Cross diffusion, segregation and aggregation

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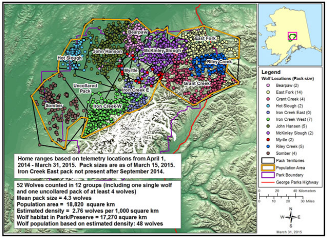
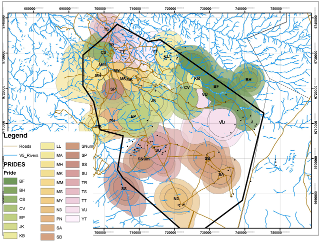
Motivation

Objective : modeling the segregation between different species
Example : populations of animals in competition

Example 1 : territories of the packs of wolves of the Denali National Park and Preserves



Example 2 : territories of the prides of lions of the Serengeti National Park



Hypothesis : the segregation originates from diffusion and repulsion
$\longrightarrow$ **cross-diffusion**

Introduction

Reaction-diffusion systems

$u_i := u_i(t,x) \geq 0$: space density of species i (for $i = 1..J$) at time $t \geq 0$.

Classical reaction-diffusion system

$$\partial_t U - \Delta_x [D\, U] = F(U),$$

with $F : \mathbb{R}^I_+ \longrightarrow \mathbb{R}^I$ and $D = \mathrm{diag}(d_1, \ldots, d_J)$ a positive diagonal matrix.

Interactions between individuals of different species affect the growth rate of the populations.

Reaction-cross diffusion systems

$u_i := u_i(t,x) \geq 0$: space density of species i (for $i = 1..J$) at time $t \geq 0$.

General reaction-cross diffusion system

$$\partial_t U - \Delta_x [A(U)] = F(U),$$

with $F : \mathbb{R}_+^I \longrightarrow \mathbb{R}^I$ and $A : \mathbb{R}_+^I \longrightarrow (R_+^*)^I$.

Interactions between individuals of different species affect the growth rate ***and the spreading*** *of the populations.*

The SKT system : modeling

$t \geq 0$: time, $x \in \Omega$: space ($\Omega \subset \mathbb{R}^N$: environment),
$u = u(t,x) \geq 0$: space density of first species at time $t \geq 0$,
$v = v(t,x) \geq 0$: space density of second species at time $t \geq 0$.

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Shigesada-Kawasaki-Teramoto (SKT) system (1979)

$$\begin{cases} \partial_t u - \Delta_x(d_1\, u + d_\alpha\, u^2 + d_\beta\, u\, v) = u\,(r_1 - r_a\, u - r_b\, v), \\ \partial_t v - \Delta_x(d_2\, v + d_\gamma\, v^2 + d_\delta\, u\, v) = v\,(r_2 - r_c\, v - r_d\, u), \\ \qquad \nabla_x u \cdot n = \nabla_x v \cdot n = 0 \quad \text{at } \partial\Omega. \end{cases}$$

Interpretation :

- $r_i > 0$ intrinsic growth rate ; $r_a > 0$, $r_c > 0$: intraspecific competition ; $r_b > 0$, $r_d > 0$: interspecific competition ;
- $d_i > 0$: standard diffusion ;
- $d_\alpha \geq 0$, $d_\gamma \geq 0$: self-diffusion ;
- $d_\beta \geq 0$, $d_\delta \geq 0$: cross-diffusion.

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$\rightarrow$ **cross/self-diffusion : repulsive effect due to the competition.**

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- show strong, nonlinear coupling / no maximum principle, existence of global strong solutions : still open,
- can lead to Turing's instability, model the segregation of species.

Derivation of the model

Derivation of cross-diffusion systems

Derivation of the SKT system

1. from individual-based models in a space-continuous setting (Fontbona-Méléard ; Moussa)
2. from individual-based models in a discrete in space setting (Daus-Desvillettes-Dietert)
3. from reaction-diffusion systems with fast reaction (Iida-Mimura-Ninomiya, Conforto-Desvillettes, Desvillettes-T.)

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Specificity : cross-diffusion term in a *Laplace form*.

Derivation of another cross-diffusion model : Maxwell-Stefan

- from kinetic models (Boudin-Grec-Salvarani, ...)

Cross-diffusion term in a *divergence (non-Laplace) form*.

1. Derivation of SKT from a continuous stochastic model

In [Fontbona-Méléard], particular case (simplified, no drift)

For $i \in [1, M]$ we track the spatial configuration over $\mathbb{R}^d$ of the population i :

$$\nu_t^{i,K} = \frac{1}{K} \sum_n \delta_{X_t^{n,i}}$$

• birth/death process in population i : exponential clock with rates r_i and $\sum_j r_{ij} G_\varepsilon * \nu_t^{j,K}$,
• diffusion process with diffusion matrix

$$A_i(G_{\varepsilon'} * \nu_t^{1,K}, \dots, G_{\varepsilon'} * \nu_t^{M,K}).$$

In the limit $K \longrightarrow \infty$, $\varepsilon \longrightarrow 0$:

$$\partial_t u_i = \sum_{k,l} \partial^2_{x_k x_l} [(A_i(G_{\varepsilon'} * u_1, \dots G_{\varepsilon'} * u_M))_{kl}\, u_i] + (r_i - \sum_j r_{ij} u_j) u_i$$

2. Derivation of SKT from a discrete-in-space stochastic model

In [Daus-Desvillettes-Dietert]

We consider the microscopic configuration over a discretized segment of $\mathbb{R}$ of the total population of size N.
• random walk with intensity depending on the presence of individuals of each population in the same cell (local interaction)

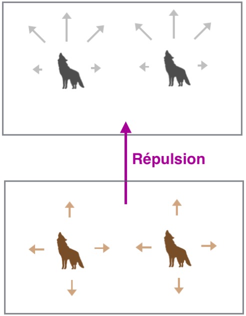
In the limit $N \longrightarrow \infty$ (formal), $\Delta x \longrightarrow 0$ (rigorous) :

$$\partial_t u_i = \partial_x^2 [d_i u_i + \sum_j d_{ij} u_j u_i]$$

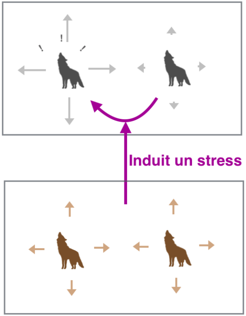
• quadratic model
• detailed balance condition : link between entropy structure and reversible Markov process
• if instead, the random walk depends on neighbouring cells $\Longrightarrow$ adding drift terms

3. Fast reaction

Relaxation model proposed by Iida, Mimura, Ninomiya



Triangular SKT system
two species - cross-diffusion



IMN model
three species - standard diffusion

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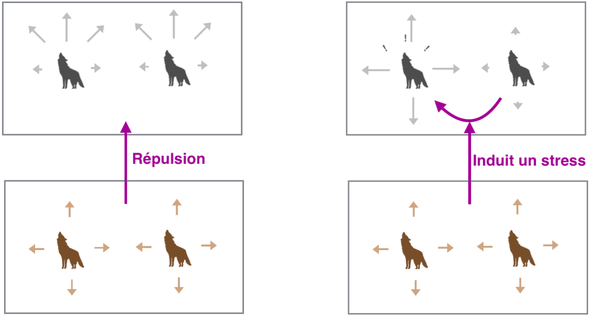

Triangular SKT system
two species - cross-diffusion

IMN model
three species - standard diffusion

When a scale parameter ε tends to zero in the IMN model, one recovers the triangular SKT system.

3. Fast reaction

$u_A^\varepsilon = u_A^\varepsilon(t,x) \geq 0$: density of population of first species in quiet state,
$u_B^\varepsilon = u_B^\varepsilon(t,x) \geq 0$: density of population of first species in stressed state,
$v^\varepsilon = v^\varepsilon(t,x) \geq 0$: density of second species.

Iida-Mimura-Ninomiya system (2006)

$$\begin{cases} \partial_t u_A^\varepsilon - d_A\,\Delta_x u_A^\varepsilon = [1-(u_A^\varepsilon+u_B^\varepsilon)-v^\varepsilon]\,u_A^\varepsilon + \dfrac{1}{\varepsilon}\,[k(v^\varepsilon)\,u_B^\varepsilon - h(v^\varepsilon)\,u_A^\varepsilon], \\ \partial_t u_B^\varepsilon - d_B\,\Delta_x u_B^\varepsilon = [1-(u_A^\varepsilon+u_B^\varepsilon)-v^\varepsilon]\,u_B^\varepsilon - \dfrac{1}{\varepsilon}\,[k(v^\varepsilon)\,u_B^\varepsilon - h(v^\varepsilon)\,u_A^\varepsilon], \\ \partial_t v^\varepsilon - \Delta_x v^\varepsilon = [1-v^\varepsilon-(u_A^\varepsilon+u_B^\varepsilon)]\,v^\varepsilon, \end{cases}$$

- the species 1 exists in a quiet state A and a stressed state B ($d_B > d_A$),
- the stress is induced by the presence of the species 2,
- the rate of switch is of order $1/\varepsilon \gg 1$.

3. Fast reaction

Equations for the densities of species

$$\begin{cases} \partial_t(u_A^\varepsilon + u_B^\varepsilon) - \Delta_x \left[(d_A \dfrac{u_A^\varepsilon}{u_A^\varepsilon + u_B^\varepsilon} + d_B \dfrac{u_B^\varepsilon}{u_A^\varepsilon + u_B^\varepsilon})(u_A^\varepsilon + u_B^\varepsilon) \right] \\ \qquad\qquad = \left[1 - (u_A^\varepsilon + u_B^\varepsilon) - v^\varepsilon\right](u_A^\varepsilon + u_B^\varepsilon), \\ \partial_t v^\varepsilon - \Delta_x v^\varepsilon = \left[1 - v^\varepsilon - (u_A^\varepsilon + u_B^\varepsilon)\right] v^\varepsilon. \end{cases}$$

Closure at the (formal) limit

If $(u_A^\varepsilon, u_B^\varepsilon, v^\varepsilon) \to (u_A, u_B, v)$ (in a strong sense) when $\varepsilon \to 0$ then $h(v)u_A = k(v)u_B$, i. e. $\frac{u_A}{u_A+u_B} = \frac{k(v)}{h(v)+k(v)}$ and $\frac{u_B}{u_A+u_B} = \frac{h(v)}{h(v)+k(v)}$.

3. Fast reaction

Equations for the densities of species at $\varepsilon = 0$

$$\begin{cases} \partial_t(u_A + u_B) - \Delta_x \left[(d_A \dfrac{k(v)}{h(v)+k(v)} + d_B \dfrac{h(v)}{h(v)+k(v)})(u_A + u_B) \right] \\ \qquad\qquad = [1 - (u_A + u_B) - v]\,(u_A + u_B), \\ \quad \partial_t v - \Delta_x v = [1 - v - (u_A + u_B)]\, v. \end{cases}$$

With accurate choices of the functions h and k, the densities $(u_A + u_B, v)$ satisfy the triangular Shigesada-Kawasaki-Teramoto system.

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The limit can be made rigourous in a generalized context (power laws in the diffusion and growth rates).
Still open (even at the formal level) for a non-triangular system.

Cross-diffusion and chemotaxis

Chemotaxis

Chemotaxis = the movement of an organism in response to a chemical stimulus.
Bacteria E. Coli :

- production of chemoattractant (signal)
- aggregation and formation of clusters

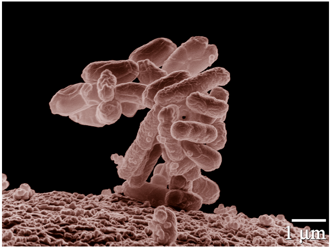

Figure: Cluster of E. Coli.

Cross-diffusion model

Model proposed by Fu *et al.* to describe stripe pattern formation

$$\begin{cases} \partial_t u = \Delta_x(\gamma(v)u), & x \in \Omega,\ t > 0, \\ \partial_t v - \varepsilon \Delta_x v = u - v, & x \in \Omega,\ t > 0, \\ \nabla_x u \cdot n = \nabla_x v \cdot n = 0 & x \in \partial\Omega\ t > 0. \end{cases} \tag{1}$$

γ : cell motility given by

$$\gamma(v) = \frac{1}{c + v^k}, \quad k > 0,\ c \geq 0.$$

γ is decreasing $\longrightarrow$ attraction.

Comparison with the Keller-Segel model

$t \geq 0$: time, $x \in \Omega$: space, $\Omega \subset \mathbb{R}^N$ $(1 \leq N \leq 3)$: environment,
$u = u(t,x)$: cell density, $v = v(t,x)$: chemical density.

$$\begin{cases} \partial_t u = \nabla_x \cdot (D(v)\nabla_x u - u\chi(v)\nabla_x v), & x \in \Omega,\ t > 0, \\ \partial_t v - \varepsilon \Delta_x v = v - u, & x \in \Omega,\ t > 0, \\ \nabla_x u \cdot n = \nabla_x v \cdot n = 0 & x \in \partial\Omega\ t > 0. \end{cases}$$

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The diffusivity D and the chemosensitivity χ are linked through the relation :

$$\chi(v) = (\alpha - 1)D'(v)$$

with $\alpha \geq 0$: effective body length of the cells (distance between receptors).

Taking $\alpha = 0$ (local sensing), we recover the previous system.

Analysis of the system

$$\begin{cases} \partial_t u = \Delta_x \left(\frac{1}{c + v^k} \, u \right), & x \in \Omega, \; t > 0, \\ \partial_t v - \varepsilon \Delta_x v = u - v, & x \in \Omega, \; t > 0. \end{cases}$$

Existence of global solutions [Desvillettes, Kim, T., Yoon]

Let $c \geq 0$, $\varepsilon > 0$ *and suppose*
$k > 0$ *if* $N = 1$, $0 < k < 2$ *if* $N = 2$, $0 < k < 4/3$ *if* $N = 3$.
Let $u_0 := u_0(x) \geq 0$ *lying in* $L^1(\Omega) \cap H_m^{-1}(\Omega)$ *and* $v_0 := v_0(x) \geq c_0 > 0$ *lying in* $W^{1,\infty}(\Omega)$.
Then, the system has a global in time (very) weak solution.

Remark : smooth solutions when Ω convex and $0 < m \leq \gamma_0(v) \leq M$ [Tao, Winkler]

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Elements of proof : the classical entropy $\int u \log u$ (for the minimal Keller-Segel model) does not work here.
Tools : energy estimates, heat kernel, and crucial use of a duality argument.

Analysis of the system : elements of proof

First note that the system preserves the cell mass : $\overline{u} = cte =: m$.
Duality argument :

$$\begin{aligned} \frac{1}{2}\frac{d}{dt}\langle (u-\overline{u}, (-\Delta)^{-1}(u-\overline{u})\rangle &= -\langle (u-\overline{u}, \gamma(v)u - \overline{\gamma(v)u})\rangle \\ &= -\int_\Omega \gamma(v)u^2 \, dx + \overline{u}\,\overline{\gamma(v)u} \\ &\leq -\int_\Omega \gamma(v)u^2 \, dx + \sup \gamma m^2. \end{aligned}$$

We end up with the estimate

$$\int_0^T \int_\Omega u^2\gamma(v) \leq C_T.$$

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Note : $\gamma(v)$ degenerates when $v \to \infty$...

Aggregation

Linear stability [Desvillettes, Kim, T., Yoon]

Let $c \geq 0$, $k > 1$, and $\mu_1 > 0$ be the principal eigenvalue of the Laplace operator $-\Delta$ on $\Omega \subset \mathbb{R}^N$ ($N \in \{1, 2, 3\}$).
Let $\bar{u} = \bar{v} > 0$ and note that $(\bar{u}, \bar{v})$ is a constant steady state of (1).
Suppose that $\bar{u} > u_1 := (\frac{c}{k-1})^{\frac{1}{k}}$. Then, $\varepsilon_1(\bar{u}) := \frac{(k-1)\bar{u}^k - c}{\mu_1(c+\bar{u}^k)} > 0$ and,

- *if $0 < \varepsilon < \varepsilon_1(\bar{u})$, then $(\bar{u}, \bar{v})$ is linearly unstable.*
- *if $\varepsilon > \varepsilon_1(\bar{u})$, then $(\bar{u}, \bar{v})$ is linearly asymptotically stable.*

Non-empty range of k with global existence and aggregation.

Numerical observation of pattern formation in 1D and 2D in the linearly unstable case.

Pattern formation (Matlab)

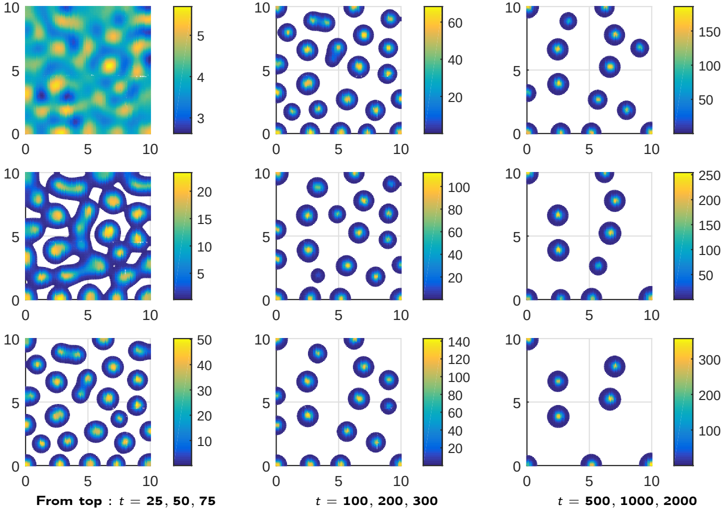

Figure: Cell density $u(t)$ for $k = 2$, $c = 1$, $u_0 = 4$, $v_0 = \text{Unif}(2, 6)$, $\varepsilon \sim 0.04$ (unstable regime).

Thank you for your attention.

A crucial tool : duality lemma

Lemma (Pierre Schmitt, 2000)

Let M be a smooth function on $[0,T] \times \overline{\Omega}$ with positive value. Then any classical solution $u \geq 0$ of

$$\begin{cases} \partial_t u - \Delta_x(Mu) \leq K \text{ in } [0,T] \times \Omega, \\ \nabla_x(Mu)(t,x) \cdot n(x) = 0 \text{ on } [0,T] \times \partial\Omega, \end{cases}$$

satisfies

$$\left\| Mu^2 \right\|_{L^1([0,T]\times\Omega)} \leq C(\Omega, T, u(0,\cdot), K)[1 + \|M\|_{L^1([0,T]\times\Omega)}].$$

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$\longrightarrow$ Back to the SKT system : estimate on $\left\| u^{2+\alpha} \right\|_{L^1([0,T]\times\Omega)}$.

Existence of solutions

Theorem (Desvillettes, Kim, T., Yoon)

Let Ω be a bounded smooth (C^2) open subset of $\mathbb{R}^N$, for $N \in \{1, 2, 3\}$. Let $c \geq 0$, $\varepsilon > 0$ and $k > 0$ if $N = 1$, $0 < k < 2$ if $N = 2$, $0 < k < 4/3$ if $N = 3$. Let $u_0 := u_0(x) \geq 0$ lying in $L^1(\Omega) \cap H_m^{-1}(\Omega)$ and $v_0 := v_0(x) \geq c_0 > 0$ lying in $W^{1,\infty}(\Omega)$. Then, **there exists a (very) weak global in time solution (u, v)** *of the cross-diffusion chemotaxis model with initial data (u_0, v_0). Furthermore,*

- *When $N = 1$, $v, v^{-1} \in L^\infty([0, T] \times \Omega)$, $u \in L^2([0, T] \times \Omega)$, $u \in L^\infty([0, T]; L^1(\Omega))$.*
- *When $N = 2$, $v \in L^{1/\eta}([0, T] \times \Omega) \cap L^\infty([0, T]; L^1(\Omega))$, $v^{-1} \in L^\infty([0, T] \times \Omega)$, $u \in L^{2-\eta}([0, T] \times \Omega) \cap L^\infty([0, T]; L^1(\Omega))$.*
- *When $N = 3$, $v \in L^{10-5k-\eta}([0, T] \times \Omega) \cap L^\infty([0, T]; L^1(\Omega))$, $v^{-1} \in L^\infty([0, T] \times \Omega)$, $u \in L^{\frac{10-5k}{5-2k}-\eta}([0, T] \times \Omega) \cap L^\infty([0, T]; L^1(\Omega))$.*

+ estimates on the gradients.

Remark : smooth solutions when Ω convex and $0 < m \leq \gamma_0(v) \leq M$ [Tao, Winkler]

Linear stability

Theorem (Desvillettes, Kim, T., Yoon)

Let Ω be a bounded smooth (C^2) open subset of $\mathbb{R}^N$, for $N \in \{1, 2, 3\}$. Let $c \geq 0$, $k > 1$, and $\mu_1 > 0$ be the principal eigenvalue of the Laplace operator $-\Delta$ on Ω.
Let $\bar{u} = \bar{v} > 0$ and note that $(\bar{u}, \bar{v})$ is a constant steady state of the cross-diffusion chemotaxis system.
Suppose that $\bar{u} > u_1 := (\frac{c}{k-1})^{\frac{1}{k}}$. Then, $\varepsilon_1(\bar{u}) := \frac{(k-1)\bar{v}^k - c}{\mu_1(c+\bar{v}^k)} > 0$ and,

- *if $0 < \varepsilon < \varepsilon_1(\bar{u})$, then $(\bar{u}, \bar{v})$ is linearly unstable.*
- *if $\varepsilon > \varepsilon_1(\bar{u})$, then $(\bar{u}, \bar{v})$ is linearly asymptotically stable.*

The triangular generalized cross-diffusion system

$$
\left.\begin{aligned}
\partial_t u - \Delta_x \left[Du + uv^{\beta}\right] = u[1 - u^a - v^b] \qquad & \text{in } \mathbb{R}_+ \times \Omega, \\
\partial_t v - \Delta_x v = v[1 - v^c - u^d] \qquad & \text{in } \mathbb{R}_+ \times \Omega, \\
\nabla_x u(t,x) \cdot n(x) = \nabla_x v^{\varepsilon}(t,x) \cdot n(x) = 0 \qquad & \forall t \geq 0, x \in \partial\Omega, \\
u(0,x) = u_{in}(x) \geq 0, \qquad v(0,x) = v_{in}(x) \geq 0 \qquad & \forall x \in \Omega.
\end{aligned}\right\} \qquad (2)
$$

Relaxation model

$$
\left.
\begin{aligned}
\partial_t u_A^\varepsilon - d_A\, \Delta_x u_A^\varepsilon &= [1 - (u_A^\varepsilon + u_B^\varepsilon)^a - (v^\varepsilon)^b]\, u_A^\varepsilon + \frac{1}{\varepsilon}\, [k(v^\varepsilon)\, u_B^\varepsilon - h(v^\varepsilon)\, u_A^\varepsilon], \\
\partial_t u_B^\varepsilon - d_B\, \Delta_x u_B^\varepsilon &= [1 - (u_A^\varepsilon + u_B^\varepsilon)^a - (v^\varepsilon)^b]\, u_B^\varepsilon - \frac{1}{\varepsilon}\, [k(v^\varepsilon)\, u_B^\varepsilon - h(v^\varepsilon)\, u_A^\varepsilon], \\
\partial_t v^\varepsilon - \Delta_x v^\varepsilon &= [1 - (v^\varepsilon)^c - (u_A^\varepsilon + u_B^\varepsilon)^d]\, v^\varepsilon, \\
\nabla_x u_A(t,x)\cdot n(x) = \nabla_x u_B^\varepsilon(t,x)\cdot n(x) &= 0 \qquad \forall t \geq 0, x \in \partial\Omega, \\
\nabla_x v^\varepsilon(t,x)\cdot n(x) &= 0 \qquad \forall t \geq 0, x \in \partial\Omega, \\
u_A(0,x) = u_{A,in}(x), \quad u_B(0,x) = u_{B,in}(x) \quad v(0,x) &= v_{in}(x) \qquad \forall x \in \Omega.
\end{aligned}
\right\}
\tag{3}
$$

Main theorem : assumptions

Assumption A

- Ω is a smooth bounded domain of $\mathbb{R}^N$,
- $d_B > d_A > 0$, $a, b, c, d > 0$,
- h, k lie in $C^1(\mathbb{R}_+, \mathbb{R}_+)$ and are lower bounded by a positive constant,
- $u_{A,in}, u_{B,in}, v_{in} \geq 0$ such that $u_{A,in}, u_{B,in} \in L^{p_0}(\Omega)$,

$v_{in} \in L^\infty(\Omega) \cap W^{2,1+p_0/d}(\Omega)$ for some $p_0 > 1$, and $\nabla_x v_{in} \cdot n(x) = 0$,

- $a > d$ or $(a \leq 1$ and $d \leq 2)$.

Theorem

Theorem (Desvillettes, T.)

Under Assumption A, When $\varepsilon \to 0$, $(u_A^\varepsilon, u_B^\varepsilon, v^\varepsilon)$ *converges (up to a subsequence) for almost every* $(t, x) \in \mathbb{R}_+ \times \Omega$ *to a limit* (u_A, u_B, v) *lying in* $L^{q_0}([0, T] \times \Omega) \times L^{q_0}([0, T] \times \Omega) \times L^\infty([0, T] \times \Omega)$ *for all* $T > 0$. *Furthermore,*

$$h(v)\, u_A = k(v)\, u_B$$

and $(u := u_A + u_B, v)$ *is a weak solution of system* (2) *with*

$$D + v^\beta = \frac{d_A k(v) + d_B h(v)}{h(v) + k(v)}$$

and initial data $u(0, \cdot) = u_{A,in} + u_{B,in}$, $v(0, \cdot) = v_{in}$.

Proof : entropy and duality methods.