

DERIVATION OF A MULTI-SPECIES CROSS-DIFFUSION MODEL FROM A LATTICE DIFFERENTIAL EQUATION AND POSITIVITY OF ITS SOLUTIONS*

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The local interaction of multi-species populations can be described by a discrete in space lattice differential equation, where the microscopic local rules of interaction are given in terms of functions that describe the incentive of individuals to move from their current site into a neighboring site. By refining the discrete microscopic description, we derive a macroscopic continuous model with cross diffusion. We present an *a priori* criterion that allows to verify whether the model preserves non-negativity of populations, which is an important property in biological applications.

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1. Introduction

Individual, or microscale, behavioral rules that describe the local movement of individuals in a population can be conveniently translated into lattice differential equations that describe the movement and spreading of the population on a regular discrete grid [1–3]. Such rules can include the incentive of individuals to leave the site they currently inhabit, as well as the attractivity of neighboring sites. Macroscale population models can be derived from this microscale description by refining the lattice and passing to the continuous limit, which typically leads to partial differential equations. This relationship between discrete microscale and continuous macroscale models is relatively well-understood for single species populations.

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The derivation of macroscopic continuous models from microscopic discrete (in space) models of several spatially interacting populations has not yet been considered in the literature to the same extent, except for [4], where it is shown that local interaction of two species leads to cross diffusion. In fact, the well-known cross-diffusion models [5, 6] are special cases of [4]. In [4], only numerical simulations were carried out, with no mathematical analysis of the resulting PDE.

The aim of our paper is to derive a generalized cross-diffusion model that includes spatial interactions among an arbitrary number of species. We use the approach in [4] for dual species models and extend it to derive our k species model. The main feature of these models is that the diffusion matrix is non-symmetric, generally not positive definite and the non-diagonal matrix elements (the cross-diffusion terms) are allowed to be large [7].

The solutions of cross-diffusion models represent population densities and must be non-negative, a question which remained open in [4] for the dual species case. For single-species models, the non-negativity of solutions is a direct consequence of the maximum principle [8]. For cross-diffusion problems, the maximum principle is not valid, wherefore the question of non-negativity is not obvious. For example, in the simplest case of cross-diffusion equations with constant coefficients, non-negativity is not preserved [9] in the sense that there exists non-negative initial data that leads to negative solutions. Based on the methods applied in [9, 10] for semilinear and quasilinear parabolic systems, we formulate a criterion that allows us to verify under which conditions on the microscopic local rules of interaction our macroscopic cross-diffusion model preserves non-negativity.

2. A generalized cross-diffusion model for k interacting species

We consider a one-dimensional spatial lattice created by an equidistant discretization of an interval. The variables u_i^j , where $i = 1, \dots, k$ and $j = 1, \dots, m$, denote the population densities for the i^{th} species in the j^{th} site on the lattice. The transfer functions $\tau_i^{j\pm}$ describe how a species u_i moves from the j^{th} grid cell into the neighbor cell $j \pm 1$. Assuming that the site's capacity to accommodate mass is limited, we can normalize the population densities with respect to their maximum densities, *i.e.* u_i^j is bounded by 1 and we can interpret it as the volume fraction of site j occupied by the population u_i .

The master equation describes the population change of a particular species in a particular site by balancing the density of populations which leaves the site to move into neighboring locations, and the density which arrives from neighboring sites. The difference between these densities is the population change of the species in the site. The master equation for the i^{th} species reads

$$\frac{\partial u_i^j}{\partial t} = \tau_i^{(j-1)+} u_i^{j-1} + \tau_i^{(j+1)-} u_i^{j+1} - \left(\tau_i^{j+} + \tau_i^{j-} \right) u_i^j + f_i^j, \quad (1)$$

where f_i^j is the net growth rate of the i^{th} species in grid cell j that can depend on the density of all populations in site j , and

$$\tau_i^{j\pm} = \alpha_i q_i \left(u_1^j, \dots, u_k^j \right) p_i \left(u_1^{j\pm 1}, \dots, u_k^{j\pm 1} \right). \quad (2)$$

Here, the constants α_i measure how fast populations move between neighboring sites. They depend on the size of lattice cells h . The non-negative functions q_i, p_i are *transfer functions* which control the local movements of a species from one site on the lattice to a neighboring site. They are taken to be continuous. In general, the transfer rates $\tau_i^{j\pm}$ can depend on the density of all populations in sites j and $j \pm 1$. The transfer function $q_i(u_1^j, \dots, u_k^j)$ is a measure of the incentive of i^{th} species u_i^j , that is currently in site j , to leave the cell; $p_i(u_1^{j\pm 1}, \dots, u_k^{j\pm 1})$ represents the attractivity of the cell population u_i^j for the incoming individuals $u_i^{j\pm 1}$ from sites $j \pm 1$.

In order to make the transition from a spatially discrete to a continuous model, we first introduce continuous functions $u_i(t, x)$ that interpolate the grid functions $u_i^j(t)$, *i.e.*, $u_i(t, x^j) = u_i^j(t)$. Assuming sufficient smoothness, we formally expand these functions around jh in terms of the variable h ,

$$u_i(t, x^{j\pm 1}) = u_i(t, x^j) \pm h \frac{\partial u_i(t, x^j)}{\partial x} + \frac{h^2}{2} \frac{\partial^2 u_i(t, x^j)}{\partial x^2} + \mathcal{O}(h^3). \quad (3)$$

We also approximate the transfer functions $q_i(u(t, x^{j\pm 1}))$ and $p_i(u(t, x^{j\pm 1}))$, where $u(t, x^{j\pm 1}) = (u_1(t, x^{j\pm 1}), \dots, u_k(t, x^{j\pm 1}))$ by second order Taylor polynomials about $u(t, x^j)$, *i.e.*

$$q_i(u(t, x^{j\pm 1})) \approx q_i(u(t, x^j)) + \sum_{l=1}^k \frac{\partial q_i(u(t, x^j))}{\partial u_l} [u_l(t, x^{j\pm 1}) - u_l(t, x^j)] + \frac{1}{2} \sum_{l=1}^k \sum_{m=1}^k \left(\frac{\partial^2 q_i(u(t, x^j))}{\partial u_l \partial u_m} [u_l(t, x^{j\pm 1}) - u_l(t, x^j)] [u_m(t, x^{j\pm 1}) - u_m(t, x^j)] \right),$$

and $p_i(u(t, x^{j\pm 1}))$ analogously. Now, we write $\hat{u} = (u_1(t, x^j), \dots, u_k(t, x^j))$ and substitute $\tau_i^{j\pm}$ and the approximations for $u_i(t, x^{j\pm 1})$, $q_i(u(t, x^{j\pm 1}))$ and

$p_i(u(t, x^{j\pm 1}))$ into (1). We obtain

$$\begin{aligned}
& \frac{\partial u_i(t, x^j)}{\partial t} \\
= & \alpha_i h^2 \left[u_i(t, x^j) p_i(\hat{u}) \sum_{l=1}^k \frac{\partial q_i}{\partial u_l}(\hat{u}) \frac{\partial^2 u_l(t, x^j)}{\partial x^2} + p_i(\hat{u}) q_i(\hat{u}) \frac{\partial^2 u_i(t, x^j)}{\partial x^2} \right. \\
& + u_i(t, x^j) p_i(\hat{u}) \sum_{l=1}^k \sum_{m=1}^k \frac{\partial^2 q_i}{\partial u_l \partial u_m}(\hat{u}) \frac{\partial u_l(t, x^j)}{\partial x} \frac{\partial u_m(t, x^j)}{\partial x} \\
& + 2p_i(\hat{u}) \frac{\partial u_i(t, x^j)}{\partial x} \sum_{l=1}^k \frac{\partial q_i}{\partial u_l}(\hat{u}) \frac{\partial u_l(t, x^j)}{\partial x} \\
& - u_i(t, x^j) q_i(\hat{u}) \sum_{l=1}^k \frac{\partial p_i}{\partial u_l}(\hat{u}) \frac{\partial^2 u_l(t, x^j)}{\partial x^2} \\
& \left. - u_i(t, x^j) q_i(\hat{u}) \sum_{l=1}^k \sum_{m=1}^k \frac{\partial^2 p_i}{\partial u_l \partial u_m}(\hat{u}) \frac{\partial u_l(t, x^j)}{\partial x} \frac{\partial u_m(t, x^j)}{\partial x} \right] \\
& + f_i(\hat{u}) + \mathcal{O}(h^3).
\end{aligned}$$

After dropping all $\mathcal{O}(h^3)$ terms, passing to the continuous limit, $h \rightarrow 0$, and rearranging the order of terms, we obtain the general system of equations as

$$\frac{\partial u_i}{\partial t} = \alpha_{i0} \frac{\partial}{\partial x} \left(\sum_{l=1}^k d_{il}(u) \frac{\partial u_l}{\partial x} \right) + f_i(u), \quad i = 1, \dots, k, \quad (4)$$

where $u = (u_1, \dots, u_k)$, $\lim_{h \rightarrow 0} \alpha_i h^2 = \alpha_{i0} > 0$, and $d(u) = (d_{il}(u))_{1 \leq i, l \leq k}$ is the diffusion matrix with components

$$\begin{aligned}
d_{ii}(u) &= u_i \left(p_i(u) \frac{\partial q_i}{\partial u_i}(u) - q_i(u) \frac{\partial p_i}{\partial u_i}(u) \right) + p_i(u) q_i(u) & \text{if } i = l, \\
d_{il}(u) &= u_i \left(p_i(u) \frac{\partial q_i}{\partial u_l}(u) - q_i(u) \frac{\partial p_i}{\partial u_l}(u) \right) & \text{if } i \neq l.
\end{aligned}$$

The same procedure applied on a two- or three-dimensional spatial lattice leads to the cross-diffusion system

$$\frac{\partial u_i}{\partial t} = \alpha_{i0} \nabla \cdot \left(\sum_{l=1}^k d_{il}(u) \nabla u_l \right) + f_i(u), \quad i = 1, \dots, k. \quad (5)$$

Solutions of population models represent densities, which are necessarily non-negative. Hence, it is important to ensure that solutions of the cross-diffusion systems (4) and (5) remain non-negative. The question whether cross-diffusion models preserve non-negativity is not trivial and we will investigate in the following section which conditions on p, q and f guarantee this property.

3. A positivity criterion

In this section, we derive explicit necessary and sufficient conditions as a criterion for the non-negativity of solutions for multi-species cross-diffusion systems of the form

$$\begin{aligned} \partial_t u &= \nabla \cdot (D(u) \cdot \nabla u) + f(u), & \Omega \times (0, T), \\ u|_{\partial\Omega} &= 0, & \partial\Omega \times [0, T], \\ u|_{t=0} &= u_0, & \Omega \times \{0\}, \end{aligned} \tag{6}$$

where $u = (u_1, \dots, u_k) : \Omega \times [0, T] \rightarrow \mathbb{R}^k$ is a vector-valued function of $x \in \Omega$ and time $t \in [0, T]$. Here, $\Omega \subset \mathbb{R}^n, n \in \mathbb{N}$, denotes a bounded domain with boundary $\partial\Omega$. The Laplace operator Δ and the gradient ∇ are applied componentwise to the vector-valued function u . We then apply the criterion to model (5) and obtain explicit conditions for the functions p, q and f .

Let $L^2(\Omega; \mathbb{R}^k)$ be the Hilbert space of vector-valued functions $u : \Omega \rightarrow \mathbb{R}^k$ such that $u_i \in L^2(\Omega), 1 \leq i \leq k$, with scalar product

$$\langle u, v \rangle_{L^2(\Omega; \mathbb{R}^k)} := \sum_{i=1}^k \langle u_i, v_i \rangle_{L^2(\Omega)}, \quad u, v \in L^2(\Omega; \mathbb{R}^k).$$

For vectors $y \in \mathbb{R}^k$, we write $y \geq 0$ if the inequality is satisfied componentwise, i.e.,

$$y_i \geq 0 \quad \text{for all } 1 \leq i \leq k,$$

and denote all non-negative vectors by $\mathbb{R}_+^k := \{y \in \mathbb{R}^k \mid y \geq 0\}$.

Definition 3.1. *The **positive cone** in $L^2(\Omega; \mathbb{R}^k)$ is the set*

$$K^+ := \left\{ u \in L^2(\Omega; \mathbb{R}^k) \mid u \geq 0 \text{ a.e. in } \Omega \right\}.$$

We say that system (6) fulfills the **positivity property** if for every initial data $u_0 \in K^+$ the corresponding solution $u(\cdot, \cdot; u_0) : \Omega \times [0, t_{max}[\rightarrow \mathbb{R}^k$ satisfies

$$u(\cdot, t; u_0) \in K^+ \quad \text{for } t \in [0, t_{max}[,$$

where $t_{max} > 0$ denotes the maximal existence interval of the solution.

The following theorem characterizes the class of cross-diffusion systems (6) satisfying the positivity property.

Theorem 3.2. *Let the coefficient functions $D_{ij} : \mathbb{R}^k \rightarrow \mathbb{R}$ of the diffusion matrix $D(u) = (D_{ij}(u))_{1 \leq i, j \leq k}$ be continuously differentiable with strictly positive diagonal elements*

$$D_{ii}(u) \geq \mu_i \quad \text{for all } i = 1, \dots, k, \tag{7}$$

where $\mu_i > 0$, and the interaction function $f = (f_1, \dots, f_k)$ be continuously differentiable, $f \in C^1(\mathbb{R}^k; \mathbb{R}^k)$. Moreover, we assume that for every initial data $u_0 \in K^+$, there exists a unique solution of system (6), and the solution and its derivatives with respect to x satisfy L^∞ -estimates

$$u(\cdot, t; u_0), \partial_{x_l} u(\cdot, t; u_0) \in L^\infty(\Omega; \mathbb{R}^k) \quad \text{for } t \in [0, t_{max}[, 1 \leq l \leq n. \tag{8}$$

Let $u_0 \in K^+$ satisfy the compatibility conditions. Then, system (6) satisfies the positivity property if and only if the coefficient functions D_{ij} fulfill

$$D_{ij}(y) = 0 \quad \text{for all } y \in \mathbb{R}_+^k \text{ such that } y_i = 0,$$

where $i \neq j, 1 \leq i, j \leq k$, and the interaction function f satisfies

$$f_i(y) \geq 0 \quad \text{for all } y \in \mathbb{R}_+^k \text{ such that } y_i = 0, \tag{9}$$

where $1 \leq i \leq k$.

The conditions on the functions D_{ij} imply that $D(u)$ can be written as

$$D(u) = \begin{pmatrix} D_{11}(u) & u_1 d_{12}(u) & u_1 d_{13}(u) & \cdots & u_1 d_{1k}(u) \\ u_2 d_{21}(u) & D_{22}(u) & u_2 d_{23}(u) & \cdots & u_2 d_{2k}(u) \\ \vdots & \vdots & \vdots & & \vdots \\ u_k d_{k1}(u) & u_k d_{k2}(u) & u_k d_{k3}(u) & \cdots & D_{kk}(u) \end{pmatrix}$$

with bounded functions $d_{ij}(u), i \neq j, 1 \leq i, j \leq k$.

Proof. Necessity: We assume the solution $u = u(\cdot, \cdot; u_0) : \Omega \times [0, t_{max}[\rightarrow \mathbb{R}^k$ corresponding to $u_0 \in K^+$ remains non-negative for $t > 0$ and prove the necessity of the stated conditions. In the following, we make formal calculations, for their validity, we refer to [11]. Taking smooth initial data u_0

and an arbitrary function $v \in K^+$, which is orthogonal to u_0 in $L^2(\Omega; \mathbb{R}^k)$, we obtain

$$\begin{aligned} \langle \partial_t u|_{t=0}, v \rangle_{L^2(\Omega; \mathbb{R}^k)} &= \left\langle \lim_{t \rightarrow 0_+} \frac{u(\cdot, t; u_0) - u_0}{t}, v \right\rangle_{L^2(\Omega; \mathbb{R}^k)} \\ &= \lim_{t \rightarrow 0_+} \left\langle \frac{u(\cdot, t; u_0)}{t}, v \right\rangle_{L^2(\Omega; \mathbb{R}^k)} - \lim_{t \rightarrow 0_+} \left\langle \frac{u_0}{t}, v \right\rangle_{L^2(\Omega; \mathbb{R}^k)} \\ &= \lim_{t \rightarrow 0_+} \left\langle \frac{u(\cdot, t; u_0)}{t}, v \right\rangle_{L^2(\Omega; \mathbb{R}^k)} \geq 0, \end{aligned}$$

where we used the orthogonality of u_0 and v as well as the hypothesis $u(\cdot, t; u_0) \in K^+$ for $t > 0$, and $t \rightarrow 0_+$ denotes the right derivative. We remark that for the particular initial data u_0 that we choose below, there always exists an orthogonal element $v \in K^+$. On the other hand, since u is the solution of (6) corresponding to u_0 , we observe that

$$\begin{aligned} \langle \partial_t u|_{t=0}, v \rangle_{L^2(\Omega; \mathbb{R}^k)} &= \left\langle D(u_0)\Delta u_0 + \sum_{l=1}^k \partial_l D(u_0) \begin{pmatrix} \nabla u_l \cdot \nabla u_1 \\ \vdots \\ \nabla u_l \cdot \nabla u_k \end{pmatrix}, v \right\rangle_{L^2(\Omega; \mathbb{R}^k)} \\ &\quad + \langle f(u_0), v \rangle_{L^2(\Omega; \mathbb{R}^k)} \geq 0, \end{aligned} \tag{10}$$

where $\partial_l D(u_0) = (\partial_l D_{ij}(u_0))_{1 \leq i, j \leq k}$. In particular, for fixed $i \in \{1, \dots, k\}$ choosing the functions $u_0 = (\tilde{u}_1, \dots, \underbrace{0}_i, \dots, \tilde{u}_k)$ and $v = (0, \dots, \underbrace{\tilde{v}}_i, \dots, 0)$

with $u_0, v \in K^+$ leads to the scalar inequality

$$\left\langle \sum_{j=1, j \neq i}^k D_{ij}(u_0)\Delta \tilde{u}_j + \sum_{l=1, l \neq i}^k \sum_{j=1, j \neq i}^k \partial_l D_{ij}(u_0)\nabla \tilde{u}_l \cdot \nabla \tilde{u}_j + f_i(u_0), \tilde{v} \right\rangle_{L^2(\Omega)} \geq 0.$$

Since this inequality holds for arbitrary non-negative $\tilde{v} \in L^2(\Omega)$, we obtain the pointwise estimate

$$\sum_{j=1, j \neq i}^k D_{ij}(u_0)\Delta \tilde{u}_j + \sum_{l=1, l \neq i}^k \sum_{j=1, j \neq i}^k \partial_l D_{ij}(u_0)\nabla \tilde{u}_l \cdot \nabla \tilde{u}_j + f_i(u_0) \geq 0 \tag{11}$$

a.e. in Ω . This implies that

$$D_{ij}(\tilde{u}_1, \dots, \underbrace{0}_i, \dots, \tilde{u}_k) = 0, \quad \tilde{u}_j \geq 0, \quad j \neq i,$$

for all $1 \leq j \leq k$, and the functions D_{ij} can be written as

$$D_{ij}(u) = u_i d_{ij}(u), \quad 1 \leq i, j \leq k, \quad j \neq i.$$

Consequently, for $j \neq i, l \neq i$, we obtain $\partial_l D_{ij}(u) = u_i \partial_l d_{ij}(u)$, and it follows that $\partial_l D_{ij}(u_0) = 0$. From inequality (11), we now deduce that the components of the interaction term satisfy

$$f_i(\tilde{u}_1, \dots, \underbrace{0}_i, \dots, \tilde{u}_k) \geq 0, \quad \tilde{u}_j \geq 0, \quad j \neq i, \quad \forall 1 \leq i, j \leq k.$$

Sufficiency: We show that the stated conditions on D and f ensure that the solution $u = u(\cdot, \cdot; u_0)$ corresponding to $u_0 \in K^+$ remains non-negative. First, we assume that the conditions on the functions D_{ij} and f_i are satisfied for all $y \in \mathbb{R}^k$ such that $y_i = 0, 1 \leq i \leq k$. System (6) takes the form

$$\partial_t u_i = \nabla \cdot \left(D_{ii}(u) \nabla u_i + \sum_{j=1, j \neq i}^k u_i d_{ij}(u) \nabla u_j \right) + f_i(u), \quad 1 \leq i \leq k,$$

where the functions $d_{ij} : \mathbb{R}^k \rightarrow \mathbb{R}$ are defined by

$$d_{ij}(y) := \int_0^1 \partial_i D_{ij}(y_1, \dots, sy_i, \dots, y_k) ds, \quad y \in \mathbb{R}^k.$$

For a function $u \in L^2(\Omega)$, we denote its positive and negative part by $u_+ := \max\{u, 0\}$ and $u_- := \max\{-u, 0\}$, respectively, and can represent it as $u = u_+ - u_-$. By the definition, immediately follows $u_- u_+ = 0$. Furthermore, if $u \in H^1(\Omega)$, then also its positive and negative part, $u_+, u_- \in H^1(\Omega)$, and

$$\partial_{x_l} u_- = \begin{cases} -\partial_{x_l} u & u < 0 \\ 0 & u \geq 0 \end{cases}, \quad \partial_{x_l} u_+ = \begin{cases} \partial_{x_l} u & u > 0 \\ 0 & u \leq 0 \end{cases}$$

for all $1 \leq l \leq n$ (cf. [12]). This implies that

$$(\partial_{x_l} u_+) u_- = u_+ \partial_{x_l} u_- = (\partial_{x_l} u_+) \partial_{x_m} u_- = 0, \quad 1 \leq l, m \leq n.$$

In order to prove the positivity of u corresponding to $u_0 \in K^+$, we show that $(u_0)_{i-} = 0$ implies that $u_{i-} := (u_i(\cdot, t; u_0))_- = 0$ for $t > 0$ and for

all $1 \leq i \leq k$. Multiplying the i^{th} equation by u_{i-} and integrating over Ω yields

$$\begin{aligned} \langle \partial_t u_i, u_{i-} \rangle_{L^2(\Omega)} &= \langle \nabla \cdot (D_{ii}(u) \nabla u_i), u_{i-} \rangle_{L^2(\Omega)} \\ &+ \sum_{j=1, j \neq i}^k \langle \nabla \cdot (u_i d_{ij}(u) \nabla u_j), u_{i-} \rangle_{L^2(\Omega)} + \langle f_i(u), u_{i-} \rangle_{L^2(\Omega)}. \end{aligned}$$

We observe that the left-hand side of the equation can be written as

$$\langle \partial_t u_i, u_{i-} \rangle_{L^2(\Omega)} = - \langle \partial_t u_{i-}, u_{i-} \rangle_{L^2(\Omega)} = -\frac{1}{2} \partial_t \|u_{i-}\|_{L^2(\Omega)}^2.$$

Taking into account the homogeneous Dirichlet boundary conditions, we obtain for the diffusion terms

$$\begin{aligned} \langle \nabla \cdot (D_{ii}(u) \nabla u_i), u_{i-} \rangle_{L^2(\Omega)} &= - \langle D_{ii}(u) \nabla u_i, \nabla u_{i-} \rangle_{L^2(\Omega; \mathbb{R}^n)} \\ &= \langle D_{ii}(u) \nabla u_{i-}, \nabla u_{i-} \rangle_{L^2(\Omega; \mathbb{R}^n)}, \\ \sum_{j=1, j \neq i}^k \langle \nabla \cdot (u_i d_{ij}(u) \nabla u_j), u_{i-} \rangle_{L^2(\Omega)} &= - \sum_{j=1, j \neq i}^k \langle u_i d_{ij}(u) \nabla u_j, \nabla u_{i-} \rangle_{L^2(\Omega; \mathbb{R}^n)} \\ &= \sum_{j=1, j \neq i}^k \langle u_{i-} d_{ij}(u) \nabla u_j, \nabla u_{i-} \rangle_{L^2(\Omega; \mathbb{R}^n)}. \end{aligned}$$

We estimate the last term by

$$\left| \sum_{j=1, j \neq i}^k \langle u_{i-} d_{ij}(u) \nabla u_j, \nabla u_{i-} \rangle_{L^2(\Omega; \mathbb{R}^n)} \right| \leq c_1 \sum_{l=1}^n \langle |\partial_{x_l} u_{i-}|, u_{i-} \rangle_{L^2(\Omega)},$$

for some constant $c_1 \geq 0$, where we used the hypothesis (8). To estimate the interaction term, we use that $f \in C^1(\mathbb{R}^k; \mathbb{R}^k)$, which leads to

$$\begin{aligned} f_i(u_1, \dots, u_k) &= f_i(u_1, \dots, \underbrace{0}_i, \dots, u_k) + u_i \int_0^1 \partial_i f_i(u_1, \dots, s u_i, \dots, u_k) ds \\ &= f_i(u_1, \dots, \underbrace{0}_i, \dots, u_k) + u_i F_i(u_1, \dots, u_k), \end{aligned}$$

where the function $F_i : \mathbb{R}^k \rightarrow \mathbb{R}$ is bounded. This representation yields

$$\begin{aligned} &\langle f_i(u), u_{i-} \rangle_{L^2(\Omega)} \\ &= \langle f_i(u_1, \dots, \underbrace{0}_i, \dots, u_k), u_{i-} \rangle_{L^2(\Omega)} + \langle u_i F_i(u_1, \dots, u_k), u_{i-} \rangle_{L^2(\Omega)} \\ &= \langle f_i(u_1, \dots, \underbrace{0}_i, \dots, u_k), u_{i-} \rangle_{L^2(\Omega)} - \langle F_i(u_1, \dots, u_k) u_{i-}, u_{i-} \rangle_{L^2(\Omega)}. \end{aligned}$$

Summing up all terms, we obtain

$$\begin{aligned} & \frac{1}{2} \partial_t \|u_{i-}\|_{L^2(\Omega)}^2 + \langle D_{ii}(u) \nabla u_{i-}, \nabla u_{i-} \rangle_{L^2(\Omega; \mathbb{R}^n)} \\ & \leq c_1 \sum_{l=1}^n \langle |\partial_{x_l} u_{i-}|, u_{i-} \rangle_{L^2(\Omega)} + c_2 \|u_{i-}\|_{L^2(\Omega)}^2 \\ & \quad - \langle f_i(u_1, \dots, \underbrace{0}_i, \dots, u_k), u_{i-} \rangle_{L^2(\Omega)} \end{aligned}$$

for some constants $c_1, c_2 \geq 0$. To estimate the mixed terms, we use Young's inequality; for every $\epsilon > 0$, there exists a constant $C_\epsilon \geq 0$ such that

$$\sum_{l=1}^n \langle |\partial_{x_l} u_{i-}|, u_{i-} \rangle_{L^2(\Omega)} \leq \epsilon \|\nabla u_{i-}\|_{L^2(\Omega; \mathbb{R}^n)}^2 + C_\epsilon \|u_{i-}\|_{L^2(\Omega)}^2.$$

If we choose $\epsilon > 0$ sufficiently small and take (7) into account, it follows that

$$\partial_t \|u_{i-}\|_{L^2(\Omega)}^2 \leq c_3 \|u_{i-}\|_{L^2(\Omega)}^2 - 2 \langle f_i(u_1, \dots, \underbrace{0}_i, \dots, u_k), u_{i-} \rangle_{L^2(\Omega)},$$

for some constant $c_3 \geq 0$. Since in the beginning we assumed that $f_i(y) \geq 0$ for all $y \in \mathbb{R}^k$ such that $y_i = 0$, $1 \leq i \leq k$, we obtain the estimate

$$\partial_t \|u_{i-}\|_{L^2(\Omega)}^2 \leq c_3 \|u_{i-}\|_{L^2(\Omega)}^2.$$

By Gronwall's Lemma and the initial condition $(u_0)_{i-} = 0$, we conclude $\|u_{i-}\|_{L^2(\Omega)} = 0$.

It remains to justify our initial assumptions on the functions f_i and D_{ij} , $1 \leq i, j \leq k$, $j \neq i$. To this end, we consider the modified system

$$\begin{aligned} \partial_t \hat{u} &= \nabla \cdot (\hat{D}(\hat{u}) \cdot \nabla \hat{u}) + \hat{f}(\hat{u}), & \Omega \times (0, T), \\ \hat{u}|_{\partial\Omega} &= 0, & \partial\Omega \times [0, T], \\ \hat{u}|_{t=0} &= u_0, & \Omega \times \{0\}, \end{aligned}$$

where the function $\hat{f}: \mathbb{R}^k \rightarrow \mathbb{R}^k$ is given by

$$\hat{f}_i(y) = f_i(|y_1|, \dots, \underbrace{0}_i, \dots, |y_k|) + y_i F_i(y), \quad y \in \mathbb{R}^k,$$

and the function F_i was defined as

$$F_i(y_1, \dots, y_k) := \int_0^1 \partial_i f_i(y_1, \dots, sy_i, \dots, y_k) ds, \quad y \in \mathbb{R}^k.$$

The modified diffusion matrix is given by

$$\hat{D}_{ij}(y_1, \dots, y_k) := D_{ij}(|y_1|, \dots, \underbrace{0}_i, \dots, |y_k|) + y_i d_{ij}(y), \quad y \in \mathbb{R}^k,$$

for $1 \leq i, j \leq k, j \neq i$. Following the same arguments, we conclude that the solution \hat{u} of the modified system remains non-negative. However, if \hat{u} is non-negative, we can remove the absolute values, and \hat{u} is a solution of the original system

$$\begin{aligned} \partial_t u &= \nabla \cdot (D(u) \cdot \nabla u) + f(u), & \Omega \times (0, T), \\ u|_{\partial\Omega} &= 0, & \partial\Omega \times [0, T], \\ u|_{t=0} &= u_0, & \Omega \times \{0\}. \end{aligned}$$

By the uniqueness of solutions follows that $u = \hat{u}$, which implies that $u(\cdot, t; u_0) \in K^+$ for $t > 0$, and concludes the proof of the theorem. \square

The diffusion matrix $D(u) = (D_{ij}(u))_{1 \leq i, j \leq k}$ in (5) is density dependent, and we assume in Theorem 3.2 that the diagonal elements are strictly positive, *i.e.* $D_{ii}(u) \geq \mu_i > 0, i = 1, \dots, k$. Applied to our cross-diffusion model, we obtain

$$u_i \left(p_i(u) \frac{\partial q_i}{\partial u_i}(u) - q_i(u) \frac{\partial p_i}{\partial u_i}(u) \right) + p_i(u) q_i(u) \geq \mu_i > 0, \quad i = 1, \dots, k, \tag{12}$$

which is satisfied, *e.g.* if the functions p_i and q_i are bounded from below by a positive constant and $p_i(u) \frac{\partial q_i}{\partial u_i}(u) \geq q_i(u) \frac{\partial p_i}{\partial u_i}(u)$. This is, for example, satisfied if $\frac{\partial p_i}{\partial u_i} < 0, \frac{\partial q_i}{\partial u_i} > 0$, which describes populations that move from locations with high density to locations with lower density. The cross-diffusion terms in model (2) obviously satisfy the conditions in Theorem 3.2. Consequently, if the functions p and q have the mentioned properties and the reaction function f satisfies (9), the generalized cross-diffusion system (5) for k interacting species preserves the non-negativity of solutions.

For example, the dual species model that presents predator-prey interaction where species u is the prey population and v is the predator population density: The functions $p_1(u, v)$ and $q_1(u, v)$ relate to the prey seeking locations with low predator density ($\frac{\partial p_1}{\partial v} < 0, \frac{\partial q_1}{\partial v} > 0, \frac{\partial p_1}{\partial u} < 0, \frac{\partial q_1}{\partial u} > 0$) and the functions $p_2(u, v)$ and $q_2(u, v)$ to the predator seeking locations with high prey density ($\frac{\partial q_2}{\partial u} < 0, \frac{\partial p_2}{\partial u} > 0, \frac{\partial q_2}{\partial v} < 0, \frac{\partial p_2}{\partial v} > 0$). Hence, the diagonal elements of the diffusion matrix of the predator-prey model are strictly positive and this model satisfies the hypothesis in Theorem 3.2.

On the other hand, in models with aggregation, one would have $\frac{\partial p_i}{\partial u_i} > 0$, $\frac{\partial q_i}{\partial u_i} < 0$, wherefore (12) is not satisfied, which reflects the known ill-posedness of PDE models of the aggregation phenomenon.

4. Conclusion

The local interaction of multi-species populations is described by a lattice differential equation, where the microscopic rules of interaction are given in terms of functions q describing the incentive for individuals to leave their current site, p describing the attractivity of a site to individuals in neighboring sites, and f describing reactive interactions in a given site. Refining the microscopic lattice-based description of the spatial interaction between species, and passing to the continuous limit, a class of macroscopic cross-diffusion models is obtained. We also present relatively easy to apply conditions on the functions p, q, f under which it is guaranteed that the model preserves non-negativity of the populations. This extends the tangent criterion for ordinary differential equations to the cross-diffusion problem at hand.

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