BIOLOGICAL CONTROL OF A PEST IN A REACTION-DIFFUSION PREDATOR-PREY SYSTEM WITH ALLEE EFFECT

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Abstract. *A common strategy in pest biological control is the release of a natural enemy of the pest. Such introduced species is sometimes named control agent. One of the explanations for biological control failure accounts for the presence of Allee effects in the control agent. An Allee effect can be defined as the positive density dependence between one (or more) fitness item of an individual and the density of its own population. The aim of biological control is to eradicate the pest or at least keep it below some economic threshold that does not affect significantly the rent of the involved activity (pest suppression). In the present work we assess how the intensity of the release of the pest enemy can be detrimental or advantageous to pest management goals. To this end we resort to numerical simulations of a reaction-diffusion prey-predator model in a one-dimensional environment where the native and exotic species interact.*

Keywords: *Allee effect, reaction-diffusion, invasive species, biological control, predator-prey system.*

1 INTRODUCTION

Invasive species increasingly threaten ecosystems worldwide. A commonly used biocontrol strategy to counteract these invasions consists of the deliberate introduction of natural enemies of an invasive pest species (Blackwood et al., 2012; Suckling et al., 2012). A particular case is the introduction of a biological control agent when a pest invades a plant cultivation in a greenhouse (Van Lenteren, 2000).

In this work, in order to assess the effectiveness of this biocontrol strategy, we develop a predator-prey dynamical model where the prey species is the pest (invasive species) and the consumer is the deliberately introduced biological control agent. That is to say, in our proposed model, both pest and control agent are supposed to be exotic species. Based on the empirical evidences (Bompard et al., 2013), it is supposed that the consumer (the biological control agent) has an Allee effect in its numerical response (Zhou et al., 2005; Verdy 2010). We first analyze a non-spatial predator-prey model based on Verdy (2010) composed of a system of two coupled nonlinear differential equations. Secondly, we analyze the corresponding spatial model adding diffusion processes to both prey and predator, converting thus the model to a system of coupled nonlinear partial differential equations. By means of numerical simulations it is shown that the amount of released enemies is crucial to the success or failure of the biocontrol strategy in both modeling contexts.

The results found in this work should not be seen as general results. Instead, they are related to a specific set of parameter values. The analyzed population models are of strategic type (May, 2001) and therefore they do not usually describe the dynamics of a specific real biological system. In this view, the analysis is based on a hypothetical set of parameters. Since the studied models have a large number of parameters, the intention is to show some possible outcomes instead of an exhaustive study for all possible outcomes (Abrams and Roth, 2004).

2 METHODS

The population framework to be analyzed is schematically displayed in figure 1 (hereinafter FR_2 denotes functional response type 2).

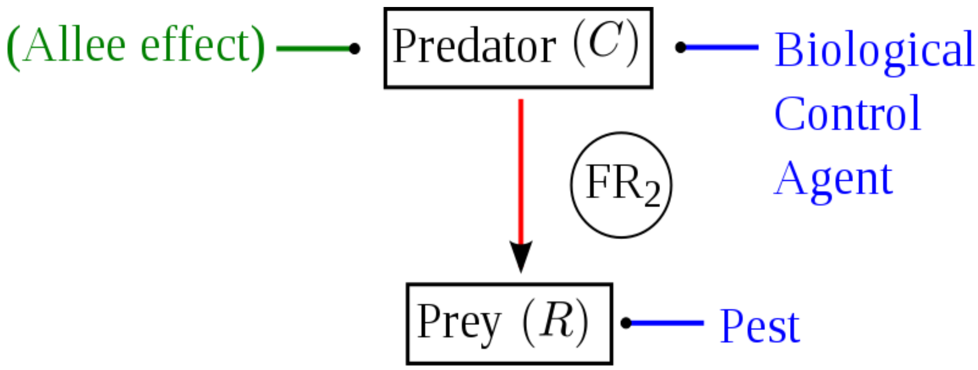


Fig. 1: An introduced control agent (C) preys upon the pest (R) with functional response type 2. Allee effect acts on the agent C. Arrow denotes consumption.

The trophic scheme of figure 1 consists basically of a ditrophic food chain: prey (pest, R); predator (an introduced biological control agent, C). The dynamics of figure 1 in an homogeneous environment can be modeled by (Verdy, 2010) :

$$\begin{aligned} \frac{dR}{dt} &= rR\left(1-\frac{R}{K}\right)-\frac{a_{CR}R}{1+a_{CR}T_{hCR}R}C; \\ \frac{dC}{dt} &= ef_{RC}\left(\frac{C}{\theta_C+C}\right)\left(\frac{a_{CR}R}{1+a_{CR}T_{hCR}R}C\right)-m_C C, \end{aligned} \tag{1}$$

where R is the density of pest individuals and C is the density of biological control agent individuals; r is the maximum per capita rate of pest growth and K is its carrying capacity; a_{CR} represents the attack coefficient of the introduced biological control agent C upon the pest R; T_{hCR} is the manipulation time of R by C, while ef_{RC} is the biological control agent's food-to-offspring (R to C) conversion efficiency coefficient. Finally, $\left(\frac{C}{\theta_C+C}\right)$ describes the Allee effect on C, where θ_C denotes its intensity, and m_C is the density independent per capita mortality rate of C.

A spatio-temporal counterpart to model (1) can be given by the following model:

$$\begin{aligned} \frac{\partial R}{\partial t} &= D_R\frac{\partial^2 R}{\partial x^2}+rR\left(1-\frac{R}{K}\right)-\frac{a_{CR}R}{1+a_{CR}T_{hCR}R}C; \\ \frac{\partial C}{\partial t} &= D_C\frac{\partial^2 C}{\partial x^2}+ef_{RC}\left(\frac{C}{\theta_C+C}\right)\left(\frac{a_{CR}R}{1+a_{CR}T_{hCR}R}C\right)-m_C C, \end{aligned} \tag{2}$$

where D_R and D_C are the diffusivity coefficients of prey and predator, respectively. The spatial domain x has the length from 0 to $L = 10$.

We assume that the initial spatial distributions of pest and agent are uniform: $R(x,0) = \alpha > 0;\ C(x,0) = \beta > 0$, except on the boundaries. This assumption may describe the uniform spatial distribution of pest among plants and a concomitant uniform spatial spreading of the agent as a measure of pest biological control. Moreover, we apply homogeneous Dirichlet boundary conditions, that is, $R(0,t) = R(L,t) = C(0,t) = C(L,t) = 0$. These boundary conditions can well represent plant cultivation in a greenhouse where pest and agent individuals cannot survive on its borders.

Model (1) is solved using a 4th Runge-Kutta method. In the following experiments we set $h = 0.05$ and $\Delta t = 0.05$, which yield convergent discrete approximations. Remark that the numerical scheme is stable independently of the parameters which are small enough to guarantee the solution accuracy. Model (2) is solved numerically by using the finite differences method. To this end both the spatial and time domains are uniformly discretized into N and M parts so that $h = \frac{L}{N}$ and $\Delta t = \frac{T}{M}$, where T is the total simulation time. Backward Euler method is used in time and the second order operator is approximated by central differences. The resulting system of algebraic equations is linearized using the Picard method and solved by uncoupling the equations with a Gauss-Seidel structure. Finally, the Gaussian elimination is used to the two linear systems.

Our intent is to assess the effects of the predator (C) initial condition on model (1) and the predator initial distribution on model (2) regarding the coexistence and/or extinction of the involved species for both models.

3 RESULTS

First, we choose a specific set of parameter values in model (1) such that species stable coexistence occurs as shown in figure 2.

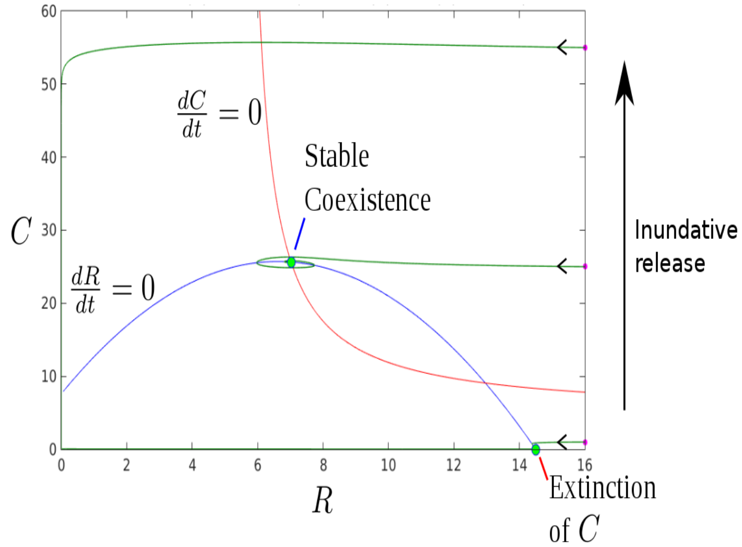
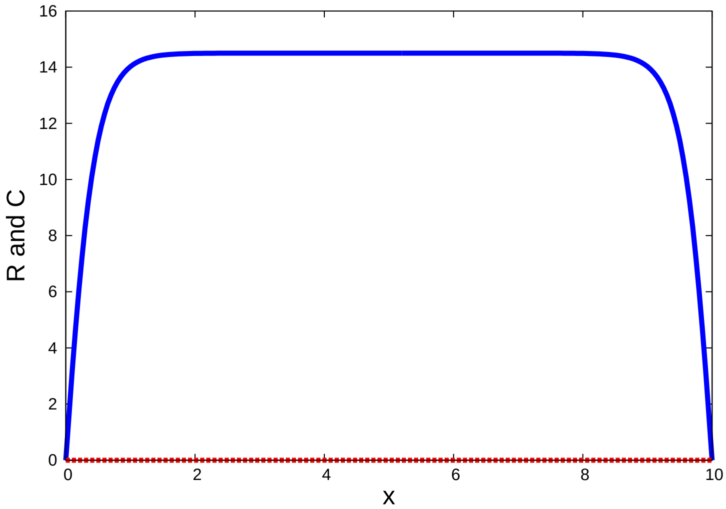


Fig. 2: One phase plane of model (1)**. Parameter values:** $r = 6; K = 14.5; a_{CR} = 0.7903; T_{hCR} = 1; ef_{RC} = 0.8; \theta_C = 1.1; m_C = 0.65$. '•' **- initial conditions:** $(16,\ 1), (16,\ 25)$ **and** $(16,\ 55)$**;** '•' **- final value for** $t = 500$**.**

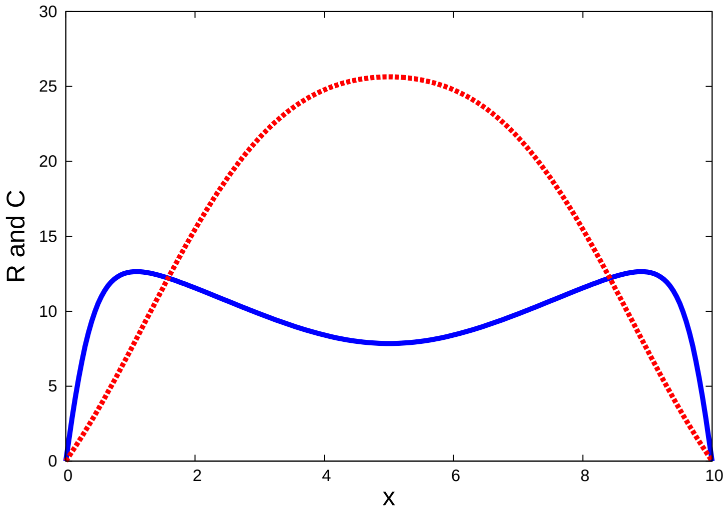
Figure 2 shows that the dependence on the initial population of agent plays a crucial role on the ultimate dynamics of model (1). Actually, this phase plane represents an inundative release of pest natural enemy (i.e., increasing agent initial population while maintaining pest population constant). Note that agent extinction occurs for inoculative as well as inundative releases. However, for intermediary values of enemy release pest and agent, stable coexistence can occur, which may portray a possible success of pest control depending on whether the stable pest level is below economic thresholds (Boukal and Berec, 2009).

These results are partially in contrast with the dynamical results pertaining to model (1) without the Allee effect in the agent (i.e., $\theta_C = 0$). In this case model (1) reduces to a Rosenzweig-McArthur model (Turchin, 2003) where according to parameter values the dynamics consist of either a globally stable limit cycle or a globally stable equilibrium point. In the former the introduction of an agent would be advantageous to pest biological control if the magnitude of the sustained oscillation is relatively small; otherwise it might imply pest outbursts. In the latter it would depend on whether the pest stabilization level is below economic thresholds (Boukal and Berec, 2009). In terms of the numerical solution of model (2), setting $\theta_C = 0$ reduces the nonlinearity, which eventually improves convergence of the iterative process.

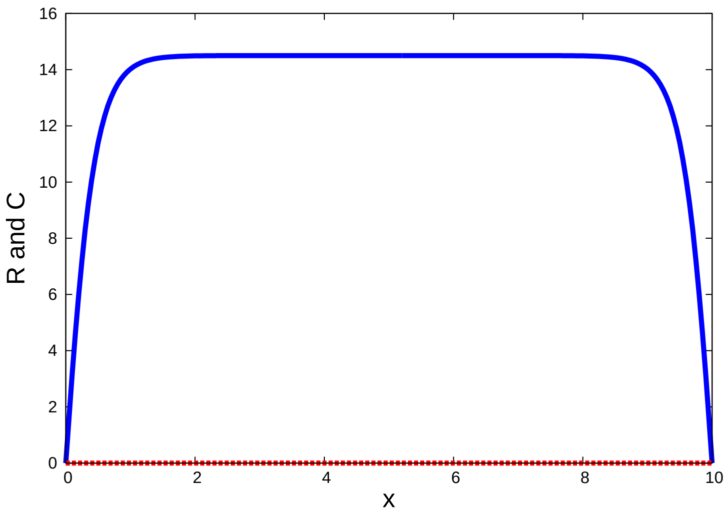
Figure 3 shows a simulation of model (2) with the same parameter values of model (1) with diffusion coefficients of pest and agent respectively given by $D_R = 0.4; D_C = 0.17$. In order to simulate an inundative release of pest enemy in a spatial context, the initial distributions of pest and agent are uniform and with the same values as the initial conditions of figure 2.



(a) Uniform initial conditions: $R = 16$ and $C = 1$.



(b) Uniform initial conditions: $R = 16$ and $C = 25$.



(c) Uniform initial conditions: $R = 16$ and $C = 55$.

Fig. 3: Spatial distribution of pest and agent along space x, $L = 10$, at $t = 100$ in model (2). Diffusion coefficients of pest and agent are respectively: ($D_R = 0.4; D_C = 0.17$); initial distributions: (a) $(16,\ 1)$; (b) $(16,\ 25)$; (c) $(16,\ 55)$. Solid blue line: pest R; dashed red line: agent C. Parameter values are the same as those of figure 2.

Similarly as in figure 2, figure 3 displays three behaviors as $C(x, 0)$ increases: C extinction, stable coexistence of C and R, and C extinction again. In terms of pest control this sequence of results points to the fact that failure of pest biocontrol can be interspersed with pest and agent coexistence (which can portray a possible success of pest control depending on the stable pest spatial distribution) as more agents are introduced in the system. This non-monotonic behavior is at variance with the view that agent inundative releases are proper to pest eradication or control. We also performed simulations of models (1) and (2) under the same structure of augmenting the pest enemy releases for $\theta_C = 1$ (in which case sustained oscillations are generated in model (1)). The results from pest biocontrol point of view were the same as the ones presented in this section. It is important to note, however, that the degree of generality of the above results awaits further analyses, such as the influence on the dynamics of model (2) generated by the relation between the magnitude of the diffusion coefficients D_R and D_C, and non-uniform initial conditions, to name a few. In this way in table 1 we present the results for some other values of D_R and D_C.

Table 1: Possible outcomes of model (2) for some values of D_R and D_C; a: intermediary initial conditions generate coexistence, b: agent extinction for all simulated initial conditions. Parameter values are the same as those of figure 2.

D_R	D_C	Outcome
0.17	0.1	a
0.17	0.17	a
0.17	0.4	b
0.4	0.17	a
0.4	0.4	b
0.4	0.74	b
0.74	0.17	a
0.74	0.74	b
0.74	0.9	b

4 DISCUSSION

In order to investigate the influence of the intensity of pest enemy releases on pest dynamics, a non-spatial and spatial predator-prey model were devised where the basal species portrayed the pest and the introduced biological control agent was cast as the predator. The main finding of this work is that the intensity of pest enemy releases is relevant to the success or failure of the proposed biocontrol strategy. However, contrary to the common belief in pest control procedures, an excessive amount of pest enemy individuals (i.e., inundative releases) may be detrimental to the effectiveness of biocontrol (Costa and dos Anjos, 2015). These results are valid for both spatial and non-spatial analyzed predator-prey models for the considered set of parameters.

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