Long-term coexistence of competing species in spatially non-homogeneous environment: existence and stability of special types solutions for systems of reaction-diffusion equations

Part I: Gradient Systems

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Diffusion equation, and **heat equation**:

$$u_t - u_{xx} = 0.$$

Here

$$u = u(x,t), \quad u_t \equiv \frac{\partial u}{\partial t}, \quad u_{xx} \equiv \frac{\partial^2 u}{\partial x^2}, \quad \text{etc.}$$

Of course, this can be extended for a more general case,

$$u_t - \Delta u = 0.$$

At a steady-state $u_t = 0$, and hence

$$\Delta u = 0.$$

Reaction-diffusion equation is
a **diffusion equation with a non-zero right part**:

$$\frac{\partial u}{\partial t} - \Delta u = f(u).$$

An **initial condition** $u(x, 0)$ and **boundary conditions** must be added, e.g.

$u(0, t) = u(1, t) = 0$ for a given function ("given temperature"), or

$\frac{\partial u(0,t)}{\partial x} = \frac{\partial u(1,t)}{\partial x} = 0$ for a given flux (no flux condition in this case).

For a single reaction-diffusion equation

$$\frac{\partial u}{\partial t} - \Delta u = f(u)$$

pretty much is known,

and mostly due to the fact that here

$$f(u) = \frac{\partial F(u)}{\partial u}.$$

The good thing about the potential $F(u)$ is that

(1) the **steady-state equation**

$$-\Delta u = f(u) \qquad (\frac{\partial u}{\partial t} \equiv 0 \ \text{ here})$$

is the Euler-Lagrange equations for the functional

$$I = \int_0^1 \left(\frac{1}{2}\left(u_x^2\right) - F(u)\right) dx = \int_0^1 E(x)\, dx.$$

Indeed, the Euler-Lagrange equations is

$$\frac{\partial}{\partial x}\left(\frac{\partial E}{\partial u_x}\right) - \frac{\partial E}{\partial u} = 0.$$

Here,

$$\frac{\partial E}{\partial u_x} = u_x, \quad \frac{\partial E}{\partial u} = -f(u), \quad \text{and hence} \quad u_{xx} = -f(u).$$

(2) For **homogeneous boundary conditions**, the functional

$$I(t) = \int_0^1 \left(\frac{1}{2}\left(u_x^2\right) - F(u)\right) dx = \int_0^1 E(x)\, dx$$

monotonically decreases for any solution $u(x,t)$ of the initial time-dependent problem

$$\frac{\partial u}{\partial t} - \Delta u = f(u).$$

Indeed,

$$\begin{aligned}
\frac{dI(t)}{dt} &= \int_0^1 \left(\frac{1}{2}\left(2u_x \frac{\partial u_x}{\partial t}\right) - \frac{\partial F}{\partial u}\frac{\partial u}{\partial t}\right) dx \\
&= \int_0^1 \left(\frac{\partial}{\partial x}(u_x\, u_t) - u_t\, u_{xx} - f(u)\, u_t\right) dx \\
&= \int_0^1 \left(\frac{\partial}{\partial x}(u_x\, u_t)\right) dx - \int_0^1 (u_{xx} + f(u))\, u_t\, dx \\
&- \int_0^1 u_t^2\, dx \le 0.
\end{aligned}$$

Here, by the Gauss divergence theorem,

$$\int_0^1 \left(\frac{\partial}{\partial x}(u_x\, u_t)\right) dx = u_x(1,t)\, u_t(1,t) - u_x(0,t) u_t(0,t) = 0$$

for the homogeneous boundary conditions.

(3) Furthermore, the function

$$E(x) = \frac{1}{2}\left(u_x^2\right) + F(u)$$

is the first integral of the steady-state equation:
that is the function $E(x)$ is constant for all x, and $\frac{\partial E}{\partial x} = 0$:

$$\begin{aligned}
\frac{\partial}{\partial x}E(x) &= \frac{1}{2}\frac{\partial}{\partial x}\left(u_x^2\right) + \frac{\partial}{\partial x}F(u) \\
&= \frac{2}{2}\frac{\partial u_x}{\partial x}u_x + \frac{\partial F}{\partial u}u_x \\
&= \left(u_{xx} + f(u)\right)u_x = 0.
\end{aligned}$$

The systems of reaction-diffusion equations, e.g.

$$u_t - \Delta u = f(u, v),$$

$$v_t - \Delta v = g(u, v),$$

are considerably more difficult.

An example

To describe the spatial spread of two competing species—

US original grey and UK indigenous red squirrels in the UK—

J. Norbury and G.C. Wake (1993) suggested

a system of two reaction-diffusion equations:

$$\begin{aligned} u_t - u_{xx} &= \lambda u(1 - u^2 - a^2 v^2), \\ v_t - v_{xx} &= \lambda v(b^2 - a^2 u^2 - c^2 v^2). \end{aligned}$$

This model is **a gradient system**: the right parts of the equations are partial derivatives of the potential

$$G(u,v) = \frac{\lambda}{2}\left(u^2 - \frac{1}{2}u^4 - a^2 u^2 v^2 + b^2 v^2 - \frac{1}{2}c^2 v^4\right).$$

A time-independent spatial distribution of the species $u(x)$ and $v(x)$ satisfies the equations

$$\frac{d^2u}{dx^2} = -G_u, \qquad \frac{d^2v}{dx^2} = -G_v.$$

(Boundary conditions should be added to close the system.)

These equations are the **Euler-Lagrange equations** for the functional

$$I = \int_0^1 \left(\frac{1}{2}\left(u_x^2 + v_x^2\right) - G(u,v)\right) dx.$$

Furthermore, the function

$$E(x) = \frac{1}{2}\left(u_x^2 + v_x^2\right) + G(u,v)$$

is the **first integral** of the system:
that is **the function $E(x)$ is constant for all x.**

Problem formulation

We consider two interacting (competing) species with densities $u(\mathbf{x},t)$ and $v(\mathbf{x},t)$ in a multi-dimensional region $\Omega \subset \mathbf{R}^n$.
(Here $n = 2$ for most biological species,
or $n = 3$ for some bacteria or in chemical reactors).
The densities of the species satisfy the equations

$$\begin{aligned}
\frac{\partial u(\mathbf{x},t)}{\partial t} &= \nabla \cdot (D_1(\mathbf{x}) \nabla u(\mathbf{x},t)) + \frac{\partial W(\mathbf{x},u,v)}{\partial u}, \\
\frac{\partial v(\mathbf{x},t)}{\partial t} &= \nabla \cdot (D_2(\mathbf{x}) \nabla v(\mathbf{x},t)) + \frac{\partial W(\mathbf{x},u,v)}{\partial v}.
\end{aligned}$$

Here we assume that the species have different and varying in space diffusion rates, $D_1(\mathbf{x})$ and $D_2(\mathbf{x})$, and that
the potential $W(\mathbf{x},u,v)$ can vary in space.

The **boundary** and **initial conditions** are

$$D_1(\mathbf{x})\frac{\partial u}{\partial n} + B(\mathbf{x}) \cdot (u - u_a(\mathbf{x})) = 0,$$
$$D_2(\mathbf{x})\frac{\partial v}{\partial n} + C(\mathbf{x}) \cdot (v - v_a(\mathbf{x})) = 0, \quad \text{and}$$

$$u(\mathbf{x}, 0) = \phi(\mathbf{x}), \quad v(\mathbf{x}, 0) = \psi(\mathbf{x}) \quad \text{for} \quad \mathbf{x} \in \Omega.$$

Examples:

(1) **"No-flux" conditions**
(*homogeneous Neumann conditions*): $B(\mathbf{x}) = C(\mathbf{x}) = 0$ here:

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \quad \text{for} \quad \mathbf{x} \in \partial\Omega.$$

(2) **"Given temperature" conditions**
(*homogeneous Dirichlet conditions*): $D_1(\mathbf{x}) = D_2(\mathbf{x}) = 0$ here:

$$u(\mathbf{x}) = v(\mathbf{x}) = 0 \quad \text{for} \quad \mathbf{x} \in \partial\Omega.$$

Naturally, only the case $u, v \geq 0$ is feasible for a population or concentration model.

Here we consider two species;
however all results can be easily generalised to a multi-species case.

Theorem 1.

There is no periodic in time t solution for this initial-boundary value problem.

Proof:

Let us consider the functional

$$F(t) = \int_{\Omega} \left(\frac{1}{2} \left(D_1 (\nabla u)^2 + D_2 (\nabla v)^2 \right) - W \right) dV$$

$$+ \frac{1}{2} \oint_{\partial \Omega} \left(B(u - u_a)^2 + C(v - v_a)^2 \right) dS.$$

For a periodic solution $u(\mathbf{x}, t), v(\mathbf{x}, t)$
the function $F(t)$ must be periodic as well.

Nevertheless,

$$
\begin{aligned}
\frac{dF(t)}{dt} &= \int_{\Omega} \left(D_1 \nabla u \cdot \nabla u_t + D_2 \nabla v \cdot \nabla v_t\right) dV \\
&- \int_{\Omega} \left(W_u \cdot u_t + W_v \cdot v_t\right) dV \\
&+ \oint_{\partial\Omega} B(u - u_a) u_t \, dS + \oint_{\partial\Omega} C(v - v_a) v_t \, dS \\
&= -\int_{\Omega} \left(u_t^2 + v_t^2\right) dV \leq 0,
\end{aligned}
$$

where $\frac{dF(t)}{dt} = 0$ only for time-independent solutions.

This contradicts the assumption about the periodicity of the functional.

Hence there are no periodic solutions for the system,
in view of the monotonicity of $F(t)$.

Corollary 1.

No Hopf bifurcation is possible for the initial-boundary value problem with gradient right parts.

Functional $F(t)$ is the Lyapunov function for this system.

Theorem 1 and **Corollary 1** hold for gradient systems of all sizes, and a single reaction-diffusion equation, **whose forcing term always may be considered as a gradient of a potential**, provides a particularly important case.

Steady-state solutions

Steady-states solutions of the system satisfy the equations:

$$\nabla \cdot (D_1 \nabla u) = -\frac{\partial W}{\partial u}, \quad \nabla \cdot (D_2 \nabla v) = -\frac{\partial W}{\partial v}, \quad \mathbf{x} \in \Omega \subset \mathbf{R}^n,$$

with boundary conditions

$$D_1 \frac{\partial u}{\partial n} = -B(u - u_a), \quad D_2 \frac{\partial v}{\partial n} = -C(v - v_a), \quad \mathbf{x} \in \partial\Omega.$$

Here $D_1(\mathbf{x}), D_2(\mathbf{x}) > 0$ are diffusion rates,
$W(\mathbf{x}, u, v)$ is a potential, and
$B(\mathbf{x}), C(\mathbf{x}), u_a(\mathbf{x})$ and $v_a(\mathbf{x})$ are given functions.

We assume $B(\mathbf{x}), C(\mathbf{x}) \geq 0$, since the case $B(\mathbf{x}), C(\mathbf{x}) < 0$ is usually not of practical interest.

Theorem 2.

If the potential $W(\mathbf{x}, u, v)$ is bounded from above and $B(\mathbf{x}), C(\mathbf{x}) \geq 0$, then, as $t \to \infty$, a solution of the initial-boundary value problem tends to a steady-state (to a solution of the time-independent boundary value problem).

Proof:

The potential $W(\mathbf{x},u,v)$ is bounded from above,
that is $W(\mathbf{x},u,v) \leq \overline{W}$ and $B(\mathbf{x}), C(\mathbf{x}) \geq 0$.
Hence the functional $F(t)$ is bounded from below, that is

$$\begin{aligned} F(t) &= \int_\Omega \left(\frac{1}{2}\left(D_1(\nabla u)^2 + D_2(\nabla v)^2\right) - W(\mathbf{x},u,v)\right) dV \\ &\quad + \frac{1}{2}\oint_{\partial\Omega}\left(B(\mathbf{x})(u-u_a)^2 + C(\mathbf{x})(v-v_a)^2\right) dS \\ &\geq -\int_\Omega W(\mathbf{x},u,v)\, dV \geq -\overline{W}\int_\Omega dV = -\overline{W}\, \|\Omega\|, \end{aligned}$$

and therefore is a Lyapunov function.

Furthermore,

$$\frac{dF}{dt} = -\int_\Omega \left(u_t^2 + v_t^2\right) dV \leq 0,$$

that is the functional monotonically decreases for all time-dependent solutions.

Since the functional $F(t)$ is bounded from below, there is a finite limit, $\overline{F} \geq -\overline{W}\ \|\Omega\|$, such that $\lim_{t\to\infty} F(t) = \overline{F}$.

Since $\dfrac{dF}{dt} = 0$ only when $u_t = v_t = 0$, this limit is achieved on a pair of time-independent functions $(u(\mathbf{x}), v(\mathbf{x}))$.

Since the system is the Euler-Lagrange equation for the functional F, this pair of functions $u(\mathbf{x}), v(\mathbf{x})$ satisfies both problems.

Stability of solutions is of importance because
only stable solution can arise in reality.

Corollary 2.

A time-independent solution is stable
if and only if it minimises the functional $F(t)$ on a class of functions satisfying the equations and boundary conditions.

A solution is asymptotically stable if and only if the corresponding minimum of the functional is isolated.

Proof:

By the Lyapunov asymptotic stability theorem with the functional $F(t)$ as a Lyapunov function.

Spatially uniform steady-states

If the boundaries of a region are impenetrable
(e.g., are given by lakes or rivers, for the biological species)
then no flux boundary conditions may be applied:

$$u_n(\mathbf{x}) = v_n(\mathbf{x}) = 0 \quad \text{for} \quad \mathbf{x} \in \partial\Omega.$$

In this case, a very specific steady-state solution,
a spatially uniform steady-state which does not depend
on the spatial variable $\mathbf{x}$, can exist.

For a spatially uniform solution $\nabla u = \nabla v = 0$,
and hence u, v satisfy the equations

$$W_u(\mathbf{x}, u, v) = 0, \quad W_v(\mathbf{x}, u, v) = 0 \quad \text{for} \quad \mathbf{x} \in \Omega.$$

That is the spatially uniform steady-states correspond to critical points of the potential function $W(\mathbf{x}, u, v)$.

Dependence of the diffusion coefficients $D_1(\mathbf{x})$ and $D_2(\mathbf{x})$ on $\mathbf{x}$ does not affect the existence of the spatially uniform solutions.

Theorem 3.

If a homogeneous Neumann initial-boundary value problem has spatially uniform steady-states, then these steady states which correspond to the maxima of the potential $W(\mathbf{x}, u, v)$ are asymptotically stable, while these that correspond to saddle points or minima are unstable.

If a maximum is unique then the steady-state is globally asymptotically stable.

Proof: A steady-state is stable if it minimises the functional $F(t)$

$$F(t) = \int_\Omega \left(\frac{1}{2} \left(D_1 (\nabla u)^2 + D_2 (\nabla v)^2 \right) - W(\mathbf{x}, u, v) \right) dV.$$

For a spatially uniform solution $\nabla u = \nabla v = 0$ holds, and the solutions correspond to critical points of the potential $W(\mathbf{x}, u, v)$.

Hence those steady-states which are isolated maxima of the potential $W(\mathbf{x}, u, v)$, minimise the functional and are asymptotically stable.

It is remarkable that the spatially uniform solutions of the system provide an absolute (on C^2) minimum of the functional. Of course this result critically depends on the Neumann boundary conditions.

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