Modeling spatial adaptation of populations by a time non-local convection cross-diffusion evolution problem ☆

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Abstract

In [19], Sighesada, Kawasaki and Teramoto presented a system of partial differential equations for modeling spatial segregation of interacting species. Apart from competitive Lotka-Volterra (reaction) and population pressure (cross-diffusion) terms, a convective term modeling the populations atraction to more favorable environmental regions is included. In this article, we introduce a modification of their convective term to take account for the notion of *spatial adaptation* of populations. After describing the model we briefly discuss its well-possedness and propose a numerical discretization in terms of a mass-preserving time semi-implicit finite differences scheme. Finally, we provied the results of two biologically inspired numerical experiments showing qualitative differences between the original model of [19] and the model proposed in this article.

Keywords: Population dynamics, evolution problem, cross-diffusion, time non-local convection, finite differences, spatial adaptation, segregation.

1. Introduction

In [19], Shigesada, Kawasaki and Teramoto introduced a model for analyzing the spatial segregation patterns arising in the evolution of populations of two species which are ruled by

- competition for similar resources,

- population pressure, and

- environmental quality.

These biological interactions are realized mathematically in the form of a time evolution drift-cross diffusion system of partial differential equations,

$$\partial_t u_i - \partial_x J_i = f_i(u_1, u_2), \quad J_i = (c_i u_i + a_{i1} u_i u_1 + a_{i2} u_i u_2)_x - d_i u_i U_x, \quad (1)$$

for $i = 1, 2$, where u_i denotes population density, U is the environmental potential, modeling areas where the environmental conditions are more or less favorable [19, 18], the non-negative diffusion coefficients c_i and a_{ij} model the random diffusion of individuals and the inter- and intra-specific population pressure, respectively, and d_i are usually assumed to be real constants determining the attraction strength of the potential maxima. Function f_i is a competition Lotka-Volterra type function,

$$f_i(u_1, u_2) = (\alpha_i - \beta_{i1} u_1 - \beta_{i2} u_2) u_i, \quad i, j = 1, 2,$$

where $\alpha_i \geq 0$ is the intrinsic growth rate of the i−species, and $\beta_{ij} \geq 0$ are the coefficients of inter- and intra-specific competition.

In this article, for simplicity, we assume Equations (1) to be satisfied in the bounded domain $\Omega \times (0, T)$, with $\Omega \subset \mathbb{R}$ an open interval, and $T > 0$, although the multi-dimnsional case $\Omega \subset \mathbb{R}^N$ with $N \leq 3$ could be also treated. The problem is completed by prescribing non-flux boundary conditions and non-negative initial data:

$$J_i \cdot \nu = 0 \quad \text{on} \quad \partial\Omega \times (0, T), \quad (2)$$
$$u(\cdot, 0) = u_{i0} \quad \text{on} \quad \Omega, \quad (3)$$

for $i = 1, 2$, where ν denotes the exterior unit normal to $\partial\Omega$.

Problem (1)-(3) has received much attention since its introduction due to the interesting spatial pattern formation of solutions, referred to as *segregation*. These patterns do not arise in the linear diffusion model, i.e. for $a_{ij} = 0$, $i, j = 1, 2$, where, if in addition $d_i = 0$, then the steady state solutions are constants determined by the zeros of the Lotka-Volterra terms. These constant solutions correspond, in general terms, to two kind of competitions: weak, which implies coexistence, and strong which implies extinction of at least one population. Lou and Ni [15, 16] analyzed the steady state problem corresponding to (1) (with $d_i = 0$) and proved the existence of non-constant solutions for some parameter combinations including weak and strong competition. Their results seem to indicate that while the intensity of diffusion

(c_i) and self-diffusion (a_{ii}) tend to suppress pattern formation, those of cross-diffusion (a_{12}, a_{21}) seems to help create segregation patterns.

The first results on the existence of solutions of problem (1)-(3) were proven under certain restrictions on the self- and cross-diffusion coefficients. For instance, for sufficiently small cross-diffusion terms (or small initial data) and vanishing self-diffusion coefficients $a_{11} = a_{22} = 0$, Deuring proved the global existence of solutions in [6]. For the case $c_1 = c_2$ a global existence result in one space dimension was obtained by Kim [14]. Furthermore, under the condition

$$8a_{11} > a_{12}, \quad 8a_{22} > a_{21}, \tag{4}$$

Yagi [20] showed the global existence of solutions in two space dimensions assuming $a_{12} = a_{21}$. A global existence result for weak solutions in any space dimension under assumption (4) can be found in [8]. Condition (4) can be easily understood by observing that in this case, the diffusion matrix is positive definite, hence yielding an elliptic operator. If the condition (4) does not hold, there are choices of c_i, a_{ij}, $u_i \geq 0$ for which the diffusion matrix is not positive definite. In [9] (see also [10] for some extensions of the result) the existence of global weak solutions for any $a_{ij} > 0$ was proven by using a suitable entropy functional. However, the proof uses the embedding $H^1(\Omega) \subset L^\infty(\Omega)$ in a crucial way, restricting the result to one space dimension. The one-dimensional result was later generalized by Chen and Jüngel [2] to up to three space dimensions without any additional restrictions than those given in [9]. We refer to [15, 16] for the corresponding stationary problem and notice that related models appear, among other fields, in chemotaxis, granular material and semiconductor theories [7, 17, 11, 3].

On the numerical side, a first approach based on a time Euler semi-discrete scheme was proven to be convergent in [9], in the one dimensional spatial case. More recently, other numerical approaches have been introduced in the context of Euler-Galerkin approximations ($N \leq 3$) by Chen and Jüngel [2], of finite element methods ($N \leq 3$) by Barret and Blowey [1] and of particle methods ($N = 1$) by Gambino et al. [12]. However, for the 1D case, the results of all these methods seems to be similar.

In all these works the focus is set either on finding conditions on the diffusion coefficients c_i and a_{ij}, and the Lotka-Volterra coefficients α_i and β_{ij} which ensure the existence of solutions of problem (1)-(3), allowing to define a convergent numerical method to approximate them, either on finding conditions which imply qualitative properties such as the co-existence or the

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extinction of populations in the steady state problem. However, the drift term responsible of directing the populations towards the maxima of the environmental potential has been always assumed to be linear and depending on constant coefficients (d_i) which express the strength of attraction of the different populations to these maxima. In this article we introduce a new drift coefficient dependence which allow us to modelize *spatial adaptation* by means of a memory mechanism which strengthen the attraction of population to a point if the population density in such point has been high in the past. More explicitly, we assume d_i to have the form

$$d_i(x,t) = \frac{1}{t} \int_0^t u_i(x,s)ds. \tag{5}$$

It is proven in [9] that under the regularity $U_x \in L^2(Q_T)$ (and other conditions on the data) the existence of weak solutions of (1)-(3) satisfying (among other properties) $u_i \in L^\infty(Q_T)$, holds true. The extension of this result to considering non-constant coefficients d_i of the form (5) is then straightforward since d_i is linear with respect to u_i and $d_i U_x \in L^2(Q_T)$ due to the estimate

$$\|d_i\|_{L^\infty} \leq \|u_i\|_{L^\infty}. \tag{6}$$

In fact, the existence of solutions of the $N-$dimensional problem $(N \leq 3)$ with these new convection coefficients and assuming the additional regularity $\nabla U \in L^\infty(Q_T)$ may be proven by adapting the proof of Chen and Jüngel [2]. As a last modification of the original problem, we consider the intrinsic growth rate coefficients α_i to be non-constant. Indeed, once that we consider an heterogeneous space domain in which populations are driven to the environmental potential maxima, it seems reasonable to assume a dependence of α_i on U such that larger growth of populations takes place in better environmental regions. We set

$$\alpha_i \equiv \alpha_i(U) \tag{7}$$

with $\alpha_i' \geq 0$. As in the case of the modified convective term, minor changes in the proof of Theorem 1 of [9] (or Theorem 1.1 of [2], for $N \leq 3$) allow to prove the existence of weak solutions of problem (1)-(3), with α_i defined by (7) and d_i by (5). In this context, let us finally mention a related population model, the *evolution of conditional dispersal* model, introduced and developed in a series of papers by Lou et al., see [5, 4, 13] and the references therein, in which

the system (1) is particularized with $a_{ij} = 0$, i.e., without cross-diffusion, with $\alpha_i(U) = U$ and with d_i constant. For this model, the authors were able to provide analytical conditions on the coefficients of the equations which ensure the stability of either positive (coexistence) or semi-trivial (extinction of one specie) steady state solutions. Although the complexity of the model described in the present paper does not allow to extract this kind of detailed information, we have numerically observed similar phenomena than those described for the conditional dispersal model.

2. Numerical discretization and examples

In this section we present numerical simulations illustrating differences between the behaviors of solutions corresponding to constant or variable convective coefficients d_i. In the first example, of qualitative nature, we simulate the situation in which a catastrophic natural event changes abruptly the spatial location of the maxima of the environmental potential, i.e., the more favored environmental region. We see that in the case of spatial adaptation, represented by d_i given by (5), the extinction of the population more intensely adapted to the initial potential maximum is possible as a result of the very low population density left in areas far from this maximum, which implies a bad competitive positioning near the new potential maximum after the catastrophic event. However, for constant d_i the population is able to recover and dominate again in the new favored region.

The second example, in which the potential maximum is kept time independent, shows two interesting biological properties. First, that the segregation of populations is more intense in the case of spatial adaptation than in the case of constant convective coefficients. Second, that intense spatial adaptation may lead to coexistence in cases where the constant convection coefficients lead to extinction.

For the numerical discretization, we use a time semi-implicit finite differences scheme similar to that used by Barret and Blowey [1] in the context of the finite elements method. We look for time independent functions u_1^k and u_2^k approximating the continuous solution u_1, u_2, respectively, in the time interval $(k\tau, (k+1)\tau]$, for $k = 0, ..., N$, for some $N \in \mathbb{N}$ and $\tau = T/(N+1)$. Naturally, for $k = 0$ we set $u_1^0 = u_{10}$, $u_2^0 = u_{20}$. For $t_k = k\tau$, let u_1^{k-1}, u_2^{k-1}

be given. We compute u_1^k, u_2^k by means of the following iterative algorithm:

$$\frac{1}{\tau}(u_1^{k,n} - u_1^{k-1}) - \left((c_1 + 2a_{11}u_1^{k,n-1} + a_{12}u_2^{k,n-1})u_{1x}^{k,n}\right)_x - \tag{8}$$

$$\left(u_1^{k,n-1}(a_{12}u_{2x}^{k,n} - d_1^{k,n-1}U_x^k)\right)_x = \alpha_1(U^k)u_1^{k,n} - (\beta_{11}u_1^{k,n-1} + \beta_{12}u_2^{k,n-1})u_1^{k,n-1},$$

$$\frac{1}{\tau}(u_2^{k,n} - u_2^{k-1}) - \left((c_2 + 2a_{22}u_2^{k,n-1} + a_{21}u_1^{k,n-1})u_{2x}^{k,n}\right)_x - \tag{9}$$

$$\left(u_2^{k,n-1}(a_{21}u_{1x}^{k,n} - d_2^{k,n-1}U_x^k)\right)_x = \alpha_2(U^k)u_2^{k,n} - (\beta_{21}u_1^{k,n-1} + \beta_{22}u_2^{k,n-1})u_2^{k,n-1},$$

in Ω, for $n = 1, 2, \ldots$, with $u_i^{k,0} = u_i^{k-1}$, $U^k = U(x, t_k)$ and $d_i^{k,n-1} = d_i$, if d_i is constant or

$$d_i^{k,n-1} = \frac{1}{k}\sum_{j=1}^{k} u_i^{j,n-1},$$

if d_i is defined by (5). We solve equations (8)-(9) together with the non-flux boundary conditions given by

$$(c_1 + 2a_{11}u_1^{k,n-1} + a_{12}u_2^{k,n-1})u_{1x}^{k,n} + a_{12}u_1^{k,n-1}(u_{2x}^{k,n} - d_1^{k,n-1}U_x^k) = 0, \tag{10}$$

$$(c_2 + 2a_{22}u_2^{k,n-1} + a_{21}u_1^{k,n-1})u_{2x}^{k,n} + a_{21}u_2^{k,n-1}(u_{1x}^{k,n} - d_2^{k,n-1}U_x^k) = 0, \tag{11}$$

on $\partial\Omega$. We iterate the scheme (8)-(11) until the stopping criterium

$$\max_{i=1,2}\|u_i^{k,n} - u_i^{k,n-1}\|_{L^\infty} < tol \tag{12}$$

is reached, and then we set $u_i^k = u_i^{k,n}$. In (12), tol is a small number that we take of the order 10^{-5} for the experiments with variable d_i and of the order 10^{-7} for those with constant d_i. In both cases, we observed good convergence properties of the iterative scheme.

For the spatial discretization we used a scheme based on centered differences, which preserves the mass of populations for zero Lotka-Volterra terms. Let $x_j = a + j(b-a)/M$, $j = 0, \ldots, M$ be a partition of the interval $\Omega = (a, b)$ and let us introduce the notation

$$U_i^j = u_i^{k,n}(x_j), \quad w_i^j = u_i^{k,n-1}(x_j), \quad U^{j,k} = U(x_j, t_k) \quad d_i^{j,k} = d_i(x_j, t_k)$$

$$\alpha_1 = c_1 + 2a_{11}w_1 + a_{12}w_2, \quad \text{and} \quad \alpha_2 = c_2 + 2a_{22}w_2 + a_{21}w_1.$$

Then, for the unknowns (U_1^j, U_2^j), for $j = 1, \ldots, M - 1$ Eq. (8) leads to

$$\frac{1}{\tau}(U_1^j - w_1^j) - \frac{1}{h^2}\big(\alpha_1^{j+1/2}U_1^{j+1} - (\alpha_1^{j+1/2} + \alpha_1^{j-1/2})U_1^j + \alpha_1^{j-1/2}U_1^{j-1}\big) -$$
$$\frac{a_{12}}{h^2}\big(w_1^{j+1/2}U_2^{j+1} - (w_1^{j+1/2} + w_1^{j-1/2})U_2^j + w_1^{j-1/2}U_2^{j-1}\big) +$$
$$\frac{a_{12}}{h}\big(w_1^{j+1/2}d_1^{j+1/2,k}U_x^{j+1/2,k} - w_1^{j-1/2}d_1^{j-1/2,k}U_x^{j-1/2,k}\big) =$$
$$\alpha_1(U^{j,k})U_1^j - (\beta_{11}w_1^j + \beta_{12}w_2^j)w_1^j,$$

where $h = (b - a)/M$ and $v_i^{j\pm1/2} = (v_i^j + v_i^{j\pm1})/2$. An analogous expression is obtained from Eq. (9), The corresponding mass preserving discretization of the boundary conditions is

$$\alpha_1^{1/2}(U_1^1 - U_1^0) + a_{12}w_1^{1/2}(U_2^1 - U_2^0) = ha_{12}w_1^{1/2}d_1^{1/2,k}U_x^{1/2,k}, \qquad (13)$$
$$\alpha_2^{1/2}(U_2^1 - U_2^0) + a_{21}w_2^{1/2}(U_1^1 - U_1^0) = ha_{21}w_2^{1/2}d_2^{1/2,k}U_x^{1/2,k}, \qquad (14)$$

for $j = 0$, and similar expressions for $j = M$. Observe that the condition for (13)-(14) to have a unique solution is

$$\alpha_1^{1/2}\alpha_2^{1/2} - a_{12}a_{21}w_1^{1/2}w_2^{1/2} \neq 0, \qquad (15)$$

which, for the continuous version of the problem, leads to condition (4). Although the continuous version of (15), for any $(x, t) \in Q_T$, is difficult to establish, the proof of existence of non-negative solutions given in [9] seems to indicate that this quantity remains always positive. For the discrete version (15), we force the solution to be positive by substituting in each time iteration u_i by $u_{i\varepsilon} = \max\{u_i, \varepsilon\}$, for $\varepsilon = 10^{-7}$ in the experiments.

Unless otherwise stated, in all the experiments we use the data given in Table 1.

Experiment 1. Intensive adaptation may lead to extinction after a catastrophic environmental event. In this example we explore the effects that sudden environmental changes may have on the extinction of populations which have adapted intensively to some region. For this experiment we use the following Lotka-Volterra functions

$$f_i(u_1, u_2) = (\alpha_i(U) - \beta_{i1}u_1 - \beta_{i2}u_2)u_i, \qquad (16)$$

Table 1: Parameter values common for all the experiments

Parameter	Symbol	Value
Spatial domain	Ω	$(0, 1)$
Nodes number	N	101
Time step	τ	0.001
Diffusion coefficients	c_1, c_2	0
Cross diffusion coefficients	a_{ij}	0.25
Initial densities	$u_{10}, \ u_{20}$	0.5
Environmental potential	U	$\exp(-\frac{(x-x_0)^2}{0.001})$

with $\alpha_1(U) = 320U$, $\alpha_2(U) = 300(0.99U + 0.01)$, and $\beta_{ij} = 150$ for $i, j = 1, 2$. For the case of variable d_i, we define them by (5). When running for constant d_i, we take

$$d_i = \lim_{t \to 0} \frac{1}{t} \int_0^t u(x, t) dt = u_{i0},$$

which is constant due to the election of the initial datum, see Table 1. The environmental potential, given also in Table 1, is first set with the maximum at $x_0 = 0.2$. We run the simulation until $t = 0.3$ is reached and a sudden change of the potential maximum, to $x_0 = 0.8$, is produced. Then we continue till the steady state is nearly reached, which we assume to be when $\|u(\cdot, t_k) - u(\cdot, t_{k-1})\|_{L^\infty} < 5 \times 10^{-6}$. For the case of constant d_i this happens at $t = 4.29$ while for d_i variable it takes till $t = 12.86$. Notice that the only difference between equations and data for populations 1 and 2 is the definition of the growth rate coefficients α_i.

In Fig. 1 we show time slices of the evolution (left to right and up to down) of both populations (u_1 continuous line, u_2 dotted line) for the case of variable d_i. In the first four slices, a notorious progressive concentration and growing of population 1 in the neighborhood of $x_0 = 0.2$ is accompanied by an almost extinction of population 2, due to $\alpha_1 > \alpha_2$ in that region. However, although hardly visible from the plots, we checked that $u_2 > u_1$ in regions far from the potential maximum. After the catastrophic event, at $t = 0.3$, population 2 is able to grow faster than population 1 as a result of the low population 1 density left in the surroundings of $x_0 = 0.8$ after the period of concentration at $x_0 = 0.2$. The subsequent evolution leads to extinction of population 1.

In Fig. 2 we show time slices of the evolution of both populations for the

case of constant d_i. We see that the initial behavior of the system is similar to the case of variable d_i. However, after the change of location of the potential maximum, at $t = 0.3$, we see a significant qualitative change: population 1, that in the case of variable d_i becomes extinct, is able to recover and win the competition against population 2, which is extincted.

Finally, in Fig. 3 we plot the spatial adaptation terms produced in the case of variable d_i, which rule the strength of the convection term. We observe that property (6) is satisfied. It also interesting to note that the biological notion of spatial adaptation represented by these terms is time varying and that intense adaptation to some region, $x_0 = 0.2$ in this example, may be weakened and practically disappear if the region is left uninhabitated for a long time.

In Figs. 1-3, time $t = 3$ gives a good approximation to the steady state.

Experiment 2. Adaptation in a stable environment may enhance segregation and promote coexistence. In this example we compare the segregation magnitudes for the cases of variable and constant d_i. We run two experiments, one with zero Lotka-Volterra functions, implying mass conservation for the continuous model, and another with similar Lotka-Volterra functions than those of Experiment 1. The environmental potential, given in Table 1, is time independent and with the maximum at $x_0 = 0.5$, to check the symmetry preserving property of the discretization scheme. In order to have some distinction between populations, we set, for the case of variable d_i,

$$d_i(x,t) = \frac{\varepsilon_i}{t} \int_0^t u_i(x,\tau)d\tau,$$

with $\varepsilon_1 = 2$ and $\varepsilon_2 = 1$. The convection coefficients for the corresponding problem with constant d_i are given by $d_i = \varepsilon_i u_{i0}$. We run the simulation until the steady state is nearly established, using the same criterium than in Experiment 1. Notice that the only difference between equations and data for populations 1 and 2 is in the parameters ε_i.

In Fig. 4 we show the steady state for constant d_i (left) and variable d_i (right), which is reached for $t_* \approx 0.714$ and $t_* \approx 8.186$, respectively. Continuous line corresponds to population 1 and dotted line to population 2. The mass conservation property is well captured by the discrete model, being the relative difference

$$\max_{i=1,2} \int_\Omega |u_i(x,t_*) - u_{0i}|dx \Big(\int_\Omega |u_{0i}|dx \Big)^{-1}$$

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lower than 8×10^{-4} for d_i constant and an order greater for d_i variable. The symmetry of the solution is also conserved, being the relative difference

$$\max_{i=1,2} \|u_i(\cdot, t_*) - \tilde{u}_i(\cdot, t_*)\| \|u_i(\cdot, t_*)\|^{-1}$$

of the order of 10^{-15}, for both d_i cases, where $\tilde{u}_i(x,t) = u_i(1-x,t)$. The concentration of mass in the neighborhood $(0.45, 0.55)$ of $x_0 = 0.5$ is, for the variable case

$$\int_{0.45}^{0.55} u_1(x, t_*)dx = 0.216 \approx 40\%, \quad \int_{0.45}^{0.55} u_2(x, t_*)dx = 0.055 \approx 10\%$$

where the percentage points are in terms of the total mass, while, for the constant case is

$$\int_{0.45}^{0.55} u_1(x, t_*)dx = 0.122 \approx 25\%, \quad \int_{0.45}^{0.55} u_2(x, t_*)dx = 0.060 \approx 12.5\%.$$

The qualitative differences between the solutions of constant or variable d_i are clearly seen in Fig. 4. In the case of variable d_i, the population with more intensive adaptation capacity (population 1 due to $\varepsilon_1 > \varepsilon_2$) concentrates in the surroundings of the potential maximum x_0 while population 2 reaches, in fact, its minimum density at this point. However, in the case of constant d_i, both populations reach their maximum value at the potential maximum $x_0 = 0.5$.

For the second example of this experiment we use the Lotka-Volterra functions given in (16) with $\alpha_i(U) = 300U$, for $i = 1, 2$ and $\beta_{ij} = 150$ for $i, j = 1, 2$. In Fig. 4 we show the steady state for constant d_i (left) and variable d_i (right), which is reached for $t_* \approx 8.1$ and $t_* \approx 3.11$, respectively. Continuous line corresponds to population 1 and dotted line to population 2. Notably, the effect of rapid concentration of population 1 around the maximum, for the case of variable d_i, leads the system to a coexistence steady state, although with a high degree of segregation in the surroundings of x_0, where population 2 attains a minimum. However, for the case of constant d_i, population 2 is extincted.

3. Conclusions

The mathematical model (1)-(3) introduced by Shigesada, Kawasaki and Teramoto (1979) [19] to reproduce the behaviour of interacting species which

are affected not only by competition or random displacement but by population pressure and attraction to favorable environmental regions has been a source of interesting mathematical and biological discussion. One of the more remarkable properties of the model is the formation of segregation patterns, which are observed in the field, and which lead to non-trivial steady state configurations. In this article we proposed the consideration of a new term in the equations, the time non-local term (5), which may be interpreted as a *spatial adaptation* intensity or capacity of the populations. From the mathematical point of view, the introduction of this new term do not pose additional difficulties for the achievement of results on existence and regularity of solutions. Moreover, the numerical discretization seems to behave well in a similar range of parameters and data than the original model since the way in which the new term induces the concentration of one of the populations in a narrow region is always bounded. However, the introduction of this new term produces important quantitative and qualitative differences with respect to the original model. We showed numerical experiments in which the behavior of solutions is qualitatively different in terms of coexistence and extinction. We also showed that the segregation-concentration effect already present in the original model is enhanced quantitatively with the introduction of the spatial adaptation term.

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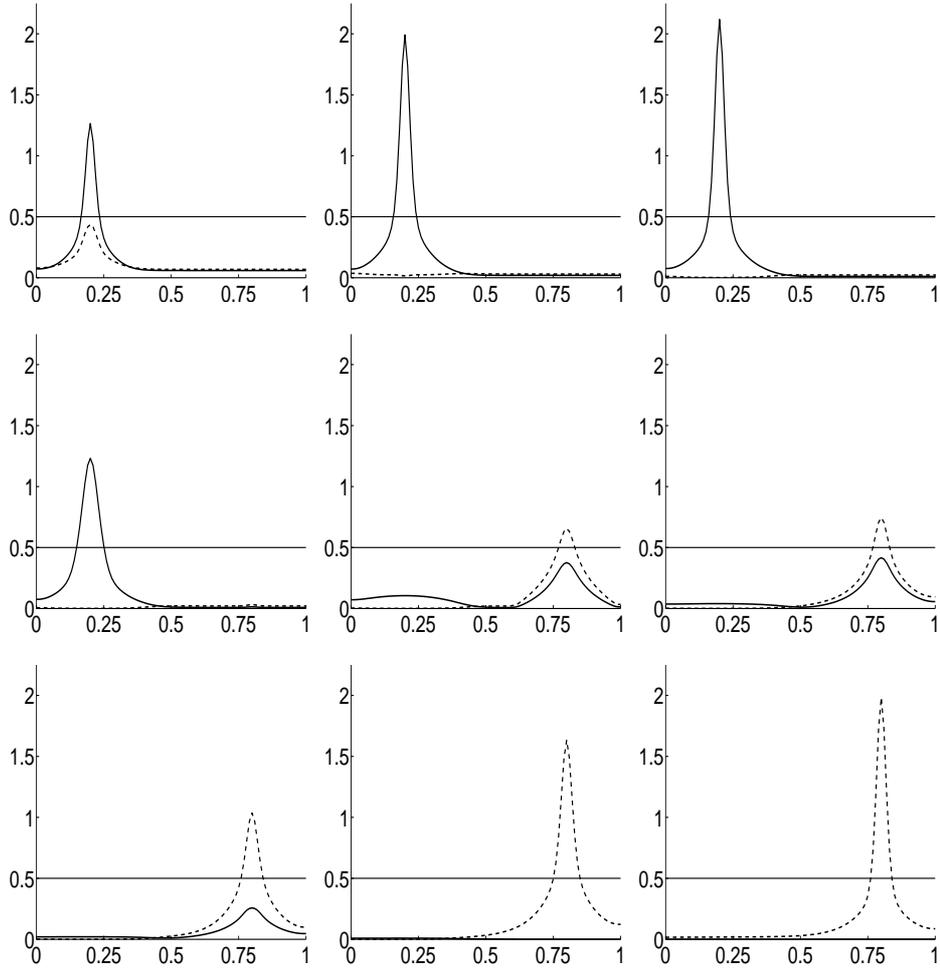
Figure 1: Experiment 1. Populations evolution for variable d_i. Time slices at $t = 0.05, 0.15, 0.25, 0.3, 0.35, 0.45, 0.6, 1, 3$, with the sudden change of environmental potential maximum at $t = 0.3$, which relocates from $x = 0.2$ to $x = 0.8$. The horizontal line corresponds to the initial populations densities.
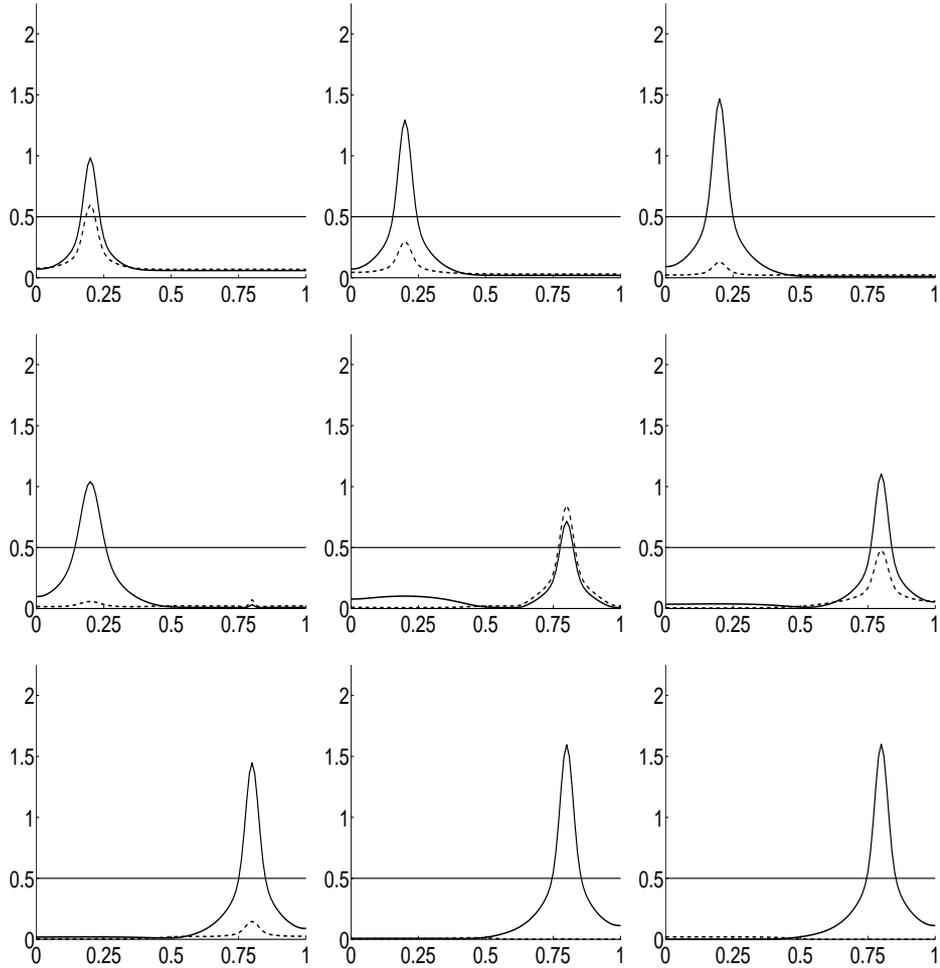
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Figure 2: Experiment 1. Populations evolution for constant d_i. Time slices at $t = 0.05, 0.15, 0.25, 0.3, 0.35, 0.45, 0.6, 1, 3$, with the sudden change of environmental potential maximum at $t = 0.3$, which relocates from $x = 0.2$ to $x = 0.8$. The horizontal line corresponds to the initial populations densities.
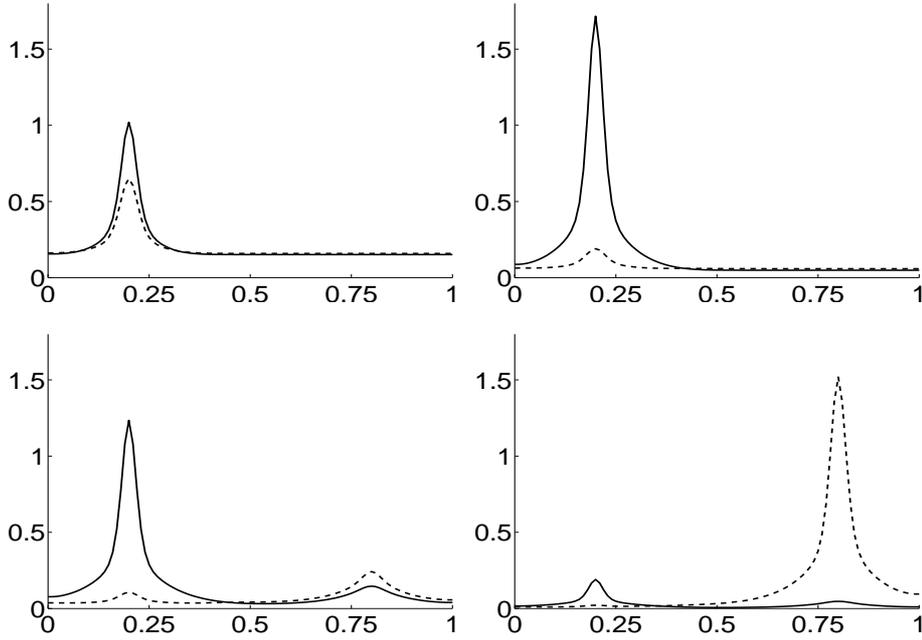
Figure 3: Experiment 1. Evolution of the adaptation intensity terms, d_i. Time slices at $t = 0.05, 0.25, 0.45, 3$, with the sudden change of environmental potential maximum at $t = 0.3$, which relocates from $x = 0.2$ to $x = 0.8$.
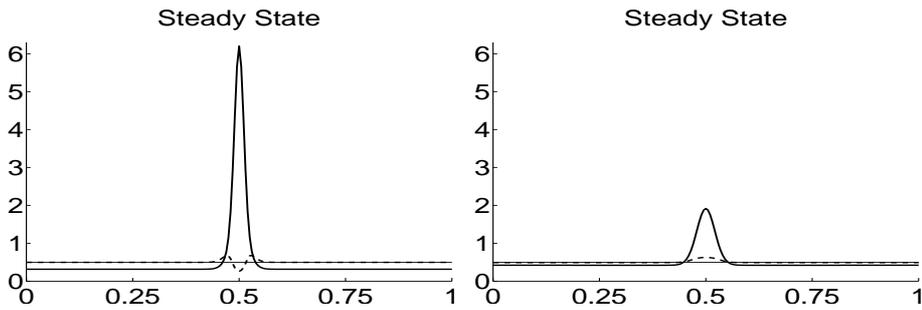

Figure 4: Experiment 2. Lotka-Volterra terms set to zero and environmental potential maximum at $x_0 = 0.5$. Case of variable d_i (left) and constant d_i (right). The horizontal line corresponds to the initial populations densities.
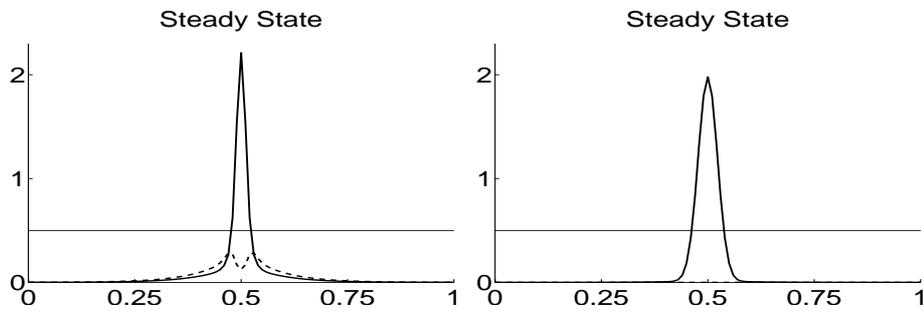
Figure 5: Experiment 2. Competitive Lotka-Volterra terms and environmental potential maximum at $x_0 = 0.5$. Case of variable d_i (left) and constant d_i (right). The horizontal line corresponds to the initial populations densities.