

Quasicycles in a spatial predator-prey model

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We use spatial models of simple predator-prey interactions to predict that predator and prey numbers oscillate in time and space. These oscillations are not seen in the deterministic versions of the models, but are due to stochastic fluctuations about the time-independent solutions of the deterministic equations which are amplified due to the existence of a resonance. We calculate the power spectra of the fluctuations analytically and show that they agree well with results obtained from stochastic simulations. This work extends the analysis of these quasicycles from that previously developed for well-mixed systems to spatial systems, and shows that the ideas and methods used for nonspatial models naturally generalize to the spatial case.

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I. INTRODUCTION

A standard paradigm of condensed matter physics involves the interaction of discrete entities (for example, atoms, molecules or spins) positioned on the sites of a regular lattice which when viewed at the macroscale can be described by a differential equation after coarse-graining. This type of structure is not unique to physics; there are many other systems which consist of a large number of discrete entities which interact with each other in a simple way, but which when viewed macroscopically show complex behavior. What is different, however, is that physicists stress the relationships between models of the same phenomena constructed at different scales, for instance, by deriving macroscopic models from those defined at the microscale. Here we will be interested in modeling species in an ecological system where the interaction between individuals of those species is of the predator-prey type. Although both “microscopic models”—individual based models (IBMs) defined on a two-dimensional lattice, for example, and “macroscopic models” such as reaction-diffusion equations, have been extensively studied [1], the derivation of the latter from the former has received very little attention. Thus it is not obvious *a priori* if the results from the two different approaches can be meaningfully compared or if the macroscopic description misses some important features which are present in the IBM.

In this paper we will build on some earlier work [2] that introduced a methodology which began from a specific IBM and derived the corresponding model which holds at the macroscopic, or population, level. The latter was called the population level model (PLM) and the former sometimes called the individual level model (ILM), rather than the IBM, by analogy. There is another reason for using the term ILM in place of IBM. The nature of the “microscopic model” can vary considerably. At one extreme are models where the constituents each have individual characteristics. They may have an age, sex, be hungry at a given time, and so on. These are essentially agent based models [3,4]. At the other extreme are very simple “physical” models, such as lattice gas models [5], where the analogies to physical processes take a pri-

mary role. The term IBM is frequently used for the former agent based models. Our starting point will be somewhere between these two extremes. We model the individuals as entities which may be born or die, may migrate to neighboring sites on the lattice in a single time interval and when on the same lattice site may interact with each other if one is a prey species of the other. Thus, the individuals act as chemical species which have given interaction rules. There are several advantages with this formulation. First, it corresponds most directly in terms of properties of the constituents to PLMs such as the Volterra equations. Second, more properties of individuals can be included if required, taking the model more towards the agent-based IBMs mentioned above. Third, it allows the stochastic nature of birth, death, predator-prey, and migratory processes to be naturally included into the model. Whereas most stochastic models have been simulated directly, we prefer to formulate them as a master equation, and use the system-size expansion [6] to derive the form they take when the system size is large.

The aim of this paper is then to investigate the nature of the PLM model both at the macroscopic or mean-field level—which is deterministic—and at what might be described as the mesoscopic scale where stochastic effects are still important, but where the discrete nature of the constituents has been lost. The former is interesting because it is not clear that the model derived in this way will coincide with those appearing in the references on the subject [7–10], but also because of the types of collective patterns frequently displayed by these systems, which often resemble those observed when studying physical and chemical systems. The latter is interesting because it has been found that in simple predator-prey models (without spatial effects being included) large predator-prey cycles are present in the stochastic model, which are lost at the deterministic level [11]. More specifically, the discrete nature of the individuals results in a demographic stochasticity at the mesoscale which acts as a driving force and creates a resonance effect, turning small cyclic fluctuations into large cycles called quasicycles [8]. Here we investigate the nature of this phenomenon in a model where spatial effects are included. The ordinary differential equations of the Volterra type will now be replaced by partial differential equations of the reaction-diffusion type, and the two coupled Langevin equations of [11] will be

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replaced by two coupled partial differential equations with additive noise.

The analysis we describe above has not been carried out previously, but there are very many studies of stochastic and/or spatial Lotka-Volterra-like systems which are described in the literature. A rather extensive discussion of the relationship between our approach and other studies was given in [2] which, together with [11], can be regarded as the precursor of the current work. A recent paper [12], as well as being representative of many of the investigations that have been carried out in this field, contains references to many of the papers presented in the area in the last 2 or 3 years. Physicists have been interested in predator-prey models for a number of reasons, for some it is the existence of a phase transition [13,14], but for us it is that the work presented here differs from almost all previous studies in that it follows the traditional physics prescription of postulating a microscopic model and deriving the macroscopic (and in our case also the mesoscopic) model from this.

The paper is organized as follows. In Sec. II, the model alluded to above is introduced and formulated as a master equation. This is followed in Sec. III by a discussion of the deterministic limit of the equation, a linear stability analysis of the stationary solution of this equation, and the linear noise correction to the deterministic equation. In Sec. IV a Fourier analysis of the linear stochastic differential equations is carried out which yields power spectra which characterize the nature of the spatial and temporal predator-prey cycles, with the analytic results being compared to the results of computer simulations. There are two Appendixes containing mathematical details. The first describes the application of the system-size expansion to the master equation and the second contains the Fourier analysis of the linear stochastic differential equations.

II. MODEL

The system we will be interested in consists of individuals of species *A* who are predators of individuals belonging to the prey species *B*. We assume that they inhabit patches, labeled by $i=1, \dots, \Omega$, which are situated at the sites of a *d*-dimensional hypercubic lattice. Of course, for applications we are interested in the case of a square lattice in two dimensions, but we prefer to work with general *d*. One reason is that it is not any more complicated to do so, another is because our stochastic simulations have been carried out in $d=1$ in order to achieve higher accuracy. Each patch possesses a finite carrying capacity, *N*, which is the maximum number of individuals allowed per site. The number of predators and prey in patch *i* will be denoted by n_i and m_i respectively. There will therefore be $(N-n_i-m_i)$ empty or vacant “spaces,” *E*, in patch *i*. These are necessary to allow the number of *A* and *B* individuals in patch *i* to independently vary with time. Further background to the modeling procedure is given in [2], where it has been applied to competition between two species.

As discussed in Sec. I, we assume that the constituents *A*, *B*, and *E* react together at given rates. The reactions corresponding to birth, death, and predation are assumed to be

local, that is, only involve individuals at a particular site. They will therefore be identical to those invoked in the predator-prey model without spatial structure [11], and since these have been shown to lead to the Volterra equations in the deterministic limit, we will adopt them here,

$$B_i E_i \xrightarrow{b} B_i B_i, \tag{1}$$

$$A_i B_i \xrightarrow{p_1} A_i A_i, \quad A_i B_i \xrightarrow{p_2} A_i E_i, \tag{2}$$

$$A_i \xrightarrow{d_1} E_i, \quad B_i \xrightarrow{d_2} E_i. \tag{3}$$

All constituents have a subscript *i* to denote that they are located in patch *i*. Equation (1) describes the birth of a prey individual, which occurs at a rate *b*. We assume that “space” is required for this to occur. Also we do not specify the birth of predator individuals as a separate event, since these also occur through predation, as described by Eq. (2), and will not lead to new terms in the evolution equations. Two types of predation are required in Eq. (2) so that only a fraction of the resources obtained from consumption of the prey are used to produce new predator individuals. Finally, Eq. (3) describes the death of individuals of species *A* and *B* at rates d_1 and d_2 , respectively.

Here we are considering an explicitly spatial model, so the additional feature which we include is the possibility of changes in the populations due to migrations between nearest-neighbor patches. These events can be described by adding the following set of reactions [2]:

$$A_i E_j \xrightarrow{\mu_1} E_i A_j, \quad B_i E_j \xrightarrow{\mu_2} E_i B_j, \tag{4}$$

$$A_j E_i \xrightarrow{\mu_1} E_j A_i, \quad B_j E_i \xrightarrow{\mu_2} E_j B_i.$$

Here *i* and *j* are nearest-neighbor sites and μ_1 and μ_2 are the migration rates for individuals of species *A* and *B*, respectively.

The state of the system at any given time is specified by the elements of the set $\{n_i, m_i: i=1, \dots, \Omega\}$. If we take the transition rates between these states to only depend on the current state of the system, the process will be Markov and can be described by a master equation in continuous time. The natural way to define such transition rates is according to a mass action law: The probability that two constituents meet is proportional to their current proportions in their respective patches. The allowed transitions and the rates at which they take place are given by Eqs. (1)–(4). Denoting the transition rates from a state with n_l predators and m_k prey to a state with n'_l predators and m'_k prey by $T_{n'_l, m'_k | n_l, m_k}$, then the transition rates corresponding to the purely local reactions (1)–(3) are

$$T_{n_i+1, m_i-1 | n_i, m_i} = p_1 \frac{2n_i m_i}{\Omega N},$$

$$T_{n_i, m_i+1 | n_i, m_i} = b \frac{2m_i(N-n_i-m_i)}{\Omega N},$$

$$T_{n_{i-1}, m_i | n_i, m_i} = d_1 \frac{n_i}{\Omega},$$

$$T_{n_i, m_{i-1} | n_i, m_i} = p_2 \frac{2n_i m_i}{\Omega N} + d_2 \frac{m_i}{\Omega}. \quad (5)$$

These are exactly as in the nonspatial form of the model [11], but with the state variables all having a subscript i to denote these are the reactions in patch i and an extra factor of Ω in the denominator since there is a choice between any one of the Ω patches when determining the probability of a transition taking place. To lighten the notation we have shown the dependence of T only on the subset of variables liable to change (in this case those on the site i). The corresponding expressions for the transition rates between nearest neighbors, which describes the migratory process, are

$$\begin{aligned} T_{n_i+1, n_j-1 | n_i, n_j} &= \mu_1 \frac{n_j(N - n_i - m_i)}{z\Omega N}, \\ T_{n_i-1, n_j+1 | n_i, n_j} &= \mu_1 \frac{n_i(N - n_j - m_j)}{z\Omega N}, \\ T_{m_i+1, m_j-1 | m_i, m_j} &= \mu_2 \frac{m_j(N - n_i - m_i)}{z\Omega N}, \\ T_{m_i-1, m_j+1 | m_i, m_j} &= \mu_2 \frac{m_i(N - n_j - m_j)}{z\Omega N}. \end{aligned} \quad (6)$$

Here, z denotes the coordination number of the lattice, that is the number of nearest neighbors of any given site, which in our case is $2d$. It needs to be included since it represents the choice of nearest neighbor j , once the patch i has been chosen.

The master equation which governs the time evolution of the system can now be constructed. Although this equation can easily be written down, and has the standard form of a sum of transition probabilities giving rise to a change in the probability distribution function with time [6], it has a rather ungainly appearance. It can be made to look neater through the introduction of a little more notation. First, the probability distribution function that the system is in state $\{n_i, m_i; i = 1, \dots, \Omega\}$ at time t is conventionally denoted by $P(n_1, m_1, \dots, n_\Omega, m_\Omega; t)$, but we will denote it by $P_{\mathbf{n}, \mathbf{m}}(t)$. Then the master equation takes the form

$$\frac{dP_{\mathbf{n}, \mathbf{m}}(t)}{dt} = \sum_{i=1}^{\Omega} \mathcal{T}_i^{\text{loc}} P_{\mathbf{n}, \mathbf{m}}(t) + \sum_{i=1}^{\Omega} \sum_{j \in i} \mathcal{T}_{ij}^{\text{mig}} P_{\mathbf{n}, \mathbf{m}}(t), \quad (7)$$

where the notation $j \in i$ means that j is a nearest neighbor of i and where $\mathcal{T}_i^{\text{loc}}$ and $\mathcal{T}_{ij}^{\text{mig}}$ are transition rates which are defined below. These transition rates may in turn be simplified by the introduction of the step operators [6] $E_{x_i}^{\pm 1}$ and $E_{y_i}^{\pm 1}$ defined by their effect on a typical function of \mathbf{n} and \mathbf{m} as follows:

$$E_{x_i}^{\pm 1} f(n_i, m_i) = f(n_i \pm 1, m_i),$$

$$E_{y_i}^{\pm 1} f(n_i, m_i) = f(n_i, m_i \pm 1). \quad (8)$$

The local transition operator $\mathcal{T}_i^{\text{loc}}$ may now be written as

$$\begin{aligned} \mathcal{T}_i^{\text{loc}} &= (E_{x_i} - 1)T_{n_{i-1}, m_i | n_i, m_i} + (E_{y_i}^{-1} - 1)T_{n_i, m_{i+1} | n_i, m_i} \\ &\quad + (E_{y_i} - 1)T_{n_i, m_{i-1} | n_i, m_i} + (E_{x_i}^{-1} E_{y_i} - 1)T_{n_{i+1}, m_{i-1} | n_i, m_i}, \end{aligned} \quad (9)$$

with the four local transition rates given explicitly in Eq. (6). Similarly, the transition operator $\mathcal{T}_{ij}^{\text{mig}}$ which involves transitions between nearest-neighbor sites can be written as

$$\begin{aligned} \mathcal{T}_{ij}^{\text{mig}} &= (E_{x_i}^{-1} E_{x_j} - 1)T_{n_{i+1}, n_j-1 | n_i, n_j} + (E_{x_i} E_{x_j}^{-1} - 1)T_{n_{i-1}, n_j+1 | n_i, n_j} \\ &\quad + (E_{y_i}^{-1} E_{y_j} - 1)T_{m_i+1, m_j-1 | m_i, m_j} \\ &\quad + (E_{y_i} E_{y_j}^{-1} - 1)T_{m_{i-1}, m_j+1 | m_i, m_j}. \end{aligned} \quad (10)$$

The master equation (7), together with the definitions of the transitions rates given by Eqs. (5) and (6) together with Eqs. (9) and (10), completely define the model once initial and boundary conditions are specified. The model is far too complicated to be solved exactly, but it can be analyzed very accurately by studying it in the limit of large system size. As previously proposed [2, 11, 15, 16], and as discussed in Appendix A, the leading order in a system-size expansion of the master equation gives deterministic equations whose stationary state can be analyzed, whereas the next-to-leading order result gives linear stochastic differential equations, which can be Fourier analyzed. From this we can investigate the possible existence of resonant behavior induced by the demographic stochasticity of the original model.

In the next section we obtain and analyze the equations describing the model. The details of the calculation required to determine these are given in Appendix A.

III. DETERMINISTIC LIMIT AND FLUCTUATIONS ABOUT IT

The deterministic limit of the model defined by Eqs. (7), (9), and (10) is derived in Appendix A. It is defined in terms of the populations $\phi_i = \lim_{N \rightarrow \infty} (n_i/N)$ and $\psi_i = \lim_{N \rightarrow \infty} (m_i/N)$ and explicitly given by Eqs. (A4), (A5), (A15), and (A16). These may be written as the 2Ω macroscopic equations

$$\frac{d\phi_i}{d\tau} = 2p_1 \phi_i \psi_i - d_1 \phi_i + \mu_1 (\Delta \phi_i + \phi_i \Delta \psi_i - \psi_i \Delta \phi_i), \quad (11)$$

$$\begin{aligned} \frac{d\psi_i}{d\tau} &= -2(p_1 + p_2 + b) \phi_i \psi_i + (2b - d_2) \psi_i - 2b \psi_i^2 \\ &\quad + \mu_2 (\Delta \psi_i + \psi_i \Delta \phi_i - \phi_i \Delta \psi_i), \end{aligned} \quad (12)$$

where $i = 1, \dots, \Omega$ and where the symbol Δ represents the discrete Laplacian operator $\Delta f_i = \frac{2}{z} \sum_{j \in i} (f_j - f_i)$. A rescaled time, $\tau = t/\Omega$, has also been introduced.

To complete the formulation of the problem, initial and boundary data should be provided. For the type of system considered here the most natural choice is to consider zero-flux boundary conditions, regardless of the initial conditions.

This corresponds to the condition that individuals are not allowed to leave or enter the fixed region designated as the system, in other words there is no immigration or emigration. The system of equations (11) and (12) possesses two limits of interest. The limit $\Omega=1$ formally corresponds to a one-site system and is simply the well-known Volterra model as studied in [11]. The limit $\Omega \rightarrow \infty$ corresponds to shrinking the lattice spacing to zero and so obtaining a continuum description in which the discrete Laplacian operator is replaced by the continuous Laplacian ∇^2 and the Eqs. (11) and (12) become a pair of partial differential equations,

$$\frac{\partial \phi}{\partial \tau} = \alpha \phi \psi - \beta \phi + \mu_1 \nabla^2 \phi + \mu_1 (\phi \nabla^2 \psi - \psi \nabla^2 \phi), \quad (13)$$

$$\frac{\partial \psi}{\partial \tau} = r \psi \left(1 - \frac{\psi}{K} \right) - \lambda \psi \phi + \mu_2 \nabla^2 \psi + \mu_2 (\psi \nabla^2 \phi - \phi \nabla^2 \psi), \quad (14)$$

where $\alpha=2p_1$, $\beta=d_1$, $r=2b-d_2$, $K=(2b-d_2)/2b$, and $\lambda=2(p_1+p_2+b)$, with ψ and ϕ representing the prey and predators densities respectively. It should be noted that in the transition to a continuum model, the population fractions go over to population densities and parameters may be scaled by factors involving the lattice spacing. An example of this involves the migration rates in Eqs. (13) and (14), which are scaled versions of those appearing in Eqs. (11) and (12) [see Eqs. (B10)].

One of the most interesting features of Eqs. (13) and (14) is the emergence of cross-diffusive terms of the type $(\psi \nabla^2 \phi - \phi \nabla^2 \psi)$. These types of contributions do not usually appear in the heuristically proposed spatially extended predator-prey models [17,18]. However, they seem to appear naturally in these types of lattice models, and cross-diffusive terms similar to those found here have been obtained as the mean-field limit of a set of models proposed by Satulovsky [19].

For the class of models we are considering here, the origin of these nonlinear diffusion terms can be seen from an examination of the transition rates for diffusion given by the expressions (6). It is the presence of the factors $(N-n_i-m_i)$ which gives rise to these extra terms, and these factors in turn are present because the reactions (4) have the structure $A_i E_j \xrightarrow{\mu_1} E_i A_j$, rather than $A_i \xrightarrow{\mu_1} A_j$. So it is the requirement that there is space available in the patch where the individual is moving to, which gives the nonlinear diffusion term. For a model which specifies a finite carrying capacity for each patch, such terms are bound to exist. In the situations where the patch occupations are not near this limit, these terms are negligible, and the usual deterministic equations with linear diffusion terms are recovered.

An inspection of Eqs. (13) and (14) leads to the conclusion that these equations do not reduce to a simple reaction-diffusion scheme for any choice of parameters. However if zero-flux boundary conditions are chosen, this implies that, after a single integration over the spatial domain, the contribution of the cross-diffusive terms for the solution vanishes,

$$\int_A (\phi \nabla^2 \psi - \psi \nabla^2 \phi) dA' = \int_C (\phi \nabla \psi - \psi \nabla \phi) \cdot d\mathbf{r} = 0, \quad (15)$$

with a similar equation with ϕ and ψ interchanged. The condition (15) also occurs if we impose the requirement that $\psi(\mathbf{r}, t)$ and $\phi(\mathbf{r}, t)$ vanish as $\mathbf{r} \rightarrow \infty$, instead of the zero-flux boundary conditions, which are those typically chosen [10].

Before discussing the equations which describe the stochastic behavior of the system, we will analyze the nature of the stationary solutions in the deterministic limit. We will be particularly interested in investigating the possibility that “diffusion-driven” instabilities may occur for the model defined by Eqs. (11) and (12) or equivalently for Eqs. (13) and (14).

A. Stationary state in the deterministic limit

One of the simplest questions one can ask about Eqs. (11) and (12) or Eqs. (13) and (14) concerns the nature of the stationary state. It is simple to verify that there are two unstable fixed points (describing the null state, $\phi^* = \psi^* = 0$, and a state with no predators, $\phi^* = 0, \psi^* = K$), and a single coexistence fixed point given by (see also [20–22], for instance)

$$\phi^* = \frac{r}{\lambda} \left(1 - \frac{\beta}{\alpha K} \right), \quad \psi^* = \frac{\beta}{\alpha}. \quad (16)$$

As an aside we remark that if we had assumed a birth process $B_i \xrightarrow{b} B_i B_i$, and not $B_i E_i \xrightarrow{b} B_i B_i$, the result would have been a deterministic equation with the factor of $[1 - (\psi/K)]$ in Eq. (14) absent. This corresponds to a situation without saturation in the predator’s capacity and leads to a nongeneric situation where the model has a conserved quantity, and therefore a family of neutrally stable cycles which are not robust to the introduction of more realistic features. In other words, this system has pathological dynamical properties [23], where the amplitude of the oscillations bears no relation to the biology of the predator and prey and only depends on the arbitrary initial population sizes [24]. The introduction of logistic growth, for instance, destroys these neutrally stable cycles and replaces them by a stable fixed point.

Finding nonhomogeneous stationary state solutions would require solving a pair of coupled nonlinear differential equations, but we can look for solutions if the homogeneous solutions (16) are unstable to spatially inhomogeneous small perturbations. That is, we look for solutions of Eqs. (11) and (12) which have the form

$$\phi_j = \phi^* + u_j, \quad \psi_j = \psi^* + v_j, \quad (17)$$

where u_j and v_j are the small perturbations. An exactly similar analysis could be carried out on the continuum versions (13) and (14), but now u and v would be functions of \mathbf{r} , a vector in the region of interest. Substituting Eq. (17) into Eqs. (11) and (12), and keeping only linear terms in u and v gives

$$\frac{du_j}{d\tau} = a_{11}u_j + a_{12}v_j + \mu_1\Delta u_j + \mu_1(\phi^*\Delta v_j - \psi^*\Delta u_j), \quad (18)$$

$$\frac{dv_j}{d\tau} = a_{21}u_j + a_{22}v_j + \mu_2\Delta v_j + \mu_2(\psi^*\Delta u_j - \phi^*\Delta v_j). \quad (19)$$

Here a_{11} , a_{12} , a_{21} , and a_{22} are the contributions which would be found if the perturbation had been assumed to be homogeneous; they are exactly the terms found in [11], namely

$$a_{11} = \alpha\psi^* - \beta, \quad a_{12} = \alpha\phi^*,$$

$$a_{21} = -\lambda\psi^*, \quad a_{22} = r\left(1 - \frac{2\psi^*}{K}\right) - \lambda\phi^*. \quad (20)$$

We may write Eqs. (18) and (19) in the unified form $\dot{\mathbf{u}}_j = \mathbf{A}\mathbf{u}_j$ with $\mathbf{u}_j = (u_j, v_j)^T$ for a given site j . The entries of the matrix \mathbf{A} will be denoted by $\alpha_{i,11}$, $\alpha_{i,12}$, $\alpha_{i,21}$, and $\alpha_{i,22}$. The solution to $\dot{\mathbf{u}}_j = \mathbf{A}\mathbf{u}_j$ has the form

$$\mathbf{u}_j(\tau) \sim \exp(\nu\tau + i\mathbf{a}\mathbf{k} \cdot \mathbf{j}), \quad (21)$$

where a is the lattice spacing and where we have explicitly indicated the vector nature of \mathbf{j} and \mathbf{k} . The ν and \mathbf{k} must satisfy

$$\begin{vmatrix} \nu - \alpha_{11} & -\alpha_{12} \\ -\alpha_{21} & \nu - \alpha_{22} \end{vmatrix} = 0, \quad (22)$$

where

$$\alpha_{\mathbf{k},11} = a_{11} + \mu_1(1 - \psi^*)\Delta_{\mathbf{k}},$$

$$\alpha_{\mathbf{k},12} = a_{12} + \mu_1\phi^*\Delta_{\mathbf{k}},$$

$$\alpha_{\mathbf{k},21} = a_{21} + \mu_2\psi^*\Delta_{\mathbf{k}},$$

$$\alpha_{\mathbf{k},22} = a_{22} + \mu_2(1 - \phi^*)\Delta_{\mathbf{k}}, \quad (23)$$

and where the discrete Laplacian, $\Delta_{\mathbf{k}}$ for a d -dimensional hypercubic lattice is (see Appendix A)

$$\Delta_{\mathbf{k}} = \frac{2}{d} \sum_{\gamma=1}^d [\cos(k_\gamma a) - 1]. \quad (24)$$

The idea that patterns can form due to a diffusion-induced instability was first put forward by Turing in 1952 in connection with his investigation into the origins of morphogenesis [25]. More generally, such patterns can arise in reaction-diffusion equations where a homogeneous stationary state is stable to homogeneous perturbations, but where irregularities or stochastic fluctuations in real systems can induce local deviations from the spatially uniform state, which can in turn grow if this state is unstable to inhomogeneous perturbations. Since Turing's seminal work, the phenomenon has been studied in many types of reaction-diffusion systems, including spatial predator-prey models [17,26–28]. In contrast to these previous studies, where the reaction-diffusion equations were

postulated phenomenologically, we have derived our equations from a ILM. Moreover they differ from the models considered previously because of the existence of nonlinear diffusive terms. Therefore, it is of interest to study if the model we have derived allows for the existence of Turing patterns.

We first need to check that the homogeneous stationary state is stable to homogeneous perturbations. A homogeneous perturbation means that the u_j and v_j in Eq. (17) are independent of j . This in turn means that the terms involving μ_1 and μ_2 are absent from Eqs. (18) and (19). Therefore the stability to homogeneous perturbations may be found from Eq. (22) with the α replaced by the a . Stability is assured if $a_{11} + a_{22} < 0$ and $a_{11}a_{22} - a_{12}a_{21} > 0$, since these conditions are equivalent to asking that the ν which are solutions of Eq. (22) have negative real parts. It is straightforward to check from the explicit forms (16) and (20) that $a_{11} = 0$, $a_{12} > 0$ and $a_{21}, a_{22} < 0$, and so that this is the case. As an aside we can also investigate the stability of the null state ($\phi^* = \psi^* = 0$) and the state without predators ($\phi^* = 0$, $\psi^* = K$). We find that, under the condition the fixed point (16) exists, $a_{11}a_{22} < 0$ and $a_{12} = 0$. Therefore, the determinant of the stability matrix is negative, and so the eigenvalues are real with different signs. This implies that both these states are unstable.

To get a diffusive instability, we need to investigate the solutions (17) which now include the spatial contributions. For an instability to occur, one of the conditions $\text{tr } \mathbf{A}_{\mathbf{k}} < 0$ or $\det \mathbf{A}_{\mathbf{k}} > 0$ must be violated. From Eq. (24) it is clear that $\Delta_{\mathbf{k}} \leq 0$ and so from Eq. (23) that $\alpha_{11} \leq a_{11}$ and $\alpha_{22} \leq a_{22}$ and so that $\text{tr } \mathbf{A}_{\mathbf{k}} < 0$. So the only possibility for a Turing pattern to arise is if $\det \mathbf{A}_{\mathbf{k}} < 0$. By direct calculation

$$\det \mathbf{A}_{\mathbf{k}} = -a_{12}a_{21} - \mu_1[a_{21}\phi^* - a_{22}(1 - \psi^*)]\Delta_{\mathbf{k}} - \mu_2a_{12}\psi^*\Delta_{\mathbf{k}} + \mu_1\mu_2(1 - \phi^* - \psi^*)\Delta_{\mathbf{k}}^2. \quad (25)$$

Now all the terms on the right-hand side of Eq. (25) are manifestly positive, except the second. However, since

$$a_{21}\phi^* - a_{22}(1 - \psi^*) = r\psi^*\left(\frac{1}{K} - 1\right), \quad (26)$$

and $K = 1 - (d_2/2b) < 1$, then this term is also positive. Therefore $\det \mathbf{A}_{\mathbf{k}} > 0$ and so the homogeneous stationary state is stable to both small homogeneous and small inhomogeneous perturbations.

It has been known for some time that the simple reaction-diffusion equations for a predator-prey model (i.e., those only containing simple diffusive terms such as $\nabla^2\varphi$ and $\nabla^2\psi$) do not lead to diffusive instabilities [10]. We have shown here that the introduction of a particular type of cross-diffusive term, which has its origins in the ILM formulation, also contains no Turing instability. It should be noted that this also holds true in the limit of zero lattice spacing where $\Delta_{\mathbf{k}}$ is replaced by $-k^2$ (up to a constant), which is also always negative for $\mathbf{k} \neq 0$. This corresponds to using Eqs. (13) and (14), rather than Eqs. (11) and (12). Since, on average, the population fractions do not exhibit any form of spatial self-organizing structure, the emergence of such structures when observing the full dynamical process should be understood as an effect due to fluctuations. So we now study the next-

to-leading order contributions which describe fluctuations around these mean values, with the aim of quantifying possible resonant behavior in both space and time.

B. Fluctuations

The next-to-leading order in the system size expansion gives a Fokker-Planck equation in the 2Ω variables ξ_i and η_i , which describe the deviation of the system from the mean fields,

$$\xi_i(t) = \sqrt{N} \left(\frac{n_i}{N} - \phi_i(t) \right), \quad \eta_i(t) = \sqrt{N} \left(\frac{m_i}{N} - \psi_i(t) \right). \quad (27)$$

The equation itself is derived in Appendix A; it is given by Eq. (A6) with coefficients defined by Eqs. (A26) and (A27). These coefficients have been evaluated at the fixed-point φ^* , ψ^* of the deterministic equations since, as explained earlier, we are interested in studying the effect of fluctuations on the system once transient solutions of the deterministic equations have died away. Rather than work with this Fokker-Planck equation, it is more convenient to use the Langevin equation which it is equivalent to. This has the form [29,30]

$$\frac{d\zeta_i}{d\tau} = \mathcal{A}_i(\zeta) + \lambda_i(\tau), \quad (28)$$

where

$$\langle \lambda_i(\tau) \lambda_j(\tau') \rangle = \mathcal{B}_{ij} \delta(\tau - \tau'). \quad (29)$$

Here $\zeta_i = (\xi_i, \eta_i)$ and $\lambda_i = (\lambda_{i,1}, \lambda_{i,2})$ with \mathcal{B}_{ij} being the constant matrix defined by Eq. (A27).

The key point here is that the system-size expansion to this order yields a function $\mathcal{A}(\zeta)$ which is *linear* in ζ_i , as can be seen from Eq. (A26). It is this linear nature of the Langevin equation which is crucial in the analysis that follows. To study possible cyclic behavior we require to calculate the power spectrum of the fluctuations (27), and to do this we need to find an equation for their temporal Fourier transforms. The linearity of the Langevin equation (28) means that this is readily achieved. The translational invariance of the solutions of the deterministic equations, together with the nature of the diffusive terms also make it useful to take the spatial Fourier transform of Eq. (28). This is discussed in detail in Appendix B; writing out the two components of the equation explicitly it has the form

$$\begin{aligned} \frac{d\xi_{\mathbf{k}}}{d\tau} &= \alpha_{\mathbf{k},11} \xi_{\mathbf{k}} + \alpha_{\mathbf{k},12} \eta_{\mathbf{k}} + \lambda_{1,\mathbf{k}}(\tau), \\ \frac{d\eta_{\mathbf{k}}}{d\tau} &= \alpha_{\mathbf{k},21} \xi_{\mathbf{k}} + \alpha_{\mathbf{k},22} \eta_{\mathbf{k}} + \lambda_{2,\mathbf{k}}(\tau), \end{aligned} \quad (30)$$

where the $\alpha_{\mathbf{k}}$ are given by Eq. (23) and by Eq. (20). The noise correlators (29) are now local in \mathbf{k} space,

$$\langle \lambda_{\mathbf{k}}(\tau) \lambda_{\mathbf{k}'}(\tau') \rangle = \mathcal{B}_{\mathbf{k}} \Omega a^d \delta_{\mathbf{k}+\mathbf{k}',0} \delta(\tau - \tau'), \quad (31)$$

where $\mathcal{B}_{\mathbf{k}}$ is derived in the Appendixes [see Eq. (B6), etc.] and is given by

$$\mathcal{B}_{\mathbf{k},11} = a^d [(d_1 \phi^* + 2p_1 \psi^* \phi^*) - 2\mu_1 \phi^* (1 - \phi^* - \psi^*) \Delta_{\mathbf{k}}],$$

$$\begin{aligned} \mathcal{B}_{\mathbf{k},22} &= a^d [2b \psi^* (1 - \phi^* - \psi^*) + d_2 \psi^* + 2(p_1 + p_2) \psi^* \phi^* \\ &\quad - 2\mu_2 \psi^* (1 - \phi^* - \psi^*) \Delta_{\mathbf{k}}], \end{aligned}$$

$$\mathcal{B}_{\mathbf{k},12} = \mathcal{B}_{\mathbf{k},21} = -2a^d p_1 \phi^* \psi^*. \quad (32)$$

It should be noted that, since $\Delta_{\mathbf{k}} < 0$, the diagonal elements of $\mathcal{B}_{\mathbf{k}}$ are all positive, as they should be.

It is interesting to consider what happens in the continuum limit $a \rightarrow 0$. For nonzero a , the wave numbers take on values in the interval $(-\pi/a) \leq k_i \leq (\pi/a)$, but this becomes an infinite interval as $a \rightarrow 0$. The wave numbers are still discrete however, due to the finite volume (area in two dimensions) of the system; we keep the volume Ωa^d fixed in the limit, so that $\Omega \rightarrow \infty$. In the limit $\Omega a^d \delta_{\mathbf{k}+\mathbf{k}',0}$ goes over to $(2\pi)^d \delta(\mathbf{k}+\mathbf{k}')$ and $\Delta_{\mathbf{k}}$ goes over to $-k^2$, as long as the migration rates are suitably scaled [see Eq. (B10)]. However, from Eq. (32), it is clear that the $\mathcal{B}_{\mathbf{k}}$ vanish in the limit due to the factor of a^d . This should not be too surprising: since $\Omega \rightarrow \infty$, the number of degrees of freedom of the system is becoming infinitely large, and thus we would expect fluctuations to vanish. If all the $\mathcal{B}_{\mathbf{k}}$ are zero, the noises $\lambda_{\mathbf{k}}(\tau)$ vanish, and therefore so do $\xi_{\mathbf{k}}(\tau)$ and $\eta_{\mathbf{k}}(\tau)$. This effect has been seen (see [31], and the references therein): Oscillatory behavior in these types of models persists as long as the number of sites remains finite, however it disappears in the so-called thermodynamic limit. However, in practice, one must go over to describing the population sizes as population densities, rather than pure numbers, in this limit. This will involve further rescalings, and depending on the exact definition of the model, these fluctuations can survive the continuum limit. For this reason we will keep a finite lattice spacing: The results for a particular continuum model variant can then be determined by taking the $a \rightarrow 0$ limit in the appropriate manner.

IV. POWER SPECTRA

To calculate the power spectra of the fluctuations about the stationary state, we first have to take the temporal Fourier transform of Eqs. (30). This reduces the equations governing the stochastic behavior of the system to two coupled algebraic equations which are linear. These can be used to obtain a closed form expression for the power spectra. In this section we first describe this analytic approach, and then go on to discuss how the power spectra can be found from numerical simulations, and then finally compare the results of these two approaches.

A. Analytic form

Taking the temporal Fourier transform of Eqs. (30) yields

$$\mathbb{M} \zeta_{\mathbf{k}}(\omega) = \lambda_{\mathbf{k}}(\omega), \quad (33)$$

where $\mathbb{M} = (-i\omega \mathbb{I} - \mathbb{A})$ and \mathbb{I} is the 2×2 identity matrix. Therefore $\zeta = \mathbb{M}^{-1} \lambda$, which implies that

$$|\xi_{\mathbf{k}}(\omega)|^2 = |p_{11}|^2 \lambda_1 \lambda_1^* + p_{11} p_{12}^* \lambda_1 \lambda_2^* + p_{11}^* p_{12} \lambda_1^* \lambda_2 + |p_{22}|^2 \lambda_2 \lambda_2^*, \quad (34)$$

with a similar expression for $|\eta_{\mathbf{k}}(\omega)|^2$ which is just Eq. (34) but with all the first subscripts of p changed to 2. Here the p_{ab} are the elements of \mathbb{M}^{-1} . Using

$$\langle \lambda_{\mathbf{k}}(\omega) \lambda_{\mathbf{k}}^*(\omega) \rangle = \mathcal{B}_{\mathbf{k}}, \quad (35)$$

the power spectra for the predators

$$P_{\mathbf{k},1}(\omega) = \langle |\xi_{\mathbf{k}}(\omega)|^2 \rangle, \quad (36)$$

and for the prey

$$P_{\mathbf{k},2}(\omega) = \langle |\eta_{\mathbf{k}}(\omega)|^2 \rangle, \quad (37)$$

may easily be found.

Since the Langevin equations are diagonal in \mathbf{k} space, the structure of the expressions for the power spectra are the same as those found in other studies [11,15,16], namely

$$P_{\mathbf{k},1} = \frac{C_{\mathbf{k},1} + \mathcal{B}_{\mathbf{k},11} \omega^2}{[(\omega^2 - \Omega_{\mathbf{k},0}^2)^2 + \Gamma_{\mathbf{k}}^2 \omega^2]}, \quad (38)$$

and

$$P_{\mathbf{k},2} = \frac{C_{\mathbf{k},2} + \mathcal{B}_{\mathbf{k},22} \omega^2}{[(\omega^2 - \Omega_{\mathbf{k},0}^2)^2 + \Gamma_{\mathbf{k}}^2 \omega^2]}, \quad (39)$$

where

$$\begin{aligned} C_{\mathbf{k},1} &= \mathcal{B}_{\mathbf{k},11} \alpha_{\mathbf{k},22}^2 - 2\mathcal{B}_{\mathbf{k},12} \alpha_{\mathbf{k},12} \alpha_{\mathbf{k},22} + \mathcal{B}_{\mathbf{k},22} \alpha_{\mathbf{k},12}^2, \\ C_{\mathbf{k},2} &= \mathcal{B}_{\mathbf{k},22} \alpha_{\mathbf{k},11}^2 - 2\mathcal{B}_{\mathbf{k},12} \alpha_{\mathbf{k},21} \alpha_{\mathbf{k},11} + \mathcal{B}_{\mathbf{k},11} \alpha_{\mathbf{k},21}^2. \end{aligned} \quad (40)$$

The spectra (38) and (39) resemble those found when analyzing driven damped linear oscillators in physical systems. A difference between that situation and the one here is that the driving forces here are white noises $\lambda(\tau)$ which excite all frequencies equally, thus there is no need to tune the frequency of the “driving force” to achieve resonance. The parameters in the denominators of Eqs. (38) and (39) are given by $\Omega_{\mathbf{k},0}^2 = \det \mathbf{A}_{\mathbf{k}}$ and $\Gamma_{\mathbf{k}} = -\text{tr} \mathbf{A}_{\mathbf{k}}$, where $\mathbf{A}_{\mathbf{k}}$ is the stability matrix found from perturbations about the homogeneous state and which has entries given by Eq. (23).

We are particularly interested in the situation where there is resonant behavior, that is, when there exist particular frequencies when the denominators of Eqs. (38) and (39) are small. The denominator vanishes when $(i\omega)^2 + (i\omega)\text{tr} \mathbf{A}_{\mathbf{k}} + \det \mathbf{A}_{\mathbf{k}} = 0$, which never occurs at real values of ω , however it does occur for complex ω with nonzero real part if $(\text{tr} \mathbf{A}_{\mathbf{k}})^2 < 4 \det \mathbf{A}_{\mathbf{k}}$. This pole in the complex ω plane indicates the existence of a resonance, and is exactly the same condition that the stability matrix $\mathbf{A}_{\mathbf{k}}$ has complex eigenvalues. This conforms with our intuition that the approach to the homogeneous stationary state needs to be oscillatory for demographic stochasticity to be able to turn this into cyclic behavior. If the ω dependence of the spectra numerators is ignored, then it is simple to show that the spectra have a maximum in ω if additionally $(\text{tr} \mathbf{A}_{\mathbf{k}})^2 < 2 \det \mathbf{A}_{\mathbf{k}}$. Using the full numerator results in a condition which is only slightly more complicated [15,16].

B. Numerical results

We expect that the deterministic equations (11) and (12), together with the stochastic fluctuations about them, given by Eqs. (30)–(32), will give an excellent description of the model defined by Eqs. (1)–(4) for moderate to large system size. We have tested this expectation by performing numerical simulations of the full stochastic process (1)–(4) using the Gillespie algorithm [32]. This is completely equivalent to solving the full master equation (7). To obtain the best results we restricted our simulations to the one-dimensional system ($d=1$), even though our theoretical treatment applies to general d and we would usually be interested in $d=2$. We took the length of the spatial interval to be unity, so that $a\Omega=1$. Therefore, once the number of lattice sites, Ω , is fixed, so is the lattice spacing, a .

The local reaction rates were chosen so as to match the values used in the nonspatial version of the model [11]. In particular this means that $\varphi^* = \psi^*$. Since the time in this spatial version is scaled by Ω ($\tau = t/\Omega$), the rates are Ω times those used in [11], namely $p_1 = 0.25\Omega$, $p_2 = 0.05\Omega$, $d_1 = 0.1\Omega$, $d_2 = 0.0$, and $b = 0.1\Omega$. Here we present only the results which relate to the nature of the fluctuations; we will be especially interested in any cyclic behavior which is most easily found from the Fourier transform of the fluctuations $\xi_{\mathbf{k}}(\omega)$ and $\eta_{\mathbf{k}}(\omega)$. These are then compared to those from the power spectra (36) and (37). In practice the Fourier transforms are calculated by employing a discrete Fourier transform, and in order to compare the amplitudes obtained numerically with the analytical results, the numerically averaged spectra contain an extra factor $|(4\delta_x \delta_t)/(\mathcal{N}_x \mathcal{N}_t)|^2$, where the δ are the spacing between consecutive points and the \mathcal{N} the number of sampled points in space and time.

We begin by showing the results of changing the number of sites, Ω . In Fig. 1 the left-hand column shows results obtained by taking $\Omega=200$ with all other parameters taking on the same values as given above. The right-hand column shows results with the same parameters again, except that $\Omega=500$. The results from simulations were obtained by averaging a large number of realizations of the process in the time interval $t \in [1000, 2000]$, when the stationary state had been established.

Figure 1 displays the results of simulations [upper graphs of Figs. 1(a)–1(d)] and the analytic expressions (38) and (39) [lower graphs of Figs. 1(a)–1(d)]. Mention should be made of the scales of these (and subsequent) figures. The k take on discrete values $2\pi n$ where n is an integer, since the length of the interval being considered is unity. In order to compare to the analytic forms, k is measured in units of $1/a$, and so effectively it is ak which is plotted. This takes on discrete values $2\pi n/\Omega$, but we are looking at sufficiently large values of Ω that the k values appear continuous. For the ω axis, the characteristic time which sets the scale is δ_t . It should also be noted that the k axis in Fig. 1(c) has been reversed to show the peak from another perspective. From Figs. 1(b) and 1(d), we see that the predator and prey spectra do not seem to differ appreciably. This was also found in the nonspatial case [11]. However, as we shall see later, if the migration rates are significantly different then the two spectra will differ. Also the fact that $\alpha_{\mathbf{k},11} \neq 0$, but that the analogous quantity in the

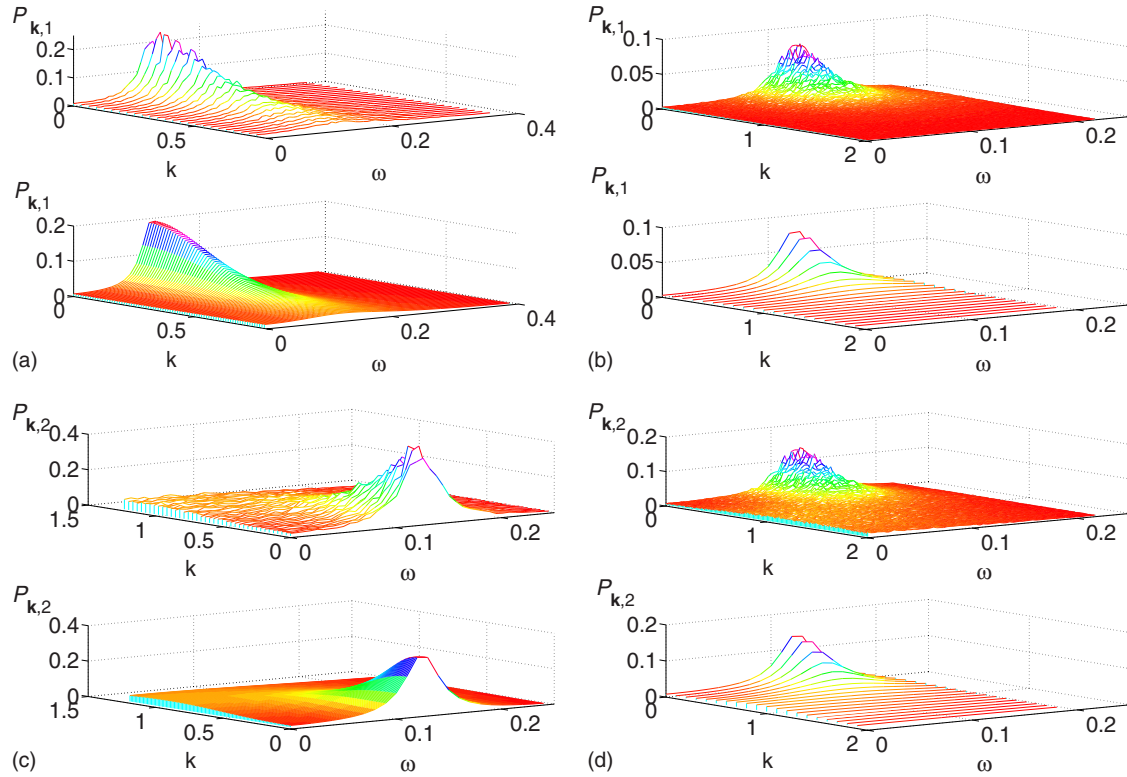


FIG. 1. (Color online) Power spectra obtained from averaging 150 independent realizations with $\Omega=200$ (left-hand column), and averaging 100 realizations with a system composed by $\Omega=500$ sites (right-hand column). The reaction rates employed were $p_1=0.25\Omega$, $p_2=0.05\Omega$, $d_1=0.1\Omega$, $d_2=0.0$, $b=0.1\Omega$, $\mu_1=0.2\Omega$, $\mu_2=0.1\Omega$, and $N=500$. The upper graphs in each panel show the results of the simulations while the lower graphs the analytic predictions (38) and (39).

nonspatial case, a_{11} , does vanish, leads to additional differences between the predator and prey spectra in the spatial version.

For both values of Ω studied, we found that the analytic expressions and those obtained from simulating the full stochastic process show good agreement, which indicates that the use of the first two orders in the van Kampen approximation are sufficient for our purposes. We see that there is a large peak at a nonzero value of ω and so resonant behavior still occurs in this spatial model, just as it did in the nonspatial case. However, the height of the peak reduces with k and eventually at some finite value of k the peak disappears altogether. There is always an additional peak at $\omega=0$; this is much smaller and is just visible in Figs. 1(c) and 1(d). We will discuss it again shortly, when a different choice of the migration rates makes it far more prominent.

In Fig. 2 similar plots are shown for two different values of the migration rates μ_1 and μ_2 , keeping all other parameters as before (except in one case where we take $d_2 \neq 0$) and taking $\Omega=500$. The value of d_2 was changed so that the fixed-point values φ^* and ψ^* were different, which makes the results displayed in Fig. 2(b) somewhat clearer than those shown in Fig. 2(a).

Finally, as shown in Fig. 3, we found that making one migration rate considerably larger than the other led to significant differences. Figures 3(a) and 3(b) show that with the predator migration rate much larger than that for the prey, the amplification is considerably enhanced for the prey. The power spectra in Figs. 3(c) and 3(d) show that although the

peaks at nonzero ω are still present, they look very different for the predator and for the prey species. Also noteworthy is the peak at zero frequency, which is now much larger than before in the case of the prey. The graph is cutoff at $k \sim 1$ only because it becomes much more noisy at larger values of k and so rather difficult to interpret. A similar result is obtained if we swap the values of the migration rates, but now it will be the predator fluctuations which will exhibit the large amplification effect.

V. CONCLUSION

In the work that we have presented here we have stressed the systematic nature of the procedures employed and the generic nature of the results obtained. The starting point was the ILM (1)–(4), but many of the results that we give are not sensitive to the precise form of the model employed. For instance, births and predator events could have an alternative (or additional) rule which would involve nearest-neighbor patches. An example would be $B_i E_j \rightarrow B_i B_j$, where i and j are nearest-neighbor sites, which would mean that a birth could only take place if there was space in the adjoining patch. The definition of the neighborhood could also vary to include next-nearest neighbors or a Moore neighborhood, rather than a von Neumann one. All these changes would give the same behavior at the population level, and in many cases exactly the same model, and leave the form of our results unchanged.

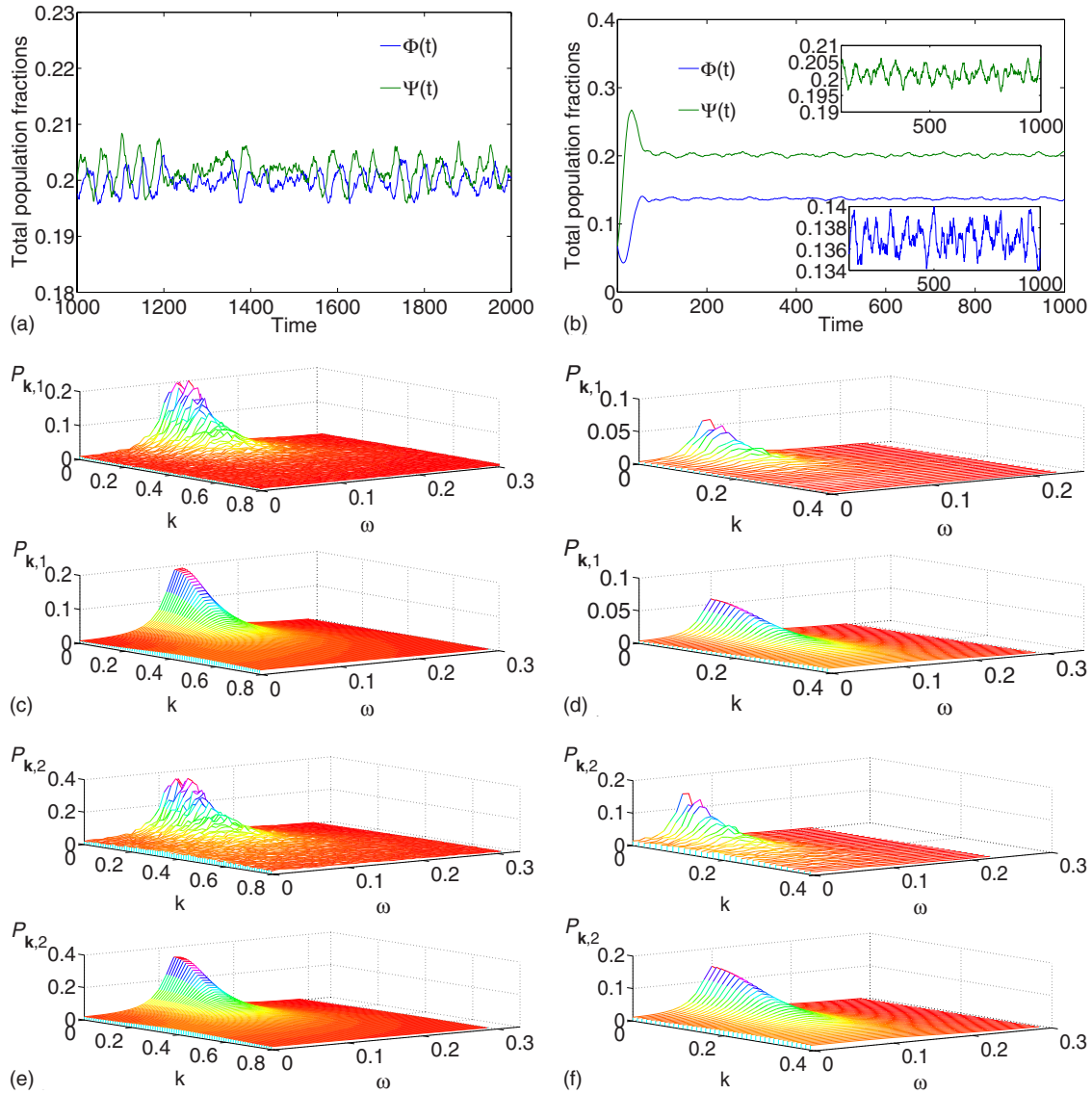


FIG. 2. (Color online) Temporal evolution of the total population fractions and spectra obtained from numerical simulations of the process (upper graphs) and from Eqs. (38) and (39) (lower graphs). The site capacity and the number of sites were $N=500$ and $\Omega=500$. The left-hand-column panels were obtained employing the same local reaction rates as in Fig. 1 and $\mu_1=0.5\Omega$, $\mu_2=0.7\Omega$, whereas the right-hand-column panels were obtained with $\mu_1=0.8\Omega$, $\mu_2=0.9\Omega$, and $d_2=0.05\Omega$. The spectra in both cases were obtained by averaging 100 independent realizations.

In a similar way, the nature of the lattice, and its dimension, only enter the differential equations through the discrete Laplacian operator $\Delta_{\mathbf{k}}$ and factors of a^d , leaving the essential aspects of quantities such as the power spectra unchanged. One consequence of this observation is that the very good agreement between the analytically calculated power spectra and those found from the one-dimensional simulations should still occur in higher dimensions and for other models. This is the main justification for restricting our simulations to one dimension and hence being able to obtain higher quality data. All these observations lead us to expect our results to be generally applicable and to be capable of straightforward generalization to other, similar, problems.

The procedure we have followed is also systematic. Rather than writing down a PLM on phenomenological grounds, we have derived it within a expansion procedure

with a small parameter ($1/\sqrt{N}$) from a more basic ILM. This allows us to relate the parameters of the PLM to those of the ILM, but also to derive the strength and nature of the noise that is a manifestation of the demographic stochasticity, rather than putting it in by hand. The two sets of equations derived from the ILM—the macroscopic, or mean-field equations and the Langevin equations describing the stochastic fluctuations about the mean fields—capture the essential aspects of the dynamics at the population level. Provided that N is not too small that stochastic extinction events are significant, they give a very good description of generic phenomena which one would expect to see in simple descriptions of systems with one predator species and one prey species.

The main focus of this paper was on the power spectra. We found that the resonant amplification present in the well-

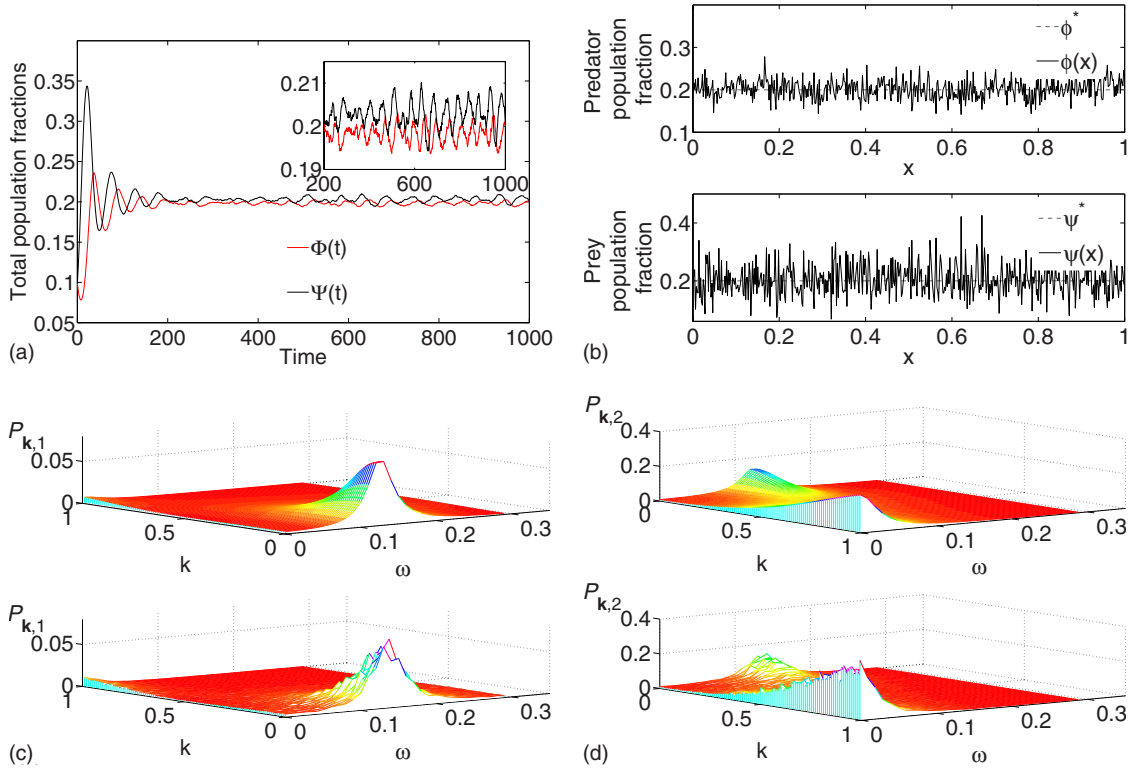


FIG. 3. (Color online) (a) Total population fractions and (b) spatial configurations for the predator and prey fractions. (c) and (d) Numerically and analytically obtained power spectra obtained from 70 realizations of the process and from expressions (38) and (39) respectively. The migration rates were $\mu_1=1.0\Omega$, $\mu_2=0.01\Omega$, and the local rates are the same as in Fig. 1. The amplification effect is stronger than in the previous cases particularly in the case of the prey spectra. Simulations have been carried out swapping the values of the rates, showing a similar effect, but for the other spectrum.

mixed system is still present in the spatial system, although the height of the peak decreases with k , at least in the one-dimensional model. The spectra for the predator and prey species can be made significantly different by making one of the migration rates much larger than the other, a freedom that was not available to us in the nonspatial case. There is also a peak at $\omega=0$. This is present in the nonspatial model, but has no physical significance. Here it does: It corresponds to periodic spatial structures. This peak is very small if the migration rates are of the same order, but can be as large as the peak at $\omega \neq 0$ if the migration rates are sufficiently different.

The existence of a large peak at nonzero ω and $|\mathbf{k}|$ means that when the system is studied at a spatial resolution defined by \mathbf{k} , there will be large amplitude oscillations of frequency $\omega_0(\mathbf{k})$, where this is the position of the peak. While we can deduce the existence of such structures for general d from our analytic calculations, our numerical work has only been undertaken for $d=1$. Since the topology of one-dimensional lattices constrain the dynamics from exhibiting more interesting structures in space and time (as have been reported in numerical studies of models of a similar nature [19,31,33]), these periodic structures may have more complicated forms in higher dimensions.

The approach which consists of defining the time evolution of a model by a master equation, and then performing some type of analysis which allows one to obtain not only the mean-field theory, but corrections to it, has proved to be very effective in understanding the results obtained from nu-

merical simulations [16,19,34]. In the case of the technique employed in this paper, there are many applications which can be envisaged—those which apply to completely different systems, but also predator-prey systems with a more complicated functional response. It would also be interesting to investigate systems whose deterministic limit exhibits Turing instabilities [27,28]. In other words, the general approach we have discussed here, and the results we have reported, have a very general nature. This implies that resonant amplification of stochastic fluctuations will be frequently seen in lattice models and lead to cyclic behavior in a wide range of systems.

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APPENDIX A: SYSTEM SIZE EXPANSION

In this Appendix the master equation for the model discussed in the main text is expanded to leading order (which gives the macroscopic laws) and next-to-leading order (which gives the linear noise approximations) in the van Kampen system-size expansion [6]. The system-size expansion is not usually applied to systems with spatial degrees of free-

dom (but see [35]), and there are a number of possible ways of proceeding. Here we will take what is perhaps the simplest case, and assume that the expansion parameter is $1/\sqrt{N}$, that is, each lattice site is treated as a subsystem for which the carrying capacity becomes large. The calculation may be performed in a way which is similar to the nonspatial case; whereas in the nonspatial model there were two degrees of freedom: The number of predators, n , and the number of prey, m , there are now 2Ω degrees of freedom, n_i and m_i , $i = 1, \dots, \Omega$. In what follows we will therefore limit ourselves to an outline of the method and to the statement of key intermediate results. For a description of the method, reference should be made to van Kampen [6] or papers that apply the method to related problems [15,16].

The system-size expansion begins with the mapping

$$\frac{n_i}{N} = \phi_i + (N)^{-1/2} \xi_i, \quad \frac{m_i}{N} = \psi_i + (N)^{-1/2} \eta_i. \quad (\text{A1})$$

Here $\phi_i(t)$ and $\psi_i(t)$ will be the variables in the PLM, and the stochastic variables $\xi_i(t)$ and $\eta_i(t)$ will appear in the Langevin equations at next to leading order.

Under this transformation, the left-hand side of the master equation (7) becomes

$$\frac{\partial \Pi}{\partial t} + \sum_{i=1}^{\Omega} \left(\dot{\xi}_i \frac{\partial \Pi}{\partial \xi_i} + \dot{\eta}_i \frac{\partial \Pi}{\partial \eta_i} \right), \quad (\text{A2})$$

where $\dot{\xi}_i = -(N)^{1/2} \dot{\phi}_i$, $\dot{\eta}_i = -(N)^{1/2} \dot{\psi}_i$ and where Π is the probability density function, but now expressed as a function of ϕ_i , ψ_i , and t . To determine the form of the right-hand side of the master equation in terms of the new variables, we need to write T_i^{loc} and T_{ij}^{mig} , given by Eqs. (9) and (10), respectively, in terms of these new variables. This consists of two stages: First writing the step operators (8) as operators involving the new variables, and second, determining their action on the transition probabilities (5) and (6).

Beginning with T_i^{loc} the first stage gives

$$E_{x_i} - 1 = N^{-1/2} \frac{\partial}{\partial \xi_i} + \frac{1}{2} N^{-1} \frac{\partial^2}{\partial \xi_i^2} + \dots,$$

$$E_{y_i} - 1 = N^{-1/2} \frac{\partial}{\partial \eta_i} + \frac{1}{2} N^{-1} \frac{\partial^2}{\partial \eta_i^2} + \dots,$$

$$E_{x_i}^{-1} - 1 = -N^{-1/2} \frac{\partial}{\partial \xi_i} + \frac{1}{2} N^{-1} \frac{\partial^2}{\partial \xi_i^2} + \dots,$$

$$E_{x_i}^{-1} E_{y_i} - 1 = N^{-1/2} \frac{\partial}{\partial \eta_i} - N^{-1/2} \frac{\partial}{\partial \xi_i} + \frac{1}{2} N^{-1} \left(\frac{\partial}{\partial \xi_i} - \frac{\partial}{\partial \eta_i} \right)^2 + \dots. \quad (\text{A3})$$

We can now list the various contributions we obtain, at order $N^{1/2}$ and N^0 , which we need in order to find T_i^{loc} as defined in Eq. (9), as follows:

$$(i) (E_{x_i} - 1) d_1 n_i,$$

$$N^{1/2}: d_1 \phi_i \frac{\partial}{\partial \xi_i},$$

$$N^0: d_1 \frac{\partial}{\partial \xi_i} \xi_i, \quad \frac{1}{2} d_1 \phi_i \frac{\partial^2}{\partial \xi_i^2}.$$

$$(ii) (E_{y_i} - 1) \left(\frac{2p_2 n_i m_i}{N} + d_2 m_i \right),$$

$$N^{1/2}: (d_2 \psi_i + 2p_2 \psi_i \phi_i) \frac{\partial}{\partial \eta_i},$$

$$N^0: (d_2 + 2p_2 \phi_i) \frac{\partial}{\partial \eta_i} \eta_i, \quad 2p_2 \psi_i \frac{\partial}{\partial \eta_i} \xi_i,$$

$$\left(\frac{d_2}{2} \psi_i + p_2 \psi_i \phi_i \right) \frac{\partial^2}{\partial \eta_i^2}.$$

$$(iii) (E_{y_i}^{-1} - 1) \left(\frac{2bm_i(N-n_i-m_i)}{N} \right),$$

$$N^{1/2}: -2b\psi_i(1-\psi_i-\phi_i) \frac{\partial}{\partial \eta_i},$$

$$N^0: 2b(2\psi_i - 1 + \phi_i) \frac{\partial}{\partial \eta_i} \eta_i,$$

$$2b\psi_i \frac{\partial}{\partial \eta_i} \xi_i, \quad b\psi_i(1-\psi_i-\phi_i) \frac{\partial^2}{\partial \eta_i^2}.$$

$$(iv) (E_{x_i}^{-1} E_{y_i} - 1) \left(\frac{2p_1 n_i m_i}{N} \right),$$

$$N^{1/2}: -2p_1 \psi_i \phi_i \frac{\partial}{\partial \xi_i}, \quad 2p_1 \phi_i \psi_i \frac{\partial}{\partial \eta_i},$$

$$N^0: 2p_1 \phi_i \frac{\partial}{\partial \eta_i} \eta_i, \quad 2p_1 \psi_i \frac{\partial}{\partial \eta_i} \xi_i, \quad p_1 \phi_i \psi_i \frac{\partial^2}{\partial \eta_i^2}, \quad p_1 \phi_i \psi_i \frac{\partial^2}{\partial \xi_i^2},$$

$$-2p_1 \phi_i \frac{\partial}{\partial \xi_i} \eta_i, \quad -2p_1 \psi_i \frac{\partial}{\partial \xi_i} \xi_i, \quad -2p_1 \phi_i \psi_i \frac{\partial^2}{\partial \eta_i \partial \xi_i}.$$

Identifying the terms of order $N^{1/2}$ on the right- and left-hand sides of the master equation gives the contributions of the local reactions to the macroscopic laws:

$$-\dot{\phi}_i = \frac{d_1}{\Omega} \phi_i - \frac{2p_1}{\Omega} \psi_i \phi_i, \quad (\text{A4})$$

$$-\dot{\psi}_i = \frac{d_2}{\Omega} \psi_i + \frac{2p_2}{\Omega} \psi_i \phi_i + \frac{2p_1}{\Omega} \phi_i \psi_i - \frac{2b}{\Omega} \psi_i(1-\psi_i-\phi_i). \quad (\text{A5})$$

If a rescaled time, $\tau = t/\Omega$, is introduced, then these equations are exactly the PLM of the nonspatial version of the model [11]. This is as it should be, since without including the nearest-neighbor couplings in T_{ij}^{mig} , the system is simply Ω copies of the nonspatial model.

Performing a similar identification of both sides of the master equation, but now for terms of order N^0 gives a Fokker-Planck equation:

$$\frac{\partial \Pi}{\partial t} = - \sum_{i=1}^{\Omega} \frac{\partial}{\partial \xi_i} \{ \mathcal{A}_i[\xi(t)] \Pi \} + \frac{1}{2} \sum_{i,j} \frac{\partial^2}{\partial \xi_i \partial \xi_j} [\mathcal{B}_{ij}(t) \Pi], \quad (\text{A6})$$

where we have introduced the notation $\xi_i = (\xi_i, \eta_i)$. The function $\mathcal{A}_i(\xi)$ and the matrix \mathcal{B}_{ij} are given by

$$\begin{aligned} \mathcal{A}_{i,1}^{\text{loc}} &= \frac{1}{\Omega} (2p_1 \psi_i - d_1) \xi_i + \frac{1}{\Omega} (2p_1 \phi_i) \eta_i, \\ \mathcal{A}_{i,2}^{\text{loc}} &= \frac{1}{\Omega} [-2(p_1 + p_2 + b) \psi_i] \xi_i + \frac{1}{\Omega} [-2(p_1 + p_2 + b) \phi_i \\ &\quad + (2b - d_2) - 4b \psi_i] \eta_i, \end{aligned} \quad (\text{A7})$$

and

$$\begin{aligned} \mathcal{B}_{ij,11}^{\text{loc}} &= \frac{1}{\Omega} (d_1 \phi_i + 2p_1 \psi_i \phi_i) \delta_{ij}, \\ \mathcal{B}_{ij,22}^{\text{loc}} &= \frac{1}{\Omega} [2b \psi_i (1 - \phi_i - \psi_i) + d_2 \psi_i + 2(p_1 + p_2) \psi_i \phi_i] \delta_{ij}, \\ \mathcal{B}_{ij,12}^{\text{loc}} &= \mathcal{B}_{ij,21}^{\text{loc}} = \frac{1}{\Omega} (-2p_1 \phi_i \psi_i) \delta_{ij}. \end{aligned} \quad (\text{A8})$$

The superscript loc denotes their origin from the local reaction contribution of the master equation, and the subscripts 1 and 2 refer to $\xi_1 = \xi$ and $\xi_2 = \eta$, respectively. These results agree with the nonspatial results found in [11], up to a factor of Ω , as required. It should also be noted that the function $\mathcal{A}_i(\xi)$ is linear in ξ_i and η_i with coefficients which are exactly those which would be obtained from a linear stability analysis of Eqs. (A4) and (A5) [6]. This is given in the main text by Eq. (20), which agrees with the results in Eq. (A7). By contrast the \mathcal{B}_{ij} cannot be obtained from the macroscopic results.

Next we carry out the same procedures on the contribution due to migration, $\mathcal{T}_i^{\text{mig}}$. To do this, the operator expressions listed below are required,

$$\begin{aligned} E_{x_i}^{-1} E_{x_j} - 1 &= N^{-1/2} \left(\frac{\partial}{\partial \xi_j} - \frac{\partial}{\partial \xi_i} \right) + \frac{1}{2} N^{-1} \left(\frac{\partial}{\partial \xi_i} - \frac{\partial}{\partial \xi_j} \right)^2, \\ E_{x_i} E_{x_j}^{-1} - 1 &= N^{-1/2} \left(\frac{\partial}{\partial \xi_i} - \frac{\partial}{\partial \xi_j} \right) + \frac{1}{2} N^{-1} \left(\frac{\partial}{\partial \xi_i} - \frac{\partial}{\partial \xi_j} \right)^2, \\ E_{y_i}^{-1} E_{y_j} - 1 &= N^{-1/2} \left(\frac{\partial}{\partial \eta_j} - \frac{\partial}{\partial \eta_i} \right) + \frac{1}{2} N^{-1} \left(\frac{\partial}{\partial \eta_i} - \frac{\partial}{\partial \eta_j} \right)^2, \\ E_{y_i} E_{y_j}^{-1} - 1 &= N^{-1/2} \left(\frac{\partial}{\partial \eta_i} - \frac{\partial}{\partial \eta_j} \right) + \frac{1}{2} N^{-1} \left(\frac{\partial}{\partial \eta_i} - \frac{\partial}{\partial \eta_j} \right)^2. \end{aligned} \quad (\text{A9})$$

These operators possess the general structure $N^{-1/2} \hat{L}_1 + N^{-1} \hat{L}_2$, with \hat{L}_1 equal to a difference of first derivatives and $\hat{L}_2 = \hat{L}_1^2/2$. In addition the transition rates (6) have a common

structure as functions of N which is $\rho(NF_1 + N^{1/2}F_2 + F_3 + \dots)$, when written in terms of the new variables, with $\rho = \mu_1/(z\Omega)$ or $\mu_2/(z\Omega)$, depending on which term one is considering. The F_k depend on the macroscopic fractions (ϕ_i and ψ_i) and on the stochastic variables (ξ_i), except for F_1 which only depends on the former. Therefore, the form of the part of the master equation involving migration terms is

$$\begin{aligned} &(N^{-1/2} \hat{L}_1 + N^{-1} \hat{L}_2) \rho(NF_1 + N^{1/2}F_2 + F_3) \Pi \\ &= \rho(N^{1/2}F_1 \hat{L}_1 + \hat{L}_1 F_2 + F_1 \hat{L}_2 + \dots) \Pi, \end{aligned} \quad (\text{A10})$$

keeping only terms of the order required. This allows us to identify the three main contributions:

(a) The order $N^{1/2}$ term is identified with the second term on the left-hand side of the master equation [Eq. (A2) with $\dot{\xi}_i = -(N)^{1/2} \dot{\phi}_i$ and $\dot{\eta}_i = -(N)^{1/2} \dot{\psi}_i$] which leads to 2Ω independent macroscopic equations.

(b) The order N^0 term $\rho \hat{L}_1 F_2$ is of the same order as the time derivative in Eq. (A2). Since it involves only first-order derivatives in ξ_i it will give contributions which will add to the \mathcal{A}_i in Eq. (A6) found for the purely local terms in the master equation.

(c) The order N^0 term $\rho F_1 \hat{L}_2$ is also of the same order as the time derivative in Eq. (A2). Since it involves only second-order derivatives in ξ_i it will give contributions which will add to the \mathcal{B}_{ij} in Eq. (A6) found for the purely local terms in the master equation.

As an example, the term $T_{n_i+1, n_j-1 | n_i, n_j}$ in Eq. (6) when written out in the new variables gives

$$\begin{aligned} &\frac{\mu_1}{z\Omega} \{ [\phi_j(1 - \phi_i - \psi_i)] N + [(1 - \phi_i - \psi_i) \xi_j - \phi_j(\xi_i + \eta_i)] N^{1/2} \\ &\quad - \xi_j(\xi_i + \eta_i) \} \Pi. \end{aligned} \quad (\text{A11})$$

In the notation we have introduced above

$$F_1 = \phi_j(1 - \phi_i - \psi_i). \quad (\text{A12})$$

The second term in Eq. (6), $T_{n_i-1, n_j+1 | n_i, n_j}$, can be obtained from the first term by interchanging i and j [and this is still true when the operators are included in Eq. (10)], so adding these expression together we find

$$- \frac{2\mu_1}{z\Omega} \left(\sum_j (\phi_j - \phi_i) + \sum_j (\phi_i \psi_j - \phi_j \psi_i) \right). \quad (\text{A13})$$

To obtain this we have identified $\partial \Pi / \partial \xi_i$, for each i , with the corresponding term on the left-hand side of the master equation (A2). Using the discrete Laplacian operator

$$\Delta f_i = \frac{2}{z} \sum_{j \in i} (f_j - f_i), \quad (\text{A14})$$

this may be written as

$$- \frac{\mu_1}{\Omega} (\Delta \phi_i + \phi_i \Delta \psi_i - \psi_i \Delta \phi_i). \quad (\text{A15})$$

A similar analysis may be carried out for the terms

$$(E_{y_i}^{-1}E_{y_j} - 1)T_{m_i+1, m_j-1 | m_i, m_j}$$

and

$$(E_{y_i}E_{y_j}^{-1} - 1)T_{m_i-1, m_j+1 | m_i, m_j}.$$

This will give the same form as above, but with the obvious changes $\mu_1 \rightarrow \mu_2$, $\psi_i \leftrightarrow \phi_i$, etc. For the macroscopic contribution one thus finds

$$-\frac{\mu_2}{\Omega}(\Delta\psi_i + \psi_i\Delta\phi_i - \phi_i\Delta\psi_i). \quad (\text{A16})$$

Adding Eq. (A15) to the right-hand side of Eq. (A4) and Eq. (A16) to the right-hand side of Eq. (A5) gives the set of macroscopic laws, Eqs. (11) and (12), for each patch i .

Returning to the stochastic contributions, the one of type (b) coming from the term

$$(E_{x_i}^{-1}E_{x_j} - 1)T_{n_i+1, n_j-1 | n_i, n_j},$$

is the F_2 -type term in Eq. (A11). Explicitly this is equal to

$$\frac{\mu_1}{z\Omega} \sum_{i,j} \left(\frac{\partial}{\partial \xi_j} - \frac{\partial}{\partial \xi_i} \right) [(1 - \phi_i - \psi_i)\xi_j - \phi_j(\xi_i + \eta_i)] \Pi. \quad (\text{A17})$$

The term

$$(E_{x_i}E_{x_j}^{-1} - 1)T_{n_i-1, n_j+1 | n_i, n_j},$$

gives precisely the same contribution, and adding these together one finds

$$-\frac{\mu_1}{\Omega} \sum_i \frac{\partial}{\partial \xi_i} \{ [\Delta - \psi_i\Delta + (\Delta\psi_i)]\xi_i + [\phi_i\Delta - (\Delta\phi_i)]\eta_i \} \Pi. \quad (\text{A18})$$

This may be written as

$$-\frac{\mu_1}{\Omega} \sum_i \frac{\partial}{\partial \xi_i} (D_{i,11}\xi_i + D_{i,12}\eta_i) \Pi, \quad (\text{A19})$$

where

$$D_{i,11} = \Delta - \psi_i\Delta + (\Delta\psi_i), \quad D_{i,12} = \phi_i\Delta - (\Delta\phi_i). \quad (\text{A20})$$

In an analogous way, the migrational contributions from the third and fourth terms in Eq. (6) give (letting $\mu_1 \rightarrow \mu_2$, $\phi_i \leftrightarrow \psi_i$, and $\xi_i \leftrightarrow \eta_i$)

$$-\frac{\mu_2}{\Omega} \sum_i \frac{\partial}{\partial \eta_i} (D_{i,21}\xi_i + D_{i,22}\eta_i) \Pi, \quad (\text{A21})$$

where

$$D_{i,22} = \Delta - \phi_i\Delta + (\Delta\phi_i), \quad D_{i,21} = \psi_i\Delta - (\Delta\psi_i). \quad (\text{A22})$$

The results (A19)–(A22) can also be obtained through a linear-stability analysis of the non-local terms in Eqs. (11) and (12). They represent diffusion and should be added to the terms in Eq. (A7) which represent reactions, to give the com-

plete contribution in the first term on the right-hand side of the Fokker-Planck equation (A6).

Finally, there are the terms of type (c), which have the form $\rho F_1 \hat{L}_2$. We have already discussed the F_1 terms, and the operators \hat{L}_2 may be read off from Eq. (A9). The four terms corresponding to those in Eq. (6) are

$$\begin{aligned} & \frac{\mu_1}{z\Omega} \sum_{i,j} \frac{1}{2} [\phi_i(1 - \phi_j - \psi_j)] \left(\frac{\partial}{\partial \xi_i} - \frac{\partial}{\partial \xi_j} \right)^2 \Pi, \\ & \frac{\mu_1}{z\Omega} \sum_{i,j} \frac{1}{2} [\phi_j(1 - \phi_i - \psi_i)] \left(\frac{\partial}{\partial \xi_i} - \frac{\partial}{\partial \xi_j} \right)^2 \Pi, \\ & \frac{\mu_2}{z\Omega} \sum_{i,j} \frac{1}{2} [\psi_i(1 - \phi_j - \psi_j)] \left(\frac{\partial}{\partial \eta_i} - \frac{\partial}{\partial \eta_j} \right)^2 \Pi, \\ & \frac{\mu_2}{z\Omega} \sum_{i,j} \frac{1}{2} [\psi_j(1 - \phi_i - \psi_i)] \left(\frac{\partial}{\partial \eta_i} - \frac{\partial}{\partial \eta_j} \right)^2 \Pi. \end{aligned} \quad (\text{A23})$$

In this paper we will only be interested in studying the equations satisfied by the stochastic variables $\xi_i = (\xi_i, \eta_i)$, $i = 1, \dots, \Omega$, when the transients in the macroscopic equations (11) and (12) have died away. Then ϕ_i and ψ_i are equal to their fixed point values ϕ^* and ψ^* , respectively, which are independent of the site label i . Adding the four contributions (A23) in this case gives

$$\begin{aligned} & \frac{2\mu_1}{z\Omega} \phi^*(1 - \phi^* - \psi^*) \sum_{i,j} \left(z\delta_{ij} \frac{\partial^2}{\partial \xi_i^2} - \frac{\partial^2}{\partial \xi_i \partial \xi_j} \right) \Pi \\ & + \frac{2\mu_2}{z\Omega} \psi^*(1 - \phi^* - \psi^*) \sum_{i,j} \left(z\delta_{ij} \frac{\partial^2}{\partial \eta_i^2} - \frac{\partial^2}{\partial \eta_i \partial \eta_j} \right) \Pi. \end{aligned} \quad (\text{A24})$$

These contributions are diagonal in the predator-prey variables (there are no mixed derivatives involving ξ and η), but is not diagonal in the site variables (there are mixed derivatives involving i and j). Comparing Eq. (A24) with the Fokker-Planck equation (A6), we see that the contributions to the matrix \mathcal{B} , which add to those in Eq. (A8) are

$$\begin{aligned} \mathcal{B}_{ij,11}^{\text{mig}} &= \frac{4\mu_1}{\Omega} \phi^*(1 - \phi^* - \psi^*) \delta_{ij} - \frac{4\mu_1}{z\Omega} \phi^*(1 - \phi^* - \psi^*) J_{(ij)}, \\ \mathcal{B}_{ij,22}^{\text{mig}} &= \frac{4\mu_2}{\Omega} \psi^*(1 - \phi^* - \psi^*) \delta_{ij} - \frac{4\mu_2}{z\Omega} \psi^*(1 - \phi^* - \psi^*) J_{(ij)}, \end{aligned} \quad (\text{A25})$$

where $J_{(ij)}$ is zero unless i and j are nearest neighbors.

In summary, the order N^0 terms give the Fokker-Planck equation (A6), with the function $\mathcal{A}_i(\xi)$ and the matrix \mathcal{B}_{ij} being given by

$$\begin{aligned} \mathcal{A}_{i,1} &= \alpha_{i,11}\xi_i + \alpha_{i,12}\eta_i, \\ \mathcal{A}_{i,2} &= \alpha_{i,21}\xi_i + \alpha_{i,22}\eta_i, \end{aligned} \quad (\text{A26})$$

where the α are exactly the coefficients found in Sec. III A by linear stability analysis, and

$$\mathcal{B}_{ij,11} = [(d_1\phi^* + 2p_1\psi^*\phi^*) + 4\mu_1\phi^*(1 - \phi^* - \psi^*)]\delta_{ij} - \frac{4\mu_1}{z}\phi^*(1 - \phi^* - \psi^*)J_{(ij)},$$

$$\mathcal{B}_{ij,22} = \{[2b\psi^*(1 - \phi^* - \psi^*) + d_2\psi^* + 2(p_1 + p_2)\psi^*\phi^*] + 4\mu_2\psi^*(1 - \phi^* - \psi^*)\}\delta_{ij} - \frac{4\mu_2}{z}\psi^*(1 - \phi^* - \psi^*)J_{(ij)},$$

$$\mathcal{B}_{ij,12} = \mathcal{B}_{ij,21} = (-2p_1\phi^*\psi^*)\delta_{ij}. \quad (\text{A27})$$

In the above we have assumed that the Fokker-Planck equation (A6) has been reexpressed in terms of the rescaled time $\tau = t/\Omega$, in order to eliminate factors of Ω^{-1} from \mathcal{A} and \mathcal{B} .

APPENDIX B: FOURIER ANALYSIS

As discussed in the main text we carry out a temporal Fourier transform in order to calculate the power spectra associated with the fluctuations about the stationary state in order to identify temporal cycles, but we also wish to carry out spatial Fourier transforms. There are a number of reasons for doing this: (a) The translational invariance of the stationary state means that quantities of interest become diagonal in Fourier space, (b) because of this the continuum limit is easily taken, and (c) the power spectra are naturally generalized from the nonspatial case to depend on the wave vector as well as on the frequency.

We largely follow the conventions of Chaitin and Lubensky [36] in introducing the spatial Fourier transforms. That is, we define the Fourier transform, $f_{\mathbf{k}}$, of a function $f_{\mathbf{j}}$ defined on a d -dimensional hypercubic lattice, with lattice spacing a , by

$$f_{\mathbf{k}} = a^d \sum_{\mathbf{j}} e^{-i\mathbf{k}\cdot a\mathbf{j}} f_{\mathbf{j}},$$

$$f_{\mathbf{j}} = a^{-d} \Omega^{-1} \sum_{\mathbf{k}} e^{i\mathbf{k}\cdot a\mathbf{j}} f_{\mathbf{k}}, \quad (\text{B1})$$

where, for clarity, we have deviated from the usual notation of the main text and written the lattice site label \mathbf{j} as a vector. Here \mathbf{k} is restricted to the first Brillouin zone, $-(\pi/a) \leq k_\gamma \leq (\pi/a)$, $\gamma = 1, \dots, d$. We will also require the result [36]

$$\sum_{\mathbf{j}} e^{-i\mathbf{k}\cdot a\mathbf{j}} = \Omega \delta_{\mathbf{j},0}. \quad (\text{B2})$$

Using the definition (B1) we may take the Fourier transform of the Langevin equation (28). This is straightforward for the time derivative on the left-hand side and for the noise term λ_i . For the \mathcal{A}_i term we use Eq. (A26) where the α are made up of the local constant terms (20) and those coming from diffusion (A20) and (A22). At the fixed point where φ and ψ are homogeneous these diffusion operators are site-independent and given by $D_{11} = (1 - \psi^*)\Delta$, $D_{12} = \varphi^*\Delta$, $D_{21} = \psi^*\Delta$, and $D_{22} = (1 - \varphi^*)\Delta$. The Fourier transform of the Langevin equation thus takes the form (30), with the α given by Eq. (23), where $\Delta_{\mathbf{k}}$ is the Fourier transform of the discrete

Laplacian operator Δ . From the definitions (A14) and (B1) this is easily shown to be given by Eq. (24).

To complete the description of the Langevin equation in \mathbf{k} space, we need to rewrite the correlation function (29). Taking the Fourier transform of both $\lambda_i(\tau)$ and $\lambda_j(\tau')$ yields

$$\langle \lambda_{\mathbf{k}}(\tau) \lambda_{\mathbf{k}'}(\tau') \rangle = a^{2d} \sum_{\mathbf{i}, \mathbf{j}} e^{-i\mathbf{k}\cdot a\mathbf{i}} e^{-i\mathbf{k}'\cdot a\mathbf{j}} \mathcal{B}_{\mathbf{ij}} \delta(\tau - \tau'). \quad (\text{B3})$$

However, $\mathcal{B}_{\mathbf{ij}}$ is given by Eq. (A27) and is only nonzero if $\mathbf{i} = \mathbf{j}$ or if \mathbf{i} and \mathbf{j} are nearest-neighbors. That is, it has the form

$$\mathcal{B}_{\mathbf{ij}} = b^{(0)} \delta_{\mathbf{ij}} + b^{(1)} J_{(\mathbf{ij})}. \quad (\text{B4})$$

The translational invariance of $\mathcal{B}_{\mathbf{ij}}$ is quite clear: It can be completely specified by the difference $\mathbf{d} = \mathbf{j} - \mathbf{i}$

$$\mathcal{B}_{\mathbf{d}} = b^{(0)} \delta_{\mathbf{d},0} + b^{(1)} \delta_{|\mathbf{d}|,1}. \quad (\text{B5})$$

Inserting the expression for $\mathcal{B}_{\mathbf{d}}$ in terms of its Fourier transform, $\mathcal{B}_{\mathbf{q}}$, in Eq. (B3), we have from Eqs. (B1) and (B2) that

$$\langle \lambda_{\mathbf{k}}(\tau) \lambda_{\mathbf{k}'}(\tau') \rangle = a^d \Omega \sum_{\mathbf{q}} \mathcal{B}_{\mathbf{q}} \delta_{\mathbf{k},\mathbf{q}} \delta_{\mathbf{k}',-\mathbf{q}} \delta(\tau - \tau') = \mathcal{B}_{\mathbf{k}} a^d \Omega \delta_{\mathbf{k}+\mathbf{k}',0} \delta(\tau - \tau'). \quad (\text{B6})$$

Now

$$\mathcal{B}_{\mathbf{k}} = a^d \sum_{\mathbf{d}} e^{-i\mathbf{k}\cdot a\mathbf{d}} \mathcal{B}_{\mathbf{d}} = a^d \left[b^{(0)} + 2b^{(1)} \left(\sum_{\gamma=1}^d \cos(k_\gamma a) \right) \right] \quad (\text{B7})$$

using Eq. (B5). In terms of $\Delta_{\mathbf{k}}$ defined by Eq. (24), this may be written as

$$\mathcal{B}_{\mathbf{k}} = a^d \left((b^{(0)} + zb^{(1)}) + \frac{zb^{(1)}}{2} \Delta_{\mathbf{k}} \right), \quad (\text{B8})$$

since for a hypercubic lattice the coordination number is $z = 2d$. Writing these out explicitly using Eqs. (A27) and (B4) gives Eq. (32) in the main text.

Finally, we can ask what happens as we take the lattice spacing, a , to zero, but keeping Ωa^d (the area, if $d=2$) fixed. Using Eq. (24) and

$$\cos(k_\gamma a) \simeq 1 - \frac{(k_\gamma a)^2}{2} + O[(ka)^4] \quad (\text{B9})$$

we see that $\Delta_{\mathbf{k}} = -a^2 k^2 / d + O(k^4)$. Since $\Delta_{\mathbf{k}}$ always appears along with the migration rates, the factor of a^2/d can always be absorbed into these rates by defining new quantities

$$\tilde{\mu}_1 = \frac{1}{d} a^2 \mu_1, \quad \tilde{\mu}_2 = \frac{1}{d} a^2 \mu_2. \quad (\text{B10})$$

So for instance, in Eqs. (23) and (32) the $\Delta_{\mathbf{k}}$ can be replaced by $-k^2$ and μ_1 and μ_2 by $\tilde{\mu}_1$ and $\tilde{\mu}_2$, respectively, as a becomes small (or equivalently Ω becomes large). In this limit $\Omega a^d \delta_{\mathbf{k}+\mathbf{k}',0}$ becomes $(2\pi)^d \delta(\mathbf{k}+\mathbf{k}')$ [36], and therefore Eq. (31) becomes

$$\langle \lambda_{\mathbf{k}}(\tau) \lambda_{\mathbf{k}'}(\tau') \rangle = \mathcal{B}_{\mathbf{k}} (2\pi)^d \delta(\mathbf{k} + \mathbf{k}') \delta(\tau - \tau'), \quad (\text{B11})$$

where $B_{\mathbf{k}}$ is given by Eq. (32), but with the small a approximation described above.

To obtain the power spectrum we need to take the temporal Fourier transform of Eq. (B11). This yields

$$\langle \lambda_{\mathbf{k}}(\omega) \lambda_{\mathbf{k}'}(\omega') \rangle = \mathcal{B}_{\mathbf{k}} (2\pi)^d \delta(\mathbf{k} + \mathbf{k}') (2\pi) \delta(\omega + \omega'). \quad (\text{B12})$$

Since there are only contributions in the above formula when $\mathbf{k}' = -\mathbf{k}$ and $\omega' = -\omega$ this is frequently written as

$$\langle \lambda_{\mathbf{k}}(\omega) \lambda_{-\mathbf{k}}(-\omega) \rangle = \mathcal{B}_{\mathbf{k}}, \quad (\text{B13})$$

or equivalently, since $\lambda_{\mathbf{k}}^*(\omega) = \lambda_{-\mathbf{k}}(-\omega)$, as in Eq. (35).

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