



Long-term effects of abrupt environmental perturbations in model of group chase and escape with the presence of non-conservative processes

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ABSTRACT

This paper examines the influence of environmental perturbations on dynamical regimes of model ecosystems. We study a stochastic lattice model describing the dynamics of a group chasing and escaping between predators and prey. The model includes smart pursuit (predators to prey) and evasion (prey from predators). Both species can affect their movement by visual perception within their finite sighting range. Non-conservative processes that change the number of individuals within the population, such as breeding and physiological dying, are implemented in the model. The model contains five parameters that control the breeding and physiological dying of predators and prey: the birth and two death rates of predators and two parameters characterizing the birth and death of prey. We study the response of our model of group chase and escape to sudden perturbations in values of parameters that characterize the non-conservative processes. Temporal dependencies of the number of predators and prey are compared for various perturbation events with different abrupt changes of probabilities affecting the non-conservative processes.

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1. Introduction

Simulation of population dynamics is a central research theme in computational biology, which contributes to understanding the interactions between predators and prey. Classical models of predator–prey systems were developed first by Lotka and Volterra [1–3]. They showed that simple predator–prey models may exhibit limit cycles during which the populations of both species have periodic oscillations in time with a 1/4-period lag between predator and prey [4]. Such oscillations in species abundances have successfully been observed in real-world systems [5–8]. As the field developed, the commonly used model schemes shifted from continuous ones based on a differential equation towards discrete and agent-based models [9–13]. Furthermore, the predator–prey systems have been studied in various contexts, such as robotics, game theory and ecology [14–19].

Many complex systems have impulsive dynamical behavior due to abrupt jumps of some parameters affecting the system at specific instants during the evolving processes. Ecological systems are often affected by environmental changes and human activities, such as vaccination, medical treatment of disease, sterilization, etc. For example, numerous species are prone to extinction due to temperature fluctuations or climatic changes, and pollution events [20–26]. Discrete nature

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of human actions or environmental changes lead to population densities changing very rapidly in a short time interval. The maintenance of existing population density requires information as to how organisms react to intended as well as unintended abrupt changes.

Short-term environmental perturbations (such as heavy rainfall, severe fires, or storms) are likely to cause the sudden death of healthy individuals within a population, which would not exhibit any changes in their biological variables within a population at a stable state. These perturbations are often assumed to be in the form of impulses in the modeling process. However, ecosystems can be exposed to various types of environmental perturbations for long periods of time, which may result in an enduring alteration of population and trait dynamics. Long-term effects of environmental perturbations frequently cause modification of the biological properties of species, such as species reproduction, mortality rates and other vital rates [23,27]. In this paper, we develop a stochastic lattice model describing the dynamics of a group chasing and escaping between predators and prey [28,29]. Non-conservative processes, such as breeding and physiological dying, are implemented in the model [30,31]. We study the dynamics of coexistence that arises due to the introducing of the abrupt changes in the values of parameters that characterize the non-conservative processes into the model.

Our model is based on the agent-based approach to simulate numerically collective chasing and escaping in a discrete space and time with periodic boundary conditions, similar to the model of hunting in groups proposed by Kamimura and Ohira [28,32–35]. In the following, we sketch the main features of our model, along the lines of Ref. [29]. Predators and prey are initially placed randomly on the sites of the lattice as pointlike particles. Thus, each site is either empty or occupied by a predator or a prey. Predators can sense the positions of the prey at an arbitrarily predefined distance and they try to move to one of the nearest neighboring sites in order to decrease the distance from the nearest prey. As predators move and approach their prey, the prey try to evade the capture by making a distance of one lattice spacing in a direction away from the nearest predator. Prey is caught upon the first encounter with a predator.

Distances in the present study are measured by the L^1 (“Manhattan”) metric. Manhattan distance between sites S_1 and S_2 on a square lattice is equal to the length of all paths connecting S_1 and S_2 sites along horizontal and vertical segments, without ever going back. In reality, predators search for prey in their vicinities. Similarly, prey can recognize the existence of nearby predators. Therefore, each species has its specific sighting range σ in which it can see the other species. Sighting range σ describes their skills at chasing or escaping. In that sense the model includes the smart pursuit of predators to prey and the escape of prey from predators. Analysis of the capture dynamics in the present study is limited to species with the same sighting ranges, i.e., $\sigma = 2$ [29]. If the value of σ equals zero, the movement is equivalent to the random walkers [28,31,36,37].

The model contains five parameters that control the breeding and physiological dying of predators and prey: the birth and two death rates of predators and two parameters characterizing the birth and death of prey. The goal of the present study is to investigate the short-time response of our model of group chase and escape to sudden perturbations in the values of parameters that characterize the non-conservative processes. In addition, we present and discuss the numerical results regarding the time evolution of the number of predators and prey for long periods of time after the abrupt changes of parameters affecting the non-conservative processes. In this paper we show that the short-time behavior is always linked to the forgetting of the initial conditions through the pursuit-evasion processes. Our numerical results suggest that this short-time evolving process is often accompanied with high amplitudes of population dynamics. The short-term memory effects observed in our model are reflected in the fact that the future evolution of the population densities after time $t_w > 0$ depends not only on the densities of predators and prey at the moment t_w , but also on the previous evolving history. This feature concerns the coding of the system history in various spatial configurations of predators and prey on the habitat. Furthermore, we try to demonstrate that the number of predators and prey in the long-term state are unambiguously determined by the probabilities for all nonconservative processes in the system. As consequence, quasi-steady state regime corresponding to perturbed probabilities does not depend on the moment of their introduction.

An outline of this paper is as follows. Section 2 describes the details of the model and simulations. In Section 3 results of numerical simulation are presented and discussed. Finally, Section 4 contains some additional comments and final remarks.

2. Definition of the model and the simulation method

The habitat where two interacting species survive and proliferate is represented by a two-dimensional square lattice of linear size L with periodic boundary conditions. In our model, the lattice is initially empty. To prepare the environment in the initially disordered state, we randomly distributed $N_1^{(0)}$ predators and $N_2^{(0)}$ prey as monomers. Spatial distribution of species on the lattice is generated using the random sequential adsorption (RSA) method [38,39]. Consequently, each site can be either empty or occupied by one particle: by a predator (chaser) or prey (escapee).

After placing the predators and the prey up to the chosen densities $\rho_1^{(0)} = N_1^{(0)}/L^2$ and $\rho_2^{(0)} = N_2^{(0)}/L^2$, we switch the species deposition events off and add the diffusive dynamics into the system. At this stage, apart from the hard core interaction between the species, there are rules governing the dynamic processes at the individual level. Movement within the lattice and the population dynamics are modeled as discrete time processes. At each Monte Carlo step a lattice site is selected at random. If the selected site is unoccupied, the configuration remains unchanged and a new site is selected at random. If the selected site is occupied by a predator or a prey, each species follow the hopping rules described below. After each Monte Carlo step, the time t is updated, $t \rightarrow t + 1/L^2$ and the process continues by choosing a new lattice site at random.

We assume that each species has its specific sighting range σ in which it can see the other species. In other words, predator has a certain pursuit region within which it can locate prey; simultaneously, prey has an escape zone inside which it can detect predators. The metric used in our model is L^1 , so e.g. the site (x, y) is at distance $|x| + |y|$ from the origin, with lattice spacing equal to unity. Here, unlike the previous model [29], both predators and prey have a sighting range $\sigma = 2$, which corresponds to the region around the individuals that includes the first and second neighbors. Accordingly, the decision for every step both of the predator and prey depends on the individuals that are found at the places of the first and second neighbors.

Suppose that predator is placed in a randomly selected site of the lattice. If the first neighbors of the selected site are entirely occupied with predators, the chosen predator stays at its original position. Then, the time t is updated, and the process continues by choosing a new lattice site at random. Suppose that some of the first neighbors of the selected site are occupied with prey. Then we randomly select a prey among them, remove the selected prey from the lattice, and move the chosen predator to this empty place. However, if the first neighbors of the chosen predator are not occupied with prey, the predator executes a jump as long as there is at least one empty nearest neighbor site. In this case, the predator moves to the empty adjacent site that is surrounded by the highest number of prey, $n_2^{(\max)}$, as its first neighbors. If two or more empty nearest neighbor sites correspond to the same highest number of prey $n_2^{(\max)}$, one of them is selected at random.

Now, suppose that a prey is placed in a randomly selected site of the lattice. If there are no empty nearest neighbors of the selected site, the chosen prey does not change its position, and the time increases by $1/L^2$. The process continues by choosing a new lattice site at random. If the selected site has empty adjacent sites, the chosen prey jumps to the empty nearest neighbor site that is surrounded by the lowest number of predators, $n_1^{(\min)}$, as its first neighbors. If two or more empty nearest neighbor sites correspond to the same lowest number of predators $n_1^{(\min)}$, one of them is selected at random. It must be emphasized that prey moves to the selected site only if $n_1^{(\min)}$ is less than or equal to the number of predators surrounding it in its original position.

The set of rules described above mimics the smart pursuit-evasion processes [29]. The competitive evolution of the populations of predators and prey is also governed by additional set of rules which defines the population dynamics. Non-conservative processes that change the number of individuals (size of the population), such as breeding and physiological dying, are also implemented in the model. We introduce the following five non-conservative processes into the model. For predators:

- Predators that have eaten a prey during the displacement can give an offspring in the previously occupied site, with probability P_{1r}^{fed} (birth probability of predators). In order to breed, it is considered that the predator must be strong enough, i.e., it must have food available in immediate surroundings.
- Predators that have not eaten a prey during the displacement can die with probability P_{1d}^{unfed} . It is assumed that the lack of food reduces the number of predators present in the habitat.
- Predators can suddenly die with probability P_{1d} (death probability of predators).

For prey:

- After displacement, prey can give an offspring filling an empty previously occupied site with probability P_{2r} (birth probability of prey).
- A prey has a probability P_{2d} of dying (death probability of prey).

Death probabilities of species describe quantitatively the dying that could be tied to any other factors and events in the eco-system, such as the old age of individuals or diseases.

Based on the above definitions we formulate the algorithm as follows. If a randomly selected site of the lattice is not empty, predator (prey) can die with probability P_{1d} (P_{2d}). If the predator (prey) died, it is removed from the lattice, and a new site is selected. Otherwise, we apply the rules for pursuit-evasion movement for individuals explained above. If the randomly selected predator survives, we check whether it ate the prey during the displacement. If so, the predator leaves an offspring in the previously occupied site, with probability P_{1r}^{fed} . However, if the predator did not eat the prey during the displacement, it dies with probability P_{1d}^{unfed} . Similarly, if the randomly selected prey survives, we check whether it moved into a new position. If so, the prey leaves an offspring in the previously occupied site, with probability P_{2r} .

The time t is counted by the number of attempts to select a lattice site and scaled by the total number of lattice sites $N = L^2$. Since in one Monte Carlo time step each lattice site is randomly checked once on the average, it can be considered that all predators and prey are active at all times and that none of the species have a priority in the number of attempts to make a move. In our study, the typical value of lattice size is $L = 128$, and the simulation data are averaged over 128 independent runs.

3. Results

At first, we present and discuss the numerical results regarding the time evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ on the lattice of size $L = 128$, for the representative set of probabilities $S_1 = \{P_{1r}^{\text{fed}} = 0.25, P_{1d}^{\text{unfed}} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$ that characterize the

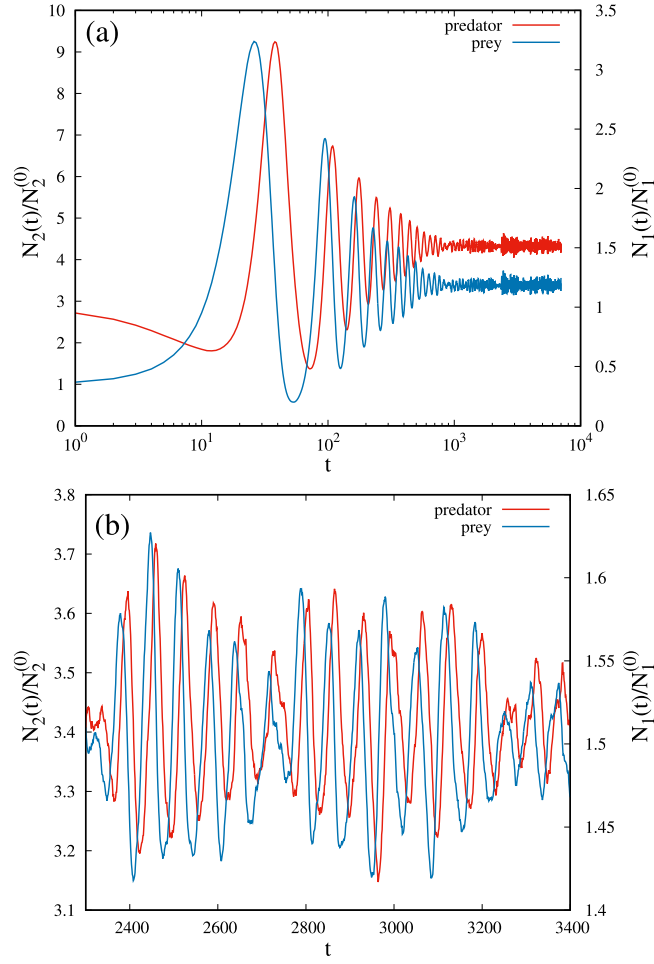


Fig. 1. (a) Time dependences of the number of the normalized number of predators $\tilde{N}_1 = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2 = N_2(t)/N_2^{(0)}$ on the lattice of size $L = 128$. (b) Shown here are the temporal dependences of the \tilde{N}_1 and \tilde{N}_2 in the oscillatory region of the quasi-steady state, between $t_1 = 2300$ and $t_2 = 3400$, obtained for the same conditions as in panel (a). The values of probabilities that characterize the non-conservative processes are $S_1 = \{P_{1r}^{\text{fed}} = 0.25, P_{1d}^{\text{unfed}} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$. The initial numbers of species are chosen as $N_1^{(0)} = 720$ and $N_2^{(0)} = 800$.

non-conservative processes (see, Fig. 1(a)). The initial numbers of species were chosen as $N_1^{(0)} = 720$ and $N_2^{(0)} = 800$, corresponding to the initial densities $\rho_1^{(0)} = N_1^{(0)}/L^2 = 0.0439$ and $\rho_2^{(0)} = N_2^{(0)}/L^2 = 0.0488$, with the ratio $\rho_1^{(0)}/\rho_2^{(0)} = N_1^{(0)}/N_2^{(0)} = 0.9$. It can be seen that in the initial stage, during which the flocks of species are not formed, the number of predators and prey oscillates periodically with large amplitudes. However, the amplitude of oscillation decreases with time. After a short transient period, the system arrives at a quasi-steady state. This state corresponds to a coexisting state when the densities of predators and prey oscillate (fluctuate) around some ‘‘average’’ values, which do not change in time. More details about the temporal behavior of the number of predators and prey for the late stage of evolution, in a time range between $t_1 = 2300$ and $t_2 = 3400$, are shown in Fig. 1(b). A common prediction can be observed: prey oscillations precede predator oscillations by up to a quarter of the cycle period [4]. When predators are sparse, prey increase in the abundance. As the number of prey increases, predators also increase in the abundance. When the predators reach sufficiently high densities, the prey population is driven down to low densities. With a lack of prey, the predator population reduces, and the cycle repeats.

In addition, Fig. 2 shows the temporal evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ for the set of probabilities $S_2 = \{P_{1r}^{\text{fed}} = 0.09, P_{1d}^{\text{unfed}} = 0.05, P_{1d} = 0.01; P_{2r} = 0.15, P_{2d} = 0.01\}$, and initial numbers of species $N_1^{(0)} = 720$ and $N_2^{(0)} = 800$. For these conditions, we get qualitatively the same results as in Fig. 1. The results presented in Figs. 1 and 2 are used to establish the response in the evolution of the density of species to a change in the probabilities $S = \{P_{1r}^{\text{fed}}, P_{1d}^{\text{unfed}}, P_{1d}; P_{2r}, P_{2d}\}$ at a given moment t_w .

It is interesting to compare the oscillatory behavior of the number of predators and prey obtained using the two different sets (S_1, S_2) of probabilities that characterize the non-conservative processes (see, Figs. 1(b) and 2(b)). In the

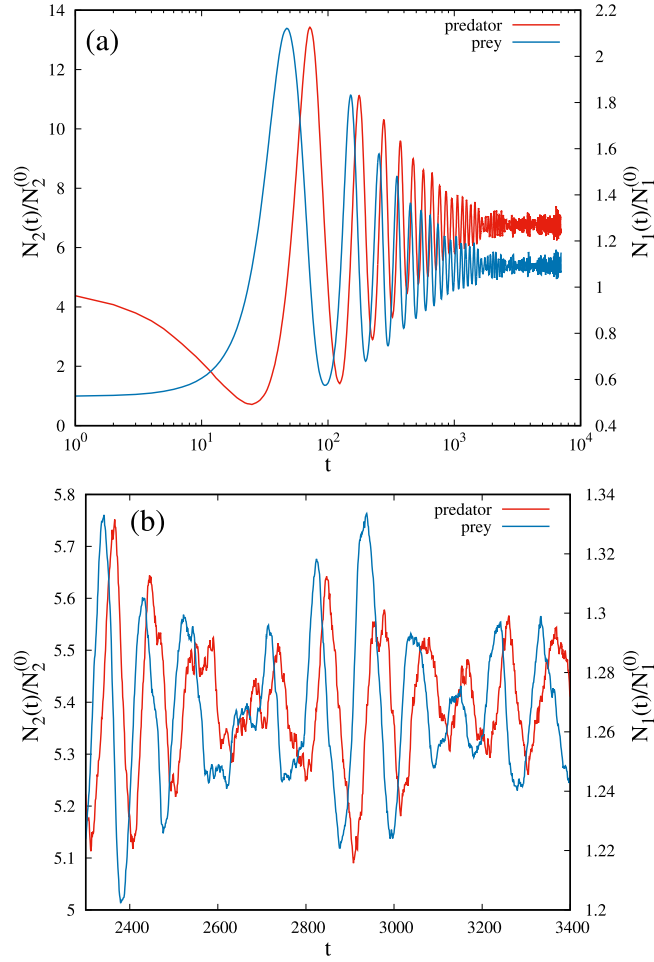


Fig. 2. (a) Time dependences of the number of the normalized number of predators $\tilde{N}_1 = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2 = N_2(t)/N_2^{(0)}$ on the lattice of size $L = 128$. (b) Shown here are the temporal dependences of the \tilde{N}_1 and \tilde{N}_2 in the oscillatory region of the quasi-steady state, between $t_1 = 2300$ and $t_2 = 3400$, obtained for the same conditions as in panel (a). The values of probabilities that characterize the non-conservative processes are $S_2 = \{P_{1r}^{\text{fed}} = 0.09, P_{1d}^{\text{unfed}} = 0.05, P_{1d} = 0.01; P_{2r} = 0.15, P_{2d} = 0.01\}$. The initial numbers of species are chosen as $N_1^{(0)} = 720$ and $N_2^{(0)} = 800$.

second set of parameters S_2 , the probabilities P_{1r}^{fed} and P_{1d}^{unfed} for the non-conservative processes related to predator feeding are significantly reduced. The predator–prey cycles are based on a feeding relationship between two species. Therefore, we can consider that the coupling of the predator and prey systems is much stronger in the case of parameters from the set S_1 . Consequently, the amplitude of oscillations of predators in the quasi-stationary regime corresponding to the set of parameters S_2 is significantly smaller than in the case of the set of parameters S_1 .

In Fig. 3 we show the temporal dependence of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ on the lattices of size $L = 64$ and 128 . It is important to note that the initial densities of predators $\rho_1^{(0)}$ and prey $\rho_2^{(0)}$ have not changed with the lattice size L . Numerical results for $\tilde{N}_1(t)$ and $\tilde{N}_2(t)$ in Fig. 3 are given for the initial densities $\rho_1^{(0)} = 0.0439$ and $\rho_2^{(0)} = 0.0488$ for both lattices. It is evident that the time evolution of the normalized number of species does not depend on the lattice size L . However, for the lattice of fixed size L , time evolution of $\tilde{N}_1(t)$ and $\tilde{N}_2(t)$ depends on the initial number of predators $N_1^{(0)}$ and prey $N_2^{(0)}$. Fig. 4 shows the dependence of the mean number of predators $\langle N_1 \rangle$ and prey $\langle N_2 \rangle$ in a quasi-stationary state on their initial number. It can be seen that the behavior of the system in the quasi-steady state ceases to depend on the initial conditions if the initial density of predators and prey is high enough. Indeed, the lower is the concentration of the targets (prey), the longer is the mean distance that a chaser (predator) crosses to find a target and catch it. Thus, at low densities of species, group chase with sight-limited chasers becomes very inefficient. Consequently, in the present paper, sufficiently large initial densities of species are chosen so that the average values of the number of predators and prey in the long-term state are unambiguously determined by the probabilities for all nonconservative processes in the system.

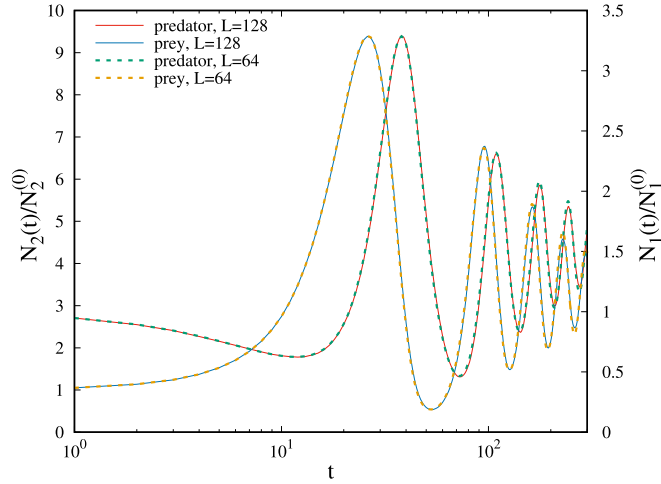


Fig. 3. Time dependences of the normalized number of predators $\tilde{N}_1 = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2 = N_2(t)/N_2^{(0)}$ on the lattices of size $L = 64$ and 128 , as indicated in the legend. Results shown here are obtained for the same initial densities $\rho_1^{(0)} = 0.0439$ and $\rho_2^{(0)} = 0.0488$, for both lattices. Initial values for the number of predators/prey are $N_1^{(0)}/N_2^{(0)} = 180/200, 720/800$ for $L = 64, 128$, respectively. The values of probabilities that characterize the non-conservative processes are $\mathcal{S}_1 = \{P_{1r}^{\text{fed}} = 0.25, P_{1d}^{\text{unfed}} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$.

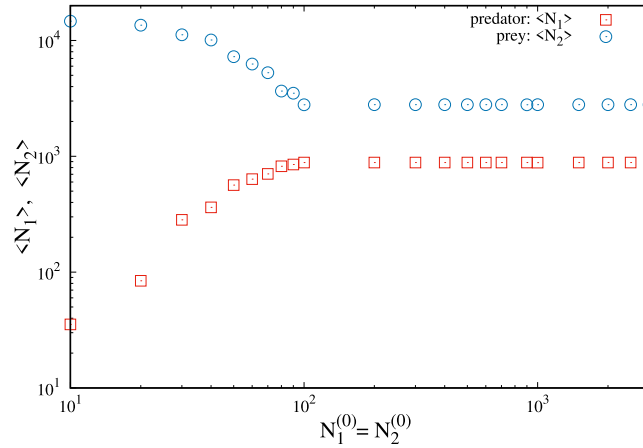


Fig. 4. Shown here is the dependence of the mean number of predators and prey in a quasi-stationary state on their initial number. The values of probabilities that characterize the non-conservative processes are: $\mathcal{S} = \{P_{1r}^{\text{fed}} = 0.25, P_{1d}^{\text{unfed}} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$. The lattice size value is $L = 128$.

One of the aims of our study were the properties of the long-term state attained by a population. We have found three possible states: (S1) the coexisting one with prey and predators, (S2) the absorbing one with prey only, and (S3) the empty one where no individual survived. Which one is the final state of a given population depends on the parameters characterizing the population dynamics. In the following example, we demonstrate the described behavior of the model. From the set of probabilities $\mathcal{S} = \{P_{1r}^{\text{fed}}, P_{1d}^{\text{unfed}}, P_{1d}; P_{2r}, P_{2d}\}$, three of them are fixed, i.e. we put $P_{1d} = 0.05, P_{2r} = 0.20$ and $P_{2d} = 0.05$. Probabilities P_{1r}^{fed} and P_{1d}^{unfed} are varied in $[0, 1]$ range, with a step of 0.1 . In Fig. 5 we show the average values of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ in the long-term state for the full range of probabilities $P_{1r}^{\text{fed}}, P_{1d}^{\text{unfed}} \in [0, 1]$. An absorbing state (S2) can be reached for each probability value $P_{1r}^{\text{fed}} \in [0, 1]$ if the probability P_{1d}^{unfed} is large enough. It corresponds to the part of the surface in Fig. 5(a) for which the number of predators is equal to zero. Figs. 5(a) and 5(b) show that the system asymptotically tends to the state (S3) when $P_{1r}^{\text{fed}} \rightarrow 1$ and $P_{1d}^{\text{unfed}} \rightarrow 0$. It can be seen from Fig. 5 that all other areas correspond to the coexisting state (S1). In order to show different possible states in a more clear manner, we presented our results also in Fig. 6 which is a two-dimensional plot where we highlighted the states (S1), (S2), (S3), and (S1&2) which is an area of both (S1) and (S2) states. In other words, the individual simulation runs corresponding to the domain (S1&S2) can be finished in one of the two final states: adsorbing or coexisting one. In the case of coexisting final state (S1), the number of prey is very high; it covers a large part

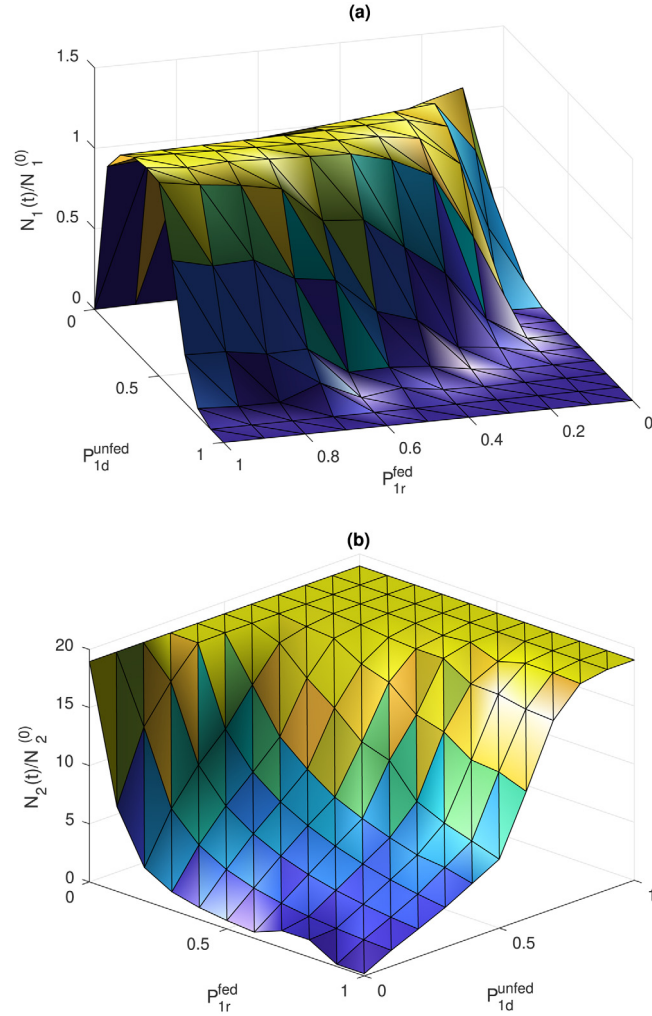


Fig. 5. Shown here is the surface plot of the normalized number of (a) predators $\tilde{N}_1 = N_1(t)/N_1^{(0)}$ and (b) prey $\tilde{N}_2 = N_2(t)/N_2^{(0)}$ in the long-term state for the full range of the probabilities $p_{1r}^{fed}, p_{1d}^{unfed} \in [0, 1]$. Initial densities of both species on the lattice of size $L = 128$ are the same, $\rho_1^{(0)} = \rho_2^{(0)} = 0.0488$, which corresponds to $N_1^{(0)} = N_2^{(0)} = 800$ predators and prey at $t = 0$.

of the lattice, but they coexist with a small number of predators. Clear boundaries between the states could be obtained by performing many more simulations with step that is less than 0.1.

3.1. Response properties of the model

In this section, we present the results of the simulations for the previously described model subject to abrupt changes in the values of probabilities $\{p_{1r}^{fed}, p_{1d}^{unfed}, P_{1d}; P_{2r}, P_{2d}\}$ that characterize the non-conservative processes. Starting from an initially disordered state, with randomly distributed predators and prey on the lattice, the system evolves at fixed probabilities $\mathcal{S} = \{p_{1r}^{fed}, p_{1d}^{unfed}, P_{1d}; P_{2r}, P_{2d}\}$. At a certain time, t_w , probability value for some selected non-conservative process $P \in \mathcal{S}$ changes from $P(I)$ to another value $P(II)$. During the further evolution of the system, the perturbed probability value $P(II)$ does not change.

At first, we present the results of simulations for the cases with abrupt changes of probabilities P_{2r} and P_{2d} that characterize the non-conservative processes of prey. In both cases, the system evolves to the time $t_w = 2500$ with constant probabilities $\mathcal{S}_1 = \{p_{1r}^{fed} = 0.25, p_{1d}^{unfed} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$. Fig. 7 shows the response in the evolution of the normalized number of predators $\tilde{N}_1(t)$ and prey $\tilde{N}_2(t)$ to an abrupt decrease in the birth probability of prey $P_{2r}(I) = 0.20 \rightarrow P_{2r}(II) = 0.10$ at instant $t_w = 2500$. When P_{2r} is abruptly lowered, the first effect is a sharp drop in the number of prey. This is followed by a significant reduction in the number of predators due to a lack of food. After the transient oscillatory regime, the system arrives at a quasi-steady state when the average number of predators remains reduced, but the average number of prey has slightly increased for the chosen parameter set.

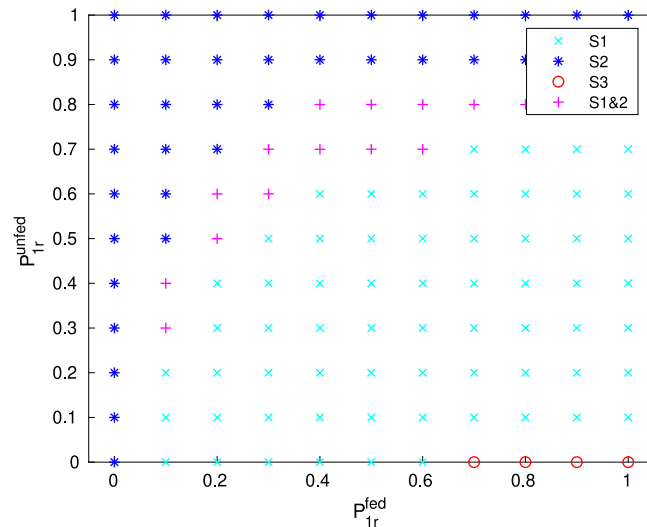


Fig. 6. Two-dimensional representation of full range of probabilities $p_{1r}^{fed}, p_{1d}^{unfed} \in [0, 1]$ that shows possible states of the model, (S1) – the coexisting one, (S2) – with prey only, (S3) – the empty one, and (S1&S2) – with both (S1) and (S2) states.

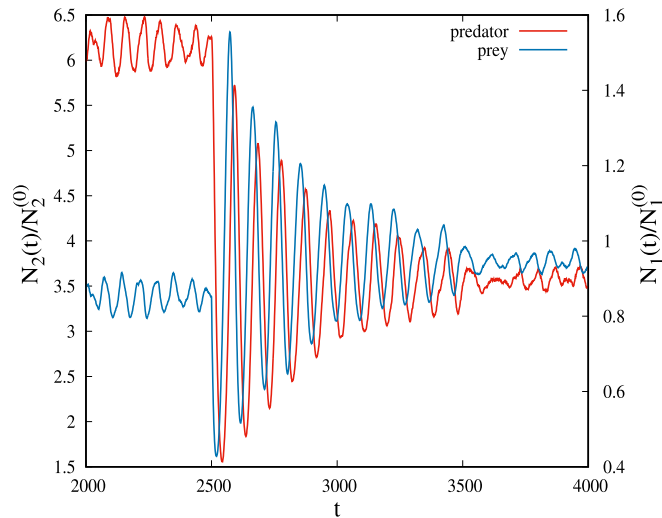


Fig. 7. Response in the evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ to an abrupt change of the probability $P_{2r}(I) = 0.20 \rightarrow P_{2r}(II) = 0.10$ at $t_w = 2500$. The values of probabilities that characterize the non-conservative processes before t_w are $S_1 = \{p_{1r}^{fed} = 0.25, p_{1d}^{unfed} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$.

Fig. 8 shows the response in the evolution of the normalized number of predators $\tilde{N}_1(t)$ and prey $\tilde{N}_2(t)$ to an abrupt increase in the death probability of prey $P_{2d}(I) = 0.01 \rightarrow P_{2d}(II) = 0.05$ at instant $t_w = 2500$. These results were obtained for the initial probability set $S_1 = \{p_{1r}^{fed} = 0.25, p_{1d}^{unfed} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$, which is identical to the previous one. Comparing **Figs. 7** and **8**, it can be seen that the response of the system to an increase in the death probability is very similar to its behavior when reducing the birth probability of prey. At short times after the probability P_{2d} is suddenly increased, we observe an abrupt decrease in the number of prey, followed by the reduction of the number of predators. After the transient oscillatory regime, the average number of predators is decreased because there is not enough available food. However, the average number of prey remains the same because there are fewer predators to catch them.

In the following, we present the results of simulations for the cases with the abrupt changes of probabilities $\{p_{1r}^{fed}, p_{1d}^{unfed}, P_{1d}\}$ that characterize the non-conservative processes of predators. These simulations are performed for two sets of initial probabilities, $S_1 = \{p_{1r}^{fed} = 0.25, p_{1d}^{unfed} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$ and $S_2 = \{p_{1r}^{fed} = 0.09, p_{1d}^{unfed} = 0.05, P_{1d} = 0.01; P_{2r} = 0.15, P_{2d} = 0.01\}$ (see **Figs. 1** and **2** showing the unperturbed evolution of the system).

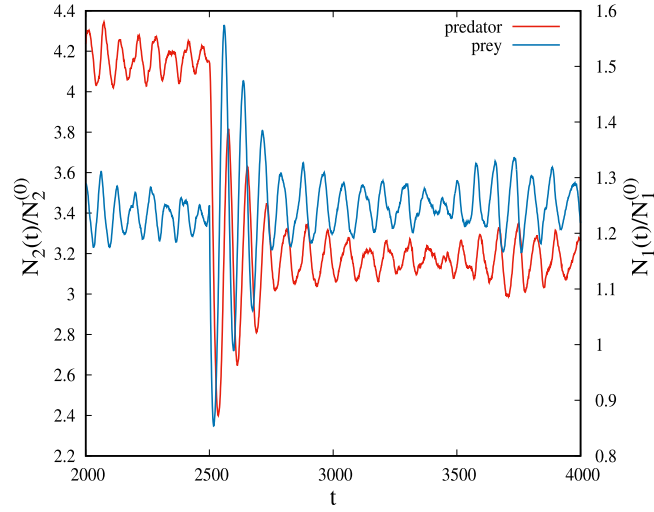


Fig. 8. Response in the evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ to an abrupt change of the probability $P_{2d}(I) = 0.01 \rightarrow P_{2d}(II) = 0.05$ at $t_w = 2500$. The values of probabilities that characterize the non-conservative processes before t_w are $S_1 = \{P_{1r}^{fed} = 0.25, P_{1d}^{unfed} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$.

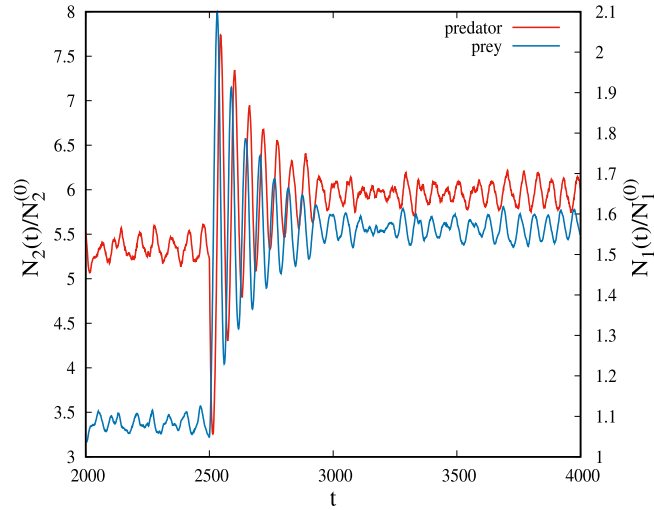


Fig. 9. Response in the evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ to an abrupt change of the probability $P_{1d}(I) = 0.01 \rightarrow P_{1d}(II) = 0.05$ at $t_w = 2500$. The values of probabilities that characterize the non-conservative processes before t_w are $S_1 = \{P_{1r}^{fed} = 0.25, P_{1d}^{unfed} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$.

In Fig. 9 we show the time evolution of the normalized number of predators $\tilde{N}_1(t)$ and prey $\tilde{N}_2(t)$ for the first set of initial probabilities S_1 , when the death probability of predators P_{1d} is changed from $P_{1d}(I) = 0.01$ to $P_{1d}(II) = 0.05$ at instant $t_w = 2500$. We can see that for short times after an abrupt change of P_{1d} the decay of the number of predators is fast. At short times, predator deficiency leads to a rapid increase in the number of prey. However, the increased food availability and the better nutrition of predators maintain their presence on the habitat after the transient oscillatory regime with almost the same average number as before the system perturbation. In other words, increasing the probability P_{1d} has not reduced the number of predators on the habitat, but it increased the average number of prey.

It must be stressed that the density evolution of predators and prey at short times after initialization ($t = 0$), or after an abrupt change of probabilities $S = \{P_{1r}^{fed}, P_{1d}^{unfed}, P_{1d}, P_{2r}, P_{2d}\}$ at instant $t = t_w$, depends not only on their density at these instants, but also on the corresponding spatial distribution of agents on the lattice. Initial spatial distribution of agents on the lattice depends on the method used to build an initial distribution of individuals within the population on the lattice. Spatial distribution of agents generated at moment $t_w = 2500$ represents the initial condition for further evolution of the system with new (perturbed) probabilities that characterize the non-conservative processes. It is clear that the spatial distributions of system agents in time $t_w = 2500$ are quite different from the spatial distributions generated by the RSA

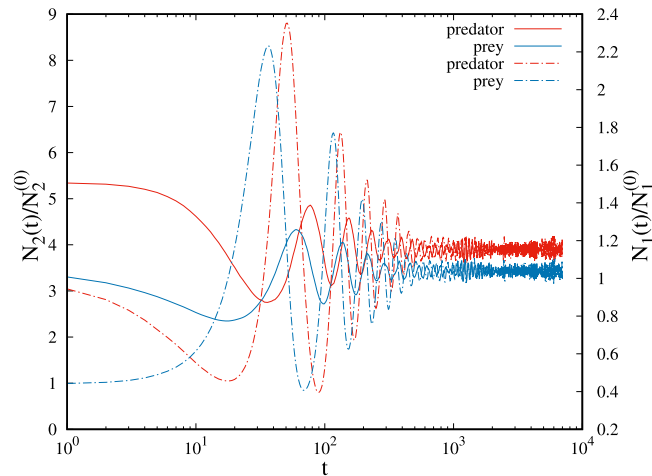


Fig. 10. Time dependences of the number of the normalized number of predators $\tilde{N}_1 = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2 = N_2(t)/N_2^{(0)}$ on the lattice of size $L = 128$. The values of probabilities that characterize the non-conservative processes are $\mathcal{S} = \{P_{1r}^{fed} = 0.25, P_{1d}^{unfed} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.05\}$. Solid lines: The results from Fig. 8, which are translated along the x-axis, $t \rightarrow t - t_w$. Dashed lines: Results obtained in the case when the initial configuration of agents are generated by the RSA method.

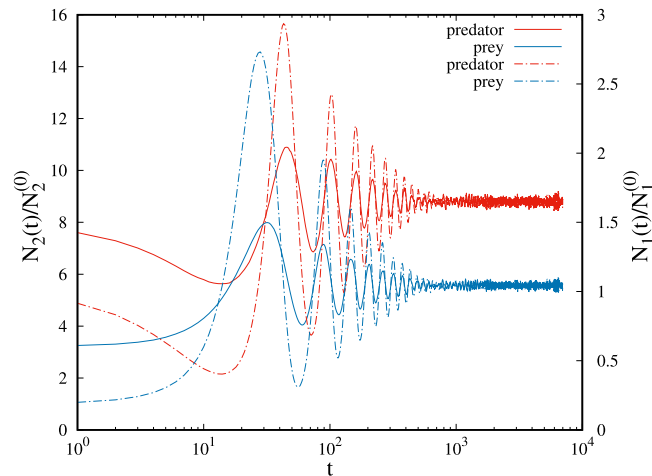


Fig. 11. Time dependences of the number of the normalized number of predators $\tilde{N}_1 = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2 = N_2(t)/N_2^{(0)}$ on the lattice of size $L = 128$. The values of probabilities that characterize the non-conservative processes are $\mathcal{S} = \{P_{1r}^{fed} = 0.25, P_{1d}^{unfed} = 0.10, P_{1d} = 0.05; P_{2r} = 0.20, P_{2d} = 0.01\}$. Solid lines: The results from Fig. 9, which are translated along the x-axis, $t \rightarrow t - t_w$. Dashed lines: Results obtained in the case when the initial configuration of agents are generated by the RSA method.

method. Therefore, the responses of the system at short times after initialization ($t = 0$) and after an abrupt change of the any of probabilities $\mathcal{S} = \{P_{1r}^{fed}, P_{1d}^{unfed}, P_{1d}; P_{2r}, P_{2d}\}$ at the time $t_w = 2500$ are quite different. In Figs. 10 and 11 we show such comparisons. This can be explained by the memory effect, which is a common phenomenon in out-of-equilibrium systems. It is well known that the system can be found in states, characterized by the same density of predators and prey, that have different spatial distribution of agents on the lattice. Memory of the hunting history up to the densities $\rho_1(t)$ and $\rho_2(t)$ is encoded in the arrangement of the agents in the environment. This implies that the knowledge of the density of agents $\rho_1(t)$ and $\rho_2(t)$ is not sufficient to predict the further evolution of the system. This feature concerns the coding of the system history in the “microscopic” configurations.

Furthermore, a quasi-steady state regime corresponding to perturbed probabilities does not depend on the moment of their introduction. This conclusion is confirmed by the results shown in Figs. 10 and 11. It can be seen that using different moments ($t = 0$ or $t = t_w = 2500$) of introducing the perturbed values of probabilities for non-conservative processes give quantitatively the same results for the temporal evolution of $\tilde{N}_1(t)$ and $\tilde{N}_2(t)$ in the quasi-steady state regime.

In order to gain a better insight into the effect of a sudden increase in P_{1d} on the population dynamics, the same set of numerical experiments is carried out as in Fig. 9, with the only difference that the set of initial probabilities for the non-conservative processes is changed from \mathcal{S}_1 to \mathcal{S}_2 . These results are shown in Fig. 12. By comparing the results shown

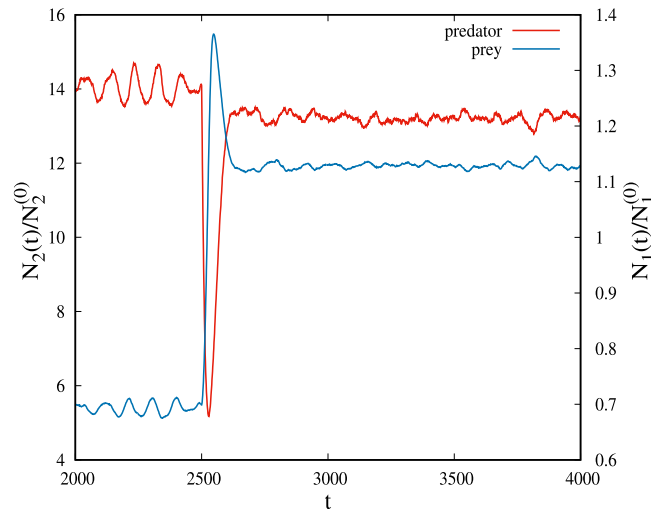


Fig. 12. Response in the evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ to an abrupt change of the probability $P_{1d}(I) = 0.01 \rightarrow P_{1d} = 0.05$ at $t_w = 2500$. The values of probabilities that characterize the non-conservative processes before t_w are $S_2 = \{P_{1r}^{fed} = 0.09, P_{1d}^{unfed} = 0.05, P_{1d} = 0.01; P_{2r} = 0.15, P_{2d} = 0.01\}$.

in Figs. 9 and 12, it is obvious that the same kind of numerical experiments for different initial probabilities S_1 and S_2 produce qualitatively similar results for the time evolution of the number of predators and prey. However, small changes in the system behavior are possible. From Fig. 12, it is evident that the change in the initial probabilities $S_1 \rightarrow S_2$ has led to a shortening of the transient oscillatory regime. The sudden increase in the death probability of predators P_{1d} causes an increase in the number of prey. However, after the transient regime, the number of predators slightly decreased, in the contrary to the behavior of the system shown in Fig. 9.

In the following, we shall demonstrate that an abrupt decrease in the birth probability of predators P_{1r}^{fed} has a very similar effect on the systems evolution as an abrupt increase of their death probability P_{1d} . Fig. 13 shows the response in the evolution of the normalized number of predators $\tilde{N}_1(t)$ and prey $\tilde{N}_2(t)$ for the set of initial probabilities S_1 , when the birth probability of predators P_{1r}^{fed} is decreased from $P_{1r}^{fed}(I) = 0.25$ to $P_{1r}^{fed}(II) = 0.15$ at instant $t_w = 2500$. Fig. 14 shows the same time dependences, but for the system whose initial probabilities are given by S_2 and the birth probability of predators P_{1r}^{fed} is abruptly changed from $P_{1r}^{fed}(I) = 0.09$ to $P_{1r}^{fed}(II) = 0.05$. Similarly to the results presented in Figs. 9 and 12, here we observe a fast decay of the number of predators for short times after an abrupt change of P_{1r}^{fed} . At short times this leads to a rapid increase in the number of prey. As previously mentioned, better food availability favorably affects the presence of predators in the habitat, so that their number increases slightly after the transient regime.

Inadequate and insufficient nutrition can lead to increased predator mortality. In our model, the predators that have not eaten any prey in the previous MC step can die with probability P_{1d}^{unfed} . In Figs. 15 and 16 we show the time evolution of the normalized number of predators $\tilde{N}_1(t)$ and prey $\tilde{N}_2(t)$, when the death probability of predators P_{1d}^{unfed} is abruptly doubled at instant $t_w = 2500$. In Figs. 15 and 16, the results are shown for the sets of initial probabilities S_1 and S_2 , respectively. After an abrupt increase of the probability P_{1d}^{unfed} , large and long-lasting oscillations in the number of predators occur, followed by large oscillations in the number of prey. As expected, the average number of prey is increased compared to the one observed before the perturbation, but the average number of predators stays almost the same. An increase in the number of prey makes the food more available, which maintains the number of predators.

4. Concluding remarks

In this paper, we have developed an intuitively clear framework for understanding the impacts of environmental perturbations on the population dynamics of the predator–prey systems. We have studied a stochastic lattice model describing a group chase and escape with sight-limited predators and prey by numerical simulations. Five probabilities that control the breeding and physiological dying of predators and prey were introduced into the model. Although the probability values used in the simulations were not taken from any specific research, our results highlight some possible consequences of perturbations in the predator–prey systems. Our MC simulations have shown that there are three possible final states into which the dynamics could lead the populations: coexistence of predator and prey, prey only, and an empty state in which both populations are extinct.

In the model, a perturbation was introduced at a specific instant during the evolving process by the abrupt change of the birth and death rates. In short times, after an abrupt change probability that characterizes the chosen non-conservative process, we have observed a sharp drop or jump in the numbers of predators and prey. Sudden changes in their number

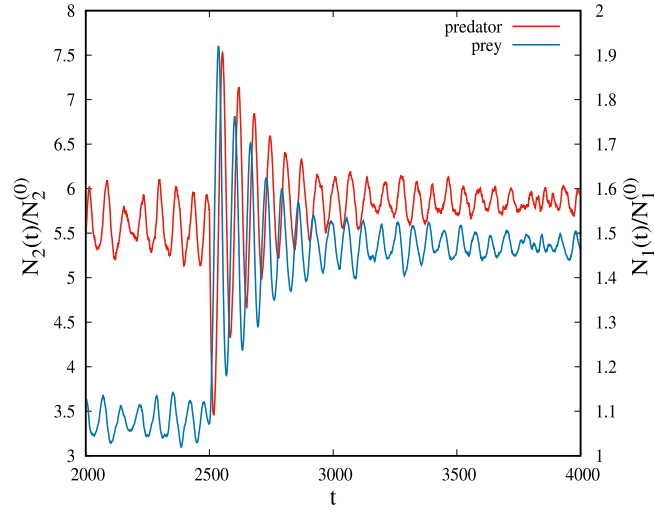


Fig. 13. Response in the evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ to an abrupt change of the probability $P_{1r}^{\text{fed}}(I) = 0.25 \rightarrow P_{1r}^{\text{fed}}(II) = 0.15$ at $t_w = 2500$. The values of probabilities that characterize the non-conservative processes before t_w are $\mathcal{S}_1 = \{P_{1r}^{\text{fed}} = 0.25, P_{1d}^{\text{unfed}} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$.

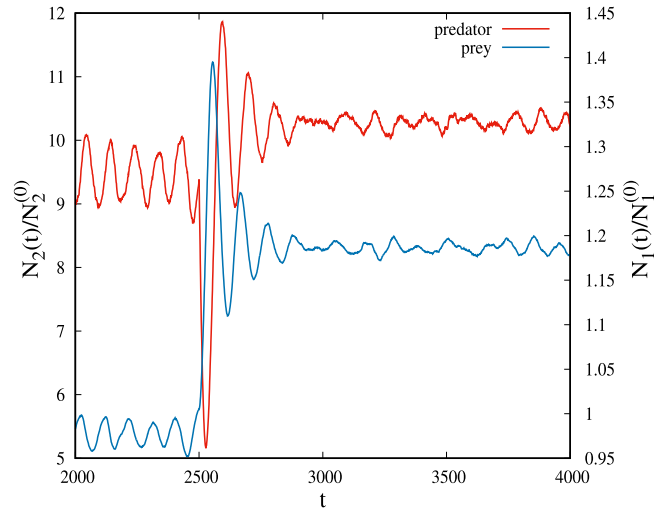


Fig. 14. Response in the evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ to an abrupt change of the probability $P_{1r}^{\text{fed}}(I) = 0.09 \rightarrow P_{1r}^{\text{fed}}(II) = 0.05$ at $t_w = 2500$. The values of probabilities that characterize the non-conservative processes before t_w are $\mathcal{S}_2 = \{P_{1r}^{\text{fed}} = 0.09, P_{1d}^{\text{unfed}} = 0.05, P_{1d} = 0.01; P_{2r} = 0.15, P_{2d} = 0.01\}$.

are stabilized during the transient oscillatory regime. After the transient oscillatory regime, the system arrives at a quasi-steady state when the densities of predators and prey oscillate (fluctuate) around some “average” values, which do not change in time. Our simulations predict the oscillations with a 1/4-period lag between predator and prey during and after the transient oscillatory regime. We have demonstrated that perturbation of a selected non-conservative process in numerical experiments with different initial probabilities produces qualitatively similar results for the time evolution of the number of predators and prey.

Our results suggest that the response of the system to an increase in the death probability of prey is very similar to its behavior when reducing the birth probability of prey. In both cases, the average number of predators is decreased after the transient oscillatory regime due to the lack of food. Further, we have found that an abrupt decrease in the birth probability of predators affects the evolution of the system similarly to an abrupt increase of their death probability. Decreasing (increasing) the birth (death) probability of predators changes their number slightly, but considerably increases the number of prey in the quasi-steady state regime. Such perturbations lead to a rapid increase in the number of prey at short times. Consequently, increased food availability maintains the presence of predators on the habitat after the transient oscillatory regime.

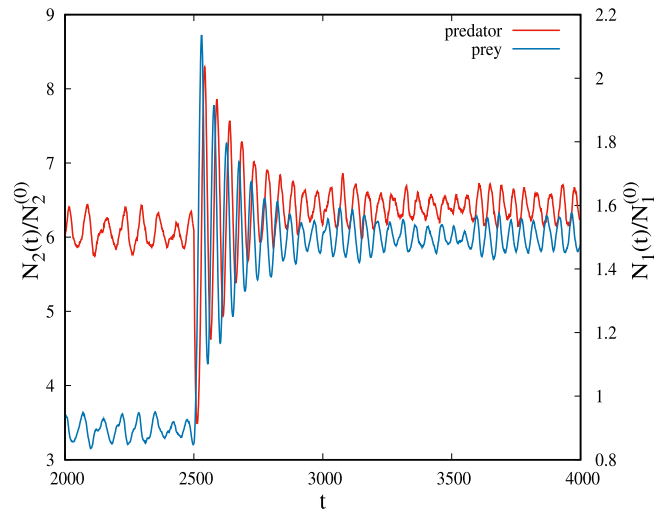


Fig. 15. Response in the evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ to an abrupt change of the probability $P_{1d}^{unfed}(I) = 0.10 \rightarrow P_{1d}^{unfed}(II) = 0.20$ at $t_w = 2500$. The values of probabilities that characterize the non-conservative processes before t_w are $S_1 = \{P_{1r}^{fed} = 0.25, P_{1d}^{unfed} = 0.10, P_{1d} = 0.01; P_{2r} = 0.20, P_{2d} = 0.01\}$.

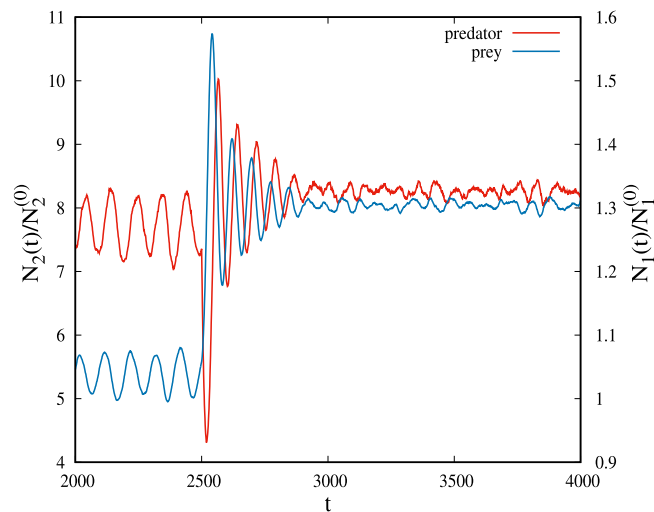


Fig. 16. Response in the evolution of the normalized number of predators $\tilde{N}_1(t) = N_1(t)/N_1^{(0)}$ and prey $\tilde{N}_2(t) = N_2(t)/N_2^{(0)}$ to an abrupt change of the probability $P_{1d}^{unfed}(I) = 0.05 \rightarrow P_{1d}^{unfed}(II) = 0.10$ at $t_w = 2500$. The values of probabilities that characterize the non-conservative processes before t_w are $S_2 = \{P_{1r}^{fed} = 0.09, P_{1d}^{unfed} = 0.05, P_{1d} = 0.01; P_{2r} = 0.15, P_{2d} = 0.01\}$.

This study could serve as a good basis for further studies of the dynamics of multi-species communities that are exposed to sudden environmental perturbations. It would be interesting to perform a similar investigation in a heterogeneous landscape, i.e., in an environment that contains obstacles [29]. This would allow us to study the role that rapid changes in the spatial structure of the natural habitat play in the time evolution of the number of predators and prey.

CRediT authorship contribution statement

J.R. Šćepanović: Conceptualization, Methodology, Software, Validation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Z.M. Jakšić:** Methodology, Validation, Formal analysis, Writing - review & editing, Supervision. **Lj. Budinski-Petković:** Methodology, Validation, Formal analysis, Writing - review & editing, Supervision. **S.B. Vrhovac:** Methodology, Software, Validation, Formal analysis, Visualization, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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