

Chaos and pattern formation in a spatial tritrophic food chain

Daniela O. Maionchi^a, S.F. dos Reis^b, M.A.M. de Aguiar^{a,c,*}

^a Instituto de Física Gleb Wataghin, Universidade Estadual de Campinas, 13083-970 Campinas, São Paulo, Brazil

^b Departamento de Parasitologia, Universidade Estadual de Campinas, 13083-970 Campinas, SP, Brazil

^c New England Complex Systems Institute, Cambridge, Massachusetts 02138, USA

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Abstract

The model of Hastings and Powell describes a tritrophic food chain that exhibits chaotic dynamics. The model assumes that the populations are homogeneously mixed, so that the probability that any two individuals interact is uniform and space can be ignored. In this paper we propose a spatial version of the Hastings and Powell model in which predators seek their preys only in a finite neighborhood of their home location, breaking the mixing hypothesis. Treating both space and time as discrete variables we derive a set of coupled equations that describe the evolution of the populations at each site of the spatial domain. We show that the introduction of local predator–prey interactions result in qualitatively distinct dynamics of predator and prey populations. The evolution equations for the predators involve averages over the local density of preys, whereas the equations for the preys involve double averages, where the local density of both preys and predators appear. Our numerical simulations show that local predation also leads to spontaneous pattern formation and to qualitative changes in the global dynamics of the system. In particular, depending on the size of the predation neighborhoods, the chaotic strange attractor present in the original model of Hastings and Powell can be replaced by a stable fixed point or by an attractor of simpler topology.

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1. Introduction

Ecological phenomena such as intra and interspecific competition, predator–prey interaction, food web dynamics, and the spread of epidemics are systems that evolve through time and are distributed in space (Levin, 1992; Murray, 2000, 2002, 2003). The classical

approach to model such ecological systems originating with Lotka (1920) and Volterra (1926) is based on the assumption that the system is homogeneously mixing. This is called the mean-field approach, following formalism long used in chemistry and physics (Lotka, 1920). Under these conditions, which ignore space completely, each individual interacts equally with all others and such individuals are, therefore, ecologically equivalent. Nevertheless, the mean field approach, based on homogeneity assumptions, has

* Corresponding author. Fax: +55 19 3289 3137.

E-mail address: aguiar@ifi.unicamp.br (M.A.M. de Aguiar).

proven inadequate in several situations to describe the complexity of phenomena occurring in natural populations, as demonstrated early by Fisher (1937) and Skellam (1951) and more recently by several authors (e.g., Durrett and Levin, 1994; Levin and Pacala, 1997; Dieckmann et al., 2000; Pascual et al., 2001; Hosseini, 2003; Levin, 2003; Rauch et al., 2003; De Aguiar et al., 2004).

Models based in the mean field approximation, however, do not necessarily display simple behavior. Interesting examples of mean field models in ecology that exhibit *chaotic* dynamics are the discrete time models of single species discussed by May (1974) and continuous time models of three-species food chains introduced by Hastings and Powell (1991). The interest in models capable of displaying chaotic behavior is that they are more realistic than those whose solutions are simply periodic. Indeed, chaotic dynamics looks periodic at a coarse scale, but the apparent cycles never actually repeat themselves exactly, which conforms to experimental observations in population ecology. Extensions and applications of the Hastings and Powell (1991) model were recently studied by Varriale and Gomes (1998) for the case of three species of fish and by Chattopadhyay and Sarkar (2003) for a microbial system. Variations of the Hastings and Powell model also displaying chaotic behavior have been also proposed by Vayenas and Pavlou (2001), Kuijper et al. (2003), Cai-lin Xu and Zi-Zhen Li (2002) and Rai and Sreenivasan (1993).

In this paper we focus our attention in the consequences of the breakdown of the homogeneously mixing hypothesis, which is an essential ingredient of all Lotka–Volterra type of models, including the Hastings and Powell model. The first question we address is how the appearance of local predation affects the evolution equations of the predators and preys. Second, we investigate whether the chaotic behavior observed in the mean field approximation persists when space is introduced in the model, or if chaos can, in this case, be only an artifact of the mean field approximation. We have chosen the model of Hastings and Powell to study these questions. This model generalizes the basic two species predator–prey model to the case of three species: the lowest level species in the food chain, X , the species Y that prey upon X , and the species Z that prey on Y . In this particular case the assumption that the full dynamics of the system, which is composed of many

individual predators feeding from individual preys, can be described only by the average populations of each kind, is non trivial (Melián and Bascompte, 2002). In other words, the assumption that each member of a species interacts with equal probability with any other member of the other species might not apply for spatially extended communities. Predators, for instance, tend to feed preferentially from nearby preys, not from far away ones (e.g., Holt, 2002).

In order to include local spatial interactions in the model of Hastings and Powell (HP), we introduce the notion of ecological neighborhoods, which are fundamental for the understanding of the dynamics of interacting species. It is defined as “the region within which an organism is active or has some influence during the appropriate period of time” (Addicott et al., 1987). An ecological neighborhood arises from the physiological and behavioral traits that determine how animals use and influence the space around them, and is conditioned primarily by the size and mobility of organisms. The concept of ecological neighborhood has been instrumental to model not only competitive interactions (e.g., Levin and Pacala, 1997; Gandhi et al., 1998), but also predator–prey interactions where predators hunt for prey by searching within a neighborhood of prescribed size (e.g., Pascual and Levin, 1999; DeAngelis and Petersen, 2001). The latter type of interaction in particular is a prime example of the need for a careful definition of ecological neighborhoods which establish the effective feeding range of a predator from a central point in its home range (De Roos et al., 1991; Pascual et al., 2001; DeAngelis and Petersen, 2001). The use of the ecological neighborhood concept has been shown to be especially relevant in the case where predator and prey populations are not well mixed, that is, when the interacting system does not obey the assumptions of the mean-field approximation (DeAngelis and Petersen, 2001). Therefore, we shall make the hypothesis that predators have a home and can only consume preys that are sufficiently close to their home location, within a critical distance R . In order to simplify the calculations we assume that preys inside this neighborhood of radius R can be predated with equal probability, whereas preys outside this range are unreachable.

We find that the implications of these modifications on the dynamics of the predators and of the preys are quite distinct. The evolution equations for the predators depend on averages over the local density of preys,

whereas the equations for the preys depend on double averages where the local densities of both preys and predators appear. We show that, depending of the range of the local interactions, groups of nearly isolated populations might appear spontaneously, giving rise to patterns in the population density. Also, the dynamics of the average population of each species in the whole range may be quite differently from the predictions of the original HP model. In particular, the strange attractor observed in HP model may be replaced either by simple equilibrium points or by different types of attractors. Finally we point out that the type of spatial coupling between neighboring individuals considered here is based on previous works on the evolution of sexually reproducing populations (Sayama et al., 2000, 2002; De Aguiar et al., 2003). We note that a similar study for the case of two competing populations (where no chaotic dynamics is possible) was presented by Durrett and Levin (1994).

2. Model formulation

2.1. The HP model and its discrete version

Before we investigate the consequences of interspecific predation for the stability of three-species food chains we briefly review the HP model. The model is a canonical representation of pairwise interactions between three species, X , Y and Z , which incorporates a Holling type II functional response (Holling, 1959) in both consumer species, namely Y and Z . In this simple scenario the model takes the following form:

$$\begin{aligned}\frac{dX}{dt} &= R_0 X \left(\frac{1-X}{K_0} \right) - C_1 F_1(X)Y, \\ \frac{dY}{dt} &= F_1(X)Y - F_2(Y)Z - D_1 Y, \\ \frac{dZ}{dt} &= C_2 F_2(Y)Z - D_2 Z\end{aligned}\quad (1)$$

where T is time, X represents the number of individuals of the species at the lowest level of the food chain, Y the number of individuals of that prey on X , and Z is the number of individuals that prey on Y . The parameters in Eq. (1) are defined as follows: R_0 and K_0 are the intrinsic rate of increase and the carrying capacity of species X . Constants C_1 and C_2 are conversion rates

of prey to predator species Y and Z , respectively, and D_1 and D_2 are constant death rate for species Y and Z , respectively. The functions F_1 and F_2 represent the predation of Y on X and Z on Y , respectively. F is a functional response, which in Hastings and Powell's model (1991) takes the form:

$$F_i(U) = \frac{A_i U}{B_i + U} \quad (2)$$

At low prey densities predation is an increasing function of prey density, whereas as prey density increases the rate of predator consumption levels off because each predator is able to handle only a finite number of prey per unit of time. This specific saturating form for the consumption of prey by predators is a common representation in mathematical models of food chains and provides a reasonable approximation to arthropod, phytoplankton, and marine food chains (Powell and Richerson, 1985).

The variables X , Y , Z and T in model Eq. (1) can be scaled according to

$$\begin{aligned}x &= \frac{X}{K_0}, & y &= \frac{C_1 Y}{K_0}, \\ z &= \frac{C_1 Z}{C_2 K_0}, & t &= R_0 T\end{aligned}\quad (3)$$

to produce a nondimensional representation of the three-species food chain as

$$\begin{aligned}\frac{dx}{dt} &= x \left[1 - x - \frac{a_1 y}{1 + b_1 x} \right], \\ \frac{dy}{dt} &= y \left[\frac{a_1 y}{1 + b_1 x} - \frac{a_2 z}{1 + b_2 y} - d_1 \right], \\ \frac{dz}{dt} &= z \left[\frac{a_2 y}{1 + b_2 y} - d_2 \right]\end{aligned}\quad (4)$$

Given the structure defined by the Holling type II, appropriate time scales for the interactions at higher trophic levels, and biologically reasonable regions of parameter space, Hastings and Powell (1991) demonstrated that the dynamic interaction between prey and predators in the simple three-species food chain is chaotic, assuming the configuration of a strange attractor in the x, y, z space.

We shall now construct a spatial version of this model. To avoid dealing with partial differential equations we shall discretize both the space and the time.

We do that in two steps as follows: first we discretize the time and write

$$\begin{aligned}x^{t+1} &= x^t \left[2 - x^t - \frac{a_1 y^t}{1 + b_1 x^t} \right], \\y^{t+1} &= y^t \left[e^{-d_1} + \frac{a_1 x^{t+1}}{1 + b_1 x^{t+1}} - \frac{a_2 z^t}{1 + b_2 y^t} \right], \\z^{t+1} &= z^t \left[e^{-d_2} + \frac{a_2 y^{t+1}}{1 + b_2 y^{t+1}} \right]\end{aligned}\quad (5)$$

Note that this map is asynchronous, i.e., the populations x , y and z are not updated simultaneously. The variable x entering the right side of the second equation is taken at the time $t + 1$, the same happening to y in the third equation. The idea behind this asynchronous version of the dynamics is that the number of preys decreases immediately after predation, but it takes some time before the feeding of the predators is converted into offspring. The discrete dynamics generated by this three dimensional map is essentially identical to that of the HP differential equations. Two important comments, however, are in order: first we note that the logistic piece of the equation for x has been simply discretized, instead of using a Beverton–Holt type of map (see for instance, Cushing and Henson, 2002). This can be done here because the map parameters are far from the logistic chaotic regions. Second, we note that the set of Eq. (5) do admit negative solutions depending on the initial conditions. These solutions do not make biological sense. Therefore, we shall restrict ourselves to the set of initial conditions where all variables are always positive. This includes a large region around the Hastings and Powell chaotic attractor. Although other discretizations of the Hastings and Powell model are possible (including some that avoid negative solutions), the version represented by Eq. (5) is the only one we found that reproduces faithfully the dynamics of the differential equations (see next section). This is the basic property we want to preserve to ensure that, when space is introduced, it can be blamed for any qualitative dynamical change.

2.2. Space and local interactions

We shall introduce space as a discrete two-dimensional regular square lattice with N by N points with periodic boundary conditions. The populations

represented by x , y and z are going to be placed only at the lattice points. In order to write down the dynamical equations describing the evolution of each species at each lattice point we need to make some assumptions about the movement of each type. We assume that the individuals of type x are fixed, like plants, for instance. They compete for resources only locally and are predated by the individuals of type y . This first assumption is only of technical character, to reduce the number of new parameters in the model. We could, of course, introduce a mobility radius A for species x .

The individuals of types y and z , on the other hand, are the predators and super-predators. Predators tend to restrict their movements to a particular segment of the available habitat, which is generally termed the home range, and to smaller areas located inside the home range, which are used more frequently, and are referred to as core areas (Burt, 1943; Gray et al., 1998; Rodriguez-Robles, 2003). Within the core areas is located the den, the home for a predator, which is a shelter, natural or constructed, used for sleeping, for thermoregulatory optima, and for giving birth and raising the young (Magoun and Copeland, 1998). The selection for den sites by small-, medium- and large sized predators is a process involving optimization along the dimensions of required resources and landscape configuration (Hiscocks and Perrin, 1991; Henner et al., 2004) in order to maximize survival and reproductive success (Oli et al., 1997; Devillard et al., 2003). In this model we shall assume that both predators and super-predators have fixed homes and that they restrict their movements to their respective home ranges. Migration is assumed to occur in a slower time scale and will be ignored. Therefore, a member of the y population whose home is located at the spatial site labeled by the vector \mathbf{n} may only feed from x preys located at a maximum distance \mathbf{B} from it, i.e., inside its home range. Similarly, the individuals of type z whose home is located at the spatial site \mathbf{n} may only feed from y preys located at a maximum distance \mathbf{C} from its home position.

In order to simplify matters, we assume that predation inside the home range is uniform. This means that all individuals of the population x inside a circle of radius B of the site \mathbf{n} can be equally predated by an individual of the specie y at \mathbf{n} , whereas individuals outside this circle cannot be predated at all. A similar rule applies for the individuals of y with respect to z and

the radius C . Although smoother neighborhoods, where the probability of being predated decreases smoothly with the distance from the predator, are more realistic, they are harder to deal with from the numerical point of view. A study of the effects of smooth neighborhoods can be found in (De Aguiar et al., 2003; see also Fuentes et al., 2003).

In order to write down the spatial version of the dynamical Eq. (5), we first calculate the rate at which individuals y at site \mathbf{n} , $y(\mathbf{n})$, feed from preys x in their neighborhood B_n . The rate is proportional to the average value of x in this neighborhood. Actually, because of the saturating function f used in the HP model, the rate at which $y(\mathbf{n})$ feeds on x becomes

$$y(\mathbf{n}) \frac{a_1 \langle x \rangle_{B_n}}{1 + b_1 \langle x \rangle_{B_n}} \quad (6)$$

where

$$\langle x \rangle_{B_n} \equiv \frac{1}{N_B} \sum_{j \in B_n} x(j) \quad (7)$$

and N_B is the number of sites inside a circle or radius B , which is approximately πB^2 . Eq. (6) has a very simple interpretation: it replaces the average value of x taken over the entire population (which is what appears in Eq. (5)) by a local average taken over the neighborhood of radius B . This is illustrated in Fig. 1.

This result allows us to calculate the rate at which the individuals of the species x at site \mathbf{n} are predated by the nearby individuals of y . First we note that only y 's in the neighborhood B_n of $x(\mathbf{n})$ can predate them. Let $y(\mathbf{k})$ be the population at the site \mathbf{k} inside B_n . Eq. (6) says that the consumption rate of $y(\mathbf{k})$ is a function of $\langle x \rangle_{B_k}$. Of this total consumption, a fraction $1/N_B$, on the average, is made of preys from the specific site \mathbf{n} . Therefore, the consumption of $x(\mathbf{n})$ by $y(\mathbf{k})$ is

$$\frac{1}{N_B} y(\mathbf{k}) \frac{a_1 \langle x \rangle_{B_k}}{1 + b_1 \langle x \rangle_{B_k}} \quad (8)$$

and the total consumption of $x(\mathbf{n})$ is the sum of consumptions over all predators $y(\mathbf{k})$ in the neighborhood of $x(\mathbf{n})$:

$$\frac{1}{N_B} \sum_{k \in B_n} y(\mathbf{k}) \frac{a_1 \langle x \rangle_{B_k}}{1 + b_1 \langle x \rangle_{B_k}} = \left\langle y(\mathbf{k}) \frac{a_1 \langle x \rangle_{B_k}}{1 + b_1 \langle x \rangle_{B_k}} \right\rangle_{B_n} \quad (9)$$

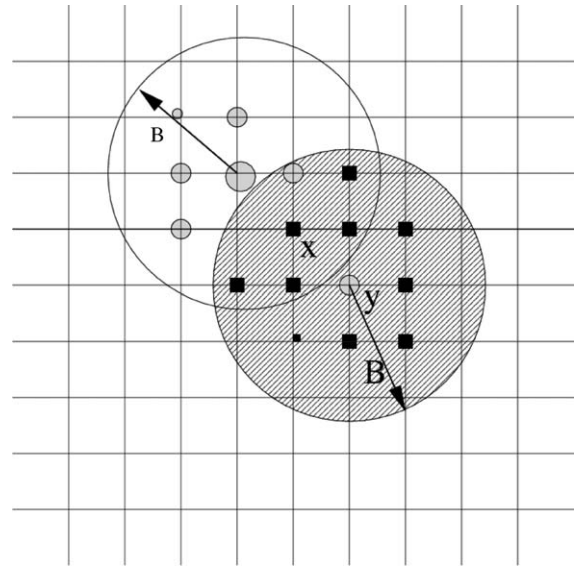


Fig. 1. Illustration of spatial grid with individuals of type y (circles) and of type x (squares). The shaded area shows the neighborhood of size B where the individual marked with the y at the center preys on x . The individual marked with the x is predated by all the y 's within a range B centered on it. It is predated, for instance, by the y at the center of the other un-shaded circle of radius B .

This shows that the effect of local predation on the predator is through a simple average. However, its effect on the prey involves the average of an average. Following the same reasoning for the interaction between y and z we obtain a set of coupled finite difference equations describing the spatial tritrophic chain that can be written in compact form as

$$\begin{aligned} x^{t+1}(\mathbf{n}) &= x^t(\mathbf{n})[2 - x^t(\mathbf{n})] - \left\langle y^t(\mathbf{k}) \frac{a_1 \langle x^t \rangle_{B_k}}{1 + b_1 \langle x^t \rangle_{B_k}} \right\rangle_{B_n}, \\ y^{t+1}(\mathbf{n}) &= y^t(\mathbf{n}) \left[e^{-d_1} + \frac{a_1 \langle x^{t+1} \rangle_{B_n}}{1 + b_1 \langle x^{t+1} \rangle_{B_n}} \right] \\ &\quad - \left\langle z^t(\mathbf{k}) \frac{a_2 \langle y^t \rangle_{C_k}}{1 + b_2 \langle y^t \rangle_{C_k}} \right\rangle_{C_n}, \\ z^{t+1}(\mathbf{n}) &= z^t(\mathbf{n}) \left[e^{-d_2} + \frac{a_2 \langle y^{t+1} \rangle_{C_n}}{1 + b_2 \langle y^{t+1} \rangle_{C_n}} \right] \end{aligned} \quad (10)$$

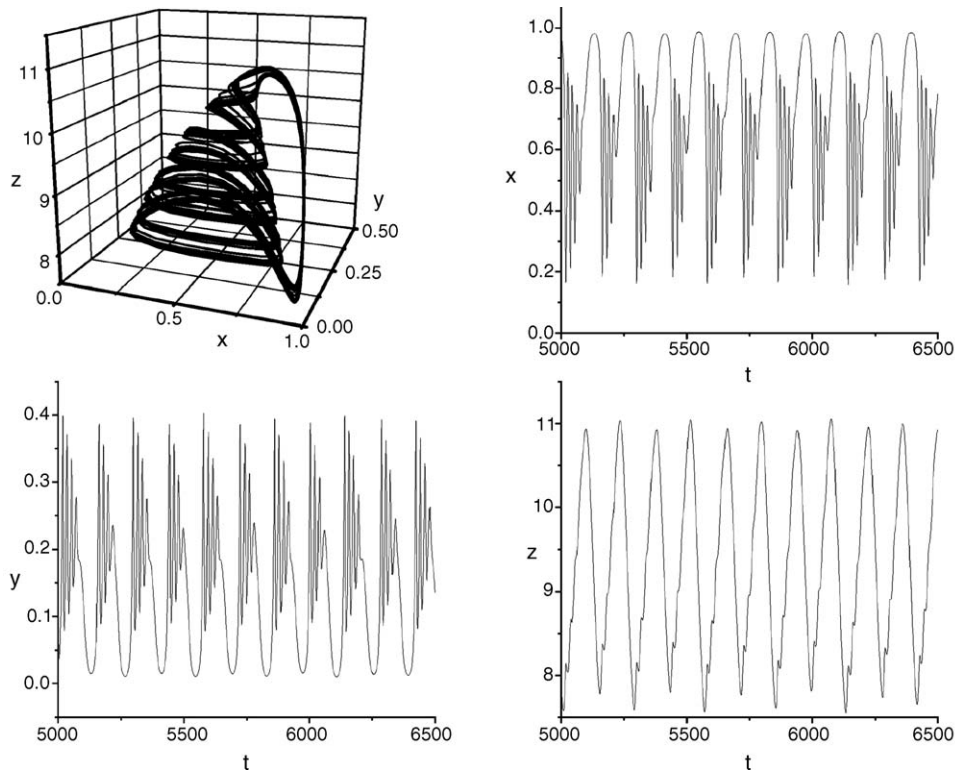


Fig. 2. Dynamics of the x , y and z populations in the HP discrete time model. (a) strange attractor in the x - y - z plane; (b)–(d) x , y and z as a function of time.

3. Results

In what follows we shall fix the parameters of the HP model as in (Hastings and Powell, 1991), namely, $a_1 = 5$, $b_1 = 3.2$, $a_2 = 0.1$, $b_2 = 2$, $d_1 = 0.45$ and $d_2 = 0.01$. Fig. 2 shows the total populations as a function of the discrete time according to Eq. (5) and a tridimensional view of the strange attractor that forms for this set of parameters.

For the spatial model we fixed the space lattice as a square of 64×64 sites with periodic boundary conditions. The total number of sites is $2^{12} = 4096$. The sizes of the B and C interaction neighborhoods have been chosen to vary between one and five lattice spaces at steps of two, generating nine different situations for the pair (B, C) : (1,1), (1,3), (1,5), etc., up to (5,5). We have actually calculated the time evolution for all values of B and C between 1 and 5 at steps of 1, totalizing 25 situations. For clarity of presentation we have chosen to present only the nine situations above, since they

are representative of the whole set. Eq. (10) were ran from a certain initial condition until equilibrium (or at least dynamical equilibrium) was reached. The initial condition for all plots is a uniform distribution of the three populations with value (x_0, y_0, z_0) over all lattice sites plus a small random perturbation corresponding to 5% of this fixed homogeneous value. The homogeneous value is chosen to be the unstable fixed point at the center of the chaotic attractor: $(x_0, y_0, z_0) = (0.820, 0.124, 10.056)$.

In order to show the three populations at the same time we plot at each spatial site a different symbol for each population. The size of the symbol is proportional to the fraction of that population at that point. We use circles for the species z , stars for y and squares for x . Fig. 3 shows an example of time evolution of the population densities for the case $(B, C) = (3, 3)$ for times 2, 16, 128 and 1000. Fig. 4 shows a detailed view of the spatial distribution for $t = 25,000$. These plots show the qualitative spatial density distribution only.

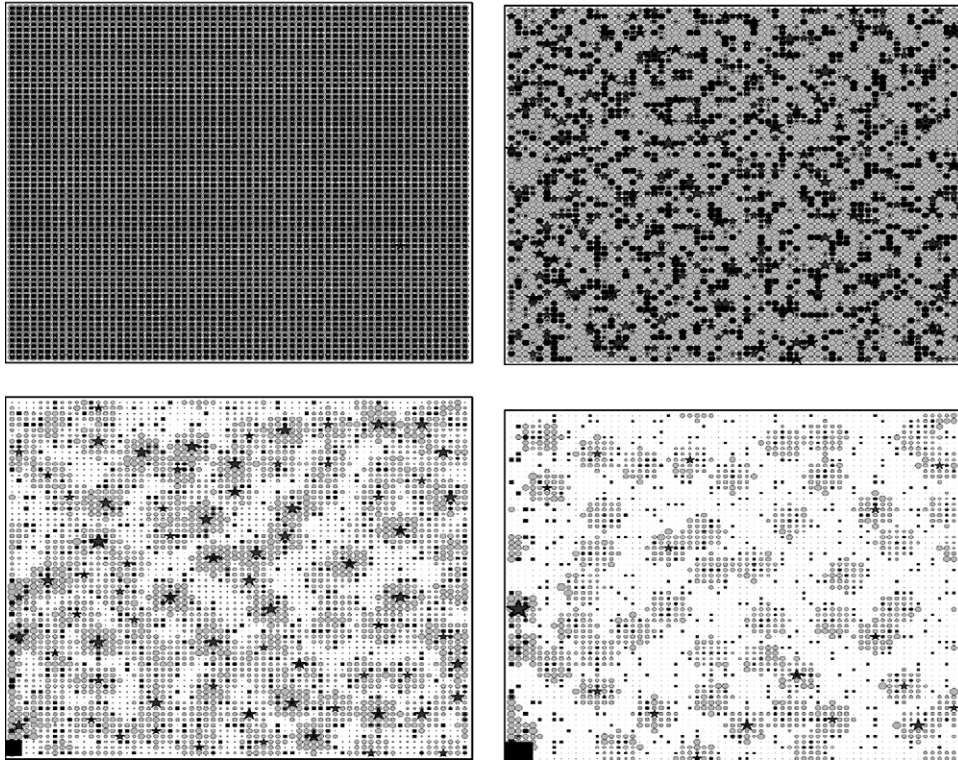


Fig. 3. Time evolution of the x (squares) y (stars) and z (circles) populations for the case $(B,C)=(3,3)$ at (a) $t=2$, (b) $t=16$, (c) $t=128$ and (d) $t=1000$.

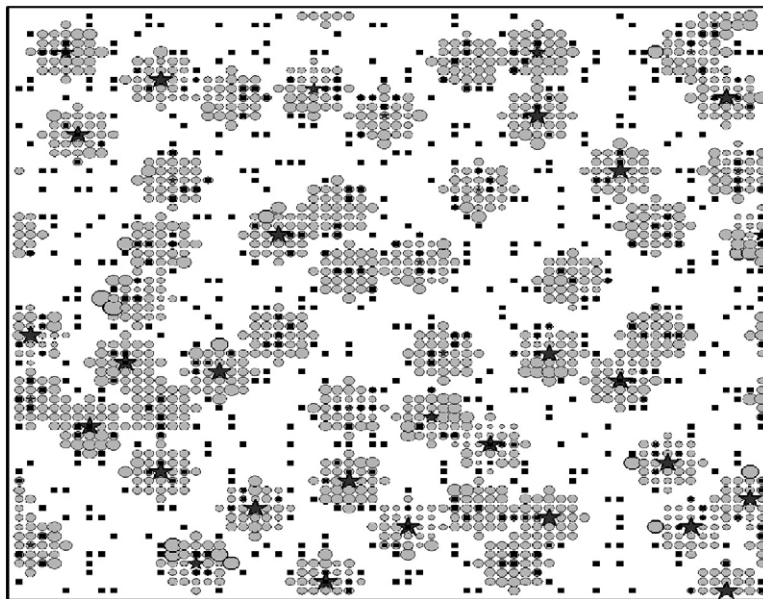


Fig. 4. Amplification of the populations distribution for the case $(B,C)=(3,3)$ at $t=25,000$.

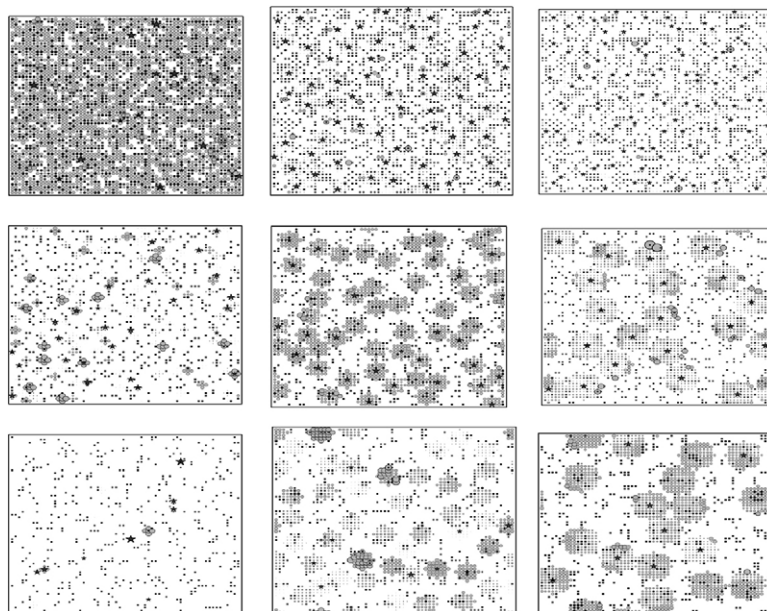


Fig. 5. Spatial distribution of the populations after 25,000 time steps. The mobility radii (B,C) is $(1,1)$, $(1,3)$ and $(1,5)$ (first line); $(3,1)$, $(3,3)$ and $(3,5)$ (second line) and $(5,1)$, $(5,3)$, $(5,5)$ (third line).

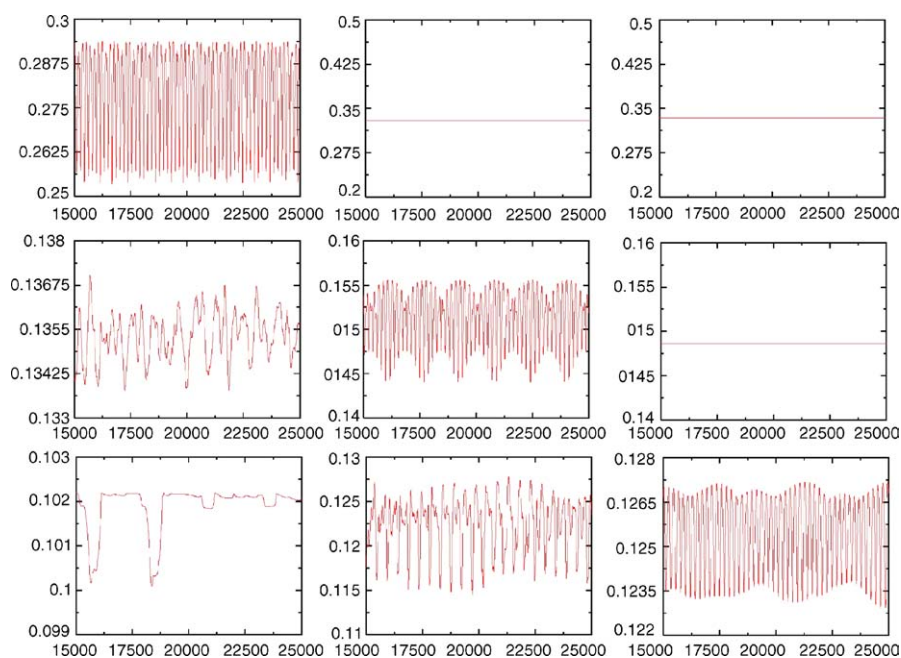


Fig. 6. Time evolution of the average x population from $t=15,000$ to $25,000$. The size (B,C) of the neighborhoods follow Fig. 4, from $(1,1)$ (upper left) to $(5,5)$ (lower right).

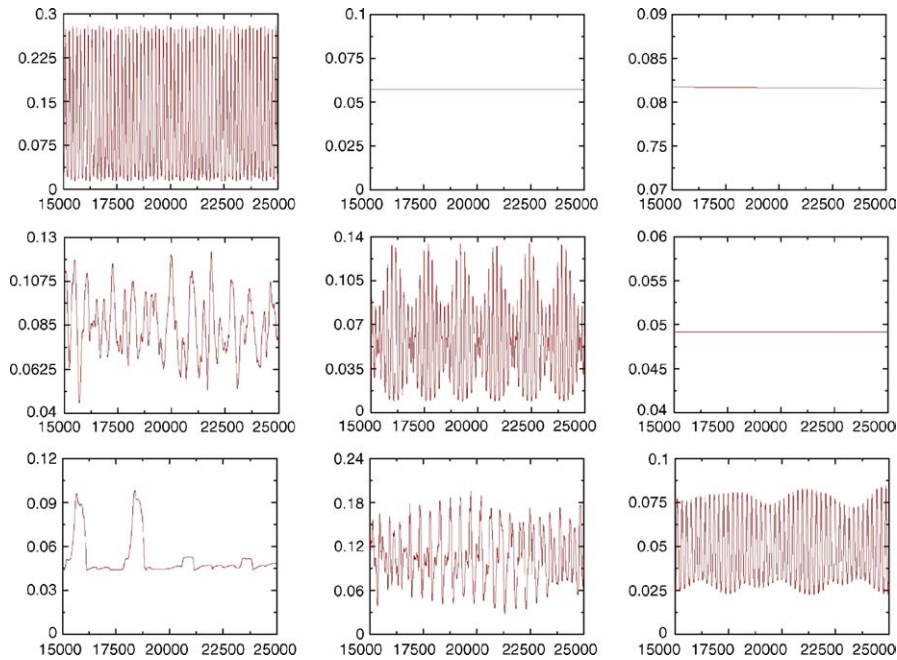


Fig. 7. Time evolution of the average y population from $t = 15,000$ to $25,000$. The size (B, C) of the neighborhoods follow Fig. 4, from $(1, 1)$ (upper left) to $(5, 5)$ (lower right).

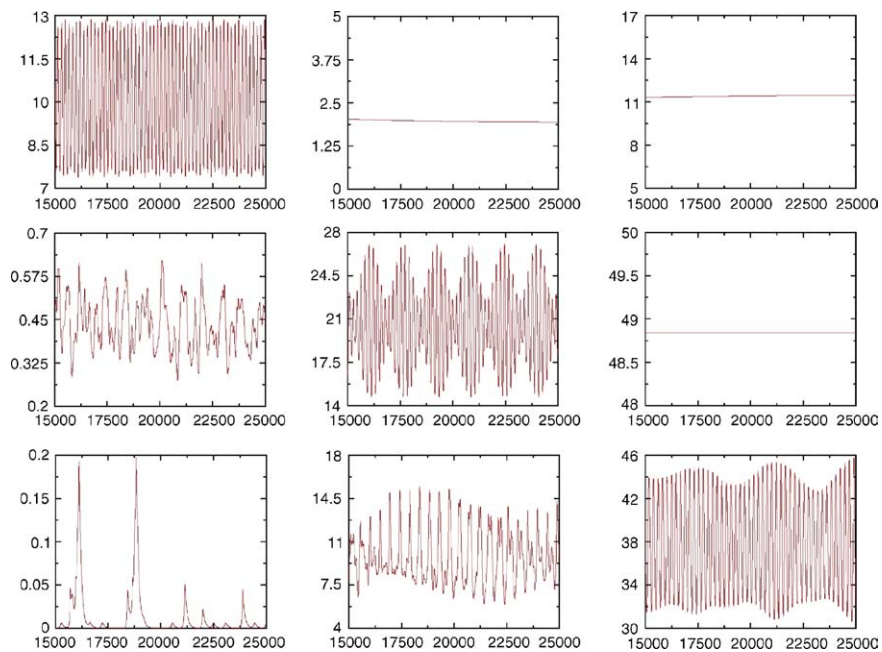


Fig. 8. Time evolution of the average z population from $t = 15,000$ to $25,000$. The size (B, C) of the neighborhoods follow Fig. 4, from $(1, 1)$ (upper left) to $(5, 5)$ (lower right).

The actual values of the population densities are plotted in Figs. 6–9, to be discussed below.

Fig. 5 shows the spatial distributions of the populations after 25,000 time steps for the 9 combinations of the B and C neighborhoods discussed above (see caption for the details). In most cases we can see the formation of isolated groups, or clusters, where the population of type z concentrates around a localized (usually single site) population of y . The species represented by x remains mostly scattered in all situations. It is interesting to notice that, although extinction is not a stable option for the homogeneous model, the spatial coupling does lead the populations to extinction in several sites outside the clusters. Even the x population has died completely in those sites. This might seem a little strange, since the species x is considered fixed, and the logistic term makes the solution $x = 0$ unstable. This happens because the model assumes, for simplicity, that a site with no x remains forever empty. Actually, the extinction of the species x , promoted by the spatial coupling, can be avoided with the introduction of a

small spontaneous growth term in model. Examples of such term are a small diffusion coefficient or a small mobility neighborhood A for the x species.

Another interesting feature of the model is the different spatial distribution of the three species involved: x tends to be uniformly distributed, although not over all sites; y is always localized in a few sites, around which a circular cluster of z are concentrated. The size of the clusters is determined by the interaction radius C , as expected. Different spatial behavior for each species is actually expected from Eq. (10), since each of them has a very distinct role in the ecosystem: x is a prey with no spatial mobility and with resources given implicitly in the logistic term; y is both prey and predator, and has a mobility B ; z is a high level predator, with mobility C . The specific form of the spatial distribution of each type, however, cannot be understood without a careful analysis with linear stability theory.

Figs. 6–8 show the time evolution of the average populations of x , y and z , respectively, in the interval

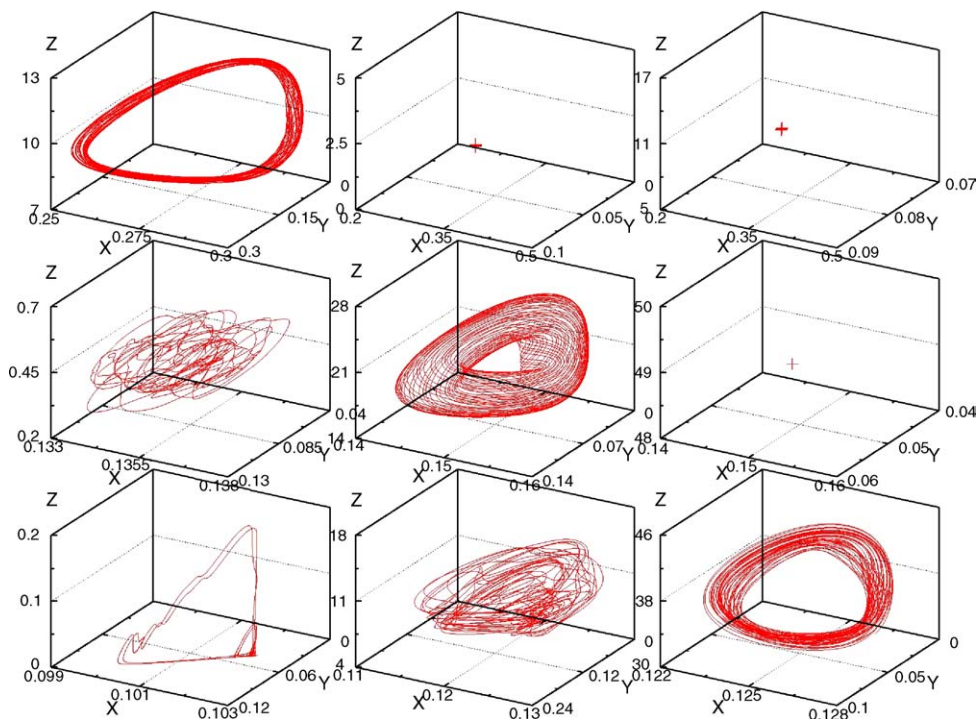


Fig. 9. Dynamics of the average populations in the three dimensional space. The size (B, C) of the neighborhoods follow Fig. 4, from (1,1) (upper left) to (5,5) (lower right).

from 15,000 to 25,000 time steps for the same values of B and C displayed in Fig. 4. The averages are computed simply by adding the total population of each species over all space and dividing by the total number of sites. These figures can be interpreted as a phase diagram in the ‘phase space’ of interaction radii. They show an interesting phase transition along the line $B = C$: for $B < C$ the dynamics tend to a simple equilibrium point, whereas for $B > C$ the behavior tends to be more complex.

Fig. 9 shows the tridimensional x – y – z plot for the average populations in this case for the same interval from 15,000 to 25,000 time steps. We see that the attractor, whenever it shows up, is very different from the one produced by the homogeneous dynamics, Eq. (5). We note that the spatial Eq. (10) do admit homogeneous solutions identical to those of (5). The fact that these solutions are not recovered by the numerical calculation indicates that they are unstable under spatial fluctuations for the parameters considered.

4. Conclusions

The usual hypothesis behind most models employing the Lotka–Volterra type of population dynamics is that each individual member of a species interacts uniformly with all other members of the other species involved. In many cases, particularly when the populations are distributed over large spatial areas, this hypothesis might not apply. In this paper we have considered a spatial version of a well-known model of Hastings and Powell for a tritrophic food chain and studied its properties with respect to the uniform model. In the spatial model the uniform interaction between individuals is replaced by local interactions of finite range. In order to avoid the difficulties of solving partial differential equations we have considered both time and space to be discrete. We first constructed a set of finite difference equations that qualitatively reproduces the dynamics of the continuous HP model. Next we assumed that the populations were distributed in space so that each site could contain individuals of the three types. The coupling between the sets of equations at different sites happens through predation in local neighborhoods.

We have shown that, depending on the size of these neighborhoods, isolated clusters of populations might form out of initially uniform populations. The appearance of spatial clustering shows that the uniform distribution becomes unstable under spatial fluctuations of the populations. In all cases studied the asymptotic distribution of the populations were such that the type x was uniformly distributed and the type y was localized in a few sites, around which a circular cluster of z were concentrated. The size of the clusters is determined by the interaction radius C . As we noted in the previous section, the different spatial behavior of each species is expected from Eq. (10), since each of them has a very distinct role in the ecosystem. The specific form of the spatial distribution of each type, however, cannot be understood without a careful analysis with linear stability theory. Such analysis involves the study of chaotically forced linear maps, and is currently under investigation.

It is important to emphasize that the spatial structures that develop spontaneously in the spatial model are not a result of randomness in the initial conditions or a consequence of the spatial model being completely different from the homogeneous model. The homogeneous discrete model, Eq. (5), is constructed in such a way that its dynamics is very similar to the continuous HP model for a large range of parameters and initial conditions. When space is introduced in this system of equations, generating Eq. (10), it can be verified that the solutions of Eq. (5) are still solutions of the new set of Eq. (10). Therefore, Eq. (10) represent an extended version of the homogeneous model, containing their solutions. We have shown that these homogeneous solutions, however, are unstable, and do not survive the introduction of small fluctuations in the spatial density. The initially homogeneous populations converge to a new solution when a small spatial fluctuation is added which displays patches and which is stable. For different initial fluctuations we get the same qualitative results, same size and number of patches, although the specific position and details on each patch changes.

We also found that the time dependence of the total populations of the spatial model can have completely different qualitative properties when compared to the uniform model. In particular, the strange attractor can be replaced by very different structures, including fixed points or attractors with simpler topologies.

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References

- Addicott, J.F., Aho, J.M., Antolin, M.F., et al., 1987. Ecological neighborhoods: scaling environmental problems. *Oikos* 49, 340–346.
- Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. *J. Mamm.* 24, 346–352.
- Chattopadhyay, J., Sarkar, R.R., 2003. Chaos to order: preliminary experiments with a population dynamics models of three trophic levels. *Ecol. Model.* 163 (1–2), 45–50.
- Ciucci, P., Mech, L.D., 1992. Selection of wolf dens in relation to winter territories in northeastern Minnesota. *J. Mamm.* 73, 899–905.
- Cushing, J.M., Henson, S.M., 2002. A periodically forced Beverton–Holt equation. *J. Diff. Eq. Appl.* 8, 1119–1120.
- De Aguiar, M.A.M., Baranger, M., Bar-Yam, Y., Sayama, H., 2003. Robustness of spontaneous pattern formation in spatially distributed genetic populations. *Braz. J. Phys.* 33, 514–520.
- De Aguiar, M.A.M., Sayama, H., Baranger, M., Bar-Yam, Y., 2004. Invasion and extinction in the mean field approximation for a spatial host-pathogen model. *J. Stats. Phys.* 114, 1417–1451.
- DeAngelis, D.L., Petersen, J.H., 2001. Importance of the predator's ecological neighborhood in modeling predation on migrating prey. *Oikos* 94, 315–325.
- De Roos, A.M., McCauley, E., Wilson, W.G., 1991. Mobility versus density limited predator–prey dynamics on different spatial scales. *Proc. R. Soc. London B* 246, 117–122.
- Devillard, S., Say, L., Pontier, D., 2003. Dispersal pattern of domestic cats (*Felis catus*) in a promiscuous urban population: do females disperse or die? *J. Anim. Ecol.* 72, 203–211.
- Dieckmann, U., Law, R., Metz, J.A.J., 2000. *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge University Press, Cambridge, UK.
- Durrett, R., Levin, S.A., 1994. Stochastic spatial models: a user's guide to ecological applications. *Phil. Trans. R. Soc. London B* 343, 329–350.
- Fisher, R.A., 1937. The wave of advance of advantageous genes. *Ann. Eugen.* 7, 355–369.
- Fuentes, M.A., Kuperman, M.N., Kenkre, V.M., 2003. Nonlocal interaction effects on pattern formation in population dynamics. *Phys. Rev. Lett.* 91, 158104.
- Gandhi, A., Levin, S., Orszag, S., 1998. "Critical slowing down" in time to extinction: an example of critical phenomena in ecology. *J. Theor. Biol.* 192, 363–376.
- Gray, S.J., Hurst, J.L., Stidworthy, R., Smith, J., Preston, R., MacDougall, R., 1998. Microhabitat and spatial dispersion of the grassland mouse (*Mus musculus*). *J. Zool.* 246, 299–308.
- Hassell, M.P., 1978. *The Dynamics of Arthropod Predator–Prey Systems*. Princeton University Press, Princeton, New Jersey, USA.
- Hastings, A., Powell, T., 1991. Chaos in a three species food chain. *Ecology* 72, 896–903.
- Henner, C.M., Chamberlain, M.J., Leopold, B.D., Burger, L.W., 2004. A multi-resolution assessment of raccoon den selection. *J. Wildl. Manage.* 68, 179–187.
- Hiscocks, K., Perrin, M.R., 1991. Den selection and use by dwarf mongooses and banded mongooses in South Africa. *S. Afr. J. Wildl. Res.* 21, 119–122.
- Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Holt, R.D., 1997. From metapopulation dynamics to community structure. In: Hanski, I., Gilpin, M. (Eds.), *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, San Diego, CA, USA, pp. 149–164.
- Holt, R.D., 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecol. Res.* 17, 261–273.
- Hosseini, P.R., 2003. How localized consumption stabilizes predator–prey systems with finite frequency of mixing. *Am. Nat.* 161, 567–585.
- Kuijper, L.D.J., Kooi, B.W., Zonneveld, C., Kooijman, S.A.L.M., 2003. Omnivory and food web dynamics. *Ecol. Model.* 163 (1–2), 19–32.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Levin, S.A., 2003. Complex adaptive systems: exploring the known, the unknown and the unknowable. *Bull. Am. Math. Soc.* 40, 3–19.
- Levin, S.A., Pacala, S.W., 1997. Theories of simplification and scaling of spatially distributed processes. In: Tilman, D., Kareiva, P. (Eds.), *The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, New Jersey, USA, pp. 271–295.
- Lotka, A.J., 1920. *Elements of Physical Biology*. Williams and Wilkins, Baltimore, MD, USA.
- Magoun, A.J., Copeland, J.P., 1998. Characteristics of wolverine reproductive den sites. *J. Wildl. Manage.* 62, 1313–1320.
- May, R., 1974. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Melián, C.J., Bascompte, J., 2002. Food web structure and habitat loss. *Ecol. Lett.* 5, 37–46.
- Murray, J.D., 2000. Pattern formation in integrative biology - a marriage of theory and experiment. *Compt. R. Acad. Sci.* 323, 5–14.
- Murray, J.D., 2002. *Mathematical Biology I*. Springer-Verlag, Berlin, Germany.
- Murray, J.D., 2003. *Mathematical Biology II*. Springer-Verlag, Berlin, Germany.
- Oli, M.K., Jacobson, H.A., Leopold, B.D., 1997. Denning ecology of black bears in the White River National Wildlife Refuge, Arkansas. *J. Wildl. Manage.* 61, 700–706.
- Pascual, M., Mazzega, P., Levin, S.A., 2001. Oscillatory dynamics and spatial scale: the role of noise and unresolved pattern. *Ecology* 82, 2357–2369.
- Powell, T., Richerson, P.J., 1985. Temporal variation, spatial heterogeneity, and competition for resources in plankton systems: a theoretical model. *Am. Nat.* 125, 431–464.
- Rai, V., Sreenivasan, R., 1993. Period-doubling bifurcations leading to chaos in a model food chain. *Ecol. Model.* 69 (1–2), 63–77.

- Rauch, E.M., Sayama, H., Bar-Yam, Y., 2003. Dynamics and genealogy of strains in spatially extended host–pathogen models. *J. Theor. Biol.* 221, 655–664.
- Rodriguez-Robles, J.A., 2003. Home ranges of gopher snakes (*Pituophis catenifer*, Colubridae) in central California. *Copeia*, 391–396.
- Sayama, H., Kaufman, L., Bar-Yam, Y., 2000. Symmetry breaking and coarsening in spatially distributed evolutionary processes including sexual reproduction and disruptive selection. *Phys. Rev. E* 62, 7065–7069.
- Sayama, H., Aguiar, M.A.M., Bar-Yam, Y., Baranger, M., 2002. Spontaneous pattern formation and genetic invasion in locally mating and competing populations. *Phys. Rev. E* 65, 051919.
- Skellam, J.G., 1951. Random dispersal in theoretical populations. *Biometrika* 38, 196–218.
- Varriale, M.C., Gomes, A.A., 1998. A study of a three species food chain. *Ecol. Model.* 110 (2), 119–133.
- Vayenas, D.V., Pavlou, S., 2001. Chaotic dynamics of a microbial system of coupled food chains. *Ecol. Model.* 136 (2–3), 285–295.
- Volterra, V., 1926. Variazioni e fluttuazioni del numero d'individui in specie animale conviventi. *Mem. R. Accad. Naz. Lincei* 2, 31–113.
- Wilson, H.B., Hassel, M.P., Holt, R.D., 1998. Persistence and area effects in a stochastic tritrophic model. *Am. Nat.* 151, 587–595.
- Xu, C.-I., Li, Z.-Z., 2002. Influence of intraspecific density dependence on a three-species food chain with and without external stochastic disturbances. *Ecol. Model.* 155 (1), 71–83.