terms multiplied by Ω^{-1} . The migration of A 's and B 's are independent of each other and so are described in exactly the same way as for single species. Details are given in Appendix B where it is shown that, after the continuum limit has been taken, the equations for

$$\phi(\mathbf{x}, \tau) \equiv \lim_{N \rightarrow \infty} \frac{\langle n_i(\tau) \rangle}{N} \quad \text{and} \quad \psi(\mathbf{x}, \tau) \equiv \lim_{N \rightarrow \infty} \frac{\langle m_i(\tau) \rangle}{N} \quad (43)$$

are

$$\begin{aligned} \frac{\partial \phi}{\partial \tau} = & \tilde{m}_1 \nabla^2 \phi + \tilde{m}_1 (\phi \nabla^2 \psi - \psi \nabla^2 \phi) + 2\tilde{b}_1 \phi (1 - \phi - \psi) \\ & - \tilde{c}_{11} \phi^2 + 2\tilde{c}_{12} \phi \psi - \tilde{d}_1 \phi \end{aligned} \quad (44)$$

and

$$\begin{aligned} \frac{\partial \psi}{\partial \tau} = & \tilde{m}_2 \nabla^2 \psi + \tilde{m}_2 (\psi \nabla^2 \phi - \phi \nabla^2 \psi) + 2\tilde{b}_2 \psi (1 - \phi - \psi) - \tilde{c}_{22} \psi^2 \\ & + 2\tilde{c}_{21} \psi \phi - \tilde{d}_2 \psi. \end{aligned} \quad (45)$$

The second version of the two-species model has $n_i=0, 1$ and $m_i=0, 1$, with birth, competition, and migration depending on nearest-neighbor occupancies. The two classes of processes are the following.

(i) For a fraction μ of the events we randomly pick a site i and then randomly pick another site j which is a nearest neighbor of i . If these sites are both E 's, no action is taken; otherwise, migration may occur according to Eqs. (41), birth according to

$$A_i E_j \xrightarrow{b_1} A_i A_j, \quad E_i A_j \xrightarrow{b_1} A_i A_j, \quad B_i E_j \xrightarrow{b_2} B_i B_j, \quad E_i B_j \xrightarrow{b_2} B_i B_j, \quad (46)$$

and competition according to

$$\begin{aligned} A_i A_j \xrightarrow{c_{11}} A_i E_j, \quad B_i A_j \xrightarrow{c_{12}} B_i E_j, \quad A_i B_j \xrightarrow{c_{21}} A_i E_j, \quad B_i B_j \xrightarrow{c_{22}} B_i E_j, \\ A_i A_j \xrightarrow{c_{11}} E_i A_j, \quad A_i B_j \xrightarrow{c_{12}} E_i B_j, \quad B_i A_j \xrightarrow{c_{21}} E_i A_j, \quad B_i B_j \xrightarrow{c_{22}} E_i B_j. \end{aligned} \quad (47)$$

TABLE III. Parameter values for Figs. 6–9.

	Samples	L	N	q_1	q_2	b_1	b_2	d_1	d_2	c_{11}	c_{22}	c_{12}	c_{21}	m_1	m_2
Fig. 6	250	100	100	1/3	1/3	0.5	0.5	0.7	0.5	0.5	0.5	0.0	0.5	1.0	1.0
Fig. 7	1000	100	10	1/3	1/3	0.5	0.5	0.7	0.5	0.5	0.5	0.0	0.5	1.0	1.0
Fig. 8	500	100	50	1/3	1/3	0.5	0.5	0.5	0.5	0.5	0.2	0.0	0.5	1.0	1.0
Fig. 9	500	100	10	1/3	1/3	0.5	0.5	0.5	0.5	0.5	0.2	0.0	0.5	1.0	1.0

(ii) For a fraction $1 - \mu$ of the events we randomly pick a site i . If the site contains an E individual, no action is taken. Otherwise, death may occur according to Eqs. (42).

The probabilities of picking two individuals, one of which is an E , are the same as in the first version of the model, but with $N=1$ and q_2 replaced by μ . The probabilities of picking a single individual are similarly related to those found in the first version. The probabilities associated with picking $A_i A_j$ is given by Eq. (40), $B_i B_j$ by $\mu m_i m_j$, and $A_i B_j$ by $\mu n_i m_j$. In Appendix B we describe how, in the limit where the number of lattice sites, N , becomes infinitely large, the continuum versions of $\langle n_i \rangle$ and $\langle m_i \rangle$ again satisfy Eqs. (44) and (45).

So, in summary, both versions of the IBM's we have discussed in this paper give rise to the same population-level equations. This is true whether there is only a single species in the system or whether two species are present. In the one-species case this equation is given in standard form by Eq. (38). To write the two-species equations (44) and (45) in standard form we make the identification (17) and introduce diffusion constants

$$D_A = \tilde{m}_1, D_B = \tilde{m}_2, D_1 = \frac{\tilde{m}_1}{N}, D_2 = \frac{\tilde{m}_2}{N}. \quad (48)$$

This gives

$$\frac{\partial N_A}{\partial \tau} = D_A \nabla^2 N_A + D_1 (N_A \nabla^2 N_B - N_B \nabla^2 N_A) + N_A (r_1 - a_{11} N_A - a_{12} N_B), \quad (49)$$

$$\frac{\partial N_B}{\partial \tau} = D_B \nabla^2 N_B + D_2 (N_B \nabla^2 N_A - N_A \nabla^2 N_B) + N_B (r_2 - a_{21} N_A - a_{22} N_B), \quad (50)$$

where $N_A = N\phi$ and $N_B = N\psi$. Unlike Eq. (38), these are *not* the standard equations found in population biology textbooks.

The additional terms which appear in Eqs. (49) and (50), but not in the standard equations, are antisymmetric in N_A and N_B and involve derivatives and so do not appear in non-spatial models or spatial models with only one species. Their structure is dictated by the way that migration is modeled at the individual level. Since their occurrence is generic, they will also appear in spatial models derived from IBM's having three or more species. Although these terms have not to our knowledge been discussed in the context of ecological models, they are well-known in the context of interspecies diffusion [43,44] in physics, and they also appear in quantum field theory [45].

VI. SIMULATIONS OF SPATIAL MODELS

The simulations of spatial competition was performed in a directly analogous fashion to the nonspatial model described in Sec. IV. We confined ourselves to one spatial dimension for simplicity. In addition, we only simulated the version of the model where a patch of size N was placed at each site of the one-dimensional lattice of size L . Within each patch the usual dynamics of competition is played out. Furthermore, in each small time step there is a small probability of dispersal of individuals from a given patch to the two neighboring patches, just as encoded in the master equation. We generally started with initial conditions in which species A and B were spatially separated and then proceed to intermix and compete as individuals diffuse from patch to patch. The mean-field equations (49) and (50) are again integrated forwards in time using second-order Runge-Kutta methods. An exhaustive list of parameter values is given in Table III.

In a spatial system such as this, extinction is much less of a problem since should a patch become empty it will soon be restocked from neighboring patches. Despite the weakened effect of discreteness in small patches, we still find that the behavior of the spatial systems differs significantly from mean-field theory when patch sizes are below a critical value (of approximate value 50 for the results presented here). As before, we have chosen to present two typical scenarios.

In Fig. 6 we show the early- and late-time behavior for a system in which initially the A individuals occupy the left half of the system and the B individuals occupy the right half. In the ensuing dynamics, the A and B individuals have identical mobilities, growth rates, and intraspecific competition parameters. However, the A individuals are disadvantaged by having a slightly higher death rate than the B 's. This is balanced by giving the A 's an interspecific competitive advantage over the B 's. On varying the strengths of these balancing forces it is possible to obtain invasion of A 's from left to right or invasion of B 's from right to left. We have chosen an example of the latter. It is seen that mean-field theory does an excellent job in predicting the long-time dynamics of the system. In this figure the patch size is rather large with a capacity of 100.

In Fig. 7 we repeat the exact simulation as before but simply reduce the patch size from 100 to 10. In this case the A individuals are severely affected by discrete extinction events and their density is in poor agreement with mean-field theory. Interestingly, the denser B individuals are fairly well described by mean-field theory throughout the range.

We also studied an alternative balance of effects as follows. In Fig. 8 we show a situation in which the death rates for the two species are the same, but now we reduce the

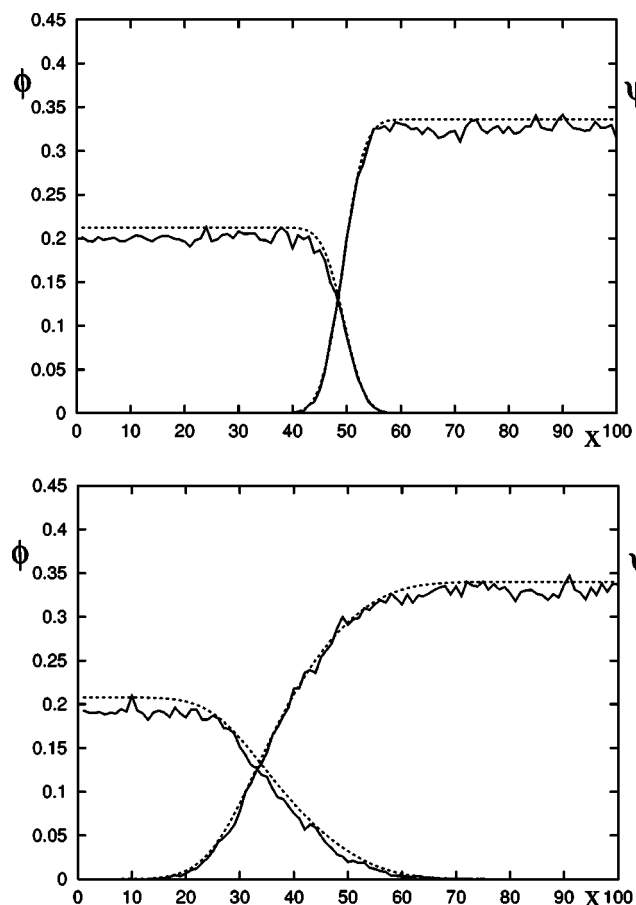


FIG. 6. Comparison of mean-field theory (smooth lines) and simulation (erratic lines) for two species A and B in a spatial setting in which initially the A individuals occupy the left half of the system and the B individuals the right half. The upper (lower) panel shows early (late) times. Here, the patch size has the relatively large value of 100. A outcompetes B (meaning that $c_{21} > c_{12}$), but has a higher death rate, and so is invaded by B . See Table III for specific parameter values used in Figs. 6–9.

amount of intraspecific competition among the B individuals. Again, the A 's have an interspecific competitive advantage over the B 's. In this case the A 's invade the B 's. Here the patch size has the intermediate value of 50 individuals. We see that mean-field theory performs relatively well.

On reducing the patch size for this particular scenario, from 50 to 10 (Fig. 9) we see the failure of mean-field theory (which predicts invasion from left to right). The enhanced fluctuations in the smaller patches lead to a quasidynamical balance in the interfacial region between A 's and B 's. In this region the A 's are beset by fluctuation-induced extinction events and this makes them too weak to invade the B 's in the usual manner of a Fisher wave. Instead, over longer scales than shown in the figure, the density of A 's slowly permeates the B -rich region in a “creeping” motion.

VII. CONCLUSIONS

There are many ways to formulate population dynamics. Popular descriptions tend to be either deterministic (mean-

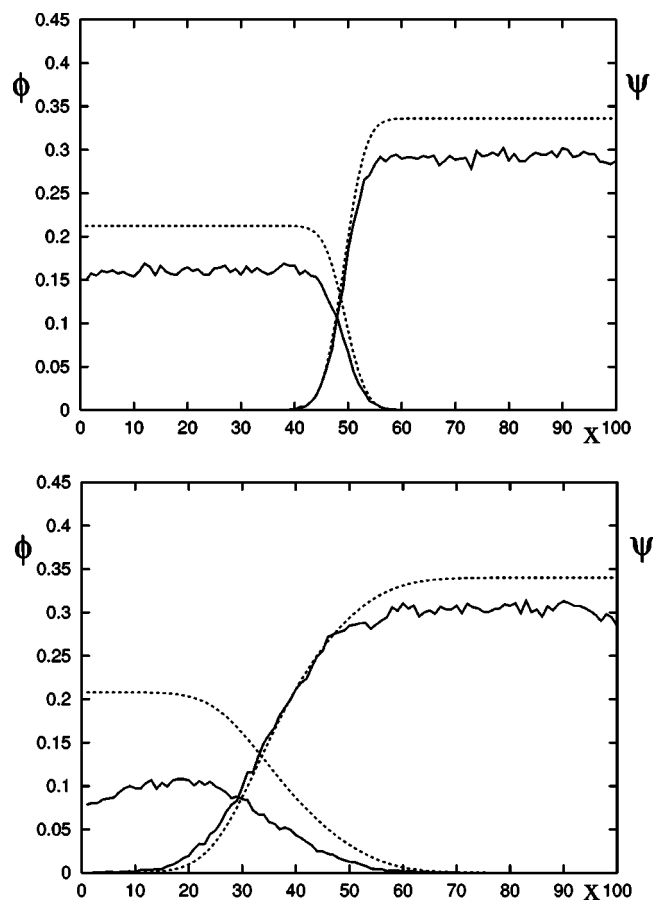


FIG. 7. The same as Fig. 6 but here the patch size is reduced from 100 to the relatively small value of 10. Note that mean-field theory is still in fairly good agreement with the high density B population, but shows significant deviation for the stochastically weakened A population.

field) equations or individual-based algorithms designed for implementation on a computer. The extreme difference in these two approaches has led to difficulties in directly comparing results. Disparities may be due to fundamental deficiencies in one or both of the techniques or else be attributable to “renormalization” of various parameters. In this paper we have attempted to bridge the gap between mean-field models and individual-based models. We have described a very general framework with which to formulate population dynamics using the language of “patches” to create a concrete picture of the stochastic process. The size of the patch is the central parameter. Mean-field theory is recovered on taking the patch size to infinity, while discrete stochastic effects become prominent for small patches containing a few individuals. Again, we emphasize that in our usage “mean field” refers to the approximation in which cross correlations between stochastic variables is neglected, but still allows for an explicitly spatial description.

From a biological perspective, a patch can be thought of as a (small) spatial region within which interactions between individuals occur. It is assumed that movement within this scale is not biologically significant. In our spatial patch model, movement of an individual between patches is biologically significant since that individual will now have in-

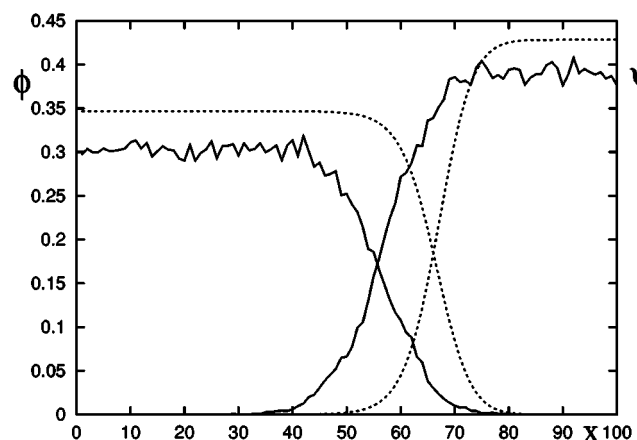
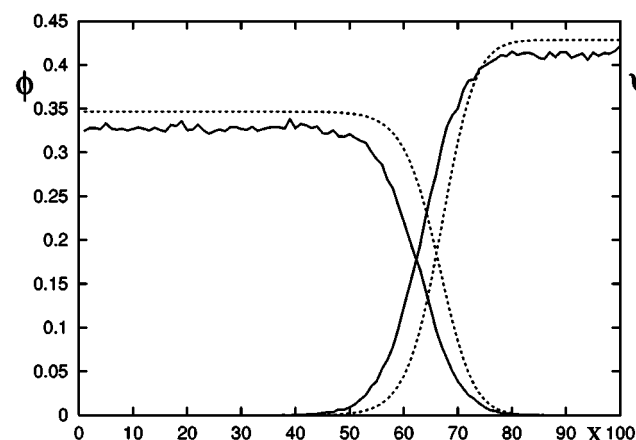
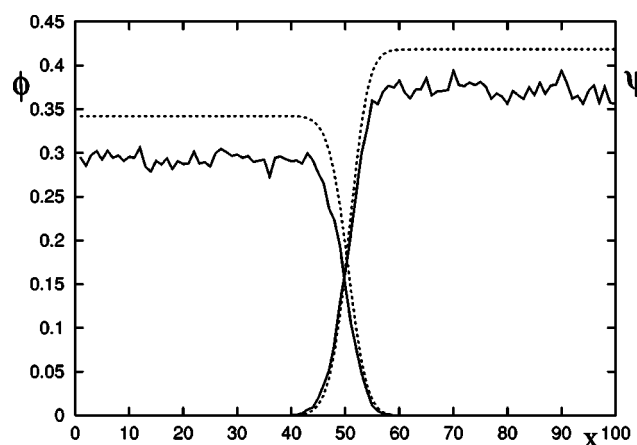
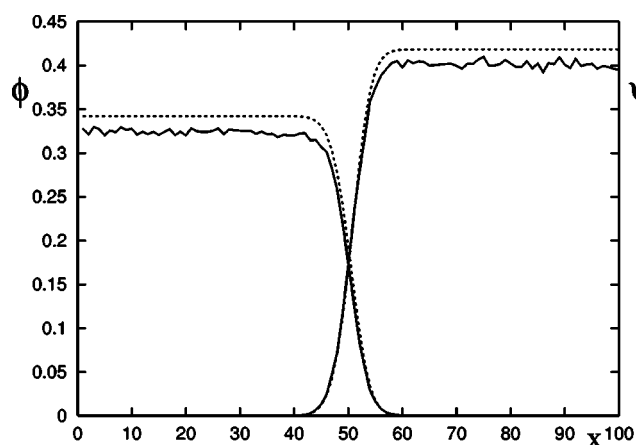


FIG. 8. A similar scenario to Fig. 6, but now A and B have identical death rates and yet B has less intraspecific competition than A . In this example A invades B . The patch size here has the relatively large value of 50.

FIG. 9. The same as Fig. 8 except that the patch size is reduced from 50 to 10. Note that the invasion of A into B is severely slowed due to the stochastic weakening of A .

interactions with a new set of individuals in a neighboring region. For systems in which interactions (not involving movement *per se*) occur over larger scales, it will be necessary to include additional inter-patch processes.

We have studied both nonspatial and spatial models. The nonspatial case corresponds to a single patch containing a number of individuals of both species. We have derived the corresponding mean-field theory and its first-order corrections (i.e., Gaussian fluctuations about the deterministic predictions). Generally, as long as the patch size is above a critical value (which tends to be of the order of 100 in the examples shown here) and the birth and death rates are such that a sizable quasi-steady-state population is possible, then the mean-field theory and its corrections give a satisfactory description of the system. For smaller patches or for situations in which there is a non-negligible probability of extinction, it is crucial to account for the discrete nature of the individuals. The population dynamics is inherently stochastic and one must dispense with a deterministic description. By tuning the patch size we have seen that the transition from a mean-field like to a stochastic regime is rather sharp and dependent on the existence of interspecific interactions (in this case, competition).

The same general picture holds for the spatially explicit models. We have discussed two types of spatial patch mod-

els. In one, at each spatial site there is a “micropatch” which may hold at most one individual. Movement and competition occurs between patches. In the other, each lattice site is a patch of tunable size and competition occurs inside the patch. Movement, of course, is still between patches. A careful formulation shows that each model has the same spatial mean-field limit. Of particular interest is the emergence of novel nonlinear diffusion terms, which are only present when two or more species are competing for space. These terms are not written down in the standard “intuitively derived” continuum equations of spatial competition models. They are especially important in spatial regions in which the density of one species is high, while the density of the other is strongly spatially varying. This would occur, for instance, in a region of space containing a population boundary for one species (due to some environmental barrier) but not for the other. We intend to investigate such effects in more detail in a follow-up paper.

In our investigation of spatial mean-field models, we have found them to be more robust than in the nonspatial case. This is primarily due to the weakening of local extinction via continual rescue effects from neighboring patches. It is still the case, however, that as the patch size is decreased, the quantitative precision of mean-field models suffers and with smaller patches still (we have in mind patches of size 10 or

less) new stochastically driven qualitative features emerge. An example of this was given (Fig. 9) in which an invasion process (in mean-field theory) was halted due to stochastic weakening of the leading edge of the invading population density.

In conclusion, we have presented a simple framework with which to discuss fluctuation effects in population biology. This framework is based on the use of patch models as concrete realizations of stochastic processes. The transition from mean-field behavior to fluctuation-dominated stochastic dynamics is effected by reducing the size of the patch. The critical patch size separating these two regimes depends sensitively on the biological interactions present. This has been an intensively theoretical work. In future work we intend to apply the patch model to a variety of multispecies population dynamics to address the importance of fluctuations and validity of mean-field theories in a quantitative and controlled manner.

ACKNOWLEDGMENTS

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APPENDIX A: LARGE- N ANALYSIS

This appendix contains the details of the large- N analysis for the two species case which was described in Sec. III in the one-species case.

It is once again useful to write the master equation (14) in the form

$$\begin{aligned} \frac{dP(n,m,t)}{dt} = & (\mathcal{E}_\xi - 1)[T(n-1, m|n, m)P(n, m, t)] \\ & + (\mathcal{E}_\xi^{-1} - 1)[T(n+1, m|n, m)P(n, m, t)] \\ & + (\mathcal{E}_\eta - 1)[T(n, m-1|n, m)P(n, m, t)] \\ & + (\mathcal{E}_\eta^{-1} - 1)[T(n, m+1|n, m)P(n, m, t)], \end{aligned} \quad (\text{A1})$$

where the step operators \mathcal{E} are defined by their actions on functions of n and m by $\mathcal{E}_\xi^{\pm 1}f(n, m, t) = f(n \pm 1, m, t)$ and $\mathcal{E}_\eta^{\pm 1}f(n, m, t) = f(n, m \pm 1, t)$.

Writing $n = N\phi(t) + N^{1/2}\xi$ and $m = N\psi(t) + N^{1/2}\eta$, van Kampen's method yields the macroscopic equations

$$\frac{d\phi}{dt} = \alpha_{1,0}(\phi, \psi), \quad \frac{d\psi}{dt} = \beta_{1,0}(\phi, \psi), \quad (\text{A2})$$

to leading order, and the linear Fokker-Planck equation

$$\begin{aligned} \frac{\partial \Pi}{\partial t} = & \left[-\frac{\partial \alpha_{1,0}}{\partial \phi} \right] \frac{\partial}{\partial \xi} (\xi \Pi) + \left[-\frac{\partial \alpha_{1,0}}{\partial \psi} \right] \frac{\partial}{\partial \xi} (\eta \Pi) \\ & + \left[-\frac{\partial \beta_{1,0}}{\partial \phi} \right] \frac{\partial}{\partial \eta} (\xi \Pi) + \left[-\frac{\partial \beta_{1,0}}{\partial \psi} \right] \frac{\partial}{\partial \eta} (\eta \Pi) \\ & + \frac{1}{2} \alpha_{2,0} \frac{\partial^2 \Pi}{\partial \xi^2} + \frac{1}{2} \beta_{2,0} \frac{\partial^2 \Pi}{\partial \eta^2}, \end{aligned} \quad (\text{A3})$$

to next order. This is a multivariate Fokker-Planck equation, but it is again linear, and so its solution is a (multivariate) Gaussian. The α and β functions are given by

$$\begin{aligned} \alpha_{1,0}(\phi, \psi) &= 2\tilde{b}_1\phi(1-\phi-\psi) - \{\tilde{c}_{11}\phi^2 + \tilde{d}_1\phi + 2\tilde{c}_{12}\phi\psi\}, \\ \beta_{1,0}(\phi, \psi) &= 2\tilde{b}_2\psi(1-\phi-\psi) - \{\tilde{c}_{22}\psi^2 + \tilde{d}_2\psi + 2\tilde{c}_{21}\phi\psi\}, \\ \alpha_{2,0}(\phi, \psi) &= 2\tilde{b}_1\phi(1-\phi-\psi) + \{\tilde{c}_{11}\phi^2 + \tilde{d}_1\phi + 2\tilde{c}_{12}\phi\psi\}, \\ \beta_{2,0}(\phi, \psi) &= 2\tilde{b}_2\psi(1-\phi-\psi) + \{\tilde{c}_{22}\psi^2 + \tilde{d}_2\psi + 2\tilde{c}_{21}\phi\psi\}. \end{aligned} \quad (\text{A4})$$

Since the solution to the Fokker-Planck equation is a Gaussian, we need once again only find the first two moments. They satisfy

$$\frac{d}{dt} \langle \xi \rangle_t = \left[+\frac{\partial \alpha_{1,0}}{\partial \phi} \right] \langle \xi \rangle_t + \left[+\frac{\partial \alpha_{1,0}}{\partial \psi} \right] \langle \eta \rangle_t, \quad (\text{A5})$$

$$\frac{d}{dt} \langle \eta \rangle_t = \left[+\frac{\partial \beta_{1,0}}{\partial \phi} \right] \langle \xi \rangle_t + \left[+\frac{\partial \beta_{1,0}}{\partial \psi} \right] \langle \eta \rangle_t, \quad (\text{A6})$$

$$\frac{d}{dt} \langle \xi^2 \rangle_t = 2 \left[+\frac{\partial \alpha_{1,0}}{\partial \phi} \right] \langle \xi^2 \rangle_t + 2 \left[+\frac{\partial \alpha_{1,0}}{\partial \psi} \right] \langle \xi \eta \rangle_t + \alpha_{2,0}, \quad (\text{A7})$$

$$\frac{d}{dt} \langle \eta^2 \rangle_t = 2 \left[+\frac{\partial \beta_{1,0}}{\partial \phi} \right] \langle \xi \eta \rangle_t + 2 \left[+\frac{\partial \beta_{1,0}}{\partial \psi} \right] \langle \eta^2 \rangle_t + \beta_{2,0}, \quad (\text{A8})$$

$$\begin{aligned} \frac{d}{dt} \langle \xi \eta \rangle_t = & \left[+\frac{\partial \alpha_{1,0}}{\partial \phi} \right] \langle \xi \eta \rangle_t + \left[+\frac{\partial \alpha_{1,0}}{\partial \psi} \right] \langle \eta^2 \rangle_t + \left[+\frac{\partial \beta_{1,0}}{\partial \phi} \right] \langle \xi^2 \rangle_t \\ & + \left[+\frac{\partial \beta_{1,0}}{\partial \psi} \right] \langle \xi \eta \rangle_t. \end{aligned} \quad (\text{A9})$$

We set the initial conditions on the macroscopic equations by asking that

$$\phi(0) = \frac{n_0}{N}, \quad \psi(0) = \frac{m_0}{N}. \quad (\text{A10})$$

This implies $\xi(0)=0$ and $\eta(0)=0$ and, by successive differentiation of the macroscopic equations, that all derivatives of $\langle \xi \rangle_t$ and $\langle \eta \rangle_t$ at $t=0$ are also zero. We therefore take

$$\langle \xi \rangle_t = 0, \quad \langle \eta \rangle_t = 0, \quad (\text{A11})$$

for all t . Since the macroscopic equations with initial conditions (A10) cannot be solved in closed form, neither can the equations for $\langle \xi^2 \rangle_t$, $\langle \eta^2 \rangle_t$, or $\langle \xi \eta \rangle_t$.

APPENDIX B: SPATIAL MODELS

In this appendix we give details of the transition probabilities and the master equations for the spatial models dis-

cussed in Sec. V of the main text. The results are frequently fairly straightforward generalizations of those found for the nonspatial model; however, there are some surprises in store: for example, the nontrivial spatial terms found in the mean-field theory of the two-species model are only found by a careful step-by-step derivation of the equations satisfied by $d\langle n_i \rangle/dt$ and $d\langle m_i \rangle/dt$.

We begin with the first version of the one-species model. The transition probabilities for the processes defined by Eqs. (33) and (35) are, by analogy with Eq. (3),

$$T(\dots n_i - 1 \dots | \dots n_i \dots) = \frac{q_1 c n_i (n_i - 1)}{\Omega N N - 1} + \frac{(1 - q_1 - q_2) d n_i}{\Omega N},$$

$$T(\dots n_i + 1 \dots | \dots n_i \dots) = \frac{2q_1 b n_i (N - n_i)}{\Omega N N - 1}. \quad (\text{B1})$$

The only change is the addition of the factor Ω^{-1} , where Ω is the number of sites in the lattice, which represents the arbitrary

choice of the lattice site. In the case where the transition probabilities involve two neighboring patches, which is the process described by Eqs. (34), the corresponding quantities are

$$T(\dots n_i - 1, n_j + 1 \dots | \dots n_i, n_j \dots) = \frac{q_2 m n_i (N - n_j)}{z \Omega N N},$$

$$T(\dots n_i + 1, n_j - 1 \dots | \dots n_i, n_j \dots) = \frac{q_2 m n_j (N - n_i)}{z \Omega N N}, \quad (\text{B2})$$

where z is the coordination number of the lattice (the number of nearest neighbors of any given site) and represents the choice of the nearest neighbor j , once i has been chosen. The master equation for this process therefore reads

$$\begin{aligned} \frac{dP(\vec{n}, t)}{dt} = & \sum_i \sum_{j \in i} \{T(\dots n_i, n_j \dots | \dots n_i + 1, n_j - 1 \dots)P(\dots n_i + 1, n_j - 1 \dots, t) + T(\dots n_i, n_j \dots | \dots n_i - 1, n_j + 1 \dots)P(\dots n_i - 1, n_j \\ & + 1 \dots, t)\} + \sum_i \{T(\dots n_i \dots | \dots n_i + 1 \dots)P(\dots n_i + 1 \dots, t) + T(\dots n_i \dots | \dots n_i - 1 \dots)P(\dots n_i - 1 \dots, t)\} \\ & - \sum_i \sum_{j \in i} \{T(\dots n_i - 1, n_j + 1 \dots | \dots n_i, n_j \dots)P(\dots n_i, n_j \dots, t) + T(\dots n_i + 1, n_j - 1 \dots | \dots n_i, n_j \dots)P(\dots n_i, n_j \dots, t)\} \\ & - \sum_i \{T(\dots n_i - 1 \dots | \dots n_i \dots)P(\dots n_i \dots, t) + T(\dots n_i + 1 \dots | \dots n_i \dots)P(\dots n_i \dots, t)\}. \end{aligned} \quad (\text{B3})$$

Although this looks rather complicated, it is a straightforward generalization of Eqs. (4). In an effort to keep it as simple as possible, only the number of individuals at sites where changes occur (i or j) have been explicitly shown on the right-hand side of the equation. The notation $j \in i$ denotes a sum over all sites j which are nearest neighbors of i . On the left-hand side of the equation, \vec{n} denotes the number of individuals in the set of all patches: $\vec{n} \equiv (n_1, \dots, n_i, \dots, n_j, \dots)$.

To obtain the rate equation, we substitute Eq. (B3) into

$$\frac{d\langle n_k \rangle}{dt} = \sum_{\{\vec{n}\}} n_k \frac{dP(\vec{n}, t)}{dt}. \quad (\text{B4})$$

Defining new quantities

$$\tilde{c} = \frac{q_1 c}{N - 1}, \quad \tilde{b} = \frac{q_1 b}{N - 1}, \quad \tilde{d} = \frac{(1 - q_1 - q_2) d}{N}, \quad \tilde{m} = \frac{q_2 m}{N}, \quad (\text{B5})$$

as in Eq. (6), and introducing a rescaled time $\tau = t/\Omega$, the following equation is found:

$$\begin{aligned} \frac{d}{d\tau} \left\langle \frac{n_i}{N} \right\rangle = & \tilde{m} \Delta \left\langle \frac{n_i}{N} \right\rangle - \tilde{c} \left\{ \left\langle \frac{n_i^2}{N^2} \right\rangle - \frac{1}{N} \left\langle \frac{n_i}{N} \right\rangle \right\} \\ & + 2\tilde{b} \left\{ \left\langle \frac{n_i}{N} \right\rangle - \left\langle \frac{n_i^2}{N^2} \right\rangle \right\} - \tilde{d} \left\langle \frac{n_i}{N} \right\rangle, \end{aligned} \quad (\text{B6})$$

where we have used the explicit forms (B1) and (B2). The symbol Δ denotes the lattice Laplacian (with unit lattice spacing):

$$\Delta f_i \equiv \frac{2}{z} \sum_{j \in i} (f_j - f_i). \quad (\text{B7})$$

The corresponding population-level description can be obtained from Eq. (B6) by letting $N \rightarrow \infty$ which eliminates the term of order N^{-1} and allows us to replace $\langle n_i^2 \rangle$ by $\langle n_i \rangle^2$, as in Sec. II. This leads to an equation for $\phi_i \equiv \langle n_i \rangle / N$ which is given by

$$\frac{d\phi_i}{d\tau} = \tilde{m}\Delta\phi_i - \tilde{c}\phi_i^2 + 2\tilde{b}\phi_i(1 - \phi_i) - \tilde{d}\phi_i. \quad (\text{B8})$$

The final step that has to be taken in order to make contact with the equations used in the traditional approach is to move from the lattice to the continuum. To do this we need to introduce a lattice spacing of ϵ and take it to zero so that

$$\lim_{\epsilon \rightarrow 0} \frac{2}{z} \sum_{j \in i} \frac{(\phi_j - \phi_i)}{\epsilon^2} \rightarrow \nabla^2 \phi(\mathbf{x}), \quad (\text{B9})$$

where the lattice site i is now replaced by the position vector \mathbf{x} . In addition, the migration parameter has to be redefined, in order to absorb a factor of ϵ^2 . The resulting equation is Eq. (37), given in the main text.

The derivation of the population-level description for the second version of the one-species model follows similar lines. The particular differences between this version and the one discussed above are described in the main text and, specifically, by Eqs. (39) and (40). The transition probabilities for this second version are

$$\begin{aligned} T(\dots n_i - 1, n_j \dots | \dots n_i, n_j \dots) &= \frac{\mu c}{zN} n_i n_j, \\ T(\dots n_i + 1, n_j \dots | \dots n_i, n_j \dots) &= \frac{\mu b}{zN} (1 - n_i) n_j, \\ T(\dots n_i + 1, n_j - 1 \dots | \dots n_i, n_j \dots) &= \frac{\mu m}{zN} (1 - n_i) n_j, \end{aligned} \quad (\text{B10})$$

with similar equations with i and j interchanged, and

$$T(\dots n_i - 1 \dots | \dots n_i \dots) = \frac{(1 - \mu)d}{N} n_i. \quad (\text{B11})$$

Note that the transition probabilities in Eqs. (B10) are zero unless n_i and n_j are both equal to 1 (competition) or $n_i = 0$ and $n_j = 1$ (birth and migration), as required. The factors zN and N account for the choices of sites i and j and replace $z\Omega$ and Ω , respectively, in the first version.

The master equation resembles Eq. (B3), except that the single-site processes are now restricted to the death process and the two-site processes are more extensive, involving birth, competition, and migration. Defining

$$\hat{c} = \frac{\mu c}{N}, \quad \hat{b} = \frac{\mu b}{N}, \quad \hat{d} = \frac{(1 - \mu)d}{N}, \quad \hat{m} = \frac{\mu m}{N}, \quad \tau = \frac{t}{N}, \quad (\text{B12})$$

we find using Eq. (B4) and the decoupling approximation $\langle n_i n_j \rangle = \langle n_i \rangle \langle n_j \rangle$,

$$\begin{aligned} \frac{d\langle n_i \rangle}{d\tau} &= \hat{m}\Delta\langle n_i \rangle - \hat{c}\langle n_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle n_j \rangle \right\} \\ &+ 2\hat{b}(1 - \langle n_i \rangle) \left\{ \frac{1}{z} \sum_{j \in i} \langle n_j \rangle \right\} - \hat{d}\langle n_i \rangle. \end{aligned} \quad (\text{B13})$$

Denoting $\langle n_i \rangle$ as ϕ_i , the terms in curly brackets become $\phi(\mathbf{x}, t)$ in the continuum limit, and so once again we recover Eq. (37), given in the main text.

The description of the IBM's when two species are present parallels that for one species. This similarity also holds for the initial stages of the derivation of the population-based equations, and so our description will be brief for both of these aspects.

For the first version of the model, the transition probabilities for birth, competition, and death processes are generalizations of Eqs. (13) [the modifications are exactly the same as those made on Eqs. (3) to give Eqs. (B1)]. Those for migration of A 's are Eqs. (B2), but with m replaced by m_1 and $N - n_j$ replaced by $N - n_j - m_j$ (or $N - n_i$ replaced by $N - n_i - m_i$). For migration of B 's, they have the same form, but with m_1 replaced by m_2 and with the substitutions $n_i \leftrightarrow m_i$ and $n_j \leftrightarrow m_j$. The master equation for $P(\vec{n}, \vec{m}, t)$ is as before, but now including the greater number of allowed processes. There are two rate equations, found by substituting the master equations into

$$\frac{d\langle n_k \rangle}{dt} = \sum_{\{\vec{n}\}} \sum_{\{\vec{m}\}} n_k \frac{dP(\vec{n}, \vec{m}, t)}{dt}, \quad \frac{d\langle m_k \rangle}{dt} = \sum_{\{\vec{n}\}} \sum_{\{\vec{m}\}} m_k \frac{dP(\vec{n}, \vec{m}, t)}{dt}. \quad (\text{B14})$$

Defining the new quantities

$$\tilde{c}_{\alpha\beta} = \frac{q_1 c_{\alpha\beta}}{N - 1}, \quad \tilde{b}_\alpha = \frac{q_1 b_\alpha}{N - 1}, \quad \tilde{d}_\alpha = \frac{(1 - q_1 - q_2)d_\alpha}{N},$$

$$\tilde{m}_\alpha = \frac{q_2 m_\alpha}{N}, \quad \tau = \frac{t}{\Omega}, \quad (\text{B15})$$

as in Eqs. (B5), we now let $N \rightarrow \infty$ and replace averages of products by products of averages to obtain the equations

$$\begin{aligned} \frac{d\phi_i}{d\tau} &= \tilde{m}_1 \Delta\phi_i + \frac{2\tilde{m}_1}{z} \sum_{j \in i} (\phi_i \psi_j - \phi_j \psi_i) - \tilde{c}_{11} \phi_i^2 - 2\tilde{c}_{12} \phi_i \psi_i \\ &+ 2\tilde{b}_1 \phi_i (1 - \phi_i - \psi_i) - \tilde{d}_1 \phi_i \end{aligned} \quad (\text{B16})$$

and

$$\begin{aligned} \frac{d\psi_i}{d\tau} = & \tilde{m}_2 \Delta \psi_i + \frac{2\tilde{m}_2}{z} \sum_{j \in i} (\psi_i \phi_j - \psi_j \phi_i) - \tilde{c}_{22} \psi_i^2 - 2\tilde{c}_{21} \psi_i \phi_i \\ & + 2\tilde{b}_2 \psi_i (1 - \phi_i - \psi_i) - \tilde{d}_2 \psi_i. \end{aligned} \quad (\text{B17})$$

Here $\phi_i \equiv \langle n_i \rangle / N$ and $\psi_i \equiv \langle m_i \rangle / N$. Writing $\phi_i \psi_j - \phi_j \psi_i$ as $\phi_i(\psi_j - \psi_i) - \psi_i(\phi_j - \phi_i)$ we obtain Eqs. (44) and (45) in the continuum limit.

For the second version of the two-species model, the transition probabilities are generalizations of the one-species forms given by Eqs. (B10) and (B11). Specifically, for the competition process the term $cn_i n_j$ becomes $c_{11} n_i n_j$ and, in addition, there are transition probabilities which are proportional to $c_{12} n_i m_j$, $c_{21} m_i n_j$, and $c_{22} m_i m_j$. For the birth process, the factor $(1 - n_i)$ is replaced by $(1 - n_i - m_i)$ and bn_j by $b_1 n_j$ or $b_2 m_j$. The same holds for migration, but with b , b_1 , and b_2 replaced by m , m_1 , and m_2 , respectively. Finally, for the death process dn_i is replaced by $d_1 n_i$ or $d_2 m_i$. The master equation is straightforward, but tedious, to write down.

Defining the new quantities

$$\hat{c}_{\alpha\beta} = \frac{\mu c_{\alpha\beta}}{N}, \quad \hat{b}_\alpha = \frac{\mu b_\alpha}{N}, \quad \hat{d}_\alpha = \frac{(1 - \mu) d_\alpha}{N}, \quad \hat{m}_\alpha = \frac{\mu m_\alpha}{N}, \quad \tau = \frac{t}{N}, \quad (\text{B18})$$

we find using the decoupling approximation — in which averages of products of any two of the variables $\{\vec{n}, \vec{m}\}$ are replaced by the products of their averages—that

$$\begin{aligned} \frac{d}{d\tau} \langle n_i \rangle = & \hat{m}_1 \Delta \langle n_i \rangle + \frac{2\hat{m}_1}{z} \left[\langle n_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle m_j \rangle \right\} \right. \\ & \left. - \langle m_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle n_j \rangle \right\} \right] - \hat{c}_{11} \langle n_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle n_j \rangle \right\} \\ & - 2\hat{c}_{12} \langle n_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle m_j \rangle \right\} + 2\hat{b}_1 (1 - \langle n_i \rangle \\ & - \langle m_i \rangle) \left\{ \frac{1}{z} \sum_{j \in i} \langle n_j \rangle \right\} - \hat{d}_1 \langle n_i \rangle, \end{aligned} \quad (\text{B19})$$

and

$$\begin{aligned} \frac{d}{d\tau} \langle m_i \rangle = & \hat{m}_2 \Delta \langle m_i \rangle + \frac{2\hat{m}_2}{z} \left[\langle m_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle n_j \rangle \right\} \right. \\ & \left. - \langle n_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle m_j \rangle \right\} \right] - \hat{c}_{22} \langle m_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle m_j \rangle \right\} \\ & - 2\hat{c}_{21} \langle m_i \rangle \left\{ \frac{1}{z} \sum_{j \in i} \langle n_j \rangle \right\} + 2\hat{b}_2 (1 - \langle n_i \rangle \\ & - \langle m_i \rangle) \left\{ \frac{1}{z} \sum_{j \in i} \langle m_j \rangle \right\} - \hat{d}_2 \langle m_i \rangle. \end{aligned} \quad (\text{B20})$$

Defining $\langle n_i \rangle$ and $\langle m_i \rangle$ as ϕ_i and ψ_i , respectively, we recover Eqs. (44) and (45) in the continuum limit, up to slightly different definitions of the birth, competition, migration, and death rates.

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