Pattern Formation in a Resource and Two Consumers Discrete Model

Formación de Patrones en un Modelo Discreto de un Recurso y dos Consumidores

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Abstract

In this work, we propose a Coupled Map Lattice model to analyse the spatio-temporal dynamics of a system of three interacting species: a resource species and two consumers. The resource is an insect with potential to become an agriculture pest while one of the consumers is a parasitoid and the other, is a predator. All the three species reproduce at the same time scale so that the dynamics is described by a system of three difference equations. The resource grows according to the Beverton-Holt function and the consumption is described by the Holling type III functional response. By means of numerical simulations, we observed that the pattern of species spatial distribution and the temporal density depend on the dynamical as well as on the movement parameters. It can be stable or oscillating heterogeneous spatial distributions but the species can also be homogeneously distributed in space. Finally, we observe that the inclusion of the space does not change the forecast of extinction obtained by the local dynamics only for some parameters.

Keywords:

Coupled Map Lattice, Discrete Models, Resource Consumers models

Resumen

En este trabajo proponemos un modelo del tipo Redes de Mapas Acoplados para analizar la dinámica espacio-temporal de un sistema de tres especies interactuantes: una especie recurso y dos consumidores. El recurso es un insecto con potencial para convertirse en plaga agrícola, mientras que uno de los consumidores es un parasitoide y el otro, un depredador. Las tres especies se reproducen en la misma escala temporal, de modo que la dinámica se describe mediante un sistema de trés ecuaciones en diferencias. La especie recurso crece según la función de Beverton-Holt y el consumo se describe mediante la respuesta funcional Holling tipo III. Mediante simulaciones numéricas, observamos que el patrón de distribución espacial de las especies y la densidad temporal dependen tanto de los parámetros de la dinámica como de los de movimiento. Pueden surgir distribuciones espaciales heterogéneas estables u oscilantes, pero las especies también pueden distribuirse homogéneamente en el espacio. Por último, observamos que la inclusión del espacio no modifica la previsión de extinción obtenida únicamente por la dinámica local para algunos parámetros.

Palabras Claves:

Redes de Mapas Acoplados, Modelos Discretos, Modelos Recurso Consumidores

1   INTRODUCTION

N atural enemies of insects represent an important tool to control insect pest populations in agriculture. They can help keeping the insect pest at acceptable densities and hence, decrease the input of pesticides. Before introducing biological species in the environment, it is important to study the dynamics in order to avoid undesirable effects such the extinction of non target species, for example. Most studies on biological control deal with the interaction of an insect pest and just one enemy. However, in natural habitats, communities of many different species interact and the use of multiple controlling agents in biological control is an important topic for theoretical investigation (Hassel and May, 1986; Jones *et al.*, 1993; Hassell, 2000).

In the present work, we propose a discrete spatio-temporal model to study the dynamics of three interacting species: a resource species and two specialist consumers. The resource species has potential to become an agriculture pest while the consumers are the pest natural enemies. It can be, for example, a rodent and two predators or an insect pest and two parasitoids. For making the description and the interpretation easier, we suppose that the resource species is an insect pest; one of the consumers is a parasitoid and the other is a predator. The resource species participates in the interaction as host and prey at the same time; however, we will refer to it by resource species in order to avoid any confusion. The resource growth process is represented by the Beverton-Holt model and its consumption by both enemies is described by the discrete equivalent to the Holling type III functional response (Kot, 2001). We also assume that all the three species grow at the same time scale.

When the environment is markedly discrete and that the dynamical processes occur at well defined time stages, a model formulated in terms of Coupled Map Lattices (CML) provide a good description (?Comins *et al.*, 1992).

The paper is organized as follows: in the *Coupled Map Lattice Model* Section we describe the CML model, the local dynamics and the movement stage. In the section *Results* we present the results of numerical implementations of the proposed model while in the section *Conclusions*, we discuss the results and make conclusions from the ecological point of view.

2   COUPLED MAP LATTICE MODEL

The proposed CML model assumes a two dimensional spatial domain, split in sites arranged as a lattice where each site is identified by the index (i,j). The state of the site (i,j) is described by three values corresponding to the species density in the site. The dynamics is composed by two different stages: the movement stage and the reaction stage which occurs alternately (?).
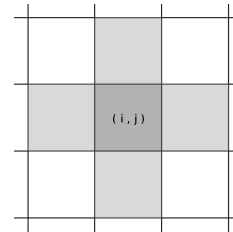
Figure 1: von Neumann neighbourhood (gray sites) of site (i,j).

During the movement stage, the individuals of each species disperse and are redistributed in the lattice. Several mechanisms can promote the individuals movement such as a random movement in homogeneous habitat; biased movement due to attraction to some source of food as well as repulsion to toxic substances or enemies; it can also be due convection of the fluid where individuals leave such as the wind or a river stream (Edelstein-Keshet, 1998). Here, we consider that the environment is homogeneous and individuals move randomly to its neighbours.

We define the neighbourhood $V_{i,j}$ of site (i,j) as those sites for which the individuals at site (i,j) can migrate. Here we consider that individuals, of all the three species, at a site can migrate to the four nearest sites. That is, we consider the von Neumann neighbourhood defined by:

$$V_{i,j} = \{(i-1,j); (i+1,j); (i,j-1); (i,j+1)\},$$

and illustrated in Figure 1.

We represent by $N'_{i,j,t}$ the density of the resource species and by $P'_{i,j,t}$ and $W'_{i,j,t}$ the density of the parasitoid and predators, respectively, in the site (i,j), after the movement stage of generation t. At each generation, during the movement stage, a constant fraction of each species: β_N for the resource, β_P for the parasitoid and β_W for the predator, leaves the site (i,j) and evenly migrates to the sites of $V_{i,j}$. Hence, a fraction $1 - \beta_x$, (where $x = N, P$ or W) of each population remains in the site (i,j).

The equations for the proposed movement stage are:

$$\begin{cases} N'_{i,j,t} = (1-\beta_N)N_{i,j,t} + \displaystyle\sum_{(x,y)\in V_{i,j}} \frac{\beta_N}{4}N_{x,y,t} \\[2mm] P'_{i,j,t} = (1-\beta_P)P_{i,j,t} + \displaystyle\sum_{(x,y)\in V_{i,j}} \frac{\beta_P}{4}P_{x,y,t} \\[2mm] W'_{i,j,t} = (1-\beta_W)W_{i,j,t} + \displaystyle\sum_{(x,y)\in V_{i,j}} \frac{\beta_W}{4}W_{x,y,t}. \end{cases} \quad (1)$$

Moreover equations (1), we consider reflective boundary conditions, so that the fraction β_x ($x = N, P, W$) of individuals located at a boundary site migrate to the three (or two, for the sites in the four corners of the domain) neighbouring sites.

That is, we suppose that the environment is uninhabitable outside the domain and that individuals can sense the habitat quality and decide do not leave it.

After the movement stage, all the interactions occur locally in each site: growth, intra-specific competition of the resource individuals, parasitism and predation. The proposed nondimensional equations for the dynamics are given by:

$$\begin{cases} N_{i,j,t+1} = N'_{i,j,t}f(N'_{i,j,t})g_1(N'_{i,j,t},P'_{i,j,t})g_2(N'_{i,j,t},W'_{i,j,t}) \\ P_{i,j,t+1} = B_1N'_{i,j,t}(1-g_1(N'_{i,j,t},P'_{i,j,t})) \\ W_{i,j,t+1} = B_2N'_{i,j,t}(1-g_2(N'_{i,j,t},W'_{i,j,t})), \end{cases}$$
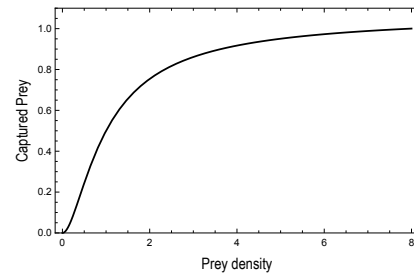(2)

where $N_{i,j,t+1}$ is the resource density, $P_{i,j,t+1}$ and $W_{i,j,t+1}$ are the density of the consumers at site (i,j) at the beginning of generation $t+1$, after the reactions have taken place. B_1 is the number of the parasitoid viable eggs in one resource individual and B_2 represents the predator growth factor. Function $f(N)$ which describes the resource growth, $g_1(N,P)$ and $g_2(N,W)$ which represent the resource density that escape from parasitism and predation, respectively, are given by

$$f(N) = \frac{\lambda}{1+(\lambda-1)\frac{N}{k}},$$

$$g_1(N,P) = e^{\left(\frac{-a_1NP}{1+(e_1N)^2}\right)},$$
(3)

$$g_2(N,W) = e^{\left(\frac{-a_2NW}{1+(e_2N)^2}\right)},$$

where $\lambda, k, a_1, e_1, a_2$ a,d e_2 are positive parameters.

In the absence of the consumers, the resource growths according to the Beverton-Holt function $f(N)$, which is equivalent to the continuous logistic growth. $\lambda > 1$ is the resource species intrinsic growth rate and k is its carrying capacity. We assume that predators and parasitoids consume the resource with Holling type III functional response. $N(1-g_x(N,1))$, $(x=1,2)$, is a sigmoidal curve which describes the density of the resource species captured by one consumer during one generation (see Figure 2). It assumes that the consumer is inefficient at low resource densities. On the other hand, consumers have a saturation effect at high resource densities. $\frac{a_x}{(e_x)^2}$, $(x=1,2)$, represents the maximum density of the resource species captured by one predator (or killed by one parasitoid) during one generation (Kot, 2001). That is, $\lim_{N\to+\infty} N(1-g_x(N,1)) = \frac{a_x}{e_x^2}$, $(x=1,2)$. $\frac{1}{e_x}$ $(x=1,2)$ corresponds to the resource density for which the fraction that is captured $(1-g_x(N,1))$ by one parasitoid is maximum; that is, $\frac{1}{e_x}$ $(x=1,2)$ is the point of maximum of function $1-g_x(N,1)$.

In order to identify the relevant groups of parameters, we introduce the nondimensional variables $n_{i,j,t} = e_2N_{i,j,t}$, $p_{i,j,t} = \frac{e_2}{B_1}P_{i,j,t}$ and $w_{i,j,t} = \frac{a_2}{e_2}W_{i,j,t}$ in system (2) to obtain the

Figure 2: Holling type III functional response: density of resource captured by one predator (or killed by one parasitoid) during a generation. That is, $N(1-g_x(N,1))$ where $x = 1,2$.

following nondimensional equations for the dynamical stage:

$$\begin{cases} n_{i,j,t+1} = n'_{i,j,t}F(n'_{i,j,t})G_1(n'_{i,j,t},p'_{i,j,t})G_2(n'_{i,j,t},w'_{i,j,t}), \\ p_{i,j,t+1} = n'_{i,j,t}(1-G_1(n'_{i,j,t},p'_{i,j,t})), \\ w_{i,j,t+1} = \mu_2 n'_{i,j,t}(1-G_2(n'_{i,j,t},w'_{i,j,t})), \end{cases}$$
(4)

where $n_{i,j,t+1}$ is the resource density, $p_{i,j,t+1}$ and $n_{i,j,t+1}$ are the density of the consumers at site (i,j) at the beginning of generation $t+1$, after the reactions have taken place. Function $F(n)$ which describes the resource growth, $G_1(n,p)$ and $G_2(n,w)$ which represent the resource density that escape from parasitism and predation, respectively, are given by

$$F(n) = \frac{\lambda}{1+(\lambda-1)\frac{n}{\alpha_2}},$$

$$G_1(n,p) = e^{\left(\frac{-\mu_1 np}{1+\alpha_1 n^2}\right)},$$
(5)

$$G_2(n,w) = e^{\left(\frac{-nw}{1+n^2}\right)}.$$

The nondimensional parameters are $\mu_1 = \frac{B_1a_1}{(e_2)^2}$, $\mu_2 = \frac{B_2a_2}{(e_2)^2}$, $\alpha_1 = (\frac{e_1}{e_2})^2$ and $\alpha_2 = e_2k$.

We observe that the equations for the movement stage (1) in the nondimensional variables do not change.

3 RESULTS

Initially, we study the local dynamics. At each site (i,j), the system (4) - (5) has five equilibrium solutions:

- $P_1 = (0,0,0)$, the trivial equilibrium;

- $P_2 = (\alpha_2,0,0)$, the resource only equilibrium;

- $P_3 = (\bar{n},\bar{p},0)$, the predator extinction equilibrium;

- $P_4 = (\bar{n},0,\bar{w})$, the parasitoid extinction equilibrium and

- $P_5 = (\bar{n},\bar{p},\bar{w})$, the coexistence equilibrium.

The standard Jury criterion for linear stability analysis, indicates that P_1 is never stable, since $\lambda > 1$. P_2 is linearly asymptotically stable given that:

(*a*)

(*b*)

(*c*)
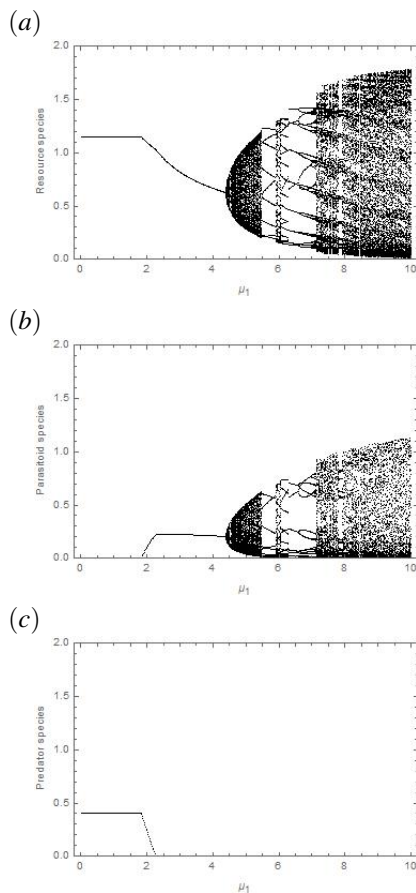
Figure 3: Bifurcation diagrams with respect to μ_1 for (*a*) resource species, (*b*) parasitoid and (*c*) predator, with $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$, $\mu_2 = 1.94$ and $\lambda = 2$.

- 1) $\lambda > 1$;

- 2) $\alpha_2^2(\mu_1 - \alpha_1) < 1$ and

- 3) $\alpha_2^2(\mu_2 - \alpha_1) < 1$.

Due to the complexity of the expressions in system (4) - (5), it is not possible to find neither the analytical expressions for P_3, P_4 and P_5 nor the conditions for their stability. Numerical simulations indicate the existence and stability of these equilibria as well as $p-$cycles and periodic limit cycles solutions. Figure 3 illustrates the typical behaviour observed in the dynamics through bifurcation diagrams of the populations with respect to μ_1. For small values of μ_1, P_4 is stable; as μ_1 increases, the three species coexist and P_5 is stable. Further increase in μ_1, which means that the parasitoid effectiveness increases, promotes the extinction of the predator population and then P_3 is stable until a bifurcation leads to the emergence o limit cycles.

In order to study the spatio-temporal dynamics of model (1), (4) and (5), we developed numerical simulations in a 50×50 square lattice for several different dynamical

and movement parameters. Our main interest is identify heterogeneous spatial distribution of the species. All the simulations start from a heterogeneous small perturbation of the asymptotic solution $(\overline{n}, \overline{p}, \overline{w})$, numerically obtained for each set of parameters. That is, $n_{i,j,0} = \overline{n}(1 + 0,1\ \xi_{i,j}^1)$; $p_{i,j,0} = \overline{p}(1 + 0,1\ \xi_{i,j}^2)$; $w_{i,j,0} = \overline{w}(1 + 0,1\ \xi_{i,j}^3)$, where ξ^1, ξ^2, $\xi^3 \in [-1,1]$ are randomly chosen according to the uniform distribution. For dynamical parameters for which the equilibrium is stable, the initial distribution corresponds to a small perturbation of the equilibrium in each site. On the other hand, for parameters promoting oscillating cycles ($p-$cycles or limit cycles), the initial value in each site corresponds to a perturbation of a solution value.

The classical Turing type patterns appearing in predator-prey systems occur for dynamical parameters for which the local equilibrium is stable. Moreover, movement parameters of prey and predators must be different (Edelstein-Keshet, 1988). In discrete models, heterogeneous patterns in predator prey models have been found from perturbations of the stable equilibrium along with discrepant movement parameters for prey and predators (Rodrigues et al., 2011). Heterogeneous spatial distributions for predator and prey have also been found close to Neimark-Sacker bifurcations (Rodrigrues et al., 2011). Since we do not have an analytical criterion for pattern formation with three species in discrete models, we consider the dynamics in different regions of the dynamical parameters space and the movement parameters with different magnitude for the three species.

We present the spatial distribution of the species trough density plots in which the dark (light) gray tones indicate high (low) densities. We also show graphs of the total density of each species over time.

In a first numerical experiment, we consider dynamical parameters for which the local coexistence of the three species is stable, that is, $\mu_1 = 2$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$ and $\lambda = 2$. Furthermore, movement parameters for each species were taken as $\beta_n = 0.91$, $\beta_p = 0.01$ and $\beta_w = 0.01$. The Figure 4 illustrates heterogeneous spatial distribution of the resource (a), parasitoids (b) and predators (c) at time-step $t = 600$. The pattern obtained also depend on the initial perturbation of the species however, the type of pattern is related to the parameters. Figure 5 shows that the total population remains constant over time.

In order to investigate the effects of the movement parameters on the spatio-temporal dynamics, we fixed the dynamical parameters as those in Figure 4 and simulate the equations for different values of β_x. Heterogeneous patterns were obtained when both consumers move at low rates. We obtained homogeneous distributions of the species when at least one of the consumers move at high rate (see Table 1).

Figure 6 shows the spatial distribution of the resource species for $\mu_1 = 4.5$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$
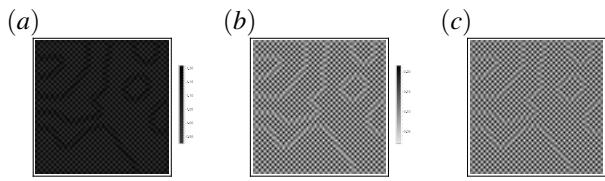
Figure 4: Spatial distribution of: (*a*) resource species, (*b*) parasitoids (*c*) predators, at $t = 600$, for $\mu_1 = 2$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$, $\lambda = 2$, $\beta_n = 0.91$, $\beta_p = 0.01$ and $\beta_w = 0.01$.
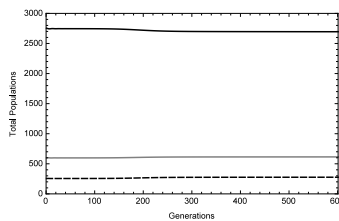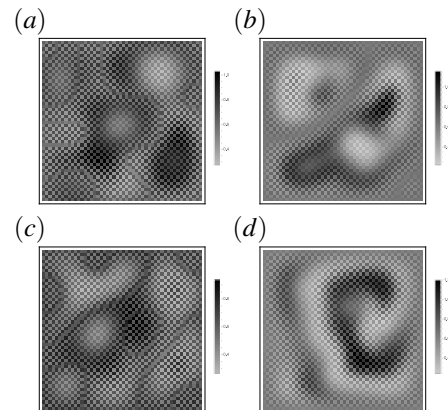

Figure 5: Total populations of the resource species (solid black curve), the parasitoids (dashed curve) and predators (gray curve). The parameters are: $\mu_1 = 2$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$, $\lambda = 2$, $\beta_n = 0.91$, $\beta_p = 0.01$ and $\beta_w = 0.01$.

Table 1: Spatial distribution for different values of β, with $\mu_1 = 2$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$ and $\lambda = 2$.

Values of β	Spatial distribution
$\beta_n = 0.01$; $\beta_p = 0.91$; $\beta_w = 0.01$	Homogeneous
$\beta_n = 0.01$; $\beta_p = 0.01$; $\beta_w = 0.91$	Homogeneous
$\beta_n = 0.91$; $\beta_p = 0.91$; $\beta_w = 0.01$	Homogeneous
$\beta_n = 0.01$; $\beta_p = 0.91$; $\beta_w = 0.91$	Homogeneous

and $\lambda = 2$, and different values of the movement parameters. For this set of dynamical parameters, the resource and parasitoids species oscillate while the predator species goes extinct in the local dynamics. The spatio-temporal dynamics of the CML, on the other hand, depends on the movement parameters. However, the predator species did not persist for any of the movement rate used in our simulations. The resource and parasitoid spatial distributions exhibited either homogeneous or heterogeneous distributions. Homogeneous distributions were obtained when resource species and parasitoid movement rate were close to each other (for example: $\beta_n = 0.01$; $\beta_p = 0.01$; $\beta_w = 0.9$; and $\beta_n = 0.91$; $\beta_p = 0.98$; $\beta_w = 0.01$, which are not illustrated here for the sake of brevity). On the other hand, when their movement rate were significantly different, heterogeneous distributions were observed (Fig. 6). Since the parasitoid spatial distribution is very similar to the resource one, Figure 6 only presents the spatial distribution of the resource species. Figure 7 illustrates the corresponding total population of the resource species (black continuous curve) and parasitoids (dashed curve). We can observe that the amplitude

Figure 6: Spatial distribution of the resource species at $t = 600$, for dynamical parameters $\mu_1 = 4.5$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$ and $\lambda = 2$ and different sets of the movement parameter β:
(a) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.01$;
(b) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.01$;
(c) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.9$;
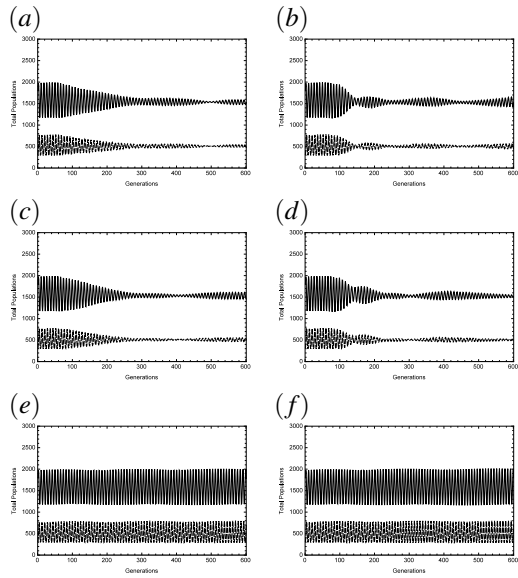(e) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.9$;

of population oscillations depends on the movement parameters. It is worth noting that Figure 7(e) and (f) correspond to oscillations with homogeneous spatial distributions (spatial distributions are not illustrated in Fig. 6). That is, the populations oscillate in time with the same density in all the sites of the habitat.

We now perform the simulation with parameters for which the local dynamics shows $p-$cycles of the resource and the predator populations while the parasitoid goes extinct: $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$, $\mu_1 = 1.84$, $\mu_2 = 5.7$ and $\lambda = 2$. The results of spatial model with this set of parameters depend on the species movement rate. Figure 8 shows the resource heterogeneous spatial distributions for different values of β_x ($x = n, p, w$). The predator distribution in space follows the resource one while the parasitoid goes extinct as it occurs in the local dynamics. The total population oscillates with amplitude dependent on the movement parameters (Figure 9). Oscillations with the species homogeneously distributed in space were obtained for movement parameters:

- $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.9$;,

- $\beta_n = 0.01$; $\beta_p = 0.01$; $\beta_w = 0.9$; and

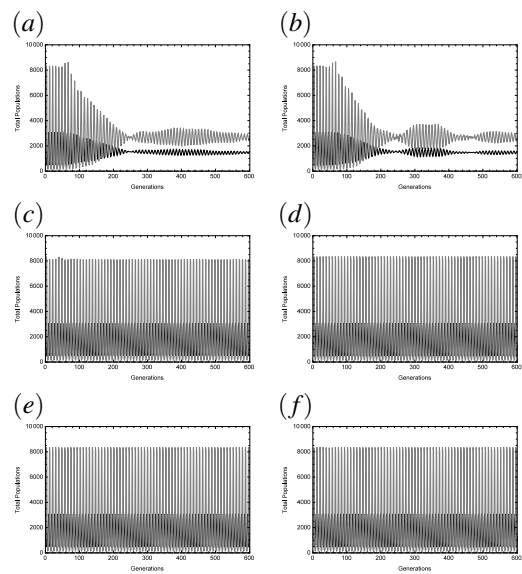- $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.9$.

Figure 9 shows the total population for these parameters; however the corresponding spatial homogeneous distribution are not illustrated in the Figure 8.

We finally simulated the system with parameters for which all the three species persist oscillating when space is not considered: $\mu_1 = 1.84$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 4$ and $\lambda = 2$. The results of the CML model simulations reveal that, depending on the species movement parameters, either
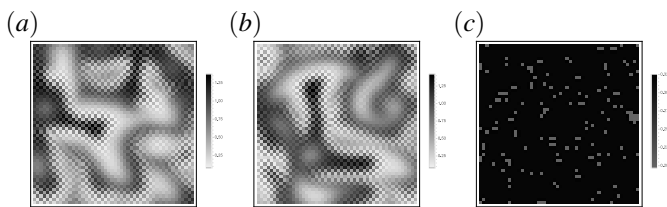
Figure 7: Total populations of the resource species (continuous black curve), parasitoid (dashed curve) and predator species (gray curve) for $\mu_1 = 4.5$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$ and $\lambda = 2$ and different sets for the movement parameters β:

(a) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.01$;
(b) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.01$;
(c) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.9$;
(d) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.9$;
(e) $\beta_n = 0.01$; $\beta_p = 0.01$; $\beta_w = 0.9$;
(f) $\beta_n = 0.91$; $\beta_p = 0.98$; $\beta_w = 0.01$.

Figure 8: Spatial distribution of resource species at $t = 600$ for $\mu_1 = 1.84$, $\mu_2 = 5.7$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$ and $\lambda = 2$ and different sets of values for β:

(a) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.01$;
(b) $\beta_n = 0.91$; $\beta_p = 0.98$; $\beta_w = 0.01$;
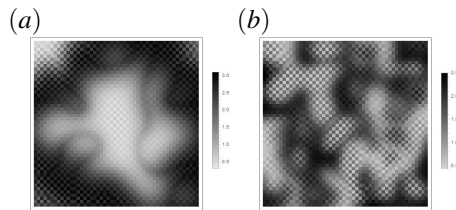(c) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.01$;

Figure 9: Total populations of the resource species (continuous black curve), the parasitoid species (dashed curve) and the predator species (gray curve) for $\mu_1 = 1.8$, $\mu_2 = 5.7$, $\alpha_1 = 1.0764$, $\alpha_2 = 1.8$ and $\lambda = 2$, and different sets of values for β:

(a) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.01$;
(b) $\beta_n = 0.91$; $\beta_p = 0.98$; $\beta_w = 0.01$;
(c) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.01$;
(d) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.9$;
(e) $\beta_n = 0.01$; $\beta_p = 0.01$; $\beta_w = 0.9$;
(f) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.9$.

(a) (b)

Figure 10: Spatial distribution of resource species at $t = 600$ for $\mu_1 = 1.84$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 4$ and $\lambda = 2$ for the different sets of values of β:
(a) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.01$;
(b) $\beta_n = 0.01$; $\beta_p = 0.01$; $\beta_w = 0.9$.

heterogeneous (see Figure 10) or homogeneous distributions can be obtained. The total populations also oscillate with great amplitude when the distribution is homogeneous (Fig. 11(e) and (f)).

4   CONCLUSIONS

We proposed a CML model for three interacting species in order to analyse the spatio-temporal dynamics of a resource species consumed by two natural enemies: a parasitoid and a predator. The resource species grows according to the Beverton-Holt dynamics while it is consumed through the Holling type III functional response by the two enemies that, implicitly compete exploiting the same resource.

Unfortunately the complexity of the equations for the local dynamics does not allow analytical results. However, through numerical simulations we observed that the local dynamics exhibit coexistence of the three species, which can be either stable or oscillating; coexistence of the resource species and one of the consumers, that is, depending on the parameters, either the parasitoid or the predator can go extinct; extinction of both the consumers and persistence of the resource only.

In the results obtained in our simulations, the movement of the species did not change the local forecast of extinction. That is, when the local dynamics results in the extinction of one the species, the CML model also lead to the extinction of this species regardless its movement rate. It is important to emphasize that this conclusion is limited to the simulations carried out, the extinction forecast of the local model can be changed for other combinations of the parameters. Oscillating local dynamics also oscillates with space with amplitude dependent on the movement parameters.

If from one hand side, the movement parameters do not change the dynamics, on the other hand side, they determine the spatial distribution of the species, whether heterogeneous or homogeneous. Heterogeneous distributions require discrepancy between the species movement rate. However,

(a) (b)
(c) (d)
(e) (f)
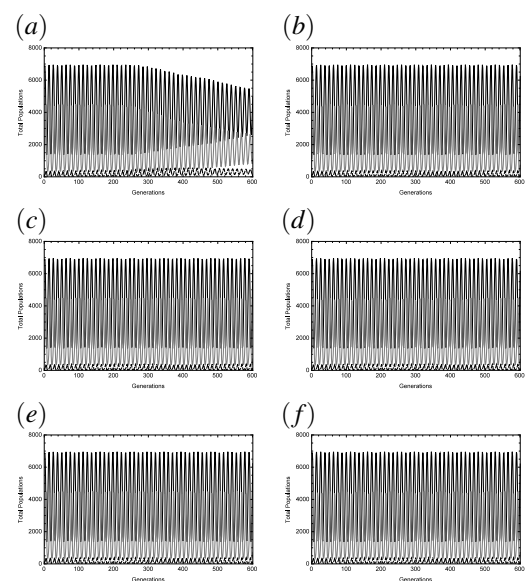
Figure 11: Total populations of the resource species (continuous black curve), the parasitoid species (dashed curve) and the predator species (gray curve) for $\mu_1 = 1.8$, $\mu_2 = 1.94$, $\alpha_1 = 1.0764$, $\alpha_2 = 4$ and $\lambda = 2$, and different sets of values for β:
(a) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.01$;
(b) $\beta_n = 0.01$; $\beta_p = 0.01$; $\beta_w = 0.9$;
(c) $\beta_n = 0.91$; $\beta_p = 0.01$; $\beta_w = 0.9$;
(d) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.01$;
(e) $\beta_n = 0.01$; $\beta_p = 0.98$; $\beta_w = 0.9$;
(f) $\beta_n = 0.91$; $\beta_p = 0.98$; $\beta_w = 0.01$.

this is not enough and there is no straightforward relation between the parameters to guarantee the existence of heterogeneous patterns. A criterion for pattern formation induced by diffusion in discrete models can be found for two interacting species (see Rodrigues *et al.* (2011)); however, we do not know, to the best of our knowledge, a similar criterion for three interacting species.

From the ecological point of view, our results suggest that it is necessary to take care with the introduction of two species for the biological control of a pest species since one of the consumers can lead the other to extinction, unless they have similar performance in terms of effectiveness of the resource consumption. The advantages of two natural enemies in biological pest control then demand more investigation and the study of more specific situation are recommended.

SUPPORT

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