Non triangular cross-diffusion systems with predator-prey reaction terms

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Abstract

A predator-prey system involving cross-diffusion is obtained at the formal level as a singular limit of a four-species reaction-diffusion system, following the approach proposed in the context of ODEs in [S. Geritz, M. Gyllenberg, A mechanistic derivation of the DeAngelis-Beddington functional response, Journal of Theoretical Biology 314 (2012) 106-108]. Part of this derivation can be made rigorous. The possibility of appearance of Turing patterns for this cross-diffusion system is studied, and compared to what happens when standard diffusion terms replace the cross diffusion terms.

1 Introduction

1.1 General presentation

The Beddington-DeAngelis functional response appearing in many works on predator-prey systems [8, 18, 6] can be directly obtained starting from modeling considerations (competition between predators, etc.) [4, 11, 3, 1]. It can also come out of a systematic process in which one starts with a system of more than two equations with simple reaction terms, and performs one or more limits.

These limits have been widely studied at the level of ODEs (see for instance [19, 15, 17] and references therein), but less at the level of (reaction-diffusion) PDEs. Such a study at the level of PDEs was performed in [10]. There, one starts with three reaction-diffusion equations, the unknown being the density of preys, and the density of two classes of predators, respectively called handling and searching predators. In this paper, it was possible to show the rigorous convergence of the solutions of this system, when some parameter tends to 0, towards the solutions of a predator-prey system involving cross-diffusion in the predator equation, and Holling II or Beddington-DeAngelis-like functional responses. A study of patterns of Turing type arising in the limiting systems was also performed there.

In the present paper, we are interested in a situation in which one starts with a system of four reaction-diffusion equations, where the reaction terms are taken from [15], and one then performs the singular perturbation analysis which was performed at the level of ODEs in [15]. The main difference with what happens in [10] is that cross diffusion terms appear in both predators and prey equations at the end (thus forming a so-called non triangular system of cross diffusion), making the analysis more difficult.

1.2 Description of the model

Following [15], in addition to the division of the predator population (of density Y) into so-called searchers (of density S) and handlers (of density H), we divide the prey population (of density X) in active prey (of density P), typically foraging and prone to predation, and invulnerable prey (of density R), typically constituted of individuals who have found a refuge.

Denoting t the time variable and x the space variable, the densities $P := P(t,x) \geq 0$, $R := R(t,x) \geq 0$, $S := S(t,x) \geq 0$, $H := H(t,x) \geq 0$ are supposed to satisfy the following system (with $X = P + R$ and $Y = S + H$):

$$\begin{cases} \partial_t P - d_P \Delta_x P = rP\left(1 - \dfrac{X}{n}\right) - aPS - \dfrac{1}{\varepsilon}\left(bPY - \dfrac{1}{\tau}R\right), \\ \partial_t R - d_R \Delta_x R = rR\left(1 - \dfrac{X}{n}\right) + \dfrac{1}{\varepsilon}\left(bPY - \dfrac{1}{\tau}R\right), \\ \partial_t S - d_S \Delta_x S = \dfrac{1}{\eta}\left(-aSP + \dfrac{1}{h}H\right) + \Gamma H - \mu S, \\ \partial_t H - d_H \Delta_x H = \dfrac{1}{\eta}\left(aSP - \dfrac{1}{h}H\right) - \mu H. \end{cases} \tag{1}$$

Here, $r > 0$ represents a growth coefficient in a logistic growth term for the prey, and $n > 0$ is the corresponding carrying capacity, while $a\,S\,P$ (with $a > 0$) is the rate at which searching predators capture vulnerable prey. The coefficients $\Gamma > 0$ and $\mu > 0$ appear in the terms $\Gamma\,H$ representing the birth of (searching) predators and $\mu\,S$, $\mu\,H$, the terms representing the death of predators.

Prey switches from vulnerable to invulnerable (and vice-versa) status with a rate $\frac{1}{\varepsilon}\,(b\,P\,Y - R/\tau)$ (with $b > 0$, $\tau > 0$) which depends on the total number Y of predators (at the considered position). This switch happens on a time scale $\varepsilon > 0$ assumed in the sequel to be small.

Predators switch from searching to handling (and vice-versa) status with a rate $\frac{1}{\eta}\,(a\,S\,P - H/h)$ (with $h > 0$). This switch happens on a time scale $\eta > 0$ assumed in part of the sequel to be small.

1.3 Presentation of the results of this paper

In the system above, it is possible to pass to the limit at the rigorous level when $\varepsilon \to 0$, and $\eta > 0$ is kept constant, when the dimension is (1 or) 2. More precisely, it is possible to show the following:

Theorem 1. *Let Ω be a bounded regular open subset of $\mathbb{R}^2$, and r, n, a, b, τ, h, Γ, μ and η be strictly positive parameters. Finally, let P_{in}, R_{in}, S_{in} and H_{in} be nonnegative initial data lying in $C^{0,\alpha}(\overline{\Omega})$ for some $\alpha \in]0,1[$, and such that $\inf_{x\in\Omega} H_{in} > 0$.*

Then, for each $\varepsilon > 0$, there exists a unique strong (nonnegative for each component) solution $P_\varepsilon := P_\varepsilon(t,x)$, $R_\varepsilon := R_\varepsilon(t,x)$, $S_\varepsilon := S_\varepsilon(t,x)$, $H_\varepsilon := H_\varepsilon(t,x)$ such that the quantities $\partial_t P_\varepsilon$, $\partial_{x_i x_j} P_\varepsilon$, $\partial_t R_\varepsilon$, $\partial_{x_i x_j} R_\varepsilon$, $\partial_t S_\varepsilon$, $\partial_{x_i x_j} S_\varepsilon$, $\partial_t H_\varepsilon$, $\partial_{x_i x_j} H_\varepsilon$ lie in $C^{0,\alpha}([0,T] \times \overline{\Omega})$ for all $T > 0$ and $i,j \in \{1,2\}$, to system (1), with homogeneous Neumann boundary condition ($\nu := \nu(x)$ being the unit normal exterior vector at a point $x \in \partial\Omega$):

$$\nabla_x P_\varepsilon(t,x) \cdot \nu(x) = 0, \qquad \nabla_x R_\varepsilon(t,x) \cdot \nu(x) = 0, \qquad \text{for } t \in \mathbb{R},\ x \in \partial\Omega, \tag{2}$$

$$\nabla_x S_\varepsilon(t,x) \cdot \nu(x) = 0, \qquad \nabla_x H_\varepsilon(t,x) \cdot \nu(x) = 0, \qquad \text{for } t \in \mathbb{R},\ x \in \partial\Omega, \tag{3}$$

and initial data:

$$P_\varepsilon(0,\cdot) = P_{in}, \quad R_\varepsilon(0,\cdot) = R_{in}, \quad S_\varepsilon(0,\cdot) = S_{in}, \quad H_\varepsilon(0,\cdot) = H_{in}. \tag{4}$$

Moreover, when $\varepsilon \to 0$, the quantities P_ε, R_ε converge (up to extraction of a subsequence) in $L^{2+\delta}([0,T] \times \Omega)$ for some $\delta > 0$ and all $T > 0$ towards functions P, R, and the quantities S_ε and H_ε converge (up to extraction of a subsequence) uniformly in $[0,T] \times \Omega$ for all $T > 0$ towards functions S and H. Then, $P, R \in L^{2+\delta}([0,T] \times \Omega)$, and $S, H \in C^{0,\alpha}([0,T] \times \overline{\Omega})$ for some $\alpha > 0$ and all $T > 0$.

Finally, those functions are weak solutions of the limiting system

$$\partial_t(P + R) - \Delta_x(d_P\,P + d_R\,R) = r\,(P + R)\left(1 - \frac{P + R}{n}\right) - a\,P\,S, \tag{5}$$

$$\partial_t S - d_S\,\Delta_x S = \frac{1}{\eta}\left(-a\,S\,P + \frac{1}{h}H\right) + \Gamma H - \mu\,S, \tag{6}$$

$$\partial_t H - d_H\,\Delta_x H = \frac{1}{\eta}\left(a\,S\,P - \frac{1}{h}\,H\right) - \mu\,H, \tag{7}$$

$$b\,P\,(S+H) = \frac{R}{\tau}, \tag{8}$$

together with homogeneous Neumann boundary conditions:

$$\nabla_x(d_P\,P(t,x) + d_R\,R(t,x))\cdot\nu(x) = 0, \qquad \textit{for } t\in I\!R,\ x\in\partial\Omega, \tag{9}$$

$$\nabla_x S(t,x)\cdot\nu(x) = 0, \qquad \nabla_x H(t,x)\cdot\nu(x) = 0, \qquad \textit{for } t\in I\!R,\ x\in\partial\Omega, \tag{10}$$

and the initial conditions:

$$P(0,x) + R(0,x) = P_{in}(x) + R_{in}(x), \qquad \textit{for } x\in\Omega, \tag{11}$$

$$S(0,\cdot) = S_{in}, \quad H(0,\cdot) = H_{in}, \tag{12}$$

in the following sense:

First, for all $\phi\in C_c^2(I\!R_+\times\overline{\Omega})$,

$$-\int_0^\infty\int_\Omega (P+R)\,\partial_t\phi\,dxdt - \int_\Omega (P_{in}+R_{in})\,\phi(0,\cdot)\,dx - \int_0^\infty\int_\Omega (d_P\,P + d_R\,R)\,\Delta_x\phi\,dxdt \tag{13}$$

$$= \int_0^\infty\int_\Omega \left(r\,(P+R)\left[1-\frac{1}{n}\,(P+R)\right] - a\,P\,S\right)\phi\,dxdt;$$

Then, for all $\phi\in C_c^2(I\!R_+\times\overline{\Omega})$,

$$-\int_0^\infty\int_\Omega S\,\partial_t\phi\,dxdt - \int_\Omega S_{in}\,\phi(0,\cdot)\,dx - \int_0^\infty\int_\Omega d_S\,S\,\Delta_x\phi\,dxdt \tag{14}$$

$$= \int_0^\infty\int_\Omega \left(\frac{1}{\eta}\,(-a\,S\,P + \frac{1}{h}\,H) + \Gamma\,H - \mu\,S\right)\phi\,dxdt;$$

Finally, for all $\phi\in C_c^2(I\!R_+\times\overline{\Omega})$,

$$-\int_0^\infty\int_\Omega H\,\partial_t\phi\,dxdt - \int_\Omega H_{in}\,\phi(0,\cdot)\,dx - \int_0^\infty\int_\Omega d_H\,H\,\Delta_x\phi\,dxdt \tag{15}$$

$$= \int_0^\infty\int_\Omega \left(\frac{1}{\eta}\,(a\,S\,P - \frac{1}{h}\,H) - \mu\,H\right)\phi\,dxdt.$$

We conclude with extra regularity properties for S, H*: indeed* $\partial_t S$, $\partial_t H$, $\partial_{x_ix_j} S$ *and* $\partial_{x_ix_j} H$ *lie in* $L^{2+\delta}([0,T]\times\Omega)$ *for some* $\delta>0$ *and all* $T>0$, $i,j\in\{1,2\}$, *so that eq. (6) and eq. (7) (and the corresponding Neumann boundary conditions and initial conditions) are both satisfied in the strong sense.*

Note that the limiting equation above can be rewritten (in strong form, without taking into account the initial and boundary conditions) as

$$\partial_t X - \Delta_x\Big(\frac{d_P + d_R\,\tau\,b\,Y}{1+\tau\,b\,Y}\,X\Big) = r\,X\,\left(1-\frac{X}{n}\right) - a\,\frac{X}{1+\tau\,b\,Y}\,S, \tag{16}$$

$$\partial_t S - d_S\,\Delta_x S = \frac{1}{\eta}\left(-a\,S\,\frac{X}{1+\tau\,b\,Y} + \frac{1}{h}H\right) + \Gamma H - \mu\,S, \tag{17}$$

$$\partial_t H - d_H\,\Delta_x H = \frac{1}{\eta}\left(a\,S\,\frac{X}{1+\tau\,b\,Y} - \frac{1}{h}\,H\right) - \mu\,H, \tag{18}$$

$$Y = S + H. \tag{19}$$

When η tends to 0, this system formally converges to the system

$$\partial_t X - \Delta_x\Big(\frac{d_P + d_R\,\tau\,b\,Y}{1+\tau\,b\,Y}\,X\Big) = r\,X\,\Big(1 - \frac{X}{n}\Big) - a\,\frac{X}{1+\tau\,b\,Y}\,S, \tag{20}$$

$$\partial_t Y - \Delta_x(d_S\,S + d_H\,H) = \Gamma H - \mu\,Y, \tag{21}$$

$$a\,S\,\frac{X}{1+\tau\,b\,Y} = \frac{1}{h}\,H. \tag{22}$$

Unfortunately, this formal limit seems quite difficult to transform in a rigorous theorem. This difficulty stems from the non-triangular structure of the cross diffusion system (20)-(22) (a cross diffusion system consisting of two equations is said to be triangular when the cross diffusion terms appear only in one of the two equations of this system). This structure can be better seen when this system is rewritten in the following (equivalent) way:

$$\begin{cases} \partial_t X - \Delta_x\left(c_X(Y)X\right) = rX\left(1 - \dfrac{X}{n}\right) - \dfrac{aXY}{haX + \tau bY + 1}, \\ \partial_t Y - \Delta_x\left(c_Y(X,Y)Y\right) = \Gamma h\dfrac{aXY}{haX + \tau bY + 1} - \mu Y, \end{cases} \tag{23}$$

where

$$c_X(Y) = d_P\frac{1}{\tau bY + 1} + d_R\frac{\tau bY}{\tau bY + 1},$$

$$c_Y(X,Y) = d_S\frac{\tau bY + 1}{haX + \tau bY + 1} + d_H\frac{haX}{haX + \tau bY + 1}.$$

Since non-triangular cross diffusion terms appear in system (23), it looks quite difficult to show the existence of strong global solutions to this system (and therefore, as previously noticed, to pass to the limit rigorously when η tends to 0 in (16)).

It is however feasible to study the possible appearance of patterns in system (23), by performing a linear stability investigation of its homogeneous steady solutions. Turing patterns are known to appear in predator-prey systems with predator-dependent trophic function and standard diffusion, under homogeneous Neumann boundary conditions [2] or Robin boundary conditions [9]. In addition, while predator-prey systems with prey-dependent trophic function and standard diffusion cannot give rise to Turing instability [2], cross-diffusion terms are the key destabilizing ingredient that leads to the emergence of spatial patterns [23, 16, 21], as in the context of competitive species [22, 13, 14].

What we want to point out in our study is the following: first the system (23) can lead to the appearance of Turing instability, for a certain range of parameters. Secondly, if the cross diffusion terms in this system are replaced by standard diffusion terms, then the Turing instability zone (that is, the zone in which the parameters lead to Turing instability) can change significantly, or even appear. We provide in this paper examples of parameters where such situations happen, that is when no Turing instability appears for the system (23), but the Turing instability appears when in this system, the cross diffusion is replaced by a (coherently chosen) standard diffusion.

Next section is devoted to the proof of Thm. 1, while in Section 3 is studied the Turing instability properties of the limiting system (23).

2 Rigorous results of convergence

In this section, we present the:

Proof of Theorem 1: We first observe that when $\varepsilon > 0$ is given, the existence and uniqueness of a strong solution to system (1) (together with Neumann boundary conditions and initial conditions) is a consequence of standard theorems for reaction-diffusion systems (cf. for example [12]).

Adding the fwo first equations in system (1), we end up (denoting by C any strictly positive constant, and using the elementary inequality $x\,(1-x/n)\le C$) with the differential inequality

$$\partial_t(P_\varepsilon+R_\varepsilon)-\Delta_x(d_P\,P_\varepsilon+d_R\,R_\varepsilon)=r\,(P_\varepsilon+R_\varepsilon)\left(1-\frac{1}{n}\,(P_\varepsilon+R_\varepsilon)\right)-a\,P_\varepsilon\,S_\varepsilon\le C, \tag{24}$$

so that (remembering that $P_\varepsilon+R_\varepsilon\ge 0$) using the improved duality Lemma of [7], we can find $\delta>0$ such that P_ε and R_ε are bounded in $L^{2+\delta}([0,T]\times\Omega)$ for all $T>0$. We deduce from this bound that, up to extraction of a subsequence, P_ε and R_ε converge weakly in $L^{2+\delta}([0,T]\times\Omega)$ towards some functions (resp. denoted by P and R) also lying in $L^{2+\delta}([0,T]\times\Omega)$ (for all $T>0$).

In the same way, adding the two last equations in system (1), we end up with the differential inequality

$$\partial_t(S_\varepsilon+H_\varepsilon)-\Delta_x(d_S\,S_\varepsilon+d_H\,H_\varepsilon)=(\Gamma-\mu)\,H_\varepsilon-\mu\;S_\varepsilon\le C\,(H_\varepsilon+S_\varepsilon), \tag{25}$$

so that (remembering that $S_\varepsilon+H_\varepsilon\ge 0$) using the improved duality Lemma of [7] (and more precisely, a variant of this Lemma found in [5]), we also can find $\delta>0$ such that S_ε and H_ε are bounded in $L^{2+\delta}([0,T]\times\Omega)$ for all $T>0$.

Next we observe that

$$\partial_t S_\varepsilon-d_S\,\Delta_x S_\varepsilon=\frac{1}{\eta}\,(-a\,S_\varepsilon\,P_\varepsilon+\frac{1}{h}\,H_\varepsilon)+\Gamma\,H_\varepsilon-\mu\,S_\varepsilon\le C\,H_\varepsilon, \tag{26}$$

so that thanks to the properties of the heat equation in dimension 2 (the convolution by the heat kernel in dimension 2 is a convolution with a function lying in L^q for all $q<2$, cf. [7] for example), we obtain the boundedness of S_ε in $C^{0,\alpha}([0,T]\times\overline{\Omega})$ for some $\alpha\in]0,1[$ and all $T>0$.

Finally, we compute

$$\partial_t H_\varepsilon-d_H\,\Delta_x H_\varepsilon=\frac{1}{\eta}\,(a\,S_\varepsilon\,P_\varepsilon-\frac{1}{h}\,H_\varepsilon)-\mu\,H_\varepsilon, \tag{27}$$

so that $\partial_t H_\varepsilon-d_H\,\Delta_x H_\varepsilon$ is bounded in $L^{2+\delta}([0,T]\times\Omega)$ for all $T>0$. Thanks again to the properties of the heat equation in dimension 2, H_ε is bounded in $C^{0,\alpha}([0,T]\times\overline{\Omega})$ for some $\alpha\in]0,1[$ and all $T>0$.

Using the bounds above, we see that $\partial_t S_\varepsilon-d_S\,\Delta_x S_\varepsilon$ and $\partial_t H_\varepsilon-d_H\,\Delta_x H_\varepsilon$ are bounded in $L^{2+\delta}([0,T]\times\Omega)$ for all $T>0$. Then, the properties of maximal regularity for the heat equation imply that $\partial_t H_\varepsilon$, $\partial_{x_ix_j}H_\varepsilon$, $\partial_t S_\varepsilon$, and $\partial_{x_ix_j}S_\varepsilon$ are bounded in $L^{2+\delta}([0,T]\times\Omega)$ for all $T>0$ and $i,j\in\{1,2\}$.

As a consequence, H_ε and S_ε converge uniformly on $[0,T]\times\Omega$ for all $T>0$ towards two functions (resp. denoted by H and S), up to extraction of a subsequence, where H and S lie in $C^{0,\alpha}([0,T]\times\overline{\Omega})$, for some $\alpha\in]0,1[$ and all $T>0$. Moreover H and S satisfy the extra properties of regularity stated in the Theorem.

We also observe that

$$\partial_t H_\varepsilon-d_H\,\Delta_x H_\varepsilon=\frac{1}{\eta}\,(a\,S_\varepsilon\,P_\varepsilon-\frac{1}{h}\,H_\varepsilon)-\mu\,H_\varepsilon\ge-\left(\frac{1}{\eta\,h}+\mu\right)H_\varepsilon,$$

so that for all $t\in[0,T]$, $x\in\Omega$,

$$S_\varepsilon(t,x)+H_\varepsilon(t,x)\ge H_\varepsilon(t,x)\ge[\inf_{x\in\Omega}H_{in}(x)]\,\exp\left(-\left(\frac{1}{\eta\,h}+\mu\right)T\right)>0. \tag{28}$$

We now compute, for any $\alpha\in]-1,1[$,

$$\frac{d}{dt}\left\{\int\left(b^\alpha\,\frac{P_\varepsilon^{1+\alpha}}{1+\alpha}\,(S_\varepsilon+H_\varepsilon)^\alpha+\frac{1}{\tau^\alpha}\,\frac{R_\varepsilon^{1+\alpha}}{1+\alpha}\right)\right\}$$

$$=\int\left(b^\alpha\,(S_\varepsilon+H_\varepsilon)^\alpha\,P_\varepsilon^\alpha\,\partial_t P_\varepsilon+\frac{1}{\tau^\alpha}\,R_\varepsilon^\alpha\,\partial_t R_\alpha+\frac{\alpha}{1+\alpha}\,b^\alpha\,P_\varepsilon^{1+\alpha}\,(S_\varepsilon+H_\varepsilon)^{\alpha-1}\,\partial_t(S_\varepsilon+H_\varepsilon)\right)$$

$$= \int \Big(b^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha\, P_\varepsilon^\alpha\, d_P\, \Delta_x P_\varepsilon + r\, b^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha\, P_\varepsilon^{1+\alpha}\, (1 - \frac{P_\varepsilon + R_\varepsilon}{n}) - a\, b^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha\, P_\varepsilon^{1+\alpha}\, S_\varepsilon$$
$$-\frac{1}{\varepsilon}\, b^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha\, P_\varepsilon^\alpha\, (b\, P_\varepsilon\, (S_\varepsilon + H_\varepsilon) - \frac{R_\varepsilon}{\tau}) + \frac{1}{\tau^\alpha}\, R_\varepsilon^\alpha\, d_R\, \Delta_x R_\varepsilon + \frac{r}{\tau^\alpha}\, R_\varepsilon^{1+\alpha}\, (1 - \frac{P_\varepsilon + R_\varepsilon}{n})$$
$$+\frac{1}{\varepsilon}\, \frac{R_\varepsilon^\alpha}{\tau^\alpha}\, (b\, P_\varepsilon\, (S_\varepsilon + H_\varepsilon) - \frac{R_\varepsilon}{\tau}) + \frac{\alpha}{1+\alpha}\, b^\alpha\, P_\varepsilon^{1+\alpha}\, (S_\varepsilon + H_\varepsilon)^{\alpha-1}\, (d_S\, \Delta_x S_\varepsilon + d_H\, \Delta_x H_\varepsilon)$$
$$+\frac{\alpha}{1+\alpha}\, b^\alpha\, P_\varepsilon^{1+\alpha}\, (S_\varepsilon + H_\varepsilon)^{\alpha-1}\, ((\Gamma - \mu)\, H_\varepsilon - \mu\, S_\varepsilon) \Big)$$
$$= -\frac{1}{\varepsilon} \int (b\, P_\varepsilon\, (S_\varepsilon + H_\varepsilon) - \frac{R_\varepsilon}{\tau})\, (b^\alpha\, P_\varepsilon^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha - \frac{R_\varepsilon^\alpha}{\tau^\alpha})$$
$$-d_P\, \alpha\, b^\alpha \int (S_\varepsilon + H_\varepsilon)^\alpha\, P_\varepsilon^{\alpha-1}\, |\nabla_x P_\varepsilon|^2 - d_R\, \alpha\, \frac{1}{\tau^\alpha} \int R_\varepsilon^{\alpha-1}\, |\nabla_x R_\varepsilon|^2$$
$$-d_P\, \alpha\, \frac{1-\alpha}{1+\alpha}\, b^\alpha \int P_\varepsilon^{1+\alpha}\, (S_\varepsilon + H_\varepsilon)^{\alpha-2}\, |\nabla_x (S_\varepsilon + H_\varepsilon)|^2$$
$$+\int \Big(r\, b^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha\, P_\varepsilon^{1+\alpha}\, (1 - \frac{P_\varepsilon + R_\varepsilon}{n}) - a\, b^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha\, P_\varepsilon^{1+\alpha}\, S_\varepsilon$$
$$+\frac{r}{\tau^\alpha}\, R_\varepsilon^{1+\alpha}\, (1 - \frac{P_\varepsilon + R_\varepsilon}{n}) + \frac{\alpha}{1+\alpha}\, b^\alpha\, P_\varepsilon^{1+\alpha}\, (S_\varepsilon + H_\varepsilon)^{\alpha-1}\, ((\Gamma - \mu)\, H_\varepsilon - \mu\, S_\varepsilon) \Big)$$
$$+\frac{\alpha}{1+\alpha}\, b^\alpha \int P_\varepsilon^{1+\alpha}\, (S_\varepsilon + H_\varepsilon)^{\alpha-1} \Big\{ (d_s + d_P)\, \Delta_x S_\varepsilon + (d_H + d_P)\, \Delta_x H_\varepsilon \Big\}.$$

Integrating w.r.t time between 0 and T leads to the following estimate:

$$\frac{b^\alpha}{1+\alpha} \int P_\varepsilon^{1+\alpha} (S_\varepsilon + H_\varepsilon)^\alpha\, dx\, (T) + \frac{1}{\tau^\alpha\, (1+\alpha)} \int R_\varepsilon^{1+\alpha}\, dx\, (T)$$
$$+\frac{1}{\varepsilon} \int_0^T \int (b\, P_\varepsilon\, (S_\varepsilon + H_\varepsilon) - \frac{R_\varepsilon}{\tau})\, (b^\alpha\, P_\varepsilon^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha - \frac{R_\varepsilon^\alpha}{\tau^\alpha})\, dxdt$$
$$+d_P\, \alpha\, b^\alpha \int_0^T \int (S_\varepsilon + H_\varepsilon)^\alpha\, P_\varepsilon^{\alpha-1}\, |\nabla_x P_\varepsilon|^2\, dxdt + d_R\, \alpha\, \frac{1}{\tau^\alpha} \int_0^T \int R_\varepsilon^{\alpha-1}\, |\nabla_x R_\varepsilon|^2\, dxdt$$
$$+d_P\, \alpha\, \frac{1-\alpha}{1+\alpha}\, b^\alpha \int_0^T \int P_\varepsilon^{1+\alpha}\, (S_\varepsilon + H_\varepsilon)^{\alpha-2}\, |\nabla_x (S_\varepsilon + H_\varepsilon)|^2\, dxdt$$
$$\le C \int_0^T \int \Big(1 + (S_\varepsilon + H_\varepsilon)^\alpha + P_\varepsilon^{1+\alpha}\, H_\varepsilon\, (S_\varepsilon + H_\varepsilon)^{\alpha-1} \Big)\, dxdt$$
$$+\, C \int_0^T \int P_\varepsilon^{1+\alpha}\, (S_\varepsilon + H_\varepsilon)^{\alpha-1} \Big(|\Delta_x S_\varepsilon| + |\Delta_x H_\varepsilon| \Big)\, dxdt$$
$$+\, C \int \Big[P_{in}^{1+\alpha} (S_{in} + H_{in})^\alpha + R_{in}^{1+\alpha} \Big]\, dx.$$

The first term in the r.h.s of the estimate above is bounded (uniformly in ε) since $S_\varepsilon + H_\varepsilon$ and $(S_\varepsilon + H_\varepsilon)^{-1}$ are bounded (uniformly in ε) in $L^\infty([0,T] \times \Omega)$ for all $T > 0$, and since P_ε is bounded in $L^{2+\delta}([0,T] \times \Omega)$ for all $T > 0$, and some $\delta > 0$.

The last term of this r.h.s. is also finite thanks to the assumptions made on the initial data.

Remembering finally that $\partial_{x_i x_j} S_\varepsilon$ and $\partial_{x_i x_j} H_\varepsilon$ are bounded in $L^{2+\delta}([0,T] \times \Omega)$ (for some $\delta > 0$, and all $T > 0$, $i, j \in \{1, 2\}$), we see that when $\alpha > 0$ is small enough, the last term is also bounded (uniformly in ε).

Still assuming that $\alpha > 0$ is small enough, we get therefore the following bounds:

$$\int_0^T \int (b\, P_\varepsilon\, (S_\varepsilon + H_\varepsilon) - \frac{R_\varepsilon}{\tau})\, (b^\alpha\, P_\varepsilon^\alpha\, (S_\varepsilon + H_\varepsilon)^\alpha - \frac{R_\varepsilon^\alpha}{\tau^\alpha})\, dxdt \le C\, \varepsilon, \tag{29}$$

and

$$\int_0^T \int (S_\varepsilon + H_\varepsilon)^\alpha \, P_\varepsilon^{\alpha-1} \, |\nabla_x P_\varepsilon|^2 \, dxdt + \int_0^T \int R_\varepsilon^{\alpha-1} \, |\nabla_x R_\varepsilon|^2 \, dxdt \le C,$$

(where the constant C does not depend upon ε).

Then, using Cauchy-Schwartz inequality and the bounds on $S_\varepsilon + H_\varepsilon$ and P_ε, we get the estimate

$$\Big(\int_0^T \int |\nabla_x P_\varepsilon| \, dxdt \Big)^2 \le \Big[\inf (S_\varepsilon + H_\varepsilon) \Big]^{-\alpha} \int_0^T \int P_\varepsilon^{1-\alpha} \, dxdt \tag{30}$$

$$\times \int_0^T \int (S_\varepsilon + H_\varepsilon)^\alpha \, P_\varepsilon^{\alpha-1} \, |\nabla_x P_\varepsilon|^2 \, dxdt \le C,$$

where the constant C does not depend upon ε. In the same way,

$$\Big(\int_0^T \int |\nabla_x R_\varepsilon| \, dxdt \Big)^2 \le \int_0^T \int R_\varepsilon^{1-\alpha} \, dxdt \int_0^T \int R_\varepsilon^{\alpha-1} \, |\nabla_x R_\varepsilon|^2 \, dxdt \le C, \tag{31}$$

where the constant C does not depend upon ε.

Using identity (24), we see that $\partial_t (P_\varepsilon + R_\varepsilon) \in L^2([0,T]; H^{-2}(\Omega)) + L^{1+\delta/2}([0,T] \times \Omega)$, so that thanks to estimates (30) and (31) and Aubin's lemma (cf. for example [20]), $P_\varepsilon + R_\varepsilon$ converges (up to extraction of a subsequence) a.e. to $P + R$ on $[0,T] \times \Omega$.

Then, using the elementary inequality (for $\alpha \in]0,1[$, and a constant C which may depend on α) $(x-y)\,(x^\alpha - y^\alpha) \ge C\,(x^{(1+\alpha)/2} - y^{(1+\alpha)/2})^2$, estimate (29) leads to the bound:

$$\int_0^T \int \Big(\Big[b \, P_\varepsilon \, (S_\varepsilon + H_\varepsilon) \Big]^{(1+\alpha)/2} - \Big[\frac{R_\varepsilon}{\tau} \Big]^{(1+\alpha)/2} \Big)^2 \, dxdt \le C \, \varepsilon.$$

We now introduce a second elementary inequality (which holds for $\alpha > 0$ small enough, and a constant C which may depend on α) $|x-y| \le C\,|x^{(1+\alpha)/2} - y^{(1+\alpha)/2}|\,(x^{(1-\alpha)/2} + y^{(1-\alpha)/2})$. Then

$$\int_0^T \int |b \, P_\varepsilon \, (S_\varepsilon + H_\varepsilon) - \frac{R_\varepsilon}{\tau}| \, dxdt$$

$$\le \int_0^T \int \Big| (b \, P_\varepsilon \, (S_\varepsilon + H_\varepsilon))^{(1+\alpha)/2} - (\frac{R_\varepsilon}{\tau})^{(1+\alpha)/2} \Big| \Big((b \, P_\varepsilon \, (S_\varepsilon + H_\varepsilon))^{(1-\alpha)/2} + (\frac{R_\varepsilon}{\tau})^{(1-\alpha)/2} \Big) dxdt$$

$$\le 2 \Big(\int_0^T \int \Big| (b \, P_\varepsilon \, (S_\varepsilon + H_\varepsilon))^{(1+\alpha)/2} - (\frac{R_\varepsilon}{\tau})^{(1+\alpha)/2} \Big|^2 dxdt \Big)^{1/2}$$

$$\times \Big(\int_0^T \int \Big[(b \, P_\varepsilon \, (S_\varepsilon + H_\varepsilon))^{1-\alpha} + (\frac{R_\varepsilon}{\tau})^{1-\alpha} \Big] dxdt \Big)^{1/2}$$

$$\le C \, \sqrt{\varepsilon}.$$

As a consequence, $b \, P_\varepsilon \, (S_\varepsilon + H_\varepsilon) - \frac{R_\varepsilon}{\tau}$ converges (up to extraction) strongly in $L^1([0,T] \times \Omega)$ a.e. to 0, and (since $S_\varepsilon + H_\varepsilon$ converges a.e. towards $S+H$) weakly in $L^1([0,T] \times \Omega)$ towards $b \, P \, (S+H) - \frac{R}{\tau}$, so that eq. (8) holds.

Remembering moreover that $P_\varepsilon + R_\varepsilon$ converges a.e. to $P + R$, we see that $b \, P_\varepsilon \, (S_\varepsilon + H_\varepsilon) + b \, R_\varepsilon \, (S_\varepsilon + H_\varepsilon)$ converges a.e. to $P\,(S+H) + b\,R\,(S+H)$, and that $(\frac{1}{\tau} + b\,(S_\varepsilon + H_\varepsilon))\,R_\varepsilon$ converges a.e. to $(\frac{1}{\tau} + b\,(S+H))\,R$. Finally, we obtain that P_ε converges a.e. towards P, and R_ε converges a.e. towards R. Thanks to the properties of boundedness in $L^{2+\delta}([0,T] \times \Omega)$ of the sequences P_ε and R_ε (for some $\delta > 0$), we see that P_ε converges towards P in such a space, and R_ε converges towards R in such a space.

We now write down a weak form of eq. (24): For all $\phi \in C_c^2(I\!\!R_+ \times \overline{\Omega})$,

$$- \int_0^\infty \int_\Omega (P_\varepsilon + R_\varepsilon) \, \partial_t \phi \, dxdt - \int_\Omega (P_{in} + R_{in}) \, \phi(0, \cdot) \, dx - \int_0^\infty \int_\Omega (d_P \, P_\varepsilon + d_R \, R_\varepsilon) \, \Delta_x \phi \, dxdt \tag{32}$$

$$= \int_0^\infty \int_\Omega \left(r\,(P_\varepsilon + R_\varepsilon)\,(1 - \frac{1}{n}\,(P_\varepsilon + R_\varepsilon)) - a\,P_\varepsilon\,S_\varepsilon \right) \phi\,dxdt.$$

Then $r\,(P_\varepsilon{+}R_\varepsilon)\,(1{-}\frac{1}{n}\,(P_\varepsilon{+}R_\varepsilon)){-}a\,P_\varepsilon\,S_\varepsilon$ converges in $L^1([0,T]{\times}\Omega)$ to $r\,(P{+}R)\,(1{-}\frac{1}{n}\,(P{+}R)){-}a\,P\,S$, so that we can pass to the limit in all the terms of eq. (32) and obtain the weak formulation (13).

We then write down a weak form of eq. (26): for all $\phi \in C_c^2(I\!R_+ \times \overline{\Omega})$,

$$- \int_0^\infty \int_\Omega S_\varepsilon\,\partial_t \phi\,dxdt - \int_\Omega S_{in}\,\phi(0,\cdot)\,dx - d_S \int_0^\infty \int_\Omega S_\varepsilon\,\Delta_x \phi\,dxdt \tag{33}$$

$$= \int_0^\infty \int_\Omega \left(\frac{1}{\eta}\,(-a\,S_\varepsilon\,P_\varepsilon + \frac{1}{h}\,H_\varepsilon) + \Gamma\,H_\varepsilon - \mu\,S_\varepsilon \right) \phi\,dxdt.$$

We can pass to the limit in this formulation and end up with the weak form of the limiting equation (14).

We finally write down a weak form of eq. (27): for all $\phi \in C_c^2(I\!R_+ \times \overline{\Omega})$,

$$- \int_0^\infty \int_\Omega H_\varepsilon\,\partial_t \phi\,dxdt - \int_\Omega H_{in}\,\phi(0,\cdot)\,dx - d_H \int_0^\infty \int_\Omega H_\varepsilon\,\Delta_x \phi\,dxdt \tag{34}$$

$$= \int_0^\infty \int_\Omega \left(\frac{1}{\eta}\,(a\,S_\varepsilon\,P_\varepsilon - \frac{1}{h}\,H_\varepsilon) - \mu\,H_\varepsilon \right) \phi\,dxdt.$$

We can once again pass to the limit in this formulation and end up with the weak form of the limiting equation (15). This concludes the proof of the Theorem.

Remark: The proof above can be rewritten without any difficulty in dimension 1. In dimension 3 and above, it is still possible to show that P_ε and R_ε are bounded in $L^{2+\delta}([0,T]{\times}\Omega)$ for some $\delta > 0$ and all $T > 0$ (the improved duality lemma of [7] works indeed in any dimension). However the properties of the heat kernel are not sufficient anymore to show that H_ε is bounded in $L^\infty([0,T]{\times}\Omega)$ for all $T > 0$. Instead one gets the following weaker estimate: H_ε is bounded in $L^{10+\delta}([0,T] \times \Omega)$ for some $\delta > 0$ and all $T > 0$, and $\Delta_x H_\varepsilon$ is bounded in $L^{5/3+\delta}([0,T] \times \Omega)$ for some $\delta > 0$ and all $T > 0$. This is however not sufficient to give a sense to a quantity like $\int_0^T \int P_\varepsilon^{1+\alpha}\,(S_\varepsilon + H_\varepsilon)^{\alpha-1} \left(|\Delta_x S_\varepsilon| + |\Delta_x H_\varepsilon| \right) dxdt$, which is used in the proof above, so that the proof fails.

It is nevertheless possible to obtain a convergence result very close to Thm. 1 in dimension 3 and above, if one supposes (in addition to the assumptions of Thm 1) that $|d_P - d_R|$ is small enough. Indeed under such an assumption, the improved duality lemma of [7] leads to a bound in $L^q([0,T] \times \Omega)$ for all $T > 0$ and $q > 2$ as large as desired (depending on $|d_P - d_R|$). Using this bound, we can recover the boundedness of H_ε in $C^{0,\alpha}([0,T] \times \overline{\Omega})$ for some $\alpha > 0$ and all $T > 0$, and conclude as in dimension 1 and 2.

Finally, the assumption that $\inf H_{in} > 0$ is technical. It is useful for the main estimate but is not based on any modeling consideration. It may be relaxed by using the properties of the heat kernel (it becomes true uniformly w.r.t. ε, at any strictly positive time $t_0 > 0$, if H_{in} is not equal to 0 a.e.).

3 Turing instability analysis

In this section, we study the stability of system (23), and we compare the (Turing) instability region with the corresponding region when the cross diffusion is replaced by a standard diffusion. In Appendix A, a comparison between the homogeneous equilibrium states of the microscopic system (1) in the case of coexistence $(X, Y > 0)$, and the ones of the limiting (when $\varepsilon, \eta \to 0$) system (23) can be found.

3.1 Adimensionalization

In order to simplify the notations and to keep only meaningful parameters, we now propose an adimensionalization procedure for system (23), that we rewrite here under the following form:

$$\partial_t X - \Delta_x \left(\left\{ d_P \frac{1}{\tau b Y + 1} + d_R \frac{\tau b Y}{\tau b Y + 1} \right\} X \right) = r X \left(1 - \frac{X}{n} \right) - \frac{a X Y}{h a X + \tau b Y + 1}, \tag{35}$$

$$\partial_t Y - \Delta_x \left(\left\{ d_S \frac{\tau b Y + 1}{haX + \tau b Y + 1} + d_H \frac{haX}{haX + \tau b Y + 1} \right\} Y \right) = \Gamma h \frac{aXY}{haX + \tau b Y + 1} - \mu Y.$$

Using the new variables $\theta,\ \xi,\ y$ instead of $t,\ X,\ Y$, where

$$t = \frac{\theta}{r}, \quad X = n\xi, \quad Y = \zeta y,$$

we obtain:

$$\partial_\theta \xi - \Delta_x \left(\left\{ \frac{d_P}{r} \frac{1}{\tau b \zeta y + 1} + \frac{d_R}{r} \frac{\tau b \zeta y}{\tau b \zeta y + 1} \right\} \xi \right) = \xi (1 - \xi) - \frac{a\zeta}{r} \frac{\xi y}{han\xi + \tau b \zeta y + 1},$$

$$\partial_\theta y - \Delta_x \left(\left\{ \frac{d_S}{r} \frac{\tau b \zeta y + 1}{han\xi + \tau b \zeta y + 1} + \frac{d_H}{r} \frac{han\xi}{han\xi + \tau b \zeta y + 1} \right\} y \right) = \frac{\Gamma hn}{\zeta} \frac{a\zeta}{r} \frac{\xi y}{han\xi + \tau b \zeta y + 1} - \frac{\mu}{r} y.$$

We then define

$$D_P := \frac{d_P}{r}, \quad D_R := \frac{d_R}{r}, \quad D_S := \frac{d_S}{r}, \quad D_H := \frac{d_H}{r},$$

$$\frac{a\zeta}{r} =: b, \quad \frac{\Gamma hn}{\zeta} =: c, \quad han =: p, \quad \tau b \zeta =: k, \quad \frac{\mu}{r} =: m,$$

so that the system becomes:

$$\partial_\theta \xi - \Delta_x \left(\left\{ D_P \frac{1}{ky + 1} + D_R \frac{ky}{ky + 1} \right\} \xi \right) = \xi (1 - \xi) - \frac{b\xi y}{p\xi + ky + 1}, \tag{36}$$

$$\partial_\theta y - \Delta_x \left(\left\{ D_S \frac{ky + 1}{p\xi + ky + 1} + D_H \frac{p\xi}{p\xi + ky + 1} \right\} y \right) = \frac{cb\xi y}{p\xi + ky + 1} - my.$$

Note that we obtain the same reaction term as in [8, 9], in which it has been proven that a globally stable equilibrium point exists under suitable conditions on the parameters.

3.2 Homogeneous steady states

We look for the homogeneous steady states of system (36). Following [8], we can prove that the system admits a total extinction equilibrium $E_0(0,0)$, and a non coexistence equilibrium $E_1(1,0)$, which do not depend on the parameters. Moreover a coexistence equilibrium $E_*(x_*, y_*)$ exists (positive and unique) if and only if

$$\frac{cb}{m} > p + 1.$$

One can also see that

$$b - k \geq 0 \quad \Rightarrow \quad y_* \geq 0 \ \text{ for } \ 0 \leq x_* \leq 1,$$

$$b - k < 0 \quad \Rightarrow \quad y_* > 0 \ \text{ for } \ \frac{k - b}{b} \leq x_* \leq 1.$$

The coordinates of this equilibrium are

$$x_* = \frac{-\left((cb - mp) - kc\right) + \sqrt{\left((cb - mp) - kc\right)^2 + 4mkc}}{2kc},$$

$$y_* = \frac{cb - mp}{mk} x_* - \frac{1}{k}, \ \text{or equivalently} \ y_* = \frac{(1 - x_*)(px_* + 1)}{b - k + kx_*}.$$

3.3 Stability properties for the ODEs

In this subsection, we consider the ODE obtained from (36) by dropping the diffusion terms, and evaluate the stability of the equilibria found in the previous subsection.

Evaluating the Jacobian matrix at the equilibrium states, we can see that E_0 is unstable (saddle point) for all parameters, while E_1 is locally asymptotically stable when E_* does not exist, and unstable otherwise.

The stability of E_* is less straightforward. The elements, the trace and the determinant of the Jacobian matrix evaluated at (x_*, y_*), are

$$J^*_{11} = \frac{mp}{cb} - \left(1 + \frac{mp}{cb}\right) x_*, \qquad J^*_{12} = -\frac{m}{c}\left(1 - \frac{k}{b}(1 - x_*)\right) < 0,$$

$$J^*_{21} = c(1 - x_*)\left(1 - \frac{mp}{cb}\right) > 0, \qquad J^*_{22} = -\frac{mk}{b}(1 - x_*) < 0,$$

$$\mathrm{tr} J^* = -x_* + \frac{m}{b}\left(\frac{p}{c} - k\right)(1 - x_*), \quad \det J^* = \frac{m}{cb}(1 - x_*)\sqrt{((cb - mp) - kc)^2 + 4mkc} > 0.$$

Note that

$$J^*_{11} > 0 \quad \text{for} \quad 0 < x_* < \frac{mp}{mp + cb} < 1,$$

and moreover

$$p < kc \qquad \Rightarrow \qquad \mathrm{tr} J^* < 0 \qquad \Rightarrow \qquad E_* \text{ locally asymptotically stable.}$$

3.4 The linearization of the cross-diffusion terms

We now study the cross-diffusion system, under the assumption that $D_P > D_R$ and $D_S > D_H$, which are biologically meaningful (handling predators should not diffuse as much as searching predators, and invulnerable preys should not diffuse as much as vulnerable preys).

The linearization of the diffusion terms around E_* gives the matrix J^*_Δ, which elements are

$$J^*_{\Delta 11} = D_P \frac{1}{ky_* + 1} + D_R \frac{ky_*}{ky_* + 1} > 0, \qquad J^*_{\Delta 12} = -(D_P - D_R)\frac{kx_*}{(ky_* + 1)^2} < 0,$$

$$J^*_{\Delta 21} = -(D_S - D_H)\frac{py_*(ky_* + 1)}{(px_* + ky_* + 1)^2} < 0,$$

$$J^*_{\Delta 22} = D_S \frac{px_*(2ky_* + 1) + (ky_* + 1)^2}{(px_* + ky_* + 1)^2} + D_H \frac{px_*(px_* + 1)}{(px_* + ky_* + 1)^2} > 0,$$

(remember that we assume that $D_P > D_R$ and $D_S > D_H$). It follows that $\mathrm{tr} J^*_\Delta > 0$, and it can be proven also that $\det J^*_\Delta > 0$. Indeed, a simple computation shows that

$$\begin{aligned} \det J^*_\Delta (ky_* + 1)(px_* + ky_* + 1)^2 = \\ = D_P D_S \left(px_* ky_* + px_* + (ky_* + 1)^2\right) + D_P D_H px_*(px_* + ky_* + 1)\big) + \\ + D_R D_S ky_* \left[px_*(2ky_* + 1) + (ky_* + 1)^2 + px_*\right] + D_R D_H ky_* (px_*)^2. \end{aligned}$$

We look at the characteristic matrix

$$M_\kappa = \begin{pmatrix} J^*_{11} & J^*_{12} \\ J^*_{21} & J^*_{22} \end{pmatrix} - \lambda_k \begin{pmatrix} J^*_{\Delta 11} & J^*_{\Delta 12} \\ J^*_{\Delta 21} & J^*_{\Delta 22} \end{pmatrix},$$

for any $\lambda_k \geq 0$ eigenvalue of $-\Delta_x$ on Ω (with Neumann boundary conditions), where $k \in \mathbb{N}$. Its trace and determinant are

$$\mathrm{tr} M_\kappa = \mathrm{tr} J^* - \lambda_k \mathrm{tr} J^*_\Delta < 0,$$

$$\det M_\kappa = \det J^* - \lambda_k (J^*_{\Delta 22} J^*_{11} + J^*_{\Delta 11} J^*_{22} - J^*_{\Delta 12} J^*_{21} - J^*_{\Delta 21} J^*_{12}) + \lambda_k^2 \det J^*_\Delta.$$

3.5 Turing instability for the cross diffusion system

We now show that there is a nonempty region of Turing instability for system (36).

In order to get instability, we need $\det M_\kappa < 0$. Since $\det J^*,\ \det J^*_\Delta > 0$, a necessary condition for instability to occur is that the coefficient of λ_k is negative. This coefficient can be rewritten as

$$\begin{aligned} C_\kappa &:= J^*_{\Delta 22} J^*_{11} + J^*_{\Delta 11} J^*_{22} - J^*_{\Delta 12} J^*_{21} - J^*_{\Delta 21} J^*_{12} \\ &= J^*_{11} \left(D_S \frac{px_*(2ky_*+1) + (ky_*+1)^2}{(px_*+ky_*+1)^2} + D_H \frac{px_*(px_*+1) + (ky_*+1)^2}{(px_*+ky_*+1)^2} \right) \\ &\qquad - (D_S - D_H) \frac{py_*(ky_*+1)}{(px_*+ky_*+1)^2} \frac{m}{c} \left(1 - \frac{k}{b}(1-x_*) \right) - D_R \frac{mk}{b}(1-x_*). \end{aligned}$$

If $J^*_{11} < 0$, then $C_\kappa < 0$, and no Turing instability can appear. If $J^*_{11} > 0$, the sign of C_κ is not prescribed *a priori*. One can easily check however that if $D_R << 1,\ D_S \approx D_H$, then $C_\kappa > 0$. Under that condition and the extra assumption $D_S >> D_P$, one can even check that

$$C_\kappa^2 - 4 \det J^* \det J^*_\Delta > 0.$$

Indeed, under the assumptions $D_R << 1,\ D_S \approx D_H$,

$$C_\kappa \approx J^*_{11} \left(D_S \frac{px_*(2ky_*+1) + (ky_*+1)^2}{(px_*+ky_*+1)^2} + D_H \frac{px_*(px_*+1) + (ky_*+1)^2}{(px_*+ky_*+1)^2} \right),$$

and

$$4 \det J^* \det J^*_\Delta \approx 4 \det J^*\, D_P \frac{1}{ky_*+1} \left(D_S \frac{px_*(2ky_*+1) + (ky_*+1)^2}{(px_*+ky_*+1)^2} + D_H \frac{px_*(px_*+1)}{(px_*+ky_*+1)^2} \right).$$

3.6 Comparison with the linear-diffusion case

In this subsection, we wish to compare the stability of the steady homogeneous state E_* for system (36), and for the standard (called in the sequel "linear") reaction-diffusion system

$$\begin{aligned} \partial_\theta \xi - D_x\, \Delta_x \xi &= \xi\,(1-\xi) - \frac{b\xi y}{p\xi + ky + 1}, \\ \partial_\theta y - D_y\, \Delta_x y &= \frac{cb\xi y}{p\xi + ky + 1} - my, \end{aligned} \tag{37}$$

where the linear diffusion rates are the cross diffusion terms of (36) evaluated at the equilibrium (x_*, y_*):

$$\begin{aligned} D_x &:= D_P \frac{1}{ky_*+1} + D_R \frac{ky_*}{ky_*+1}, \\ D_y &:= D_S \frac{ky_*+1}{px_*+ky_*+1} + D_H \frac{px_*}{px_*+ky_*+1} = D_S \left(1 - \frac{mp}{cb}\right) + D_H \frac{mp}{cb}. \end{aligned}$$

Note that both D_x and D_y are convex combinations of $D_P,\ D_R$ and $D_S,\ D_H$, respectively. Furthermore $D_x = J^*_{\Delta 11}$.

The characteristic matrix related to the equilibrium $E_* = (x_*, y_*)$ is now

$$M^L_\kappa = \begin{pmatrix} J^*_{11} & J^*_{12} \\ J^*_{21} & J^*_{22} \end{pmatrix} - \lambda_k \begin{pmatrix} D_x & 0 \\ 0 & D_y \end{pmatrix}.$$

The trace is still negative and the determinant is

$$\det M^L_\kappa = \det J^* - \lambda_k (D_y J^*_{11} + D_x J^*_{22}) + \lambda_k^2 D_x D_y.$$

Also in this case, if $J_{11}^* < 0$, then no Turing instability can appear. If $J_{11}^* > 0$, we can get Turing instability by choosing $D_x << 1$ and $D_y >> 1$.

Such a behavior occurs when one chooses $D_R << 1$, $D_S \approx D_H$, $D_S >> 1 >> D_P$. We now wish to compare the Turing instability regions for systems (36) and (37). In order to do so, we try to compare the determinants

$$\det M_\kappa^L = \underbrace{D_x D_y}_{A_L} \lambda_k^2 - (\underbrace{D_y J_{11}^* + D_x J_{22}^*}_{B_L})\lambda_k + \det J^*,$$

$$\det M_\kappa = \underbrace{\det J_\Delta^*}_{A_C} \lambda_k^2 - (\underbrace{J_{\Delta 22}^* J_{11}^* + J_{\Delta 11}^* J_{22}^* - J_{\Delta 12}^* J_{21}^* - J_{\Delta 21}^* J_{12}^*}_{B_C})\lambda_k + \det J^*.$$

One can in fact show that $A_L < A_C$ for all parameter values, and that

$$B_L > B_C \qquad \Leftrightarrow \qquad (D_S - D_H) p x_* \frac{\sqrt{\Delta}}{c} > (D_P - D_R) \frac{mkcb}{cb - mp}, \tag{38}$$

where $\Delta := ((cb - mp) - kc)^2 + 4mkc$.

We now present examples of parameters (corresponding to the case when $B_L > B_C$) corresponding to the following cases:

1. There are no regions of strictly negative determinant for both linear and cross diffusion (Figure 1(a)), so that no Turing instability occurs for both linear and cross diffusions.

2. The linear diffusion case has a Turing instability region, but the determinant of the cross diffusion case is positive for all λ_k (Figure 1(b)), so that the cross diffusion case does not lead to Turing instability.

3. Both cases lead to nonempty Turing instability regions (Figure 1(c)) and we check that

$$\frac{\sqrt{B_L^2 - 4A_L \det J_*}}{2A_L} > \frac{\sqrt{B_C^2 - 4A_C \det J_*}}{2A_C},$$

   which means that the Turing instability region for the cross diffusion case is strictly included in the Turing instability region of the linear diffusion case.

In all the cases presented above, we see that the use of the cross-diffusion model leads to a possibility of obtaining nontrivial patterns which is less likely than when the linear diffusion model is considered, so that using linear diffusions may lead to some bad evaluation of the possibility to obtain patterns.

We show in Figure 1 the determinants of the characteristic matrices with respect to λ_k, for the following set of parameter values:

$$m = 0.01,\ c = 0.31,\ b = 0.91,\ p = 1.51,\ h = 0.21,$$

(for which the coexistence equilibrium state exists and it is l.a.s with $J_{11}^* > 0$), and we propose different choices of the diffusion coefficients leading to different cases:

- Figure 1(a): $D_P = 0.01,\ D_R = 0.005,\ D_S = 10,\ D_H = 9$;
- Figure 1(b): $D_P = 0.01,\ D_R = 0.005,\ D_S = 70,\ D_H = 69$;
- Figure 1(c): $D_P = 0.01,\ D_R = 0.005,\ D_S = 100,\ D_H = 99$.

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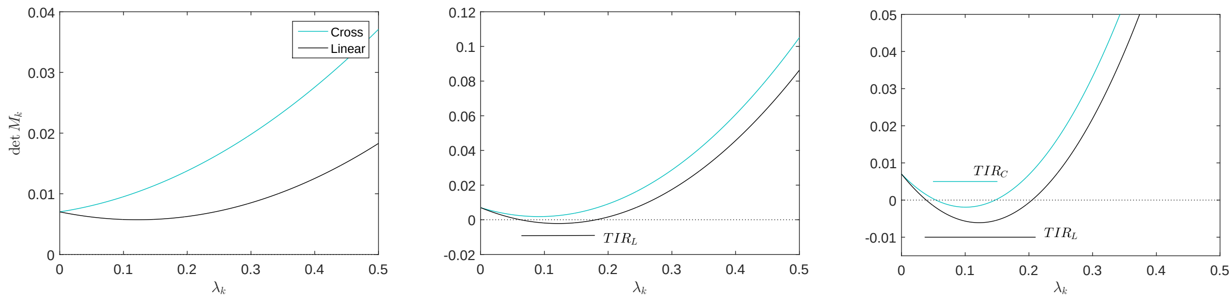

(a) (b) (c)

Figure 1: Turing Instability regions for linear diffusion and cross diffusion cases. (a) There are no regions of strictly negative determinant for both linear and cross diffusion, so that in both cases Turing instability cannot appear. (b) The linear diffusion case has a Turing instability region (TIR_L), but the determinant of the cross diffusion case is positive for all λ_k, so that the cross diffusion case does not lead to Turing instability. (c) Both cases lead to nonempty Turing instability regions, but the Turing instability region for the cross diffusion (TIR_C) case is strictly included in the Turing instability region of the linear diffusion case (TIR_L).

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Appendix A: Homogeneous equilibrium states

We provide here a short study of the homogeneous equilibrium states of the microscopic system (1) in the case of coexistence ($X, Y > 0$), and compare them to the ones of the limiting (when $\varepsilon, \eta \to 0$) system (23).

We start therefore with the system

$$\begin{cases} rP\left(1-\dfrac{X}{n}\right) - aPS - \dfrac{1}{\varepsilon}\left(bPY - \dfrac{1}{\tau}R\right) = 0, \\ rR\left(1-\dfrac{X}{n}\right) + \dfrac{1}{\varepsilon}\left(bPY - \dfrac{1}{\tau}R\right) = 0, \\ -\dfrac{1}{\eta}\left(aSP - \dfrac{1}{h}H\right) + \Gamma H - \mu S = 0, \\ \dfrac{1}{\eta}\left(aSP - \dfrac{1}{h}H\right) - \mu H = 0, \\ X = P + R, \\ Y = S + H. \end{cases}$$

Adding the first and second equations on one hand, and the third and fourth equation on the other end, we see that it is equivalent to

$$\begin{cases} rX\left(1-\dfrac{X}{n}\right) = aPS, \\ -\varepsilon rR\left(1-\dfrac{X}{n}\right) = bPY - \dfrac{R}{\tau}, \\ (\Gamma-\mu)H = \mu S, \\ aSP - \dfrac{H}{h} = \eta\mu H, \\ X = P + R, \\ Y = S + H. \end{cases}$$

From the third and sixth equations, we obtain

$$H = \frac{\mu}{\Gamma}Y, \quad S = \left(1-\frac{\mu}{\Gamma}\right)Y,$$

which leads to an equivalent 4-equations system:

$$\begin{cases} rX\left(1-\dfrac{X}{n}\right) = a\left(1-\dfrac{\mu}{\Gamma}\right)PY, \\ bPY - \dfrac{R}{\tau} = -\varepsilon rR\left(1-\dfrac{X}{n}\right), \\ a\left(1-\dfrac{\mu}{\Gamma}\right)YP - \dfrac{\mu}{\Gamma h}Y = \dfrac{\eta\mu^2}{\Gamma}Y, \\ X = P + R. \end{cases}$$

Under the condition $Y \neq 0$ (we look only for the case of coexistence), we can simplify the third equation and get a value $P_*(\eta)$ for P (which does not depend upon ε, and is strictly positive as soon as $\Gamma > \mu$):

$$P_*(\eta) := \frac{1}{a}\frac{\mu}{\Gamma-\mu}\left(\frac{1}{h}+\eta\mu\right), \tag{39}$$

so that using $R = X - P_*(\eta)$, the system becomes

$$\begin{cases} rX\left(1-\dfrac{X}{n}\right) = a\left(1-\dfrac{\mu}{\Gamma}\right)P_*(\eta)Y, \\ bP_*(\eta)Y - \dfrac{1}{\tau}\left(X-P_*(\eta)\right) = -\varepsilon r(X-P_*(\eta))\left(1-\dfrac{X}{n}\right). \end{cases}$$

This can be rewritten as a second order equation on X:

$$rX\left(1-\frac{X}{n}\right) = \frac{a}{b}\left(1-\frac{\mu}{\Gamma}\right)\left[\frac{1}{\tau}\left(X-P_*(\eta)\right) - \varepsilon r\left(X-P_*(\eta)\right)\left(1-\frac{X}{n}\right)\right], \tag{40}$$

or equivalently

$$-\frac{r}{n}\left(1+\varepsilon\frac{a}{b}\left(1-\frac{\mu}{\Gamma}\right)\right)X^2 + \left[r - \frac{a}{\tau b}\left(1-\frac{\mu}{\Gamma}\right)\left(1-\varepsilon r\tau\left(1+\frac{P_*(\eta)}{n}\right)\right)\right]X + \frac{a}{b}\left(1-\frac{\mu}{\Gamma}\right)\left(\frac{1}{\tau}-\varepsilon r\right)P_*(\eta) = 0.$$

The limiting equation (when η and ε tend to 0) is therefore

$$rX\left(1-\frac{X}{n}\right) = \frac{a}{\tau b}\left(1-\frac{\mu}{\Gamma}\right)\left(X-P_*(0)\right), \quad \text{with } P_*(0) = \frac{1}{ah}\frac{\mu}{\Gamma-\mu},$$

and it is identical to the second order equation in X obtained when looking for the homogeneous equilibria in system (23).

As a consequence, in the case when this limiting equation has a (unique) strictly positive solution X for which the corresponding Y is also strictly positive (coexistence equilibrium for the limiting problem, which entails the necessary condition $\Gamma > \mu$), then for $\varepsilon, \eta > 0$ small enough, a (unique) coexistence equilibrium also exists and converges (when $\varepsilon, \eta \to 0$) towards the (unique) coexistence equilibrium of the limiting problem.