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Stable oscillations of a predator–prey probabilistic cellular automaton: a mean-field approach

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Abstract

We analyze a probabilistic cellular automaton describing the dynamics of coexistence of a predator–prey system. The individuals of each species are localized over the sites of a lattice and the local stochastic updating rules are inspired by the processes of the Lotka–Volterra model. Two levels of mean-field approximations are set up. The simple approximation is equivalent to an extended patch model, a simple metapopulation model with patches colonized by prey, patches colonized by predators and empty patches. This approximation is capable of describing the limited available space for species occupancy. The pair approximation is moreover able to describe two types of coexistence of prey and predators: one where population densities are constant in time and another displaying self-sustained time oscillations of the population densities. The oscillations are associated with limit cycles and arise through a Hopf bifurcation. They are stable against changes in the initial conditions and, in this sense, they differ from the Lotka–Volterra cycles which depend on initial conditions. In this respect, the present model is biologically more realistic than the Lotka–Volterra model.

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1. Introduction

The simplest model exhibiting time oscillations in a two-component system is the model proposed independently by Lotka [1–3] and Volterra [4]. In this model, the individuals of two species are dispersed over an assumed homogeneous space. It is implicitly assumed in this approach that any individual can interact with any other one with equal intensity implying that their positions are not taken into account. The time evolution of the densities of the two species in the Lotka–Volterra model is given by a set of two ordinary differential equations [5–8] and is set up in analogy with the laws of mass action. Depending on the level of description wanted, the approach based on mass-action laws, contained on the Lotka–Volterra model, suffices. However, there are situations in which the coexistence takes place in a spatially heterogeneous habitat such that the population densities can be very low in some regions. In this case, we need to proceed beyond the mass-law equations and consider the space structure of the habitat. In other words, it becomes necessary to analyze the coexistence by taking explicitly into account spatial structured models.

In fact, the role of space in the description of population biology problems has been recognized by several authors in the last few years [9–32]. In a very clear manner, Durrett and Levin [13] have pointed out that the modeling of population dynamics systems which are spatially distributed by interacting particle systems [13, 33–35] is the appropriate theoretical approach that is able to give the more complete description of the problem. We include in this approach probabilistic cellular automata (PCA) [14, 35–37], which will concern us here. We refer to interacting particle systems and PCA as stochastic lattice models. They are both Markovian processes defined by discrete stochastic variables residing on the sites of a lattice; the former being a continuous time process and the latter a discrete time process.

In the present work, we study the coexistence and the emergence of stable self-sustained oscillations in a predator–prey system by considering a PCA previously studied by numerical simulations [30, 32]. This PCA is defined by local rules, similar to those of the contact process [33], that are capable of describing the interaction between prey and predator. Here, we focus on the analysis of the PCA by means of dynamic mean-field approximations [12, 34–36, 38, 39]. In this approach, the equations for the time evolution of correlations of various orders are truncated at a certain level and high-order correlations of sites are written in terms of small-order correlations. The simplest approximation is that in which all correlations are written in terms of one-site correlation, called simple approximation. In a more sophisticated approximation, called pair approximation [12, 35], any correlation is written in terms of one-site and two-site correlations.

The simple mean-field approximation is capable of predicting coexistence of individuals in a stationary state where the densities of each species, and of empty sites, are constant. However, it is not capable of predicting possible time oscillating behavior of the population densities and we have proceed to the next order of mean-field approximation. The simple approximation, on the other hand, can be placed in an explicit correspondence with a patch model [7, 15, 40], where unoccupied patches can be colonized by prey and patches occupied by prey can be colonized by predators that in turn may become extinct. In this approximation, the PCA can be seen as an extended version of the Lotka–Volterra model which includes an extra logistic term related to the empty sites.

The pair-mean-field approximation is able to predict possible time oscillating behavior of the population densities that are self-sustained and are attained through Hopf bifurcations. This is in contrast with the Lotka–Volterra model which presents no stable oscillations but instead infinite exhibits cycles that are associated with different initial conditions. However, from the biological point of view, one does not expect that a small variation in the initial densities of prey and predator results in different amplitudes of oscillations. Within our approach, a PCA treated in the pair approximation, the oscillations are associated with limit cycles what mean to say that they are stable against the changes in the initial conditions. According to our point of view, the pair approximation, in which the correlation between neighboring sites are treated exactly, provides a basic description of the predator–prey spatial interactions. For this reason, we will refer to the PCA in this approximation as a quasi-spatial-structured model.

In references [26, 30] we have found, by numerical simulations of the present PCA, oscillations that are coupled to interesting spatial pattern of coexistence. The oscillations reported by the numerical simulations are not observed at a global level, that is, they are not synchronized oscillations, but they can stabilize at a local level as clarified in these papers. The lack of global synchronization in stochastic lattice models in two dimensions has also been addressed by several authors [41–44].

2. Model

2.1. Probabilistic cellular automaton

We consider interacting particles living on the sites of a lattice and evolving in time according to Markovian local rules. The lattice is the geometrical object that plays the role of the spatial region occupied by particles, in a general case, or by individuals of each species in the present case. The lattice sites are the possible locations for the individuals. Each site can be either empty or occupied by one individual of different species and a stochastic variable η_i is introduced to describe the state of each site at a given instant of time. The state of the entire system is denoted by $\eta = (\eta_1, \ldots, \eta_i, \ldots, \eta_N)$, where N is the total number of sites. The transition between the states is governed by the interactions between neighbor sites in the lattice and by a synchronous dynamics.

The probability $P^{(\ell)}(\eta)$ of configuration η at time step ℓ evolves according to the Markov chain equation

$$P^{(\ell+1)}(\eta) = \sum_{\eta} W(\eta|\eta')P^{(\ell)}(\eta'), \tag{1}$$

where the summation is over all the microscopic configurations of the system, and $W(\eta|\eta')$ is the conditional transition probability from state η' at time ℓ to state η at time $\ell + 1$. This transition probability does not depend on time and contains all the information about the dynamics of the system. Taking into account that all the sites are simultaneously updated, which is the fundamental property of a PCA, the transition probability can be factorized and written in the form [35, 36]

$$W(\eta|\eta') = \prod_{i=1}^{N} w_i(\eta_i|\eta'), \tag{2}$$

where $w_i(\eta_i|\eta')$ is the conditional transition probability that site i takes the state η_i given that the whole system is in state η'. Being a probability distribution, the quantity $w_i(\eta_i|\eta')$ must satisfy the following properties: $w_i(\eta_i, \eta') \geqslant 0$ and

$$\sum_{\eta_i} w_i(\eta_i|\eta') = 1. \tag{3}$$

The average of any state function $F(\eta)$ is evaluated by

$$\langle F(\eta)\rangle_\ell = \sum_{\eta} F(\eta)P^{(\ell)}(\eta). \tag{4}$$

The time-evolution equation for $\langle F(\eta)\rangle$ is obtained from definition (4) and equation (1). For example, we can derive the equations for the time evolution of densities and two-site correlations.

2.2. Predator–prey probabilistic cellular automaton

To model a predator–prey system by a PCA, the stochastic variable η_i associated with site i will represent the occupancy of the site by one prey, or the occupancy by one predator or the vacancy (a site devoid of any individual). The variable η_i is assumed to take the value 0, 1

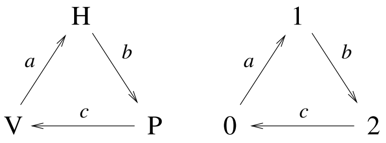

Figure 1. Transitions of the predator–prey model. The three states are prey or herbivorous (H or 1), predator (P or 2) and empty or vegetable (V or 0). The allowed transitions obey the cyclic order shown.

or 2, according to whether the site is empty (V), occupied by a prey individual (H) or by a predator (P), respectively. That is

$$\eta_i = \begin{cases} 0, & \text{empty (V)}, \\ 1, & \text{prey (H)}, \\ 2, & \text{predator (P)}, \end{cases} \tag{5}$$

which defines a three state per site PCA.

The stochastic rules, embodied in the transition rate $w_i(\eta_i|\eta')$, are set up according to the following assumptions. (a) The space is homogeneous, which means to say that no region of the space will be privileged against the others, that is, in principle the individuals have the same conditions of surveillance in any space region. (b) The space is isotropic, which means to say that there is no preferential direction in this space for any interaction. (c) The allowed transitions between states are only those that obey the cyclic order shown in figure 1. Prey can only born in empty sites; prey can give place to a predator, in a process where a prey individual dies and a predator is instantaneously born; finally a predator can die leaving an empty site. The empty sites are places where prey can proliferate and can be seen as the resource for prey surveillance. The death of predators completes this cycle, reintegrating to the system the resources for prey.

The predator–prey PCA has three parameters: a, the probability of birth of prey, b, the probability of birth of predator and death of prey and c, the probability of predator death. Two of the process are catalytic: the occupancy of a site by prey or by a predator is conditioned, respectively, to the existence of prey or predator in the neighborhood of the site. The third reaction, where predator dies, is spontaneous, that is, it occurs, with probability c, independently of the neighbors of the site. We assume that

$$a + b + c = 1, \tag{6}$$

with $0 \leqslant a, b, c \leqslant 1$.

The transition probabilities of the predator–prey PCA are described in what follows:

(a) If a site i is empty, $\eta_i = 0$, and there is at least one prey in its first neighborhood there is a favorable condition for the birth of a new prey. The probability of site i being occupied in next time step by a prey is proportional to the parameter a and to the number of prey that are in the first neighborhood of the empty site.

(b) If a site is occupied by a prey, $\eta_i = 1$, and there is at least one predator in its first neighborhood then the site has a probability of being occupied by a new predator in the next instant of time. In this process the prey dies instantaneously. The transition probability is proportional to the parameter b and the number of predators in first neighborhood of the site.

(c) If site i is occupied by a predator, $\eta_i = 2$, it dies with probability c.

The transition probabilities associated with the three processes above mentioned can be summarized as follows:

$$w_i(0|\eta) = c\delta(\eta_i, 2) + [1 - f_i(\eta)]\delta(\eta_i, 0), \tag{7}$$

$$w_i(1|\eta) = f_i(\eta)\delta(\eta_i, 0) + [1 - g_i(\eta)]\delta(\eta_i, 1), \tag{8}$$

$$w_i(2|\eta) = g_i(\eta)\delta(\eta_i, 1) + (1 - c)\delta(\eta_i, 2), \tag{9}$$

where

$$f_i(\eta) = \frac{a}{4}\sum_k \delta(\eta_k, 1), \qquad g_i(\eta) = \frac{b}{4}\sum_k \delta(\eta_k, 2), \tag{10}$$

and the summation is over the four nearest neighbors of site i in a regular square lattice. The notation $\delta(x, y)$ stands for the Kronecker delta function. These stochastic local rules, when inserted in equation (2), define the dynamics of the PCA for a predator–prey system.

The present stochastic dynamics predicts the existence of states, called absorbing states, in which the system becomes trapped. Once the system has entered such a state it cannot escape from it anymore remaining there forever. There are two absorbing states. One of them is the empty lattice. Since the predator death is spontaneous, a configuration where just predators are present is not stationary. This situation happens whenever the prey have been extinct. In this case, the predator cannot reproduce anymore and also get extinct, leaving the entire lattice with the empty sites. The other absorbing state is the lattice full of prey. This situation occurs if there are few predators and they become extinct. The remaining prey will then reproduce without predation filling up the whole lattice. The existence of absorbing stationary states is an evidence of the irreversible character of the model or, in other words, of the lack of detailed balance [35]. However, the most interesting states, those that we are concerned with in the present study, are the active states characterized by the coexistence of prey and predators.

2.3. Time-evolution equations for state functions

We start by defining the densities, which are the one-site correlations and the two-site correlations. These quantities will be useful in our mean-field analysis to be developed below. The density of prey, predator and empty sites at time step ℓ are defined through the expressions

$$P_i^{(\ell)}(1) = \langle\delta(\eta_i, 1)\rangle_\ell, \tag{11}$$

$$P_i^{(\ell)}(2) = \langle\delta(\eta_i, 2)\rangle_\ell, \tag{12}$$

$$P_i^{(\ell)}(0) = \langle\delta(\eta_i, 0)\rangle_\ell. \tag{13}$$

The evolution equations for the above densities are obtained from their definitions as state functions, as given by equation (4), and by using the evolution equation for $P^{(\ell)}(\eta)$, given by equation (1). The resulting equations can be formally written as

$$P_i^{(\ell+1)}(1) = \langle w_i(1|\eta)\rangle_\ell, \tag{14}$$

$$P_i^{(\ell+1)}(2) = \langle w_i(2|\eta)\rangle_\ell, \tag{15}$$

$$P_i^{(\ell+1)}(0) = \langle w_i(0|\eta)\rangle_\ell, \tag{16}$$

where the transition probabilities for this model are given in equations (7)–(9).

The correlation between a prey localized at site i and a predator localized at site j at time step ℓ is defined by

$$P_{ij}^{(\ell)}(1,2) = \langle \delta(\eta_i, 1)\delta(\eta_j, 2)\rangle_\ell. \tag{17}$$

The other two-site correlations are defined similarly. The time-evolution equation for the correlation of two neighbor sites i and j, one being occupied by a prey and the other by a predator, is given by

$$P_{ij}^{(\ell+1)}(1,2) = \langle w_i(1|\eta) w_j(2|\eta)\rangle_\ell. \tag{18}$$

The other two-site evolution equations are given by similar formal expressions. We can also derive equations for three-site correlations. Since we are interested here on approximations in which only the one-site and two-site correlations should be treated exactly, the above equations suffice.

We call the attention to the fact that equation (18) includes the product of two transition probabilities. This is a consequence of the synchronous update of the PCA which allows that both the neighboring sites i and j have their states changed at the same time step. This situation does not occur when we consider a continuous time one-site dynamics. Therefore, although local interaction in the present PCA and in the continuous time model considered in [12] is the same, the predator–prey system evolves according to different global dynamics which leads to different time-evolution equations for the densities and the correlations.

The exact evolution equations for the one-site correlations are

$$P_j'(1) = \frac{a}{\zeta}\sum_i P_{ji}(01) - \frac{b}{\zeta}\sum_i P_{ji}(12) + P_j(1), \tag{19}$$

$$P_j'(2) = \frac{b}{\zeta}\sum_i P_{ji}(12) + (1-c)P_j(2), \tag{20}$$

where the summation in j is over the ζ nearest neighbors of site i. To simplify notation we are using unprimed and primed quantities to refer to quantities taken at time ℓ and $\ell+1$, respectively.

The exact evolution equations for the correlations of two nearest neighbor sites j and k are

$$\begin{aligned} P_{jk}'(01) = {} & \frac{a}{\zeta}\sum_{n(\neq j)}\left[P_{jkn}(001) - \frac{a}{\zeta}\sum_{i(\neq k)} P_{ijkn}(1001)\right] \\ & + \left(1-\frac{a}{\zeta}\right)\left[P_{jk}(01) - \frac{b}{\zeta}\sum_{n(\neq j)} P_{jkn}(012)\right] \\ & - \frac{a}{\zeta}\sum_{i(\neq k)}\left[P_{ijk}(101) - \frac{b}{\zeta}\sum_{n(\neq j)} P_{ijkn}(1012)\right] \\ & + c\left[\left(1-\frac{b}{\zeta}\right)P_{jk}(21) - \frac{b}{\zeta}\sum_{n(\neq j)} P_{jkn}(212)\right] + \frac{a}{\zeta}c\sum_{n(\neq j)} P_{jkn}(201), \end{aligned} \tag{21}$$

$$
\begin{aligned}
P'_{jk}(12) = {} & \frac{ab}{\zeta^2} \sum_{n(\neq j)} \left[P_{jkn}(012) + \sum_{i(\neq k)} P_{ijkn}(1012) \right] \\
& + \frac{b}{\zeta} \sum_{n(\neq j)} \left[P_{jkn}(112) - \frac{b}{\zeta} \sum_{i(\neq k)} P_{ijkn}(2112) \right] \\
& + (1-c) \left[\left(1 - \frac{b}{\zeta}\right) P_{jk}(12) - \frac{b}{\zeta} \sum_{i(\neq k)} P_{ijk}(212) \right] \\
& + \frac{a}{\zeta}(1-c) \sum_{i(\neq k)} P_{ijk}(102)
\end{aligned}
\tag{22}
$$

and

$$
\begin{aligned}
P'_{jk}(02) = {} & \frac{b}{\zeta} \sum_{n(\neq j)} \left[\left(1 - \frac{a}{\zeta}\right) P_{jkn}(012) - \frac{a}{\zeta} \sum_{i(\neq k)} P_{ijkn}(1012) \right] \\
& + (1-c) \left[c P_{jk}(22) + P_{jk}(02) - \frac{a}{\zeta} \sum_{i(\neq k)} P_{ijk}(102) \right] \\
& + \frac{b}{\zeta} c \left[P_{jk}(21) + \sum_{n(\neq j)} P_{jkn}(212) \right],
\end{aligned}
\tag{23}
$$

where the summation in i is over the nearest neighbors of j and the summation in n is over the nearest neighbors of k.

3. Mean-field approximation

3.1. One- and two-site approximations

The evolution equation for a density in any interacting particle system which evolves in time according to local interaction rules always contains terms related to the correlations between neighbor sites in a lattice. The evolution equations for the correlations of two neighbor sites includes the correlation of clusters of three or more sites in the lattice and so on. In this way we can have an infinite set of coupled equations for the correlations which is equivalent to the evolution equation for the probability $P^{(\ell)}(\eta)$, described in equation (1) for the automaton. The scope of the dynamic mean-field approximation consists in the truncation of this infinite set of coupled equations [36–39].

The lowest order dynamic mean-field approximation is that where the probability of a given cluster is written as the product of the probabilities of each site. That is, all the correlations between sites in the cluster are neglected. For example, let us consider the cluster constituted by a center (C) site and its first neighboring sites to the north (N), south (S), east (E) and west (W) as shown in figure 2.

Within the one-site approximation the probability $P(N, E, W, S, C)$ corresponding to the cluster shown in figure 2 is approximated by

$$
P(N, E, W, S, C) = P(N)P(E)P(W)P(S)P(C),
\tag{24}
$$

where $P(X), X = N, E, W, S, C$ are the one-site probabilities corresponding to each site. For some stochastic dynamics models this approximation is able to give qualitative results that are in agreement with the expected results.

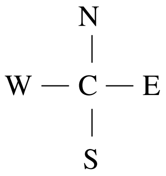

Figure 2. A site (C) of the square lattice and its four nearest neighbor sites (N, E, W, S).

In order to get a better approximation we must include fluctuations. The simplest mean-field approximation that includes correlations is the pair-mean-field approximation. This approximation is better explained by taking again, as an example, the cluster constituted by a center site which and its four nearest neighbors, shown above. Within the pair approximation the conditional probability $P(N, E, W, S|C)$ is approximated by

$$P(N, E, W, S|C) = P(N|C)P(E, |C)P(W|C)P(S|C), \tag{25}$$

that is, the conditional probability $P(N, E, W, S|C)$ is written in terms of the product of the conditional probabilities $P(X|C)$, $X = N, E, W, S$. Now using the definition of conditional probability, we have

$$\frac{P(N, E, W, S, C)}{P(C)} = \frac{P(N, C)}{P(C)} \frac{P(E, C)}{P(C)} \frac{P(W, C)}{P(C)} \frac{P(S, C)}{P(C)} \tag{26}$$

or

$$P(N, E, W, S, C) = \frac{P(N, C)P(E, C)P(W, C)P(S, C)}{[P(C)]^3}. \tag{27}$$

We see that the resulting probability is written as a function of two-site correlations $P(X, C)$ and the one-site correlation $P(C)$.

3.2. *Patch model*

The simple mean-field approximation of the predator–prey PCA describes exactly the same properties of an extended Levins patch model [7, 40]. That is, the PCA with local rules similar to the contact process becomes, in the simple mean-field approximation, analogous to the Levins model for metapopulation with empty patches, patches colonized by prey and patches colonized by predators.

In the one-site mean-field approximation we consider that the probability of any cluster of sites can be written as the product of the probabilities of each site, as in equation (24). Using this approach, and writing $x = P_i(1)$, $y = P_i(2)$ and $z = P_i(0)$ it can be seen that the set of equations can be reduced to the following two-dimensional map [32]:

$$x' = x + axz - bxy, \tag{28}$$

which is an evolution equation for prey density x and

$$y' = y + bxy - cy, \tag{29}$$

which is an evolution equation for predator density y_ℓ. Note that

$$z = 1 - x - y. \tag{30}$$

The fixed point of this map are those that represent the stationary solutions $x' = x$ and $y' = y$, and they correspond to the three following solutions $x_1 = 0, y_1 = 0$, and

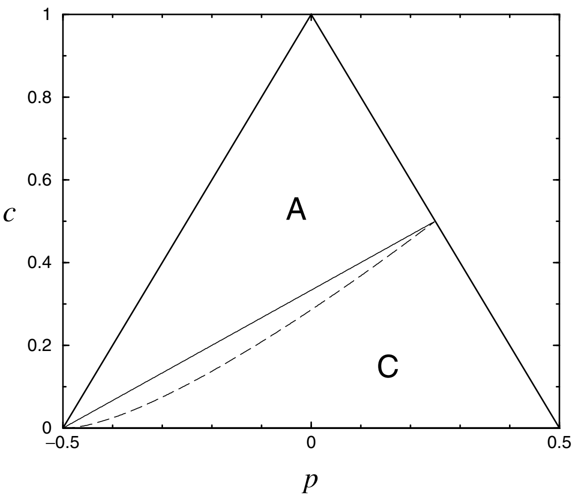

Figure 3. Phase diagram of the patch model. The continuous line represents the transition, $c_1(p)$, between the prey absorbing (A) state and the active species coexistence (C) state. The dashed line separates the two asymptotic time behavior of the active state.

$x_2 = 1$, $y_2 = 0$, and $x_3 = a/b$, $y_3 = (1 - c/b)/(1 + b/a)$. The first solution corresponds to an absorbing state where both species have been extinct. The second corresponds to an absorbing state where predators have gone extinct. The third solution corresponds to an active state where prey and predator coexist.

Due to the constraint (6), the parameters a, b and c are not all independent and only two can be chosen as independent. For this reason it is convenient to introduce the following parametrization [12]:

$$a = \frac{1-c}{2} - p, \qquad b = \frac{1-c}{2} + p, \tag{31}$$

and consider p and c as the independent variables. The parameter p is such that $-1/2 \leqslant p \leqslant 1/2$ and $0 \leqslant c \leqslant 1$ as before. This parametrization will be useful in the determination of the different phases displayed by the model.

A linear stability analysis reveals that the solution (x_1, y_1) is a hyperbolic saddle point for any set of the parameters a, b and c and so it is always unstable. The empty absorbing state will never be reached. A linear stability analysis also shows that the solution (x_2, y_2) is a stable node in the following region of the phase diagram $c > c_1$, where

$$c_1(p) = \tfrac{1}{3}(1 + 2p). \tag{32}$$

The active solution (x_3, y_3) is stable in the region $c < c_1$ and is attained in two ways: by an asymptotic stable focus, where the successive interactions of the map show damped oscillations, or trough an asymptotic stable node. In the phase diagram of figure 3, we show the transition line between the prey absorbing state and the active state given by $c = c_1$.

In figure 4, it is shown the behavior of the densities against the parameter c, the probability of predators death, for the special case $p = 0.2$. In terms of phase transitions what happens is that in the phase diagram there is a transition line separating the absorbing prey phase and the active phase which is characterized by constant and nonzero densities of prey and predator.

We may conclude that the mean-field approximation for the predator–prey probabilistic cellular automaton with rules (7)–(9) is capable to show, under a robust set of control

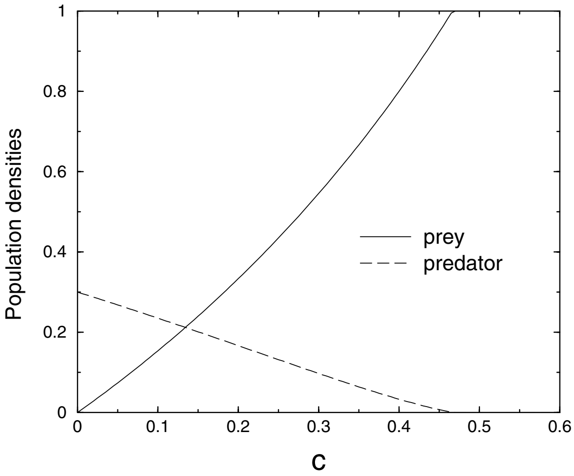

Figure 4. Densities of predator and prey as functions of the parameter c for $p = 0.2$, for the patch model.

parameters, that prey and predators can coexist without extinction. However, the map defined by equations (28) and (29) is not able to describe self-sustained oscillations of species population densities.

3.3. *Quasi-spatial model*

In order to find if oscillations in the species populations can be described within a mean-field approach we consider a more sophisticated approximation, the pair approximation, where correlations of two neighbor sites are included in the time-evolution equations for the densities. This is the lowest order mean-field approximation which takes into account the spatial localization of neighboring individuals.

In this analysis, we will maintain the correlations of one site and the correlations of two-sites in the equations. Correlations of three and four neighbor sites will be approximated by means of equation (27). With these approximation the model is described by the following set of five coupled equations:

$$x' = au - bv + x, \tag{33}$$

$$y' = bv + (1-c)y, \tag{34}$$

$$u' = \alpha a\left[\frac{qu}{z} - \alpha a\frac{qu^2}{z^2}\right] + \left[(1-\beta a) - \alpha a\frac{u}{z}\right]\left[u - \alpha b\frac{uv}{x}\right] + \alpha ac\frac{wu}{z} + c\left[(1-\beta b)v - \alpha b\frac{v^2}{x}\right], \tag{35}$$

$$v' = \alpha b\left[\beta a\frac{uv}{x} + \alpha a\frac{u^2v}{zx}\right] + \alpha a(1-c)\frac{wu}{z} + \alpha b\left[\frac{rv}{x} - \alpha b\frac{rv^2}{x^2}\right] + (1-c)\left[(1-\beta b)v - \alpha b\frac{v^2}{x}\right] \tag{36}$$

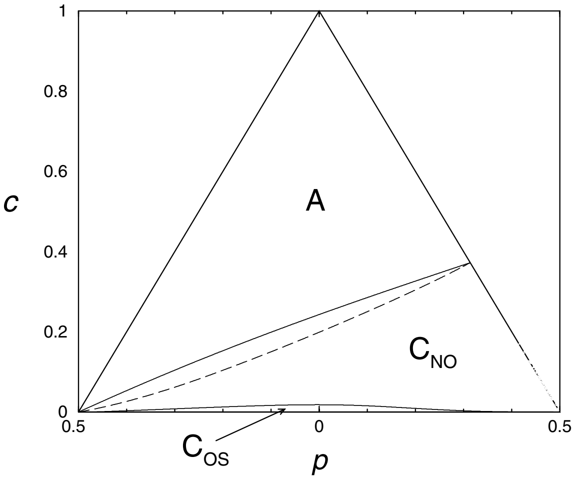

Figure 5. Phase diagram of the quasi-spatial model. The upper continuous line represents the transition, $c_1(p)$, between the prey absorbing (A) state and the nonoscillating coexistence ($\mathrm{C_{NO}}$) state. The lower continuous line represents the transition, $c_2(p)$, between the nonoscillating coexistence and the oscillating ($\mathrm{C_{OS}}$) coexistence state. The dashed line separates the two asymptotic time behavior of the nonoscillating coexistence state.

and

$$
\begin{aligned}
w' = \alpha b\left[(1-\beta a)\frac{uv}{x} - \alpha a\frac{u^2 v}{zx}\right] + (1-c)\left[w - \alpha a\frac{uw}{z}\right] \\
+ c\left[\beta b v + \alpha b\frac{v^2}{x}\right] + c(1-c)s, \qquad (37)
\end{aligned}
$$

where α and β are numerical fractions defined by $\alpha = (\zeta - 1)/\zeta$ and $\beta = 1/\zeta$ where ζ is the coordination number of the lattice. For the present case of a square lattice, $\zeta = 4$ so that $\alpha = 3/4$ and $\beta = 1/4$. We are using the following notation: $u = P(0, 1)$, $v = P(1, 2)$ and $w = P(0, 2)$, and also $r = P(1, 1)$, $q = P(0, 0)$ and $s = P(2, 2)$. The last three correlations are not independent but are related to each other by

$$r = x - u - v, \qquad (38)$$

$$q = z - u - w, \qquad (39)$$

$$s = y - v - w. \qquad (40)$$

We used the properties $P(1, 0) = P(0, 1)$, $P(1, 2) = P(2, 1)$ and $P(2, 0) = P(0, 2)$ that follows from the assumption that space is isotropic and homogeneous.

We have analyzed numerically the five-dimensional map, described by the set of equations (33)–(37), and we have obtained four types of solutions. Two solutions are trivial and are given by $x = y = u = v = w = 0$ and $x = 1$, $y = u = v = w = 0$. They correspond to the empty and prey absorbing states, respectively. The empty absorbing state, where both species have been extinct is an unstable solution and never occurs. However, the prey absorbing state is one of the possible stable stationary solutions and is stable above the critical transition line $c = c_1(p)$ shown in figure 5. Below this line it becomes unstable giving rise to the active state.

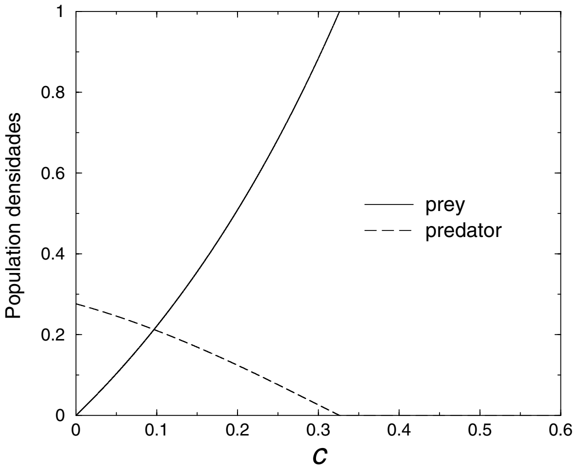

Figure 6. Densities of predator and prey as functions of c for the quasi-spatial model, for $p = 0.2$.

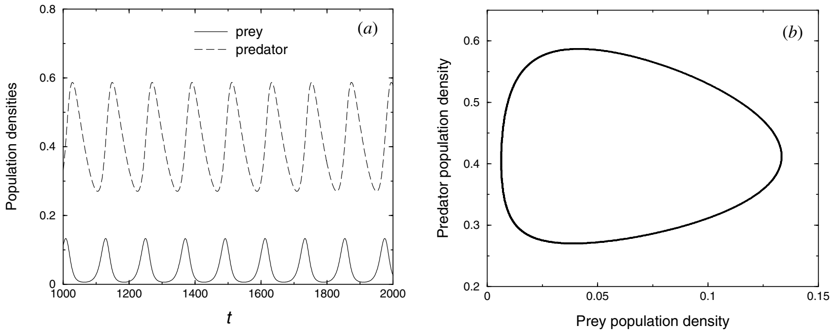

Figure 7. (a) Densities of predator and prey as functions of time and (b) density of predator versus density of prey, for the quasi-spatial model, for $p = 0$ and $c = 0.016$.

The other solutions correspond to the active states where both prey and predator coexist. These solutions are of two kinds: a stationary solution where there is a coexistence of the two species with densities constant in time, which we call the nonoscillating (NO) active state, and another solution where both population densities oscillate in time. This solution corresponds to a self-sustained oscillation of the predator–prey system and will be called the oscillating (O) active state. In the phase diagram of figure 5 there is a line $c = c_2(p)$ that separates the NO and O active phases. Figure 6 shows the behavior of the densities as a function of c for $p = 0$.

3.4. Oscillatory behavior

In figure 7, we show an example of self-sustained oscillations of the densities of prey and predators as functions of time. The oscillating solutions are attained from the nonoscillating solutions by a Hopf bifurcation [19]. The fixed point associated with this solution is an unstable center which produces a stable limit cycle as trajectories in the phase space of the

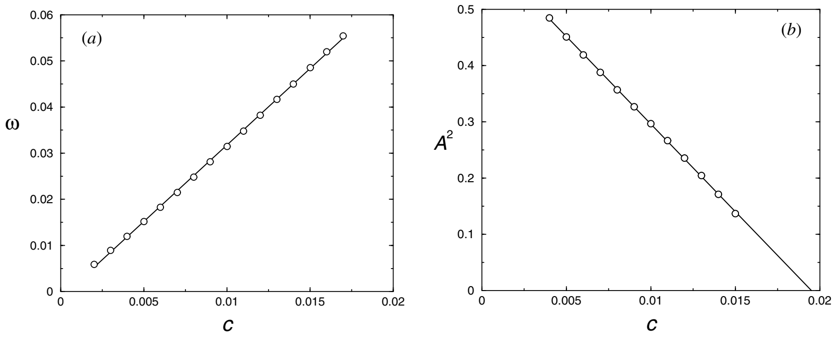

Figure 8. (*a*) Frequency of oscillations ω versus the parameter c. The frequency vanishes linearly as one approaches $c = 0$. (*b*) Amplitude A of oscillations versus c near the Hopf bifurcation point $c_2 = 0.019$. The quantity A^2 vanishes linearly when $c \to c_2$ in accordance with a Hopf bifurcation.

predator density versus prey density, as can be seen in figure 7. Note that the oscillations are not damped and have a well-defined period which is the same for the prey density and for the predator density, which implies that the oscillations are coupled. A maximum of predators always follow a maximum of prey. This means that the abundance of prey is a condition that favors the increase in the number of predators. As the predator number increases the prey population decays. The evanescence of prey is followed by a decrease in the predator number, giving conditions for the increase of prey population until the cycle starts again.

Oscillatory behavior can be found in many biological population systems [7, 8], the most famous being the one related to the time oscillations of the population of lynx and snowshoe hare [7, 8] although there are some claims that the observed cycles are not coupled with each other [45, 46]. The hare cycle can result from the time variation of the hare food supply [46] or is caused by an external source [45]. However, there are observed examples of coupled oscillations of predator–prey systems as the one studied by Huffaker [47]. The oscillations shown by the present model reproduces qualitatively some of the features of observed predator–prey systems.

Next we analyze the behavior of the frequency and amplitude of oscillations. Fixing the parameter p and varying the parameter c, we verify that in all the oscillating region the frequency of oscillation is proportional to parameter c,

$$\omega \sim c, \tag{41}$$

as can be seen in figure 8. Low frequencies are associated with low values of c; what means that, for small values of c, the greater the predator lifetime the greater will be the period of the oscillation. As to the amplitude A of the oscillations, we have verified, that fixing the value of p and varying the parameter c, it increases as c decreases. Our results show that

$$A \sim (c - c_2)^{1/2}, \tag{42}$$

as expected for a Hopf bifurcation [19] and shown in figure 8. The transition line $c = c_2$ from the oscillating phase to the nonoscillating phase can either be obtained by using the criterion given by equation (42) or by analyzing the eigenvalues associated with the map given by the set of equations (33)–(37). This last criterion means to find the points of phase diagram such that the real part of the dominant complex eigenvalue equals 1.

4. Discussion and conclusion

The main result coming from the pair-mean-field approximation applied to the predator–prey PCA is that it is possible to describe coexistence and self-sustained time oscillations. Moreover, these are stable oscillations. Given a set of parameters, just one limit cycle is achieved, no matter what the initial conditions are. This property is essential in describing a biological system since a small variation in the initial condition cannot modify the amplitude, frequency and mean value of the time oscillation densities of a predator–prey system. Similar results were obtained from a continuous time version of the present model [12]. Although the simple mean-field equations are essentially the same in both versions this is not the case concerning the pair-mean-field approximation. The time evolutions of the pair correlations for the PCA, presented here, depend on higher order correlations (up to fourth) when compared to those of the continuous version (up to third).

The model studied here is a spatially structured model with individuals residing in sites of a lattice and described by discrete dynamic variables. When we perform simple mean-field approximation we neglect all the correlations of sites in the lattice. But we take into account that there are limited resources for the surveillance of each species. For example, in the time-evolution equation for the density of prey we have an explicit term relative to reaction of birth of prey which is the product of the density of prey x by the density of empty sites $z = (1 - x - y)$. This coincides with an extended patch model approach for predator–prey systems. The presence of this term is what differs the simple mean-field equations from the Lotka–Volterra equations. However, taking into account the limitation of space and resources the simple mean-field equations are not sufficient to get self-sustained oscillations although able to describe damped time oscillations of population densities.

To get self-sustained time oscillations we had to proceed to the next level of approximation in which a pair of nearest neighbor sites is treated exactly. This approximation can be seen as representing a pair of nearest neighbor sites immersed in a mean field produced by the rest of the lattice. The most important feature being the fact that the two sites of this pair can be seen as localized in space. The set of five equations which results from the pair approximation for the PCA is indeed able to produce self-sustained oscillations of population densities. It presents an important property that the Lotka–Volterra model lacks, namely the oscillating solutions are stable and are unique for a given set of the control parameters.

Finally, we discuss another important issue, namely the possible effect of update either synchronous or asynchronous upon the threshold of species coexistence. We have verified that both types of update furnish the same qualitative results and quite similar quantitative results. Here, we considered the global synchronized dynamics embodied in the PCA; in a previous paper [12], we have considered an asynchronous dynamics, a continuous time Markov process, with the same local rules. Both versions at the same level of mean-field approximation display the same type of stable oscillations and a continuous transition line from an active to an absorbing state. However, some small quantitative differences are found. The synchronous dynamics provides a threshold of coexistence greater than those coming from the asynchronous update. In conclusion, the local dynamic rules and not the type of update are the essential ingredient to be taken into account in the present mean-field analysis.

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