Original Research Article

Analyzing the spatial dynamics of a prey–predator lattice model with social behavior

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ABSTRACT

A lattice prey–predator model is studied. Transition rules applied sequentially describe processes such as reproduction, predation, and death of predators. The movement of predators is governed by a local particle swarm optimization algorithm, which causes the formation of swarms of predators that propagate through the lattice. Starting with a single predator in a lattice fully covered by preys, we observe a wavefront of predators invading the zones dominated by preys; subsequent fronts arise during the transient phase, where a monotonic approach to a fixed point is present. After the transient phase the system enters an oscillatory regime, where the amplitude of oscillations appears to be bounded but is difficult to predict. We observe qualitative similar behavior even for larger lattices. An empirical approach is used to determine the effects of the movement of predators on the temporal dynamics of the system. Our results show that the algorithm used to model the movement of predators increases the proficiency of predators.

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1. Introduction

The relationship between the long-term dynamics and the patterns observed in population dynamics and in particular in prey–predator spatial models has been a matter of extensive research in theoretical ecology: reaction diffusion equations, cellular automata, patch models, coupled map lattices and individual based models are only a subset of the tools used to analyse phenomena such as phase transitions (Antal and Michel, 2000; Bagnoli et al., 2001), scaling and finite size effects (Sutherland and Jacobs, 1994; Pascual and Levin, 1999; Pascual et al., 2002; Xu et al., 2005), oscillatory behavior (Blasius et al., 1999; Lipowski, 1999; Zhang et al., 2006), chaos (Jansen, 2001; Li et al., 2005; Maionchi et al., 2006; Gibson and Wilson, 2013) and noise induced effects (Fiasconaro et al., 2004; La Cognata et al., 2010). Given the nature of ecological models, most of these phenomena are closely related.

The dispersal of individuals is one of the central mechanisms behind pattern formation in spatially explicit models (Hosseini, 2006; Filotas et al., 2008). A good approach to model such phenomenon is to use transition rules that describe a diffusion process: in Comins et al. (1992), the authors study a host-parasitoid model on a rectangular grid of patches. The effects of the diffusion on the spatial dynamics of the model manifest as a wavefront of hosts traveling at constant speed; this event is followed by a front of parasitoids that consumes the original wave of hosts. Depending on the fraction of hosts that disperse each generation several spatial patterns might be observed including spatial chaos, spirals and "crystal" patterns. The authors note that despite the fact that the presence of any of these patterns leads to the coexistence of both species, there is a threshold for the size of the grid below which extinction is always observed.

A comparative study of the effects of diffusion processes in spatial models appears in Sherrat et al. (1997). The authors analyse the behavior of four different spatial prey–predator models (reaction–diffusion equations, coupled map lattices, cellular automata and integrodifference equations) where prey suffer the invasion of predators. Simulations of one-dimensional versions of each model show the expected wave front of predators invading the prey-only state and leaving behind a coexistence state. The

authors focus their attention on the spatial dynamics behind the initial wavefront of predators where three different phenomena are observed:

- Regular spatio-temporal oscillations. For this case, periodic travelling waves moving at a different speed than the original front are observed. Such waves correspond to a family of solutions for the model based on reaction diffusion equations.
- Irregular spatio-temporal oscillations. For the reaction diffusion equations, certain parameters might force the travelling wave solution into irregular oscillations, the authors note that such pattern might be associated with spatial chaos. Irregularities expand from the focus of the invasion suggesting again that such dynamics are chaotic.
- Irregular fluctuations. Here, there is a band of periodic waves immediately behind the invasive front. Following this band there are irregular oscillations with no apparent pattern. This behavior corresponds to a transient phase due to an unstable periodic wave solution.

Similar patterns were obtained in Arashiro and Tomé (2007) for a probabilistic cellular automaton. By carrying numerical simulations, the authors were able to obtain the critical exponents for the automaton, thus allowing the classification of the model into the directed percolation universality class.

Diffusion-like transition rules offer a simple and mathematically tractable way to describe the dispersal of individuals. In Filotas et al. (2008) the authors state that because of a lack of common rules behind the dispersal of species, ecologists often have to make the simplest assumptions (e.g., a density independent rate of dispersion) when modeling such phenomenon; even if for many species factors such as the local population size, resource availability, or habitat quality influence the mobility of individuals. However, there has been efforts to develop strategies that better mimic the phenomena found in natural ecosystems (Li et al., 2005; Boccara et al., 1994; Rozenfeld and Albano, 2001; Szwabiński, 2012; Wang et al., 2012). In these approaches, cooperation is neglected in favour of intraspecific competition, i.e., only the negative effects of the aggregation of individuals are considered. However, it is reasonable to expect that under certain circumstances, a group of individuals has better chances of survival than those that remain isolated, e.g., to flee from a predator, or to hunt for prey. Allee effects are a good example where aggregation leads to positive density dependence, albeit only for small populations; however recent works have shown that such effects are key for the stability of a prey–predator system (Wang et al., 2011), or even determine the success of an invading species (Mistro et al., 2012). In some animal communities, social behavior is also the source of many extraordinary patterns, e.g., bird flocking or insect swarms. By incorporating social behavior on the dispersal rules of predators, we attempt to study the effects that such process have on the global dynamics of an ecosystem.

In the present paper we analyse a prey–predator lattice model where a local Particle Swarm Optimization (PSO) algorithm is used to model social interactions among the individuals of the predators species. PSO is an evolutionary computation algorithm typically used to find an optimal solution in a search space that defines the set of possible solutions to a particular problem. The foundations of the algorithm come from the observation of the social behavior of animal communities previously mentioned: insect swarms, bird flocks or fish schools (Trelea, 2003). In a PSO algorithm there is a population of particles called the "swarm", the position of each particle determines a candidate solution to the problem under study. Typically, social interactions among the members of the swarm occurs through one of two information sharing schemes:

- Global. A particle moves according to its own knowledge of the search space, and the information it receives from the particle at the location that represents the best solution found by the swarm.
- Local. In this scheme, a neighborhood comprising a particle and some of its nearest neighbors is created. To move, a particle uses its own knowledge of the search space and the information provided by the particle with the "best" position among its neighbors.

In our model, these interactions help a predator to determine the best direction of movement in order to secure food for its survival and reproduction. Cooperation among predators manifest itself as an interesting spatial pattern: predators group into clusters that maintain cohesion as they move through the lattice hunting for preys; the analysis of such phenomenon is the main focus of the present article. In a previous work (see Martínez Molina et al., 2013) we showed that the population dynamics corresponding to the formation and propagation of clusters of predators is characterized by oscillations with a very regular period. Similar behavior has been associated with variations in the mobility of the individuals of a species (Boccara et al., 1994; Shigefumi et al., 2014), large migration rates in patch models (Blasius et al., 1999; Li et al., 2005), or the aggregation of populations at small or intermediate scales (Pascual and Levin, 1999; Pascual et al., 2001; Durrett, 1994; Mobilia et al., 2007). In light of these results, we investigate the relationship between the social behavior of predators and the observed population dynamics. The main result of this work is that cooperation through a local PSO increases the proficiency of predators, which behavior is characterized by a transient phase followed by an oscillatory regime. Such behavior was taken into account to build a mean field model that accurately predicts the mean densities of the populations.

The proposed model is defined in Section 2; here, we describe each stage of the model, and explain the main consequence of the use of a local PSO algorithm for the movement of predators, i.e., the grouping of predators into swarms. In Section 3 we analyse the invasion of prey dominated zones by predators using initial conditions close to the absorbing state where the lattice is full of preys. In Section 4 we show that the movement of predators reduces the death probability of predators, which in turn increases the death rate of preys. Finally, in Section 5 we explore some properties of the model for different sizes of the lattice. Our conclusions appear in Section 7.

2. Proposed model

Our model describes the interactions between a sessile prey and its predator, such interactions are local in nature and occur on a two-dimensional lattice L where periodic boundaries have been implemented. Each site of the lattice may be occupied by a prey, a predator, both or be empty. Time proceeds in discrete time steps. The evolution of the model is controlled by a life cycle, known as "season", that determines the transition function that is applied at each time step. Depending on the function being applied, preys and predators may interact within a neighborhood whose size (the number of sites within the neighborhood) is defined as follows:

$$|M_r| = (2r + 1)^2 \tag{1}$$

where r is the radius of the neighborhood. Thus an M_1 neighborhood comprises the eight nearest neighbors of a particular site, and the site itself; an M_2 neighborhood the nearest

24 neighbors, and the site itself, and so on. The transition functions are as follows:

1. *Intraspecific competition.* During this stage the probability that a prey dies due to competitive pressure is given by:

$$\frac{\alpha y}{|M_c| - 1} \tag{2}$$

   The quantity $\alpha \in [0, 1]$ is the intraspecific competition coefficient, which determines the intensity of the competition exercised by other preys in the neighborhood M_c of a site, y is the number of preys within such neighborhood.
2. *Migration.* When migrating, predators move from zones where the density of preys is low, to zones highly populated by preys. The movement occurs according to a local PSO algorithm, which give predators the capacity to interact with other members of their species.
3. *Reproduction of predators.* During the reproduction stage, each predator chooses randomly a site in its reproduction neighborhood. If the site is not already populated by a predator, then a new predator is created at the chosen site, otherwise, no reproduction occurs. This process is repeated as many times as the reproductive capacity ϵ_Z of the species allows.
4. *Death of predators.* If a predator is not located at a site containing a prey, it dies with probability 1.
5. *Predation.* If a prey is located at a site containing a predator, it dies with probability 1.
6. *Reproduction of preys.* Like predators, preys spawn new individuals at random within a M_y neighborhood. Reproduction is only successful if the chosen sites do not contain already a predator.

   With exception of the migration rule, which is applied for five consecutive time steps, all other rules are applied during a single time step. Therefore, a season is equivalent to 10 time steps. The following pseudocode illustrates how the transition functions are scheduled in the proposed model. Such "architecture" is useful to observe the model after a transition function has been applied, and not only when a season ends.

function MAIN
  INITIALIZE
  for $j \leftarrow 1$, *totalTimeSteps* **do**
    NEXTGEN
  end for
end function

function INITIALIZE
  nextStage ← INTRASPECIFICCOMPETITION ▷ Store address of function
  migrationCounter = 0
end function

function NEXTGEN
  nextStage ▷Call the function pointed by *nextStage*
end function

function INTRASPECIFICCOMPETITION
  for $i \leftarrow 1$, *totalPreys* **do**
    Determine if the prey i dies due to competition
  end for
  nextStage ← MIGRATION ▷ Store address of function

end function

function MIGRATION
  for $i \leftarrow 1$, *totalPredators* **do**
    Update the position of predator i according to the PSO algorithm
  end for
  migrationCounter ← *migrationCounter* + 1
  if *migrationCounter* = 5 **then**
    migrationCounter = 0
    nextStage ← REPRODUCTIONOFPREDATORS
  end if
end function

function REPRODUCTIONOFPREDATORS
  for $i \leftarrow 1$, *totalPredators* **do**
    for *birthCount* $\leftarrow 1$, ϵ_Z **do**
      If possible spawn a new predator at a randomly chosen site
    end for
  end for
  nextStage ← DEATHOFPREDATORS
end function

function DEATH OF PREDATORS
  for $i \leftarrow 1$, *totalPredators* **do**
    Kill all predators not located in a cell without a prey
  end for
  nextStage ← PREDATION
end function

function PREDATION
  for $i \leftarrow 1$, *totalPreys* **do**
    Kill all preys located in a cell with a predator
  end for
  nextStage ← REPRODUCTIONOFPREYS
end function

function REPRODUCTIONOFPREYS
  for $i \leftarrow 1$, *totalPreys* **do**
    for *birthCount* $\leftarrow 1$, ϵ_Y **do**
      If possible spawn a new prey at a randomly chosen site
    end for
  end for
  nextStage ← INTRASPECIFICCOMPETITION
end function

   The migration stage deserves additional explanation; however, a deep review of PSO algorithms is beyond the scope of this article, detailed information can be found in Kennedy and Eberhart (2001). In order to use PSO as a migration algorithm, it is necessary to enhance the capabilities of the predators. In particular each predator records the position of the site with the highest density of preys visited so far. Such a measure is assigned to every site of the lattice based on the number of preys in a neighborhood of size M_c. Each predator also possesses a velocity vector which indicates the current magnitude and direction of its movement. As stated in Section 1, PSO is commonly used to solve optimization problems,

e.g., finding the maximum or the minimum of a given function. We adapt such behavior to model the movement of predators: when moving, a predator aims to maximize its chances of survival, it does so by moving to zones with a high density of preys. In contrast to a typical local PSO where the neighbors of a given particle remain fixed, in our algorithm the neighborhood of a predator changes as it moves through the lattice. During the migration stage, the position of every predator in the lattice is updated using the following equations:

$$V_i^{\tau+1} = \omega V_i^{\tau} + k_1 q_1 (P_i^{\tau} - X_i^{\tau}) + k_2 q_2 (P_{l_i}^{\tau} - X_i^{\tau}) \qquad (3)$$

$$X_i^{\tau+1} = X_i^{\tau} + V_i^{\tau+1} \qquad (4)$$

where X_i^{τ} is the position of predator i at time step τ and V_i^{τ} is the velocity vector of predator i at time step τ. Each term of Eq. (3) plays a different role in the PSO algorithm:

- The term ωV_i^{τ} is responsible for keeping the current direction of movement of the particle, this term is known as the inertia component. The parameter $\omega \in [0, 1]$ is called inertia weight; values of ω close to one produces long range movements, while values close to zero produce small movements. It must be noted that the value of ω is linearly decreased over the duration of the algorithm. If ω were to remain constant, then a predator would move around a zone with a high density of preys; however it is unlikely that the final position of the predator would be within such zone. Thus, during the first iterations predators execute long range movements that favours the exploration of their neighborhood. As migration nears its end, the movement of predators is more constrained, which encourages the search in zones with a good density of preys.
- The term $k_1 q_1 (P_i^{\tau} - X_i^{\tau})$ is known as the cognitive component and serves to guide the movement of a predator towards zones where it has previously found a good density of preys. P_i^{τ} denotes the position with the highest prey density found by predator i up to time τ. The parameter k_1 is known as the cognitive factor, while $q_1 \in [0, 1]$ is a uniformly chosen random number. Both of these parameters determine the magnitude of the contribution of the term to the new velocity vector of the predator.
- The term $k_2 q_2 (P_{l_i}^{\tau} - X_i^{\tau})$ is known as the social component, its objective is to direct the movement of the predator towards the position with the highest density of preys among the neighboring predators (social neighborhood). The parameter k_2 is known as the social factor, $q_2 \in [0, 1]$ is a uniformly chosen random number; both parameters determine the contribution of the term to the velocity vector of the predator. $P_{l_i}^{\tau}$ denotes the position with the highest prey density found by the neighbors of predator i at time τ (prey density is measured using the competition neighborhood).

The parameters q_1 and q_2 are randomly chosen in order to produce an uneven movement around a point which is the weighted average of P_i^{τ} and $P_{l_i}^{\tau}$, the goal is to force a predator to "explore" the neighborhood of a potentially good zone. Once the contribution of each term has been obtained, the new velocity vector is added to the current position X_i^{τ} of a predator to obtain its position at the time step $\tau + 1$. Fig. 1 shows the position updating of a predator for a M_l neighborhood of radius $l = 2$, and a M_c neighborhood of radius $c = 1$.

In a previous work (see Martínez Molina et al., 2013) we showed that the spatial dynamics of the proposed model is characterized by the aggregation of predators into well defined clusters that propagate through the lattice as shown in Fig. 2. Here and thereafter, we refer to such clusters as "swarms" in order to
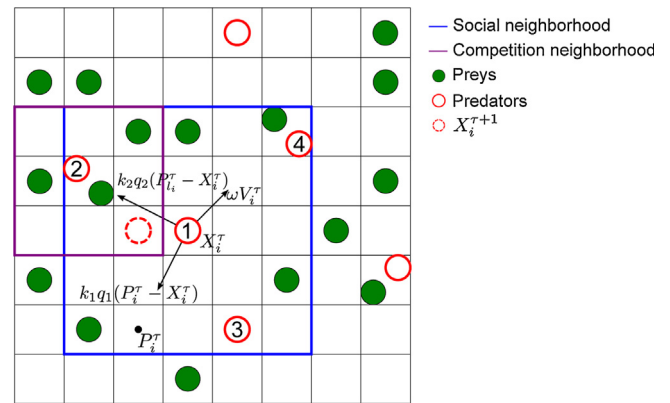

Fig. 1. Local position updating.

avoid confusion with the usage of the term "cluster" in previous works (cells u and v belong to the same cluster if both have the same state and they are "adjacent" to each other, i.e., v is located at one of the nearest neighbors of u, Sutherland and Jacobs, 1994; Fu et al., 2010). Such phenomena is driven by the following processes:

- *Formation.* This process occurs when a predator located at a zone with a high density of preys attracts predators within its social neighborhood M_l to its location.
- *Fragmentation.* Due to the cognitive component of the local PSO algorithm, it is possible for one or more predators to move beyond the social neighborhoods of the other individuals that comprise a swarm.
- *Merging.* When two or more swarms collide, the social neighborhoods of their predators overlap, what follows is an aggregation of individuals into an even bigger swarm. However, such aggregations are short lived: due to an increase in the local density of predators, resources are rapidly consumed which produces local extinction events.
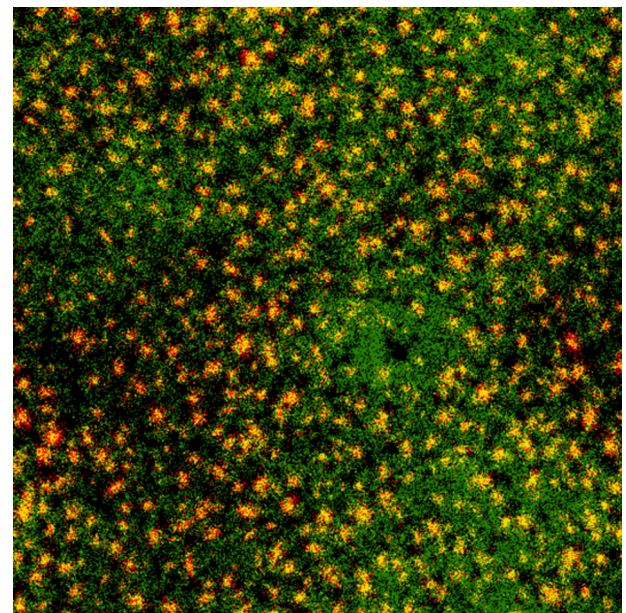

Fig. 2. Swarms of predators moving through the lattice. Preys are depicted in green, predators in red, and preys invaded by a predator are depicted in yellow. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Parameters used in computer simulations. The value specified for Φ_0 is the density that corresponds to a single predator. The values for ω specify the range over which the parameter is linearly decreased.

Preys	Value	Description
Ψ_0	1	Initial density
ϵ_Y	1	Reproductive capacity
y	3	Radius of the reproduction neighborhood
α	0.05	Intraspecific competition coefficient
c	3	Radius of the competition neighborhood

Predators	Value	Description
Φ_0	3.8147×10^{-6}	Initial density
ϵ_Z	3	Reproductive capacity
z	1	Radius of the reproduction neighborhood

| Migration	Value	Description
k_1	1	Cognitive factor
k_2	2	Social factor
l	7	Radius of the social neighborhood
ω	0.9–0.2	Inertia weight

3. Swarm dynamics

Computer simulations of the proposed model were performed using the parameters presented in Table 1. 10,000 seasons (100,000 time steps) were simulated using a lattice of 512 × 512 sites with periodic boundaries. Our experiments start with the system close to the prey-only absorbing state, i.e., the lattice starts with an initial density of preys $\Psi_0 = 1$, and an initial density of predators Φ_0 corresponding to a single predator. Where appropriate, the following color code is used to identify the state of a site:

- *Black*: an empty site.
- *Green*: a site populated by a prey.
- *Red*: a site inhabited by a predator.
- *Yellow*: a site containing a prey and a predator at the same time.

Fig. 3 shows the invasion of the prey domain by predators. In Fig. 3a several swarms of predators grouped at the source of the invasion can be observed. Due to the high density of preys, the formation of these patterns occurs quickly after the start of the simulation: if the starting predator and its progeny survive the first "death of predators" stage, then the first swarm appears after the reproduction of predators. Since the recently born predators inherit their best know position from their parent, and since the size of the reproduction neighborhood is smaller than the size of the social neighborhood, both the starting predator and its progeny remain "bounded". We may define then (somewhat arbitrarily) the time of creation of the first swarm as the time when the starting predator and at least one of its progeny survive the "death of predators" stage. As predation takes place, swarms move outwards
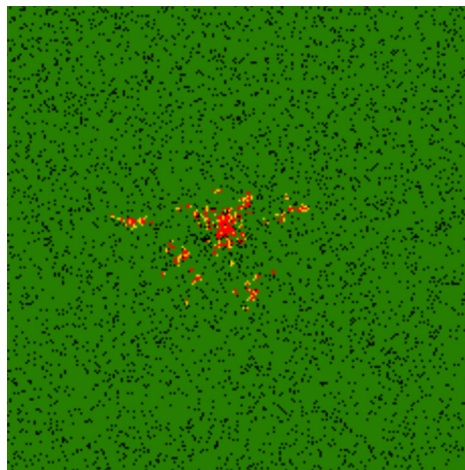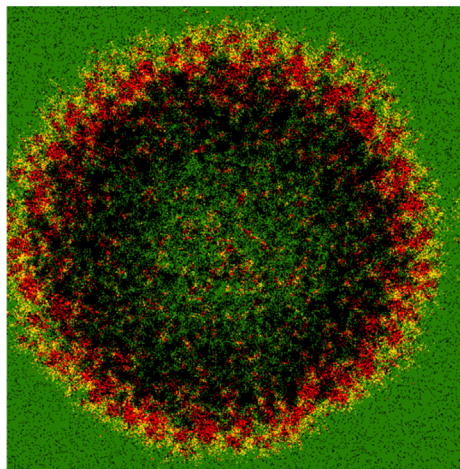

(a) 6 seasons
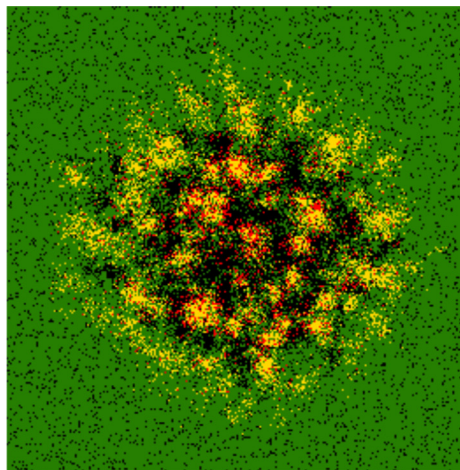
(b) 10 seasons
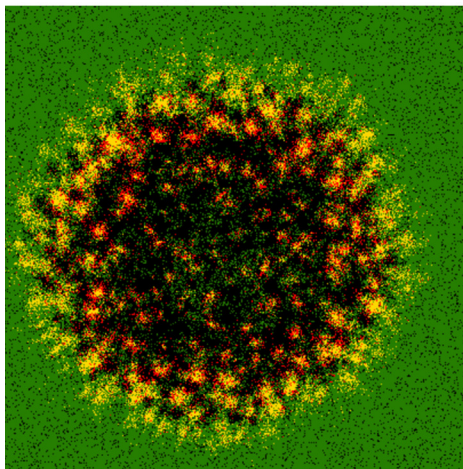
(c) 14 seasons

(d) 18 seasons

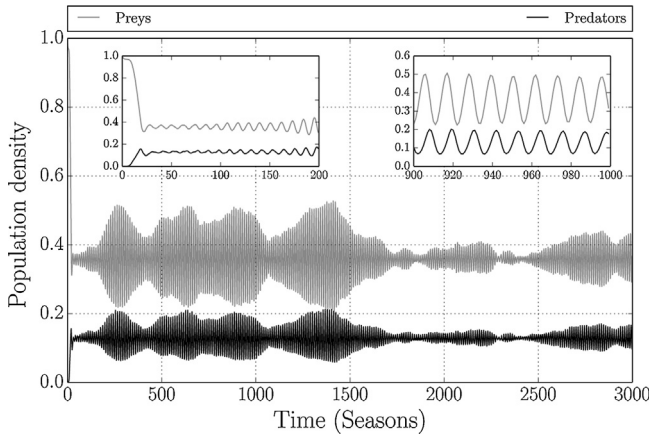**Fig. 3.** Invasion of preys by predators.

Fig. 4. Temporal dynamics of the proposed model under the parameters of Table 1. The left inset shows a monotonic approach to a fixed point during the transient phase of the simulations, which corresponds to traveling wavefronts that appear during the invasion process. The right inset shows that oscillations have a very regular period and are out of phase.

following the direction of highest prey density. However, the movement of swarms located near the source of the invasion is limited by swarms located far from the source of the invasion: if an "inner" swarm tries to expand, it is possible for its destination to be already occupied by an "outer" swarm, or it may also be the case that its destination is a recently predated zone, since these zones have a low density of preys, moving to any of these locations would increase the death probability of every individual in the swarm. Such process results in an expanding wavefront of "outer" swarms moving at the same speed, while "inner" swarms remain behind (see Fig. 3b). It must be noted that the wavefront is not homogeneous; i.e., swarms do not cover the whole perimeter of the wave (see Fig. 3c), which in turn allows some preys to survive the invasion. Zones with a low density of preys behind the wavefront are repopulated by the survivors, thus creating new clusters of preys (see Fig. 3d), which become the target of the "inner" swarms of predators. There is then a division between a prey-only state ahead of the invasion front, and a coexistence state behind, where swarms continuously migrate from zones with a low density of preys to zones highly populated by them. Similar divisions have been analysed previously: for a two-dimensional coupled map lattice and two-dimensional reaction diffusion equations, Sherrat et al. (1997) observed periodic travelling waves that persist or decay into irregular spatio-temporal oscillations due to being intrinsically unstable. Arashiro and Tomé (2007) obtained a similar division for a probabilistic cellular automaton; behind the initial wave front they observed a coexistence characterized by local time coupled oscillations where small clusters of predators invade large clusters of preys. A second coexistence state where both populations are grouped into small clusters isolated from each other was observed for a low death probability of predators which is compensated by higher birth probabilities.

The population dynamics for the proposed model under the parameters specified by Table 1 is shown in Fig. 4. The expansion of the initial wavefront produces a monotonic approach to a non-trivial fixed point during the transient period of the system; once such approach ends, it is possible to observe weak oscillations around the fixed point, which corresponds to subsequent travelling waves that are produced when surviving preys repopulate the space behind the wavefront, only to be consumed by the "inner" swarms. Such process is short lived, and waves will eventually disappear; after the transient phase, both populations oscillate with a very regular period and the typical "out of phase" behavior of prey–predator systems (see the right inset of Fig. 4).

4. Mean field analysis

It is possible to formulate the following set of mean field equations (details about such process are given in Appendix A) by considering the changes in density that occur through each season of the model:

$$\Psi_I = \Psi_t - \alpha\Psi_t^2 \tag{5}$$

$$\Phi_R = \Phi_t + (1 - \Phi_t)(1 - (1 - P_Z)^{\epsilon_Z \bar{z}_t}) \tag{6}$$

$$\Phi_{t+1} = \Phi_R - (1 - \Psi_I)\Phi_R \tag{7}$$

$$\Psi_D = \Psi_I - \Psi_I \Phi_{t+1} \tag{8}$$

$$\Psi_{t+1} = \Psi_D + (1 - \Psi_D)(1 - (1 - P_Y)^{\epsilon_Y \bar{y}_t}) \tag{9}$$

where:

- t is measured in seasons.
- Φ_t is the density of predators at time t.
- Ψ_t is the density of preys at time t.
- Ψ_I is the density of the prey species after the intraspecific competition stage.
- Φ_R is the density of predators after the corresponding reproduction stage.
- Ψ_D is the density of preys after the predation stage.
- $\bar{y}_t$ is the mean number of preys in a neighborhood of size $|M_y|$ of a site.
- $\bar{z}_t$ is the mean number of predators in a neighborhood of size $|M_z|$ of a site.
- $P_Y = 1/|M_y|$ is the probability that a site that does not contain a prey is selected for reproduction by one of its neighboring preys.
- $P_Z = 1/|M_z|$ is the probability that a site devoid of a predator is selected for reproduction by a neighboring predator.

A pair of mean field equations that describe the changes for both populations can be obtained from Eqs. (5)–(9); however, since we were not able to obtain an analytical solution to such system, we keep the equations in their original form. Note that since no change in density occurs during the migration stage, there is no mean field term associated to this rule. These equations will be used to provide a comparison of the behavior of the proposed model against a model that considers a "well mixed" environment. We will also show that by considering the effects of the migration stage in the mean field equations, an accurate prediction of the mean densities of both populations can be made.

In agreement with computer simulations of the proposed model, the mean field equations have two fixed points that correspond with the absorbent states of the proposed model: the first corresponds to an ecosystem where both populations go extinct; the second is obtained when all the individuals of the predator species die, leaving behind an ecosystem only populated by preys. Numerical simulations of the mean field model, according to the parameters of Table 1, also show an evolution toward a fixed point characterized by the coexistence of preys and predators (see Fig. 5); it is worth noting however, that the long-term density of the populations is not accurately predicted, and no oscillatory behavior can be observed. Both of these outcomes are to be expected, it is well known that mean field models, such as the one given by Eqs. (5)–(9), provide only a rough description of the dynamics of a lattice model, since they do not take space into account and assume a "well mixed" environment where individuals are randomly distributed on the lattice.
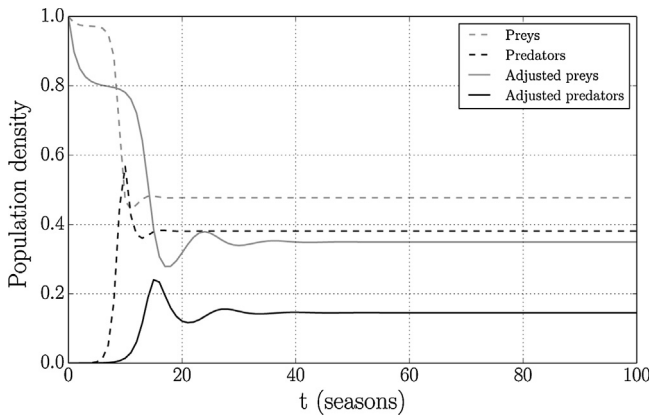
Fig. 5. Long-term mean densities predicted by the mean field model given by Eqs. (5)–(9); dashed lines correspond to the mean field model that omits the effect of the migration stage, solid lines correspond to the adjusted mean field model that considers such effects.

4.1. The role of the migration stage

Our mean field model has an additional shortcoming: it does not take into account the effects of the migration stage on the populations of preys and predators. An immediate effect of the movement of predators from zones low on resources to zones with a higher density of preys, is that the death probability of predators must be different from that when no migration occurs. Ideally, migration should provide better conditions for the survival of a predator, or the survival of its progeny; however, the effects of such change on a global scale are not easily predicted. To test our hypothesis, we have selected the parameter sets shown in Table 2: set A disables the movement of predators, so parameters like k_1 and k_2 are set to zero; parameters in set B are identical to those shown in Table 1 and are repeated to provide an easy reading of the article.

For both simulations, we have measured the following quantities: (a) the density of preys at the start of the death of predators stage Ψ_I; (b) the death probability of predators; (c) the density of predators at the start of the predation stage Φ_{t+1}; and (d) the predation probability. Fig. 6 shows these measurements: it is easy to see that when set A is used, our data concentrates in an small area, which corresponds to an orbit towards a fixed point obtained when no migration occurs. Due to the oscillatory behavior resulting from the movement of predators, the data obtained for set B follow a pattern akin to a limit cycle, thus spanning a wider area. It is worth noting that most of the

Table 2
Parameters used to analyse the migration stage.

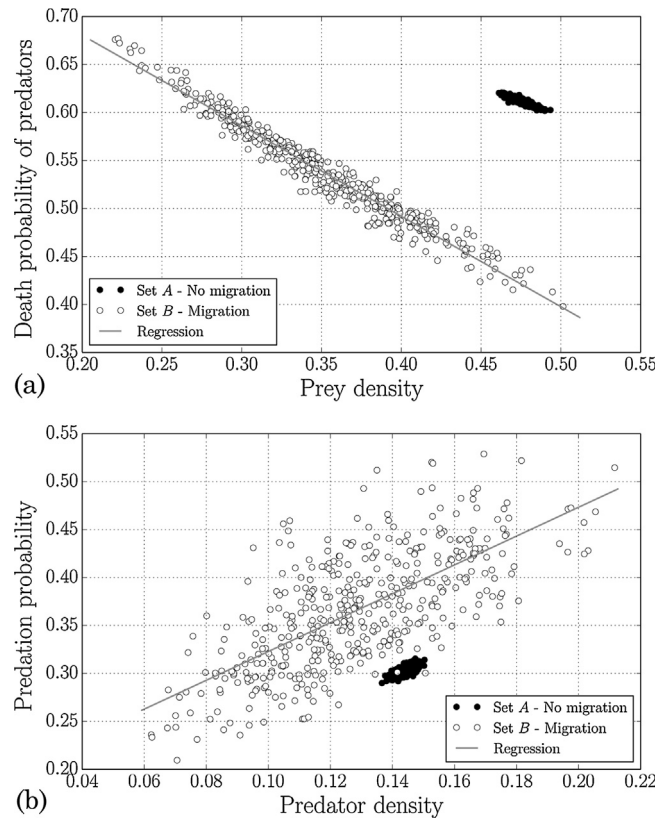| Parameter	Set A	Set B
Ψ_0	1	1
ϵ_Y	1	1
y	3	3
α	0.05	0.05
c	3	3
Φ_0	0.00000384147	0.00000384147
ϵ_Z	3	3
z	1	1
Migration parameter	Set A	Set B
k_1	0	1
k_2	0	1
l	1	7
ω	0	Linear decrease from 0.9 to 0.2

Fig. 6. Effects of the migration stage on the death probabilities of preys and predators. (a) Due to the movement of predators following the direction of highest prey density, there is a decrease on the death probability of predators with respect to a simulation where no migration occurs. In (b) it is possible to observe that, when predators do not migrate, the predation probability is lower with respect to the case in which predators move.

measurements obtained for the simulations using set B lie below the data obtained for set A (see Fig. 6a). When the migration stage is enabled, there is a decrease in the long-term density of the preys species; however, even under these "harsh" conditions, the death probability of predators is lower with respect to the case in which no migration occurs. A similar behavior can be observed in Fig. 6b. Measurements obtained using set A lie below the results obtained from set B, due to the movement of predators there is an increase in the predation probability.

To include the changes in the death probability of predators and predation probability in our mean field model, we follow a procedure first developed by Pascual et al. (2001) to determine the long-term dynamics at different spatial scales of a stochastic lattice model; the method parts from the result that certain quantities, e.g., the growth rates of preys and predators, preserve their functional form at different spatial scales. By first measuring such quantities directly from the computer simulations, and then performing suitable statistical regression methods on the obtained data, it is possible to adjust the parameters that control the mean field terms of the quantities of interest.

To apply this methodology in our simulations it is necessary to also measure the growth rate of both populations. The functional form of these quantities is similar: $(1 - \Psi_D)(1 - (1 - P_Y)^{\epsilon_Y \bar{y}_t})$ for the preys and $(1 - \Phi_t)(1 - (1 - P_Z)^{\epsilon_Z \bar{z}_t})$ for the predators, these terms are controlled by the parameters ϵ_Y and ϵ_Z respectively. To obtain a fitted curve for the data a least-squares regression was used. The results obtained show that the growth rate of preys behaves as if in average the reproductive capacity of preys $\epsilon_Y = 0.8744$; meanwhile the reproductive capacity of predators behaves as if $\epsilon_Z = 1.4693$. It is interesting to note that both

parameters are lower than the values specified for the simulation, such results is to be expected given the local nature of the interactions between individuals.

The mean field term for the death probability of predators $1 - \Psi_I$ assumes a linear relationship with respect to the number of sites not populated by preys. In its present form, the term is only valid for a "well mixed" environment where individuals are randomly placed on the lattice. However, as shown by Fig. 6a the data for the death probability of predators, obtained using sets A and B, clearly show a linear relationship with Ψ_I; the slope of the data shown in Fig. 6b suggests a similar behavior that depends on Φ_{t+1}. However, the data obtained from set B exhibit a greater deviation from the line representing such a relationship; this outcome has to be expected given the magnitude of the oscillations due to the movement of predators. Since we are dealing with linear functions, a polynomial regression is enough to adjust our mean field terms. Note that the only parameters that define the behavior of the death probability of predators and the predation probability are the coefficients of the first order polynomial for each data set. Let us call such coefficients a, b, d, and e, therefore the mean field term for the death probability of predators can be written as follows:

$$b + a\Psi_I \tag{10}$$

with $a = -1$ and $b = 1$, meanwhile the term for the predation probability can be expressed as:

$$e + d\Phi_{t+1} \tag{11}$$

with $e = 0$ and $d = 1$. It is possible to rewrite Eqs. (7) and (8) as follows:

$$\Phi_{t+1} = \Phi_R - (1 - \Psi_I)\Phi_R = \Phi_R - (b + a\Psi_I)\Phi_R \tag{12}$$

$$\Psi_D = \Psi_I - \Psi_I\Phi_{t+1} = \Psi_I - \Psi_I(e + d\Phi_{t+1}) \tag{13}$$

The results of the regression method for the data of set B give the coefficients $a = -0.9434$, $b = 0.8626$, $d = 1.5034$, and $e = 0.1726$ (additional details about these results can be found in Table 3). The effects of the adjusted parameters on the mean field model are shown in Fig. 5, a non-trivial fixed point where both populations coexist can be observed; it is easy to see, that the densities predicted by the adjusted mean field model correspond to the points around which the densities of preys and predators oscillate when the migration stage is enabled (see Fig. 4). We may summarize the effects of the movement of predators on the carrying capacity of the populations as follows: when moving towards zones where the density of preys is high, a predator increases their chance of survival; also, it increases the probability that its progeny survives the "death of predators" stage. With a greater number of predators surviving, there is an increase in the predation probability, which increases the death rate of preys. It is interesting to note that by increasing their odds of survival, the population of predators create harsher conditions for their species. Despite the fact that predators are able to survive under such conditions, the carrying capacity of both preys and predators is lower than the densities observed under a "well mixed" environment.

Table 3
Additional details for the linear regressions.

Set B	R^2	p-Value
Regression for a and b	0.9595083345163955	0.0
Regression for d and e	0.48146049419825371	0.0

5. Oscillatory behavior and spatial scale

Besides changing the mean density of the populations, the movement of predators also causes a transition to the oscillatory behavior. The oscillations have a very regular period, however, their amplitude, while bounded, is very difficult to predict (see Fig. 4). Previous works have shown that such oscillations in a prey–predator system should vanish in the thermodynamic limit (see Antal and Michel, 2000; Lipowski, 1999; Boccara et al., 1994; Durrett, 1994; Mobilia et al., 2007; Petrovskii et al., 2004), i.e., their amplitude diminishes as the size of the lattice is increased. To investigate such phenomenon, we performed additional computer simulations for lattices of size 2^{6+i} for $i = 0, 1, 2, 3, 4, 5, 6, 7$, i.e., from a lattice of size 64×64 sites to a lattice of size 8192×8192 sites; 10000 seasons were simulated using the parameters of Table 1. To obtain a measure of the amplitude of the oscillations, we calculated the standard deviation of the time series of the density of preys. Since the predators species has a similar behavior, we do not report those data. Fig. 7 shows the results of our simulations, as expected, the amplitude of the oscillations decays as the size of the lattice increases: for small lattices, an evolution towards a noisy limit cycle can be observed; as the size increases, the limit cycle destabilizes and the pattern of Fig. 4 appears. Additional increments in the size of the lattice further diminish the amplitude; however, in stark contrast to the results reported in Boccara et al. (1994), where noisy oscillations of low amplitude are observed for large lattices, we have found that the qualitative behavior of the density of preys remains unchanged: the amplitude of the oscillations is still bounded, but difficult to predict, and their period is preserved. Such behavior raises the need to emphasize the differences between our model and previous work where scaling effects are studied. First it must be noted that our predators have a mobility higher than that commonly found in other lattice models, where dispersal (whether by movement, reproductive processes, or both) is restricted to first neighbors. It is well known that large dispersal ranges bring the distribution of individuals on the lattice close to the "well mixed" case (Durret and Levin, 1994; Brännström and Sumpter, 2005), so oscillations might arise as a consequence of long range movement. Second, the spatial dynamics of oscillating prey–predator systems are commonly characterized by patterns akin to the initial invasion process, i.e., there are fronts of predators that invade prey rich areas leaving behind a few site populated by preys. These survivors quickly repopulate predated areas and the process starts again. Rozenfeld
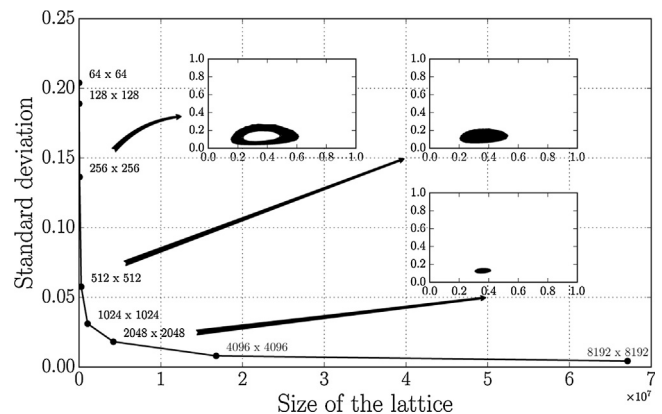

Fig. 7. Scaling behavior of the amplitude of the oscillations observed in the population of preys. Small lattices produce orbits to a noisy limit cycle; as the size of the lattice increases, the amplitude of the oscillations diminishes and the limit cycle destabilizes. For large lattices a new decrease of the amplitude is observed; however, the oscillations still have a regular period and their amplitude remains bounded, yet difficult to predict.

and Albano refers to these phenomena as "alternating percolation events" (Rozenfeld and Albano, 2001). As noted in section 3, in the proposed model such events are only observable during the transient phase; afterwards, we observe predators grouped together as swarms moving through the whole lattice while searching for zones with a "good" density of preys (a curious enough reader might wish to compare the spatial patterns found in Antal and Michel (2000), Boccara et al. (1994), Mobilia et al. (2007) and Rozenfeld and Albano (2001) with Fig. 2). The oscillatory behavior observed when migration is enabled, suggests that the time lapse between the predation of a particular zone by a swarm and the moment until such zone is qualified again as "good" by a swarm is regular.

6. Future work

The mean-field equations developed in Section 4 are only able to partially predict the behavior of the proposed model. We have shown that by including additional information about the populations of preys and predators in these equations, such prediction becomes more accurate. Is it possible to make further modifications to the mean-field equations, in such a way the they predict the oscillatory behavior of the proposed model at small and intermediate scales? Consider as an example the size of the swarms, it is reasonable to expect that individuals belonging to them are subjected to Allee effects. In particular there should be a threshold for the number of predators in a swarm, below which a swarm cannot survive for any extended period of time, i.e., a local extinction occurs. Above such threshold the swarm coexists and move. In (Pascual et al., 2011) it is shown that when local densities can be described as functions of global densities, the dynamics of the system, not only in the long-term, but also during the transient phase, can be approximated by a mean field model whose functional forms include power-laws of the local densities. It remains to be investigated if a similar process can be applied in our model. The size of the clusters of predators depends on the value taken by the parameters k_1, k_2 and l, so it is reasonable to expect that that quantities such as birth rate of predators and predation rate can be estimated using this information.

7. Conclusions

In the present work we have analysed the behavior of a prey–predator lattice model where predators hunt according to a local PSO algorithm. We have shown that for initial conditions near the absorbing state, where the lattice is fully covered by preys, there is an initial wavefront of predators moving outwards at the same speed. Such behavior is reflected as a monotonic approach to a non-trivial fixed point where preys and predators coexist. However, there are weak oscillations around the fixed point due to subsequent travelling waves produced by preys that survive the initial invasion of predators. Once the transient phase ends the systems exhibits oscillations with a regular period, but with an amplitude which is difficult to predict.

We have also shown that our local PSO algorithm increases the proficiency of predators, which produces a decrease in their death probability with respect to a simulation where no migration occurs. A higher density of predators results in an increase in the predation probability with a corresponding decrease in the density of preys. By taking into account these changes in a mean field model, we were able to accurately predict the mean densities around which the densities of both populations oscillate when the migration stage is enabled.

Finally we have explored the behavior of the proposed model for different sizes of the lattice; we found that even though the amplitude of the oscillations diminishes as the size of the lattice is increased, the same qualitative behavior is still observed for large lattices, and the period of oscillations is preserved.

PSO algorithms have the advantage of being the result of the study of cooperative behavior found in animal communities (bird flocks being a major influence). Moreover, we are only proposing a very simple use case for the algorithm; it is certainly possible to adapt our PSO algorithms to more complex scenarios, e.g., to model social hierarchies in a community; here, an individual takes only into account the information that members of "high rank" provide. So far we have found that through cooperation it is possible to observe an interesting spatial pattern that is quite different than the patterns reported in previous works. Yet, such phenomenon also leads to oscillatory behavior, which has been a matter of extensive research in ecological theory.

Appendix A. Mean field equations

1. *Intraspecific competition.* In order to derive a mean field equation that describes the intraspecific competition stage, let us ask the following: what is the expected number of deaths in a season due to the intraspecific competition? As it was shown previously, the death of a prey depends on the number of individuals of the prey species contained in the neighborhood M_c, it is reasonable then to expect that the mean number of deaths each season depends on the mean number of individuals in the neighborhood of each cell, let $\bar{y}_t$ represent this number. To calculate $\bar{y}_t$ we proceed as follows: it is clear that if $\Psi_t = 0$, then the mean number of preys in each neighborhood M_c is also zero, similarly if $\Psi_t = 1$, then the mean number of preys within each neighborhood M_c (excluding the prey at the center) is $|M_c| - 1$, an interpolation between the points $(0, 0$ and $(1, |M_c| - 1)$ (see Fig. 8) gives the equation:

$$\bar{y}_t = (|M_c| - 1)(\Psi_t) \tag{14}$$

Then, the probability that a prey dies as a consequence of the intraspecific competition is:

$$\frac{\bar{y}_t}{|M_c| - 1} = \frac{(|M_c| - 1)(\Psi_t)}{|M_c| - 1} = \Psi_t \tag{15}$$

The death of the all preys in the lattice is a sequence of events that can be described through a random variable with binomial distribution X. If Y_t denotes the number of preys in
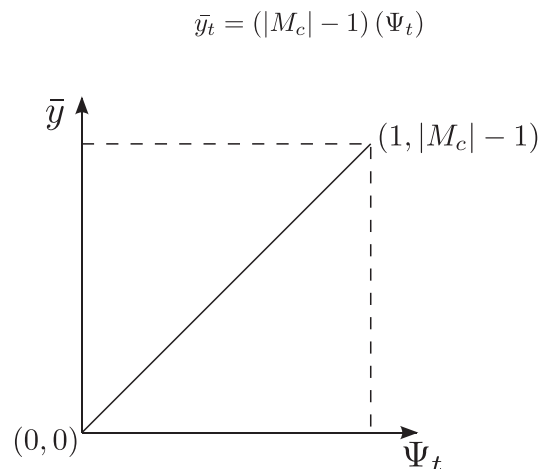
$$\bar{y}_t = (|M_c| - 1)(\Psi_t)$$

Fig. 8. The interpolation assumes proportionality between Ψ_t and the number of preys in the neighborhood M_c.

the lattice at time t, then the expected number of prey deaths is given by:

$$EX = \Psi_t Y_t \tag{16}$$

where E is the expected value operator, and Y_t is given by:

$$Y_t = \Psi_t |L| \tag{17}$$

thus:

$$EX = \Psi_t^2 |L| \tag{18}$$

To incorporate this quantity in the mean field equation, it must be converted into a density, this is done by dividing EX by $|L|$, and scaling the result by the coefficient α, obtaining that the density of preys that is eliminated each season is $\alpha \Psi_t^2$. Finally the mean field equation that describes the intraspecific competition is:

$$\Psi_{t+1} = \Psi_t - \alpha \Psi_t^2 = \Psi_t (1 - \alpha \Psi_t) \tag{19}$$

2. *Reproduction of preys.* Consider a cell with no prey, let us call such cell u. During the reproduction stage, all neighbors of u containing a prey might change its state, the number of neighbors being equal to $|M_y| - 1$. Since each neighbor chooses the location for new preys at random, the probability that a cell chooses cell u during reproduction is:

$$P_u = \frac{1}{|M_y| - 1} \tag{20}$$

The mean number of preys in the neighborhood of u is given by $\bar{y}_t$, thus the total number of reproduction "attempts" is:

$$\epsilon_Y \bar{y}_t \tag{21}$$

where:

- ϵ_Y is the reproductive capacity of preys.
- $\bar{y}_t = (|M_y| - 1)(\Psi_t)$ is the mean number of preys in the neighborhood of cell u.

Let X denote the random variable that counts the number of times cell u is chosen for reproduction, it is clear that X is a binomial random variable with parameters $(P_u, \epsilon_Y \bar{y}_t)$. Now $(1 - P_u)^{\epsilon_Y \bar{y}_t}$ is the probability that none of the preys in the neighborhood of u chooses it for reproduction, then $1 - (1 - P_u)^{\epsilon_Y \bar{y}_t}$ is the probability that cell u is chosen at least once during the reproduction stage. The mean density of cells with no preys that are chosen for reproduction during the corresponding stage is:

$$(1 - \Psi_t)(1 - (1 - P_u)^{\epsilon_Y \bar{y}_t}) \tag{22}$$

3. *Death of predators.* Each season, if a predator is not located at a cell containing a prey, it dies with probability 1. The number of predators that die each season is proportional to the number of cells not containing a prey, the probability of finding a cell with such a property is given by:

$$\frac{|L| - Y_t}{|L|} = 1 - \frac{Y_t}{|L|} = 1 - \Psi_t \tag{23}$$

Then the expected number of deaths that occur each season is given by:

$$(1 - \Psi_t) Z_t$$

where Z_t is the number of predators at time t. Finally the expected decrease in density is:

$$(1 - \Psi_t) \Phi_t \tag{24}$$

4. *Reproduction of predators.* This process behaves just as the reproduction of preys.

5. *Predation.* Each season if a prey is located at a cell containing a predator, it dies with probability 1. The probability of finding a cell with a predator is:

$$\frac{Z_t}{|L|} = \Phi_t \tag{25}$$

The expected number of preys dying each season is:

$$\Phi_t Y_t \tag{26}$$

And the expected decrease in density is given by:

$$\Phi_t \Psi_t \tag{27}$$

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