Cross-diffusion models in Ecology

Gonzalo Galiano

Dpt. of Mathematics -University of Oviedo

Outline

1. **Ecological models with cross-diffusion**
   - Introduction: The SKT and BT models
   - The BT model deduced from particle systems
   - What about the SKT model?
   - Models deduction from splitting and differentation
   - State of the art

2. **The BT model**

Outline

Introduction

First ecological model of interacting populations taking into account **drifts caused by the other population** seems to be due to Kerner (1959):

$$\partial_t u_1 - \operatorname{div}\big(a_{11}\nabla u_1 + a_{12}\nabla u_2\big) = u_1(\alpha_1 - \beta_1 u_2),$$
$$\partial_t u_2 - \operatorname{div}\big(-a_{21}\nabla u_1 + a_{22}\nabla u_2\big) = u_2(-\alpha_2 + \beta_2 u_1),$$

with $a_{ij},\ \alpha_i,\ \beta_i$ positive.

Later on, Jorné (1977) produced a **linear stabilty analysis** of the model demonstrating that:

"while self-diffusion tends to damp out all spatial variations in the Lotka-Volterra system, cross-diffusion may give rise to instabilities and to non-constant stationary solutions."

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Nonlinear models

First nonlinear cross-diffusion models seem to have been introduced by

- Shigesada, Kawasaki and Teramoto (1979), and
- Busenberg and Travis (1983),

from different modeling points of view.

Shigesada et al. starts from a single continuity equation

$$\partial_t u - \operatorname{div} J(u) = u(\alpha - \beta u), \quad \text{with } J(u) = \nabla((c + au)u) + bu\nabla\Phi.$$

The flow J is composed by three terms:

- Random dispersal, $c\nabla u$,
- Dispersal due to *population pressure* (avoiding over-crowding), $\frac{a}{2}u\nabla u$,
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Generalizing the scalar equation to two populations (**SKT model**)

$$\partial_t u_1 - \operatorname{div}\Big(\nabla\big((c_1 + a_{11}u_1 + a_{12}u_2)u_1\big) + b_1 u_1 \nabla\Phi\Big) = f_1(u_1, u_2),$$
$$\partial_t u_2 - \operatorname{div}\Big(\nabla\big((c_2 + a_{21}u_1 + a_{22}u_2)u_2\big) + b_2 u_2 \nabla\Phi\Big) = f_2(u_1, u_2),$$

with competitive Lotka-Volterra source

$$f_i(u_1, u_2) = u_i\big(\alpha_i - (\beta_{i1}u_1 + \beta_{i2}u_2)\big).$$

Nonlinear models

Busenberg and Travis generalize the one-population flow $J(u) = au\nabla u$ in the following way:

Each individual population flow J_i is proportional to the gradient of the total population density, e.g.

$$J_i(u_1, u_2) = au_i\nabla(u_1 + u_2).$$

More in general, for a potential Ψ, they consider

$$J_i(u_1, u_2) = a\frac{u_i}{u_1 + u_2}\nabla\Psi(u_1 + u_2).$$

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As remarked by Gurtin and Pipkin (1984),

the individual flows J_i may depend, instead of in the total population density $u_1 + u_2$, in a general linear combination of both population densities, possibly different for each population.

These weighted sums are motivated when considering a set of species with different characteristics, such as size, behavior with respect to overcrowding, etc.

Assuming, in addition, environmental and random effects,

$$J_i(u_1, u_2) = u_i \nabla (a_{i1} u_1 + a_{i2} u_2 + b_i \Phi) + c_i \nabla u_i.$$

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The BT model deduced from particle systems

Two populations of particle ($i = 1, 2$) described by their trajectories (stochastic processes)

$$t \in \mathbb{R}_+ \to X^i_{j_i}(t) \in \mathbb{R}^m,$$

$j_i = 1, \ldots, N_i$ ($N_1 = N_2 = n$ to simplify).

Lagrangian approach: specify interacting laws $\to$ trajectories are solutions of

$$dX^i_j(t) = F^i_j(X^1_1(t), \ldots, X^1_n(t), X^2_1(t), \ldots, X^2_n(t))dt + \sigma^i_n dW^i_j(t),$$

$X^i_j(0) = X^i_{j0}$. Here,

- $F^i_j : \mathbb{R}^{2n} \to \mathbb{R}^m$ describe deterministic interactions.
- $\sigma^i_N \in \mathbb{R}$ are intensities of random dispersal (Brownian motions).

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Particle state modeled as positive Radon measure

$$\epsilon_{X_j^i(t)}(B) = \begin{cases} 1 & \text{if } X_j^i(t) \in B \\ 0 & \text{if } X_j^i(t) \notin B \end{cases} \qquad \text{for all } B \in \mathcal{B}(\mathbb{R}^m),$$

Collective behavior in terms of spatial distribution t (**empirical measures**):

$$u_n^i(t) = \frac{1}{n} \sum_{j=1}^{n} \epsilon_{X_j^i(t)} \in \mathcal{M}(\mathbb{R}^m),$$

giving **spatial relative frequency** of i-th population, at time t.

Lagrangian description:

$$dX_j^i(t) = F^i[u_n^1(t), u_n^2(t)](X_j^i(t))dt + \sigma_n^i dW_j^i(t).$$

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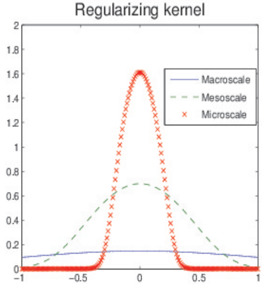
Deterministic interactions

Force exerted on $X_j^i(t)$ due to the interaction with all the other particles:

$$I_j^i = \sum_{k=1}^{2} \frac{a_{ik}}{n} \sum_{l=1}^{n} \zeta_\varepsilon(X_j^i(t) - X_l^k(t)),$$

with ζ_ε a regularizing kernel. In terms of the empirical measure,

$$I_j^i = \sum_{k=1}^{2} a_{ik}(u_n^k(t) * \zeta_\varepsilon)(X_j^i(t)).$$



Two kinds of deterministic interactions, $F^i = F_1^i + F_2^i$,

- **Repulsive:**

$$F_1^i[u_n^1(t), u_n^2(t)](X_j^i(t)) = -\nabla I_j^i = -\sum_{k=1}^{2} a_{ik}(u_n^k(t) * \nabla\zeta_\varepsilon)(X_j^i(t)).$$

- **Local attraction**, independent of scale, derived from a potential

$$F_2[u_n^1(t), u_n^2(t)](X_j^i(t)) = b_i \nabla\Phi(X_j^i(t)).$$

For the stochastic part, we assume

$$\lim_{n\to\infty} \sigma_n^i = \sigma_i \geq 0.$$

In some contexts, σ_n^i stands for the *mean free path*: average distance covered by a moving particle between successive collisions.

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The Euler description

Notation: $\langle \mu, g \rangle = \int g(s)\, d\mu(s).$

Ito's formula (changing to Eulerian): for any smooth $f : \mathbb{R}^m \times \mathbb{R}_+ \to \mathbb{R}$

$$
\begin{aligned}
\Big\langle u_n^i(t), f(\cdot,t) \Big\rangle = \quad & \frac{1}{n}\sum_{j=1}^{n} f(X_j^i(t),t) = \Big\langle u_n^i(0), f(\cdot,0) \Big\rangle \\
& - \sum_{k=1}^{2} a_{ik} \int_0^t \Big\langle u_n^i(s), (u_n^k(s) * \nabla\zeta_\varepsilon)(\cdot)\nabla f(\cdot,s) \Big\rangle\, ds \\
& + b_i \int_0^t \Big\langle u_n^i(s), \nabla\Phi \cdot \nabla f(\cdot,s) \Big\rangle\, ds \\
& + \int_0^t \Big\langle u_n^i(s), \frac{\partial}{\partial s} f(\cdot,s) + \frac{1}{2}(\sigma_n^i)^2 \Delta f(\cdot,s) \Big\rangle\, ds \\
& + \frac{\sigma_n^i}{n} \sum_{j=1}^{n} \int_0^t \nabla f(X_j^i(s),s) \cdot dW_j^i(s).
\end{aligned}
$$

The last term is the only explicit source of stochasticity, present for any $n < \infty$:

$$M_n^i(f,t) = \frac{\sigma_n^i}{n} \sum_{j=1}^{n} \int_0^t \nabla f(X_j^i(s), s) \cdot dW_j^i(s)$$

Doob's inequality implies

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Finally...

Assume $u_n^i(t) \to u_\infty^i(t)$ (deterministic process) represented by a density u_i:

$$\lim_{n\to\infty} \left\langle u_n^i(t), f(\cdot,t) \right\rangle = \left\langle u_\infty^i(t), f(\cdot,t) \right\rangle = \int_{\mathbb{R}^m} f(x,t) u_i(x,t) dx.$$

Then, for $n \to \infty$, we obtain

$$\begin{aligned}\int_{\mathbb{R}^m} f(x,t)u_i(x,t)dx = & \int_{\mathbb{R}^m} f(x,0)u_i(x,0)dx \\ & -\sum_{k=1}^{2} a_{ik} \int_0^t \int_{\mathbb{R}^m} u_i(x,s)\nabla u_k(x,s)\cdot\nabla f(x,s)dxds \\ & +b_i \int_0^t \int_{\mathbb{R}^m} u_i(x,s)\nabla\Phi(x)\cdot\nabla f(x,s)dxds \\ & +\int_0^t \int_{\mathbb{R}^m} u_i(x,s)\left(\frac{\partial}{\partial s} f(x,s) + \frac{1}{2}\sigma_i^2 \Delta f(x,s)\right)dxds.\end{aligned}$$

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Which is a weak formulation of the Cauchy BT model:

$$\partial_t u_i - \text{div}\left(u_i(a_{i1}\nabla u_1 + a_{i2}\nabla u_2 - b_i\nabla\Phi)\right) - c_i\Delta u_i = 0$$

$u_i(\cdot, 0) = u_{i0}$, and $c_i = \sigma_i^2/2$.

The passing to the limit is justified: Capasso et al. (2008), Lachowicz (2011),..

What about the SKT model?

Two (unsatisfactory) ways of fitting to the particle method:

- Diffusion coefficient:

$$\sigma_i = (c_i + a_{i1} u_1 + a_{i2} u_2)^{\frac{1}{2}}.$$

  But diffusion should decrease with concentration (sense of mean free path).

- Convection:

$$\begin{aligned}\nabla(u_1(a_{11}u_1 + a_{12}u_2)) &= u_1(2a_{11}\nabla u_1 + a_{12}\nabla u_2) + a_{12}u_2\nabla u_1 \\ &= u_1\left((2a_{11} + a_{12}\frac{u_2}{u_1})\nabla u_1 + a_{12}\nabla u_2\right)\end{aligned}$$

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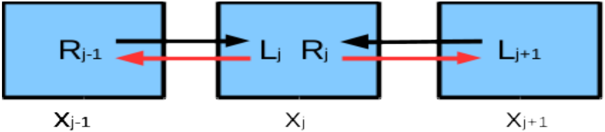
Lattice modeling



Let $\{x_j\}$ denote a mesh of size h of a 1D interval, and consider, for $i = 1, 2$,

$$\frac{d}{dt} u_i(x_j) = R^i_{j-1} u_i(x_{j-1}) + L^i_{j+1} u_i(x_{j+1}) - (R^i_j + L^i_j) u_i(x_j). \qquad (1)$$

Dispersal rates, R^i_j and L^i_j, may depend on concentrations. Assuming

$$R^i_j = L^i_j = \sigma_0 p_i(u_1(x_j), u_2(x_j)), \quad \sigma_0 > 0,$$

Eq. (1) is a finite differences formula for $\Delta(u_i p_i(u_1, u_2))$, when $\sigma_0 = \dfrac{1}{h^2}$.

Thus, for

- Constant $p's$, $p_i = c_i = const \Rightarrow$ linear diffusion ,

$$\partial_t u_i = c_i \Delta u_i.$$

- Linear $p's$, $p_i = c_i + a_{i1} u_1 + a_{i2} u_2 \Rightarrow$ SKT model

$$\partial_t u_i = c_i \Delta \big(u_i (c_i + a_{i1} u_1 + a_{i2} u_2) \big).$$

- BT model can, in general, not be cast in this form, since

$$u_i (a_{i1} \nabla u_1 + a_{i2} \nabla u_2)$$

  is not conservative.

Model deduction from differentation and splitting

Species U splits into two species U_1 and U_2, but keeping *most* of original behavior (Sánchez-Palencia, 2011).

Thus, if U satisfies

$$U'(t) = U(t)\big(\alpha - \beta U(t)\big), \quad \text{for } t \in (0, t^*), \quad U(0) = U_0 > 0. \tag{2}$$

after splitting, (U_1, U_2) satisfies

$$U_i'(t) = U_i(t)\big(\alpha - \beta\big(U_1(t) + U_2(t)\big)\big), \quad \text{for } t \in (t^*, T),$$

$$U_i(t^*) = U_{i0} > 0, \quad \text{with } U_{10} + U_{20} = U(t^*)$$

Under this splitting *without differentiation*, $U_1 + U_2$ still satisfies (2) for $t \geq t^*$.

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By splitting **with differentiation** we mean that (U_1, U_2) satisfies

$$U_i'(t) = U_i(t)\big(\alpha_i - \big(\beta_{i1} U_1(t) + \beta_{i2} U_2(t)\big)\big)$$

Under this splitting, $U_1 + U_2$ does not satisfy, in general, the original problem for $t \geq t^*$.

The splitting model in terms of PDEs: cross-diffusion

We start with one species, satisfying

$$\begin{cases} \partial_t u - \operatorname{div} J(u) = f(u) & \text{in } Q_{(0,t^*)} = (0,t^*) \times \Omega, \\ J(u) \cdot \boldsymbol{\nu} = 0 & \text{on } \Gamma_{(0,t^*)} = (0,t^*) \times \partial\Omega, \\ u(0,\cdot) = u_0 \geq 0 & \text{on } \Omega, \end{cases}$$

with

- $J(u) = u\nabla u + u\mathbf{q}$,
- $f(u) = u(\alpha - \beta u)$.

$\mathbf{q}$ usually determined as $\mathbf{q} = -\nabla\varphi$.

After splitting,

$$\begin{cases} \partial_t u_i - \operatorname{div} J_i(u_1, u_2) = f_i(u_1, u_2) & \text{in } Q_{(t^*,T)}, \\ J_i(u_1, u_2) \cdot \boldsymbol{\nu} = 0 & \text{on } \Gamma_{(t^*,T)}, \\ u_i(t^*, \cdot) = u_{i0} & \text{on } \Omega, \end{cases}$$

$u_{10} + u_{20} = u(t^*, \cdot)$.

If differentiation only takes place through the LV term,

$$\begin{aligned} J_1(u_1, u_2) + J_2(u_1, u_2) &= J(u_1 + u_2) \\ &= (u_1 + u_2)\nabla(u_1 + u_2) + (u_1 + u_2)\mathbf{q} \end{aligned}$$

After splitting,

$$\begin{cases} \partial_t u_i - \operatorname{div} J_i(u_1, u_2) = f_i(u_1, u_2) & \text{in } Q_{(t^*,T)}, \\ J_i(u_1, u_2) \cdot \boldsymbol{\nu} = 0 & \text{on } \Gamma_{(t^*,T)}, \\ u_i(t^*, \cdot) = u_{i0} & \text{on } \Omega, \end{cases}$$

$u_{10} + u_{20} = u(t^*, \cdot)$.

If differentiation only takes place through the LV term,

$$\begin{aligned} J_1(u_1, u_2) + J_2(u_1, u_2) &= J(u_1 + u_2) \\ &= (u_1 + u_2)\nabla(u_1 + u_2) + (u_1 + u_2)\mathbf{q} \end{aligned}$$

The linear terms differentiate in a natural way, e.g.

$$(u_1 + u_2)\mathbf{q} = u_1\mathbf{q} + u_2\mathbf{q}.$$

The nonlinear term admits several reasonable decompositions.

1. Leading to (a special case of) the **SKT model** (G. 2012),

$$u_i \nabla u_i + b_i \nabla(u_1 u_2), \quad b_i \geq 0, \quad b_1 + b_2 = 1.$$

2. Leading to **BT model** (G. and Selgas, 2015)

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State of the art: SKT model

Existence of solutions

Amann (1989) Local in time. Need L^∞ bounds to extend to $T = \infty$.

- First existence result for full matrix: Yagi (1993)
  Under assumption
  $$a_{12} < 8a_{11}, \quad a_{21} < 8a_{22}$$
  i.e. diffusion matrix positive definite.
- 1D case without restrictions on coefficients: G., Garzón and Jüngel (2003)
- Extension to 3D case: Chen and Jüngel (2004)
- Generalizations: Desvilletes et al. (2014), Jüngel (2015), G., Jüngel and Milisic (in progress).

State of the art: SKT model

- **Pattern formation**: Gambino, Lombardo and Sammartino (2012, 2013), Ruiz-Baier and Tian (2013),...
- **Numerical discretization**: G., Garzón and Jüngel (2001, 2003), Gambino, Lombardo and Sammartino (2009), Andreianov, Bendahmane, and Ruiz-Baier (2011),...
- **Travelling wave, exact solutions**: Zhao (2005), Cherniha (2008)
- **Ecological models**: G. and Velasco (2011, 2013),...
- **Steady state**...

State of the art: BT model

Existence of solutions
A series of papers by Bertsch, Gurtin, Hilhorst, Mimura, Peletier, and others (1984, 1985, 2010, 2013, 2015) $\rightarrow$ **Contact-inhibition problem**

G. and Selgas (2014, 2015, 2016) $\rightarrow$ **existence for BT model, numerics**

G., Shmarev and Velasco (2015) $\rightarrow$ **Contact-inhibition problem: existence, nonuniqueness**

Outline

The BT model

For $T > 0$ and $\Omega \subset \mathbb{R}^m$, find $u_i : \Omega \times (0, T) \to \mathbb{R}$ such that, for $i = 1, 2$,

$$\begin{aligned}
&\partial_t u_i - \operatorname{div} J_i(u_1, u_2) = f_i(u_1, u_2) && \text{in } Q_T = \Omega \times (0, T), \\
&J_i(u_1, u_2) \cdot n = 0 && \text{on } \Gamma_T = \partial\Omega \times (0, T), \\
&u_i(\cdot, 0) = u_{i0} && \text{in } \Omega,
\end{aligned}$$

with flow and competitive Lotka-Volterra functions given by

$$\begin{aligned}
J_i(u_1, u_2) &= u_i\big(a_{i1}\nabla u_1 + a_{i2}\nabla u_2 + b_i q\big) + c_i \nabla u_i, \\
f_i(u_1, u_2) &= u_i\big(\alpha_i - \beta_{i1} u_1 - \beta_{i2} u_2\big).
\end{aligned}$$

Assumptions

1. $\Omega \subset \mathbb{R}^m$ ($m = 1, 2$ or 3) bounded, $\partial\Omega$ Lipschitz continuous.
2. $a_{ij},\ c_i,\ \alpha_i,\ \beta_{ij} \geq 0$ and $L^\infty(Q_T)$, $b_i \in L^\infty(Q_T)$. Besides, $\exists a_0 > 0$ such that

$$4a_{11}a_{22} - (a_{12} + a_{21})^2 > a_0 \quad \text{a.e. in } Q_T.$$

3. $q \in (L^2(Q_T))^m$.
4. $u_{i0} \geq 0$, and $L^\infty(\Omega)$.

Main tool for the analysis is the entropy functional

$$E(t) = \sum_{i=1}^{2} \int_\Omega F(u_i(\cdot,t)) \geq 0, \quad \text{with } F(s) = s(\ln s - 1) + 1.$$

Using $F'(u_i) = \ln u_i$ as a test function,

$$E(t) + \int_{Q_t} \Big(\sum_{i=1}^{2} (a_{ii}|\nabla u_i|^2 + 2c_i|\nabla \sqrt{u_i}|^2) + (a_{12}+a_{21})\nabla u_1 \cdot \nabla u_2 \Big)$$

$$= E(0) + \int_{Q_t} \sum_{i=1}^{2} \Big(- b_i\, q \cdot \nabla u_i + f_i(u_1,u_2) \ln u_i \Big),$$

and, from assumptions,

$$E(t) + a_0 \int_{Q_t} (|\nabla u_1|^2 + |\nabla u_2|^2) \leq (E(0) + C_1)\, e^{C_2 t}.$$

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The limit case $4a_{11}a_{22} = (a_{12} + a_{21})^2$

Parabolic-hyperbolic problem
Solved in (at least) two cases:

- **General initial data**, but strong assumptions on coefficients:

$$\partial_t u_i - \text{div}\left(au_i\nabla(u_1 + u_2) + bqu_i + c\nabla u_i\right) = u_i(\alpha - \beta(u_1 + u_2)),$$

The key is that $u = u_1 + u_2$ satisfies a porous medium type PDE. Thus, if $u_{10} + u_{20} > 0$ in Ω then u is smooth.
An approximation is constructred via nonlinear regularization (SKT type), adding

$$a\frac{\delta}{2}\Delta(u_i(u_1 + u_2))$$

for which $u_1^\delta + u_2^\delta$ still satisfies a PM equation.
u_i^δ only converges weakly* in L^∞, but u^δ strongly in $H^1(\Omega)$

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- **Contact-inhibition problem.** Initial data segregated:

$$u_{10} + u_{20} > 0 \quad \text{and} \quad supp(u_{10}) \cap supp(u_{20}) = \emptyset$$

Bertsch et al. introduce

$$u = u_1 + u_2, \quad r = \frac{u_1}{u},$$

solving

$$(\mathrm{P})_B \begin{cases} \partial_t u - \partial_x(u(\partial_x u)) = F_1(u,r) & \text{in } Q_T, \\ \partial_t r - \partial_x u\, \partial_x r - \delta\partial_{xx} r = F_2(u,r) & \text{in } Q_T, \\ \partial_x u = \partial_x r = 0 & \text{on } \Gamma_T, \\ u(0,\cdot) = u_0, \quad r(0,\cdot) = r_0^\delta & \text{in } \Omega, \end{cases}$$

with F_i given in terms of f_i.

Bertsch et al. show existence in 1D and multi-dimensional (more restrictions) using

- parabolic regulariztion of the auxiliar problem,
- characteristics.

Using part of their arguments, we also show existence in 1D with the direct parabolic regularization.
The key is a $BV(\Omega)$ bound, maximal regularity expected.

Example: an explicit solution

H Heaviside and B Barenblatt.

$$u_{10}(x) = H(x - x_0)B(0, x), \quad u_{20}(x) = H(x_0 - x)B(0, x).$$

The $L^\infty(0, T; BV(\Omega))$ functions

$$u_1(t, x) = H(x - \eta(t))B(t, x), \quad u_2(t, x) = H(\eta(t) - x)B(t, x),$$

with $\eta(t) = x_0(1 + \frac{t}{t^*})^{1/3}$, are a weak solution of

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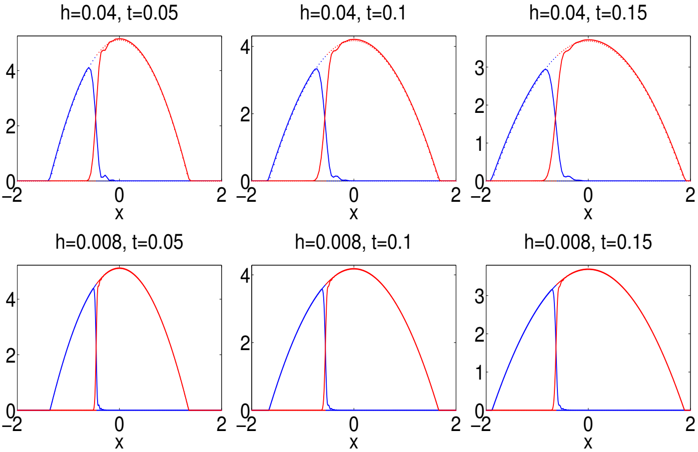
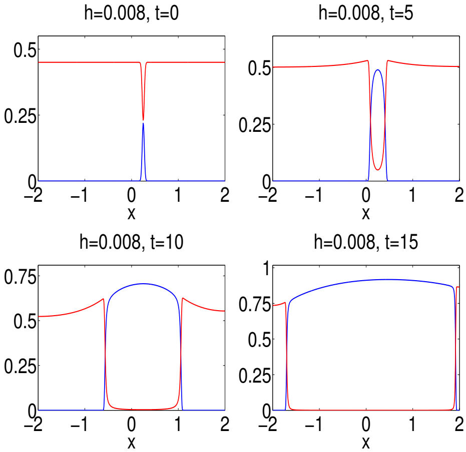
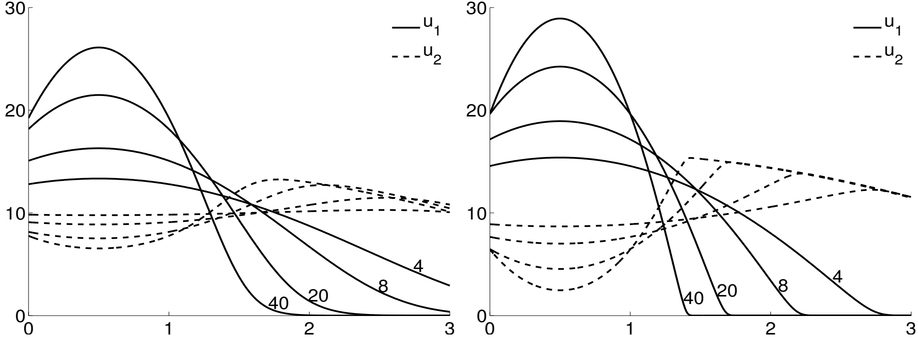
Heaviside-Barenblatt example



Invasion example



SKT versus BT



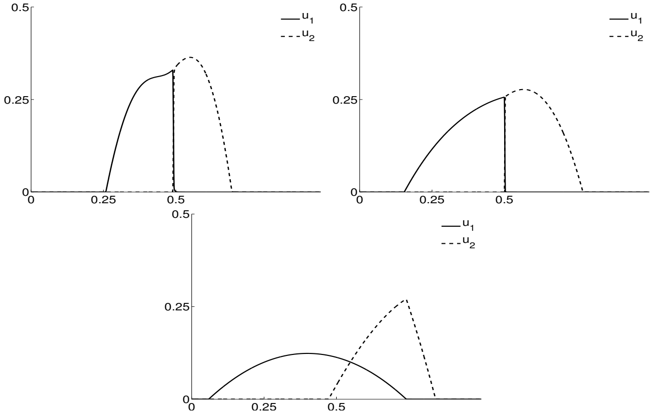


Figure : Transient states corresponding to: top left: $b_1 = 1, \ b_2 = 10$, top right: $a_{11} = a_{12} = 3$, $a_{21} = a_{22} = 1$, bottom: $a_{11} = 4, \ a_{12} = 0, \ a_{21} = 3.9, \ a_{22} = 1$.

Thank you!