Spontaneous emergence of spatial patterns in a predator-prey model

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We present studies for an individual based model of three interacting populations whose individuals are mobile in a two-dimensional lattice. We focus on the pattern formation in the spatial distributions of the populations. Also relevant is the relationship between pattern formation and features of the populations' time series. Our model displays both traveling wave solutions, clustering and uniform distributions, both related to the parameter values. We also observed that the regeneration rate, the parameter associated to the primary level of trophic chain, the plant, regulated the presence of predators, as well as the type of spatial configuration. This result corroborates the theory that the enrichment of prey can stabilize the predator-prey dynamic in more realistic models.

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I. INTRODUCTION

Mathematical modeling of population dynamics is widely recognized as a useful tool in the investigation of many interesting features found in the organization of individuals in nature [1]. In order to study the spatial distribution of individuals in their habitats, it is essential to take into account factors such as individual mobility and hunting and escaping skills.

When populations are treated as continuous functions of space and time, motion of individuals appears in these equations as diffusion terms. Diffusion is a very common natural phenomenon in many areas of science [2]. Thus much can be learned, by analogy, about the distribution of individuals in their habitats from others diffusive phenomena. For instance, if interacting populations are described by sets of reaction-diffusion equations, it is possible to infer that individuals may be distributed heterogeneously even in homogeneous habitat. It is possible to observe phenomena like traveling waves and chaos [3] even in simple models.

Predator-prey models can have their stability properties changed by diffusive terms. It has been stated by Wilson and De Roos [4] that spatial predator-prey systems are considerably more stable than the aspatial ones. Originally, population dynamics models were formulated in terms of differential equations [1]. This allowed the application of analytical methods developed to treat problems in many other areas of science and engineering in spatial ecology. With the advent of cheap computing power, it became possible to build more sophisticated models that are not easily translated into differential equations or that result in equations too difficult to be solved.

Some strategies of analyzing and simulating these models include individual based models (IBMs) using cellular automata [5]; IBMs without cellular automata [4]; and mean field approximation [6]. Finite element methods and perturbative methods [7] are also alternative approaches to study these systems. In the present work we use individual based models (IBMs) with cellular automata. This method applies simple rules inspired on natural events of real systems on a discrete group of individuals lying over a discrete finite lattice. These rules are organized as a set of events and determine how individuals will behave in each time step. We intend to investigate the global response of the system due to little modifications on parameters of the model.

The main advantage of IBMs is the possibility of accounting for many additional features observed on real systems attributing to each individuals particular information, like genetics and age [8,9], without increasing the computational cost exponentially, as we have in approaches which take into account time delayed effects and/or history-dependent models [10]. In general, there are not analytical solutions for these kinds of models.

Our work focuses mainly on the spatial patterns that emerge in an open three-trophic food chain and their relationships to the populations time series. Keitt *et al.* [11] discussed emergent patterns in diffusion-limited predator-prey interaction introducing spatial heterogeneity in the model. We observed emergent spatial patterns without the necessity of this mechanism. Our model presents self-organization [12] derived mainly from the dynamics of the system. Here we propose an IBM consisting of a fixed plant population and a prey population, which eats the plant population. The prey is able to diffuse through the system. There is also a predator population which feeds on prey in order to reproduce and that is able to diffuse through the system as well.

This paper is organized as follows. In the next section we present a description of the IBM for a three-trophic predator-prey system that motivated this work. The simulation method is presented and the details of the implementation of the cellular automata rules are described. In Sec. III, we present the results and a discussion about the main points of the paper and in Sec. IV our conclusions and future perspectives are discussed.

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II. MODEL

We consider a square lattice of linear size L with periodic spatial boundary conditions. Each cell can be occupied by plant, occupied by a prey, occupied by a predator, or occupied by both. So there will be four states for a cell: plant ($x_{ij}=0$), prey ($x_{ij}=1$), predator ($x_{ij}=2$), or both ($x_{ij}=3$). Time works as a discrete variable ($t=1,2,3,\ldots$). All the cells have a real number that expresses the quantity of the plant resources available on them. The sum of the values of all cells represents the total number of the plant population. Each mobile individual, prey or predator, has a intrinsic counter called hunger which is incremented every time step. This counter represents the total number of time steps that individuals do not eat. The adopted neighborhood is the Von Neumamm type [13,14], which includes four first neighbors. The events will be applied to each individual on each time step in the simulation according to stochastic rules.

Based on the simplest actions of individuals in nature, we propose the following rules for the cellular automata.

(i) Movement. Predators and prey have different probabilities to move to a neighboring site. At time step t, each individual receives a random number to decide its next location on the next time $t+1$. There are five possibilities and all of them are related to the diffusive rates d_1 and d_2 associated to prey and predator, respectively. They stay at the original site; going up, down, left or right. Initially, there is a probability of leaving the original cell which is divided by the four first neighbors. The complement of this probability is the chance of being at the same cell. If two individuals migrate to the same neighbor cell, only one remains on it due to the carrying capacity, considered equal to one individual per site. The individual with less hunger is chosen to occupy the cell. If all of the neighborhood is already full, the individual is forced to stay at it original point. As mentioned above, the cell can be occupied by a prey, by a predator, or by both.

(ii) Natural death. Prey and predators can have different probabilities to die. The mortality rates δ_1 and δ_2 are associated to prey and predator, respectively. At each time step it is done a draw for each individual that will die with the corresponding probability. Drawn individuals are removed from the system on the next time step. Plants do not have natural death draws, but there is a mechanism in their growth rule that prevents them from growing exponentially.

(iii) Plant growth. Plants have a constant growth rate and a carrying capacity associated with them. Each site has a float counter that indicates the quantity of resources on each time step and it generally changes after a prey visit. All sites in the lattice have their plant counters increased by the fixed constant value determined in the program, without any draws, until the limit imposed by the carrying capacity that has been reached. The plant growth in a current site do not affect the neighbor cells.

(iv) Plant gathering. When one prey comes to a site, the main rule is to gather the maximum quantity of food until its hunger counter is reduced to zero. If its hunger is less than the quantity of resources, it eats what it needs, setting its counter to zero and leaving the remaining food quantity at the site. If the opposite is verified, it eats all the site resources setting the site's counter to zero and keeps its hunger counter set equal to the difference between the two quantities. The plant gathering process does not have any draw.

(v) Predation. This event occurs when the prey and the predator share the same cell. In these cases, a draw is done to decide if the hunter is successful or not. In positive cases, predators have the hunger counter set to zero and prey will leave the system in the next time step. In negative cases, nothing will change.

(vi) Reproduction. After all events described above have been applied, the population is allowed to reproduce. Both populations have different probabilities to reproduce and only individuals whose hunger counter is zero will have a chance to do it. Predators and prey can reproduce only one offspring per time step and it will be placed in one of the available neighbor sites. If all neighbor sites are already occupied the birth will be canceled.

The individuals of the initial populations are distributed randomly around the lattice at the beginning of the simulation and the events are applied in the order that they are described previously. The upgrade of the population occurs at the end of each iteration. Individuals which died on the time t will be removed from the system, new individuals will be placed on the region, and the position of the existing individuals will be updated. Dying individuals from the death draw at the time t are allowed to reproduce at this step and then be removed from the system at the next one.

The results were obtained in square lattices of linear size $L=100$, with periodic spatial boundary conditions. Each simulation consisted of 10^6 time steps spending about 20 min in machines with the following characteristics: 32-bits Athlon MP processor with 512 MB using GNU C++ compiler 4.0.

III. RESULTS AND DISCUSSION

Continuous and deterministic models for predator-prey system present coexistence of three populations, extinction of predators or extinction of prey and predators as possible steady states [15].

We tested many cases with different sets of parameter values in order to look for all these steady states. Our analyses showed that variation of the parameter plant regeneration rate is enough to sweep up all possible steady states. As prey and predator populations rely on plant population, this parameter can control directly the presence of any population on the system. The results presented below are organized according to growing values of this parameter. For small values of regeneration rate both populations go to extinction and for higher values the system presents coexistence among three populations. We intend to focus on states whose behavior is close to the critical one. We mean by critical state a steady point in the phase space which under a small change on the parameter values can lead the system to a different point, such as extinction of one population or distinct behavior of the time series. We choose a set of parameters to present in this paper, nevertheless, many other sets were tested and similar results were found.

One important consequence of the discretization of the individuals in the model is the increase of the possibility of extinction of the populations. In the continuous model, the numerical solution of some special states shows that their respective population diminishes, almost reaching zero, but instead of going to extinction they present oscillatory behavior [16]. In discrete individual simulation, this cannot be verified because the populations are not capable of increasing their number after they have gone to zero. Simulation tests are very sensitive to stochasticity when the populations are small.

To test the stability of the system, we run several cases, using a specific set of parameters, under various initial values of the populations. Figure 1 shows the phase space of these four simulations. We can observe that all simulations predict the same steady point, independently of their initial conditions. This result indicates that the system has a wide basin of attraction. However, prey and predator populations have higher probabilities to go to extinction when they start from small values. Extinction cases frequently occur when initial populations are close to the stochasticity fluctuations.

We observe two nontrivial steady states of this system according to set of parameters that we choose. The first one is the coexistence of plant and prey. The other is the coexistence of the three populations. It is possible to verify some distinct population's behaviors and to control the existence of prey and predator populations on the region changing the regeneration rate of the plant population and keeping other parameter values constant.

A. Coexistence of two populations

Using the set of parameters C1, shown in Table I, and regeneration rate below 0.015, both mobile populations go to the extinction and the plant grow until their carrying capacity. For regeneration rates between 0.015 and 0.03, prey are capable of surviving and predators are still go to the extinction. This result indicates the existence of multiple steady states to this system.

To verify the system behavior under the value variation of the regeneration rate but maintaining fixed the other parameters, we run several cases and compare the results. Figure 2 shows the result of the simulation using the set C1 (see Table I) and the regeneration rate equal to 0.02. We observe that the time series in part *a* show an oscillatory behavior for the plant and the prey, opposing the classical logistic function property. The Fourier transform of the autocorrelation function in part *c* indicates the presence of one fundamental frequency for the plant population and two harmonics of it. This characterizes the existence of only one characteristic time for the system. This behavior is the same for both populations, showing that both of them oscillate in a synchronous way. Simulations values of regeneration rate around 0.02 show the same frequency of oscillation.

Comparing the time series and the corresponding spatial distribution, we observe the emergence of population waves migrating toward to the food gradient as we can see in Fig. 3. These population waves are nonlinear and one consequence of the nonlinearity is the annihilation of the individuals behind the wave fronts. Wave collisions are very common due

TABLE I. Sets of probabilities for the parameter values used in the simulations.

Quantity	C1	C2	C3	C4
Hunter	40	40	90	60
Prey reproduction	80	80	50	80
Predator reproduction	40	40	85	50
Prey death	1	1	5	5
Predator death	5	5	5	5
Prey mobility	80	40	80	80
Predator mobility	80	80	80	80
Carrying capacity	20	20	20	20

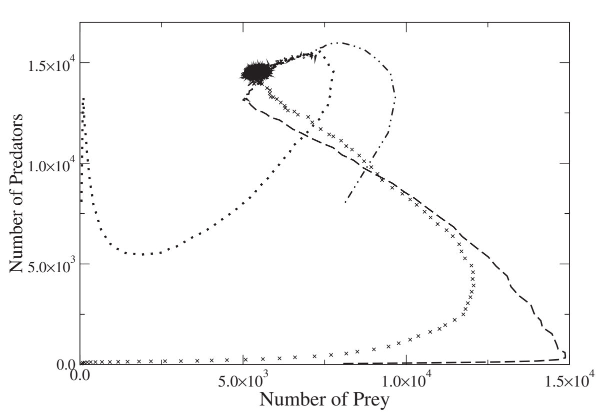

FIG. 1. Phase space portrait of plant and prey populations of four simulations with parameter values given in Table I, set C1. Values of initial populations are different in all simulations.

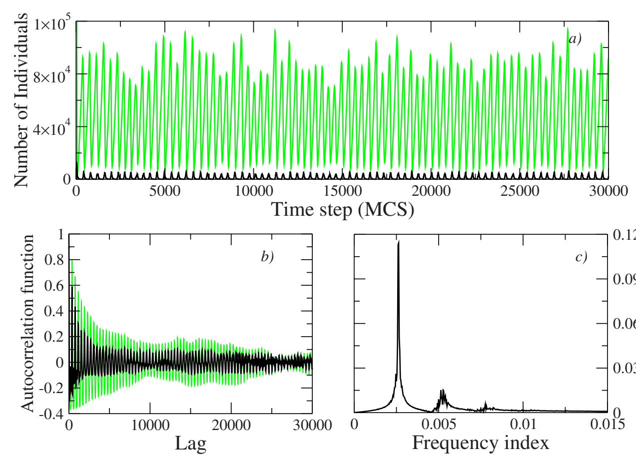

FIG. 2. (Color online) Results of simulation using the set of parameter C1 in Table I and regeneration rate equal to 0.02. The predators go to the extinction at the beginning of the simulation. (a) The time series; (b) the autocorrelation functions; and (c) the frequency spectrum of the plant population. The plant population has the same spectrum. The black curves represent prey and the green (light gray) represent the plant populations. Simulation has taken 10^6 Monte Carlo time steps. We are using one time step of the simulation as a unit of time.

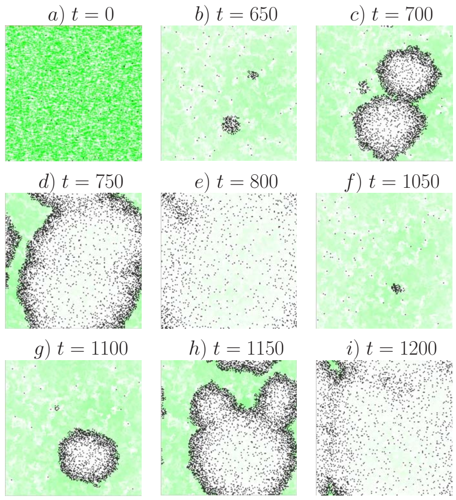

FIG. 3. (Color online) Spatial distribution of simulations adopting a regeneration rate 0.02 and the parameters set C1 (see Table I). Each figure corresponds to a different time step of the same simulation. The main feature is the appearance of a big prey wave throughout the lattice. In the figure, the plant is represented in a green (light gray) scale and prey in black.

to the imposed periodic boundary conditions. The behavior of the times series in Fig. 2 corroborates with our observations of the distribution of the individuals in Fig. 3. The population time series has a huge oscillatory amplitude that is verified on spatial distribution. Small population clumps emerge and diffuse on the region like a wave, leaving some individuals behind on the path. With the wave collision, many individuals die due to the carrying capacity of the cells and to the local lack of food. We can suppose that the low value of the regeneration rate is responsible for this kind of behavior. Plants expend some time to recover their population level. During this period there are not many sites that are able to sustain the prey and their offspring. The probability of new waves appearing is linked to regeneration rate of plant: as this rate increases more waves propagate in different places of the distribution. Oscillatory behavior is verified until the regeneration rate reaches values around 0.034 for the set of parameter C1.

For the regeneration rate in the interval from 0.03 up to 0.04, see Fig. 4, a change in the behavior of the time series happens. Figure 4 shows a few plant time series for a regeneration rate equal to 0.033. A plant's population changes its oscillatory regime from a high amplitude to a low amplitude in an unpredictable way. The oscillatory behavior with low amplitude seems to be more stable than the other one and the prey populations do not go to extinction in any future time when they have this behavior.

Figure 5(a) shows one of these time series that presents one characteristic frequency and one harmonic associated to its high amplitude region, shown in Fig. 5(b). The low amplitude region of the time series presents only one frequency, as can be seen in Fig. 5(c) and it is different from the frequency found in Fig. 5(b). Population waves still appear after the transition time, in the region with the low amplitude and it is shown in Fig. 6. In this situation, the prey population is

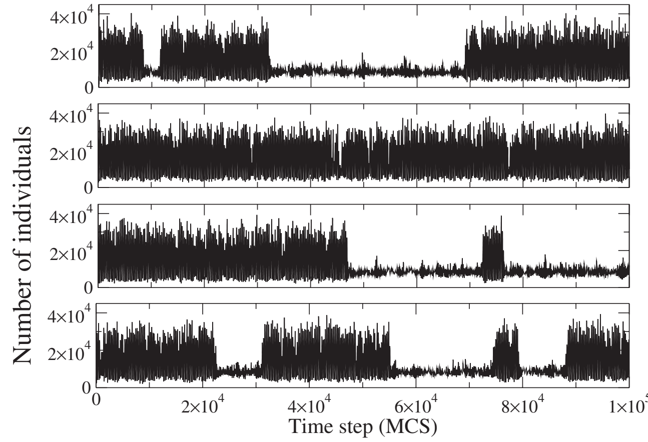

FIG. 4. Results of four simulations with the parameters set C1 in Table I, under the same initial conditions, and with the regeneration rate equal to 0.033. The behavior of the time series are distinct in each one of the simulations.

much less localized on the space and the waves are not as big as in the previous ones but both oscillate in a synchronous way.

In order to identify some features of the phenomena shown in Fig. 4, we ran 3500 simulations using the same parameter values. We measured the size of each low amplitude oscillation region larger than 1000 time steps. The results, shown in Fig. 7, obey an exponential function. The system oscillates between two states, one with high amplitude and other with low amplitude oscillation in an unpredictable way. This behavior can be associated to the self-regulation of the system and also can be found in other

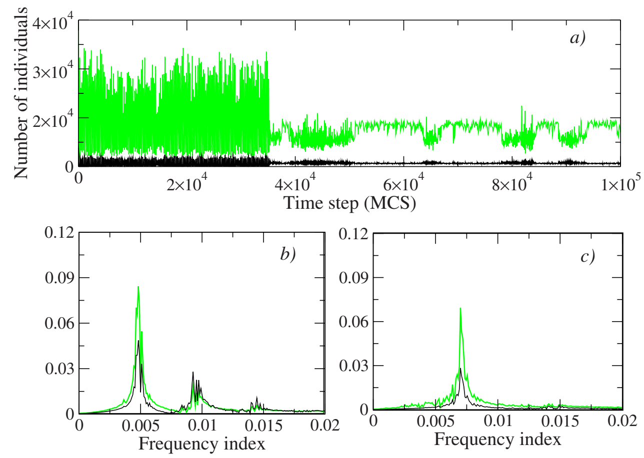

FIG. 5. (Color online) Frequency analysis of two distinct parts of the time series of populations obtained with the set C1 and the regeneration rate equal to 0.033. (a) The time series with two distinct regions. The first part corresponds to a region with high amplitude and the second corresponds to a region with low amplitude. (b) The presence of one characteristic frequency and two harmonics associated to a region with high amplitude in (a). (c) presents only one frequency related to a region with a low amplitude in part (a). These frequencies are different in two regions. Plants are green (light gray) curves and prey are black curves.

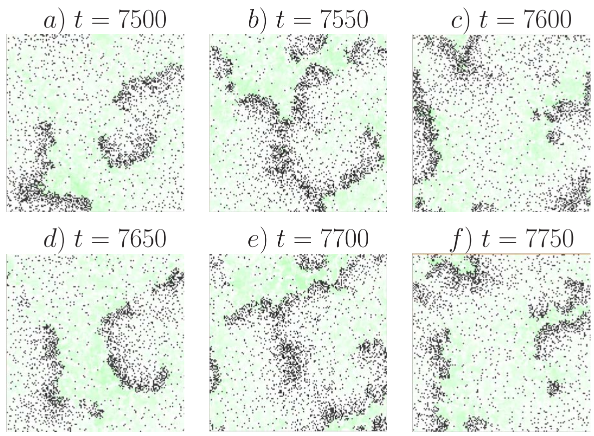

FIG. 6. (Color online) Spatial distribution of simulation for a regeneration rate equal to 0.033 with the parameter set C1. Each figure corresponds to a different time step of the same simulation. The figure represents one time interval to which the system oscillates with a low amplitude. It can be seen that population waves are smaller than the case with high amplitude oscillations. Besides this the individuals are more spread in the region. The plant population is represented in green (light gray) scale and prey in black.

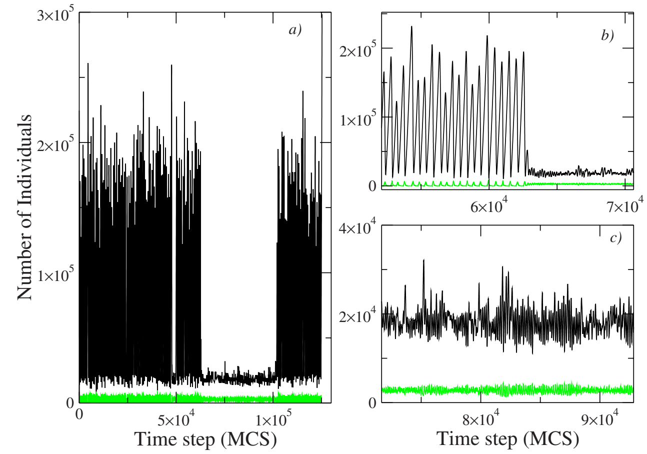

FIG. 8. (Color online) Simulations with different parameter sets show the same transition effect. Graphs (b) and (c) show a "zoom" in different parts of the graph (a). After the time 125 000, the prey population goes to extinction. Results obtained with the parameter set C2 in Table I and the regeneration rate is 0.025. Plants are represented in green (light gray) and prey in black.

different parameter sets, as we can see in Fig. 8, where we use the set $C2$.

In this interval of the regeneration rate, the time series of the system show a behavior that alternates between the solutions found with the regeneration rate under 0.03, which has high amplitude oscillations, and the solution found with a regeneration rate above 0.04 that presents low amplitude oscillations and a more stable state. Figure 9 shows the same simulation adopting a regeneration rate of 0.05. For higher values to the regeneration rate the system begins to oscillate in a low amplitude regime and become more stable. The frequency associated to the time series for both populations slowly vanishes when we increase this parameter.

Figure 10 shows a phase space portrait corresponding to the simulations shown in Figs. 5 and 8. We removed the transient points of the simulations and displayed the stationary values only. In Fig. 10(a), the system initially oscillates through a closed orbit around the equilibrium point, characterizing a high amplitude oscillation regime to the corresponding time series. Due to the stochasticity of the system, it is not possible to define clearly the orbit, however, it is possible to identify the region where it happens. The system jumps suddenly to an equilibrium point characterizing a nonoscillatory behavior for long time intervals or a low amplitude oscillation regime. In Fig. 10(b), a simulation is shown that initially oscillates along a large orbit and jumps to a point indicated in the left rectangle in the figure. Subsequently it returns to the larger orbit and goes to extinction after some time steps later, as indicated on the right rectangle

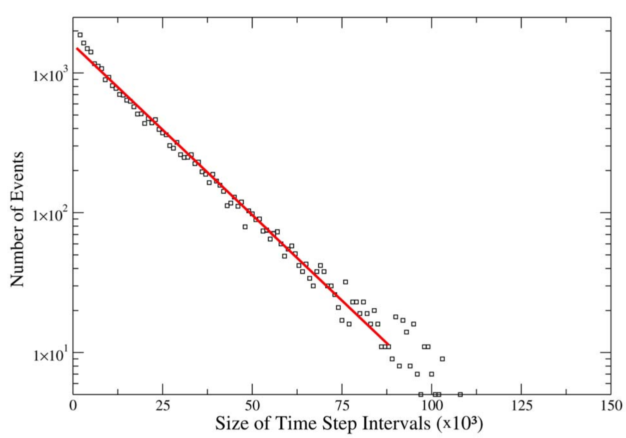

FIG. 7. (Color online) Distribution of the sizes of the intervals of each low amplitude oscillation for regions larger than 1000 time steps. The fitted exponential curve, from the data, is $y = 1596e^{-0.005\,62x}$.

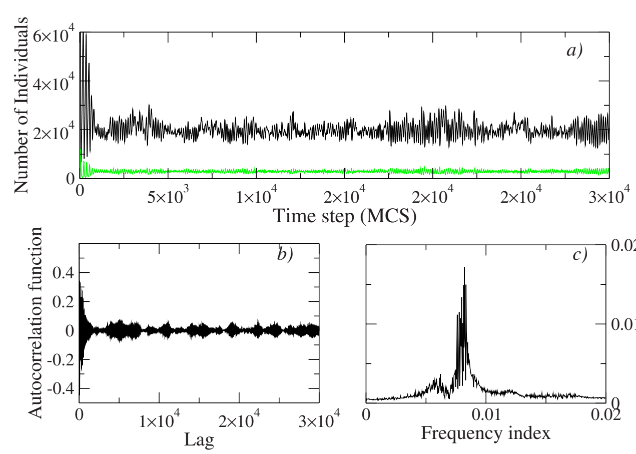

FIG. 9. (Color online) Results obtained with parameter set C1 and a regeneration rate equal to 0.05. It shows a more stable behavior. Graph (a) shows the time series of prey [green (light gray) curve] and plant (black curve), (b) the autocorrelation function, and (c) the Fourier transform. As we can see at the Fourier transform, oscillations of the time series do not show any relevant frequency.

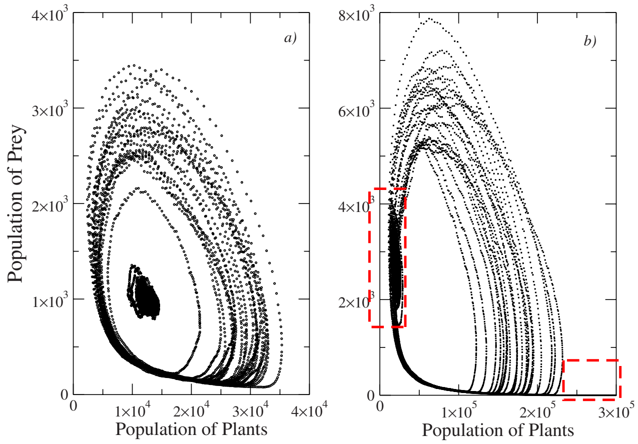

FIG. 10. (Color online) Two phase portrait from a distinct parameter set. The first one is the result from the simulation presented in the Fig. 5, and the second one is the result from the simulation presented in Fig. 8. The small rectangles in (b) indicate the points where the simulation stays during different time steps. The system oscillates between a large orbit and a steady point, represented by the left rectangle in the figure and then goes to the extinction, as we can see in the right rectangle in the figure.

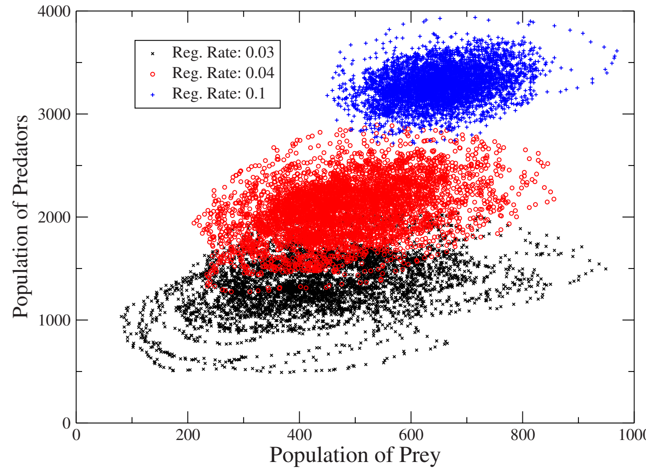

FIG. 11. (Color online) Phase space portrait of the prey and the predator populations of three simulations with parameter set C3 in Table I and using different values of regeneration rates.

in the same figure. This indicates that the system has multiple steady states and the stochasticity is responsible for the transitions among them. As we said before, populations have a higher probability to go to extinction when they have this high oscillatory behavior because they assume small values and the stochasticity is very relevant in this situation.

B. Coexistence of the three species

As we increase the regeneration rate, the wave behavior starts to disappear and prey spread along the lattice in a uniform way. After the prey population reaches a more stable behavior, predators are able to survive because there is more available food and then the coexistence of the three species is possible.

In some simulations, we observe that the number of predators is directly related to the regeneration rate of the plant. As we increase the regeneration rate of the plant we dislocate the equilibrium point of the system in a positive way. Figure 11 shows three simulations using parameter set C3 in Table I and choosing different values for the regeneration rate. These parameter sets were chosen in order to guarantee that predators would survive, although the regeneration rate was low. Increasing the regeneration rate also makes the population reduce the oscillation around the equilibrium point leading the system to a more stable state.

We have distinct spatial distribution in the case of coexistence between the three species. These distributions are dependent on the abundance of each population. The constants that affect directly those quantities are the regeneration rate, the prey birth rate, the predator birth rate, and the hunter rate. The last one is important because according to the cellular automata rule only predators which ate on the current iteration could reproduce.

Situations with a high prey birth rate and a high regeneration rate result in a uniform spatial distribution, as we show in Fig. 12. Preys are constantly reproducing, occupying the whole region. The predators and the prey are distributed uniformly. Time series obtained with this distribution is shown in Fig. 13. From this figure we can notice that the plant population has a lower level due to the high number of prey gathering it. The populations have a very stable behavior with no relevant oscillations. The Fourier transform in the graph *d* indicates the presence of a few frequencies with very low weight compared to ones we obtained previously. We consider this behavior closest logistic equation behavior, since it reaches a steady state point and it does not have any relevant oscillation or a characteristic frequency.

This result can be understood as a trend opposite to the paradox of the enrichment of prey [17]. Simple models of predator-prey dynamics predict that enrichment reduces stability by increasing prey carrying capacity or population growth rate and causes population circles that increase in amplitude [18]. The increase of the regeneration rate in our model can be seen as the increase of the carrying capacity to the prey because there will be more resources available for them and consequently the prey population growth rate will

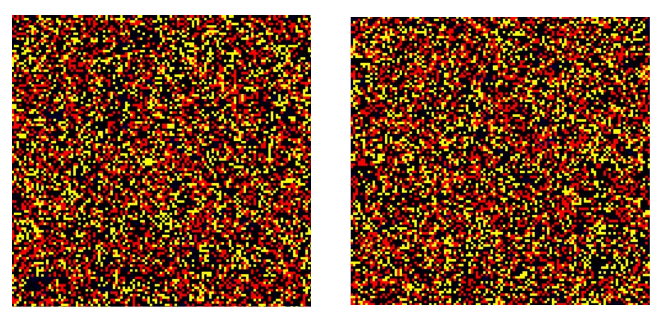

FIG. 12. (Color online) Spatial configurations correspondent to the case shown in Fig. 13. Predators are yellow (light gray) and prey are red (dark gray) points. Black points represent predator and prey in the same site.

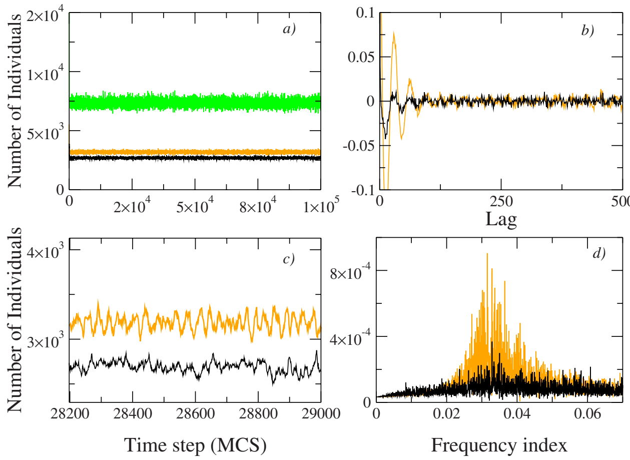

FIG. 13. (Color online) Results of simulation using parameter set C4 values in Table I and regeneration rate equal to 0.2. (a) The time series for three populations. Plants are green (light gray), predators are orange (gray), and prey are black curves. (c) A zoom on the time series for the predators and the prey, emphasizing the oscillatory behavior of both. (d) The frequency spectrum of the autocorrelation functions (b).

be higher. The results presented here corroborate with theories and experiments where the enrichment can stabilize the predator dynamics [19,20]. This behavior can be associated to the specific dynamics that govern the system and can be related to the local spatial characteristic of our model.

However, if we decrease the prey's availability by reducing their birth rate and increasing predators by adding predators birth rate and the hunter rate, we obtain a different distribution. The prey are distributed in clumps with the predators around them as we can see in Fig. 14. The prey are now rare and the predators need to stay near these clumps to reproduce and survive. Our observations of clumping agree with Kareiva's [21] considerations. He states that one unavoidable outcome of local interactions and local dispersion, when we are working with cellular automata, is the clumping. The characteristics of the clumps are strongly related to the parameter set of the model such as birth and mortality

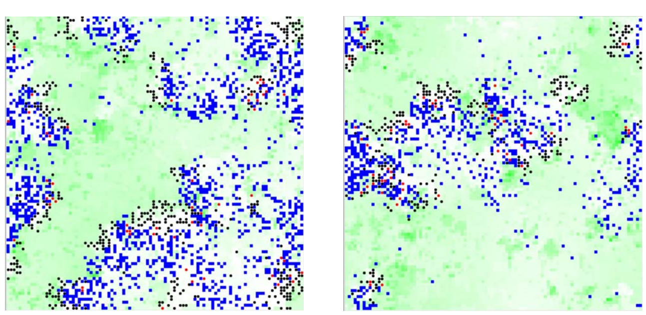

FIG. 14. (Color online) Spatial configurations corresponding to a case using parameter set C3 values in Table I and regeneration rate equal to 0.03. Plants are green (light gray), predators are black, prey are red (gray), and predator and prey are blue point. As we can see, the prey are distributed in clumps with predators localized around them.

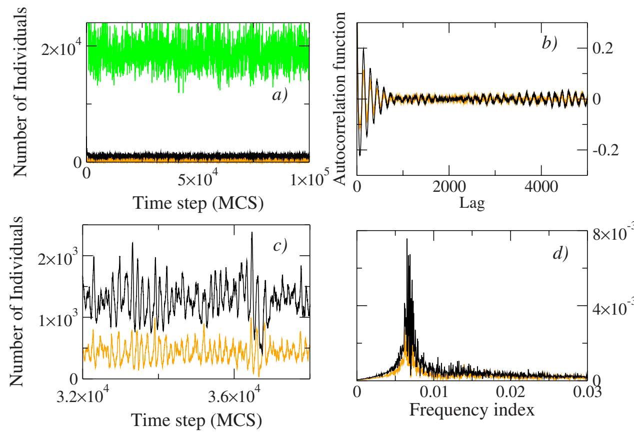

FIG. 15. (Color online) Results of simulation using parameter set C3 values in Table I and the regeneration rate equal to 0.03. (a) The time series for three populations. Plants populations are green (light gray), predators are orange (gray), and prey are black curves. (c) A zoom of the time series for the predators and the prey, emphasizing the oscillatory behavior of both. (d) The frequency spectrum to the autocorrelation functions of (b).

rates. In these cases, as we can see in Fig. 15, the plant reach higher values due to the small number of the prey and the predators have higher values due to a favorable parameter set in the simulation. All the populations time series have oscillations and the Fourier transform indicates the presence of one characteristic frequency that is equal to both.

IV. CONCLUSIONS

We develop a spatial model of a predator-prey system considering a three trophic food chain and use the individual based model (IBM), with cellular automata rules. We focus, basically, on the relationships between spatial configurations and the time series behavior.

All simulations were run with initial random spatial distributions. According to the set of parameters assigned to the simulation, different kinds of spatial patterns spontaneously emerged. In all situations under consideration here, no inhomogeneous spatial conditions were applied, so we can attribute all of these different spatial configurations as a result of the cellular automata rules that characterize the dynamics of the system. In this sense the system presents a self-organization due to these dynamics rules.

The results allow us to conclude that the regeneration rate of the plant is the critical parameter of the system. It is strongly related to the stability of the steady point of the system as well as the behavior of the system at this point.

Adopting low values of regeneration rate and using a set of parameters that allows the coexistence between prey and plant, it is possible to observe the occurrence of traveling waves on spatial distributions. Time series related to these distributions oscillate with a high amplitude and present a characteristic frequency associated to them. Increasing the value of this parameter we observe a different kind of traveling waves and distinct time series behavior, which now have a low amplitude region in their oscillations and different characteristic corresponding frequencies. In this situation the system has two possible states and alternates between them according to the value of this parameter. Jansen [22] has shown that spatial interactions can produce this kind of behavior and can stabilize the predator-prey system. Our results corroborate with his affirmative and show that the system has a critical parameter. The alternation is nondeterministic and the size distribution of intervals to these two states obeys an exponential function.

Another spatial configuration that we observed was a uniform distribution. This kind of configuration appears when resources are abundant and prey grow up until reaching the carrying capacity of the region and can be understood as a prey enrichment. This result is in accordance with others experimental and theoretical results [19,20] which assure that the enrichment of the prey stabilize the more complex predator-prey systems. This configuration is more stable than the traveling waves and within this configuration the system is capable of maintaining the three species. Situations with a high number of prey present uniform spatial distributions. However, this configuration disappears when the predators are smarter and the number of prey is lower and in its place appear a population clump configuration. In terms of time series, this distribution has a similar frequency spectrum.

The appearance of different patterns in the spatial distributions is a consequence of the dynamics of the system and is closely related to the parameter values used to describe the relations between the individuals as well as the stochastic characteristic of the process. The presence of a characteristic frequency in the corresponding time series is a signalization of the pattern type formed in the spatial distribution. In order to create a more precise connection between spatial pattern and the corresponding time series we are working now on a spatiotemporal statistical analysis of the presented data.

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