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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.

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

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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