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A STEFAN-LIKE PROBLEM IN BIOLOGY

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Abstract: In this paper we consider the spatial segregation limit for a reaction-diffusion (RD) system to describe the interaction of two competing species. We derive a new free boundary problem from the RD system when the interspecific competition rate tends to infinity. The free boundary problem is the two phase Stefan problem with reaction term where the latent heat is zero.

1. Introduction

Spatio and/or temporal patterns arising in ecological and biological problems have been theoretically investigated by using partial and ordinary differential equation models. One of the contributors in this field in Ecology would be the great mathematician V. Volterra who introduced different types of differential equation models to understand the interaction of biological species in ecological systems. Following his line, many differential equation models have been proposed so far. In particular, for the situation where each individuals randomly migrates, reaction-diffusion (RD) systems have been often used. One general form of the equations for the population density $u = (u_1, u_2, \ldots, u_N)$ is given by

$$u_{it} = d_i \Delta u_i + f_i(u)u_i$$

(1.1)

where $d_i$ is the diffusion rate of $u_i$ and $f_i(u)$ are the growth rate of $u_i$ which generally depend on $u$ ($i = 1, 2, \ldots, N$).

In this paper, we are concerned with mathematical treatment on the interaction of two ecologically similar species which strongly compete each other and move by diffusion. The resulting model is described by the following 2-component reaction-diffusion (RD) systems:

$$u_{1t} = d_1 \Delta u_1 + f_1(u)u_1$$

$$u_{2t} = d_2 \Delta u_2 + f_2(u)u_2$$

(1.2)

The result shown here has been obtained by the joint work with D. Hilhorst and L. A. Peletier[1].
with \( f_1 = r_1 \cdot a_1 u_1 \cdot b_1 u_2 \) and \( f_2 = r_2 \cdot b_2 u_1 \cdot a_2 u_2 \) where \( r_i \) is the intrinsic growth rate, \( a_i \) is the intraspecific competition rate and \( b_i \) is the interspecific competition rate which are all positive constants\(^2\). \( \Omega \) is a bounded domain in \( \mathbb{R}^n \). For \((1.2)\), we impose the zero-flux boundary conditions on the boundary \( \partial \Omega \)

\[
    u_1 \nu = 0 = u_2 \nu ,
\]

where \( \nu \) is the outward normal unit vector on \( \partial \Omega \). We define here strong competition for two species by the following inequalities

\[
a_1/b_2 < r_1/r_2 < b_1/a_2.
\]

If both \( b_1 \) and \( b_2 \) are much larger than \( a_i \) and \( r_i \) \((i = 1, 2)\), the inequalities \((1.3)\) are always hold.

For \((1.2)\) with the inequalities \((1.3)\) in the absence of diffusion, one easily finds that there are four equilibrium solutions \((0, 0), (r_i/a_i, 0), (0, r_2/a_2) \) and \((u^*, v^*)\). The fourth solution is given by the intersection point of two lines \( r_1 \cdot a_1 u_1 \cdot b_1 u_2 = 0 \) and \( r_2 \cdot b_2 u_1 \cdot a_2 u_2 = 0 \), and that \((0, 0)\) and \((u^*, v^*)\) are unstable, while \((r_i/a_i, 0)\) and \((0, r_2/a_2)\) are stable. Therefore, we find that the solution \((u_1(t), u_2(t))\) tends generically to either \((r_i/a_i, 0)\) or \((0, r_2/a_2)\). In ecological terms, it implies that two competing species can never coexist under strong competition. This is called Gause's competitive exclusion principle in ecology.

On the other hand, in the presence of diffusion, the structure of existence and stability of equilibrium solutions of \((1.2)- (1.4)\) are different from the ODE version. If the domain \( \Omega \) is convex, any non-constant equilibrium solutions are unstable, even if they exist\([2]\). This indicates that stable equilibrium solutions of \((1.2)-(1.4)\) are \((r_i/a_i, 0)\) and \((0, r_2/a_2)\) only, that is, the competitive exclusion principle still holds. On the other hand, if the domain \( \Omega \) is not convex, the solution structure is more complicated, depending on the shape of \( \Omega \)\([3]\). If \( \Omega \) takes suitable dumb-bell shape, for instance, there exist stable non-constant equilibrium solutions, in addition to the above two trivial equilibria\([3]\). These solutions have spatial distributions where \( u \) and \( v \) take nearly \((r_i/a_i, 0)\) in one subregion, and take nearly \((0, r_2/a_2)\) in the other, that is, two competing species show spatial segregation in the whole domain \( \Omega \).

From the ecological viewpoint on regional segregating problem for competing species, it is interesting to know how the time-evolution of segregating regions of two species is.

Our aim is to derive the evolutionary equation to describe the segregating boundary between two competing species from the problem \((1.2)-(1.4)\). In order to do it, it is convenient to rewrite \((1.2)\) as
\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + r_1 (1 - u_1)u_1 - bu_1u_2, \\
\frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + r_2 (1 - u_2)u_2 - \alpha bu_1u_2,
\end{align*}
\tag{1.5}
\]

where \(b\) and \(\alpha\) are positive constants. We assume that \(b\) is sufficiently large and the others are of order \(O(1)\). Ecologically it means that the competition between two species is very strong and that if \(\alpha > 1\), the competition from \(u_1\) to \(u_2\) is stronger, whereas the situation is opposite if \(\alpha < 1\).

We first demonstrate some numerical simulations of the 1-dimensional problem of (1.2)-(1.4) for different values of \(b\). For not large (but not small) \(b\), it is shown that \(u_1\) and \(u_2\) exhibit spatial segregation with an overlapped zone, because of strong competition. When the value of \(b\) increases, the overlapped zone becomes narrower (see Fig. 1). Thus, taking the limit \(b \uparrow \infty\), one can expect that \(u_1\) and \(u_2\) possess disjoint supports (habitats) with only one common point, which separates the habitats of the two competing species. The purpose of this paper is to derive the limiting system as \(b \uparrow \infty\), which is called the spatial segregation limit to describe the time evolution of the supports of \(u_1\) and \(u_2\). As will be proven below, the limiting system is a free boundary problem which is regarded as the two phase Stefan-like problem with reaction terms. For the Stefan problem, the readers refer to [4], for instance. Only difference is that no latent heat effect is included in the problem.

\[\begin{align*}
&\text{b = 1000} \\
&\text{b = 5000} \\
&\text{b = 30000}
\end{align*}\]

\[\begin{align*}
&\text{r}_1 = \text{r}_2 = 20 \\
&\text{d}_1 = \text{d}_2 = 0.05 \\
&\alpha = 1
\end{align*}\]

Fig. 1
Let \( \Gamma(t) \) be an interface which separates two subregions

\[
\Omega_1(t) = \{ x \in \Omega, \ u_1 > 0 \ \text{and} \ u_2 = 0 \} 
\]

and

\[
\Omega_2(t) = \{ x \in \Omega, \ u_2 > 0 \ \text{and} \ u_1 = 0 \} 
\]

in \( \Omega \) (see Fig. 2).

Then \( u_1 \) and \( u_2 \) are described by

\[
u_{1t} = d_1 \Delta u_1 + r_1 (1 - u_1) u_1 \quad t > 0, \ x \in \Omega_1(t) \tag{1.5}\]

\[
u_{2t} = d_2 \Delta u_2 + r_2 (1 - u_2) u_2 \quad t > 0, \ x \in \Omega_2(t) \tag{1.6}\]

\[
u_{1v} = 0 = u_{2v} \quad t > 0, \ x \in \partial \Omega. \tag{1.7}\]

On the interface,

\[
u_1 = \nu_2 = 0 \quad t > 0, \ x \in \Gamma(t) \tag{1.7}\]

and

\[
0 = -\alpha d_1 u_{1v} - d_2 u_{2v} \quad t > 0, \ x \in \Gamma(t), \tag{1.8}\]

where \( v \) is the outward unit vector. The initial conditions are given by

\[
u_i(0,x) = u_{i0}(x) \quad x \in \Omega_i(0) \quad (i = 1,2) \tag{1.9}\]

which is separated by the curve

\[
\Gamma(0) = \Gamma_0. \tag{1.10}\]

The problem is to find \( (u_1(t,x),u_2(t,x)) \) and \( \Gamma(t) \) which satisfy (1.5) - (1.10). If this problem can be solved, the interface \( \Gamma(t) \) determines the segregating boundary between two strongly competing species. One
could notice that the problem (1.5)-(1.10) is quite similar to the classical two phase Stefan problem except for
the following two different points: (i) the system (1.5) is not the heat equation but the logistic growth
equation which is well-known in theoretical ecology; (ii) the interface equation (1.8) is such that the latent
heat is zero and it contains the strength ratio $\alpha$ of the interspecific competition between $u_1$ and $u_2$.

2. Formulation of the problem
We rewrite the system (1.5) in more general form

$$u_t = d_1 \Delta u + (fu) - kvu$$

in $Q = \Omega \times R^+$ (2.1)

$$v_t = d_2 \Delta v + (g(v) - \alpha ku)\nu.$$

and make the following hypotheses on the functions $f$ and $g$:

(H) The functions $f$ and $g$ are locally Lipschitz continuous on $[0, +\infty)$ such that

$$f(s) > 0, \ g(s) > 0 \text{ for } s \in (0,1) \text{ and } f(s) < 0, \ g(s) < 0 \text{ for } s > 1.$$

We shall write

$$p_0 = \max\{f(s) : 0 \leq s \leq 1\} \text{ and } p_1 = \max\{sf(s) + f(s) : 0 \leq s \leq 1\},$$

$$q_0 = \max\{g(s) : 0 \leq s \leq 1\} \text{ and } p_1 = \max\{sg(s) + g(s) : 0 \leq s \leq 1\}.$$

The boundary and initial conditions are

$$u_\nu = 0 = v_\nu \quad \text{ on } S = \partial \Omega \times R^+ \quad (2.2)$$

and

$$u(0,x) = u_0(x), \quad v(0,x) = v_0(x) \quad x \in \Omega \quad (2.3)$$
where

\[(H_0) \quad u_0, v_0 \in C^{2+\gamma}(\Omega) \quad \text{and} \quad 0 \leq u_0 \leq 1, \quad 0 \leq v_0 \leq 1\]

By a solution of the problem (2.1)-(2.3), we shall understand a pair of functions \((u, v)\) such that \(u_0, v_0 \in C^{2+\gamma,1+\gamma/2}(Q)\).

3. The limiting problem

We shall refer to the solution \((u, v)\) of the problem (2.1)-(2.3) as \((u_k, v_k)\) to emphasize its dependency on the parameter \(k\) contained in the reaction terms in (2.1). First we prepare some results on a-priori bounds for the solution \((u_k, v_k)\) of (2.1)-(2.3) which enable to study the properties of the family of solutions \((u_k, v_k)\) for large values of \(k\). By using them, it is shown that the families \(\{u_k\}\) and \(\{v_k\}\) are bounded in \(W^{1,1}(Q_T)\) and hence in \(BV(Q_T)\) where \(Q_T = \Omega \times (0,T)\). We find that there exists sequences \(\{u_k\}\) and \(\{v_k\}\) and functions \(u^*, v^* \in H^1(\Omega)\) such that \(0 \leq u^* \leq 1, \quad 0 \leq v^* \leq 1\) and

\[u_k \to u^* \quad \text{and} \quad v_k \to v^* \quad \text{as} \quad k \to \infty \quad \text{in} \quad L^1(Q_T)\]  

and

\[u_k \to u^* \quad \text{and} \quad v_k \to v^* \quad \text{as} \quad k \to \infty \quad \text{in} \quad L^2(0,T; H^1(\Omega)).\]  

We now consider the function \(w_k = u_k - \alpha^{-1}v_k\) and eliminating the interaction terms involving \(k\) from (2.1), we have

\[w_t = d_1 \Delta u - \alpha^{-1}d_2 \Delta v + u f(u) - \alpha^{-1}v g(v) \quad \text{in} \quad Q_T\]  

\[w = 0 \quad \text{on} \quad S_T,\]

where \(S_T = \partial \Omega \times (0,T)\). Furthermore, we find that the pair of functions \((u^*, v^*)\) defined in (3.1) is a distributional solution of the equation.
\[(u^* - \alpha^{-1}v^*)_t = \Delta(d_1u^* - \alpha^{-1}d_2v^*) + u^*f(u^*) - \alpha^{-1}v^*g(v^*). \quad (3.4)\]

We now define the function \(w = u^* - \alpha^{-1}v^*\) and show that \(w\) is a weak solution of the following problem:

\[w_t = \text{div}(d(w)w) + F(w) \quad \text{in} \quad Q \quad (3.5)\]

\[w_v = 0 \quad \text{on} \quad \partial \Omega \times R^+ \quad (3.6)\]

\[w(x,0) = w_0(x) = u_0(x) - \alpha^{-1}v_0(x) \quad x \in \Omega \quad (3.7)\]

where \(d(s) = d_1\) if \(s > 0\) and \(d(s) = d_2\) if \(s < 0\). \(F(s) = f(s)s\) if \(s > 0\) and \(F(s) = g(-\alpha s)s\) if \(s < 0\).

**Definition.** A function \(w\) is a weak solution of the problem \((3.5)-(3.7)\), if

(i) \(w \in L^\infty(\Omega \times R^+) \cap L^\gamma(0,T;H^1(\Omega)) \cap C([0,\infty); L^2(\Omega))\)

(ii) \(\int_\Omega w(T)\phi - \int_\Omega w_0\phi = \int_\Omega w_0(0)\)

hold for all \(\phi \in C^1(\Omega \times R^+)\) and all \(T > 0\).

We now arrive at the following theorems:

**Theorem 1.**

(i) The problem \((3.5)-(3.7)\) has exactly one weak solution \(w \in C^{\alpha,\alpha/2}(\Omega \times [0,\infty))\) for all \(\alpha \in (0,1)\);

(ii) The function \(w\) defined in \(w = u^* - \alpha^{-1}v^*\) is a weak solution of the problem \((3.5)-(3.7)\).

**Theorem 2.**

Let \(w\) be a weak solution of the problem \((3.5)-(3.7)\) such that there exists a family of closed hypersurfaces \(\Gamma = \{ \Gamma(t), t \in [0,T] \}\) such that \(\Gamma(t)\) in \(\Omega\) for all \(t \in [0,T]\), \(w(t) > 0\) in side \(\Gamma(t)\), say in \(\Omega_t^{\text{int}}\) and \(w(t) < 0\) outside \(\Gamma(t)\), say in \(\Omega_t^{\text{ext}}\) for each \(t \in [0,T]\). Then if \(\Gamma\) is smooth enough and if the functions

\[u^* = w_+ \quad \text{and} \quad v^* = -\alpha w_- (s_- = \min(0,s))\]
are smooth up to $\Gamma_1$, $u^*$ and $v^*$ satisfy

\[
\begin{align*}
\frac{\partial u^*}{\partial t} &= d_1 \Delta u^* + f(u^*)u^* \quad \text{in } \bigcup \{ \Omega^\text{int}_t, t \in (0,T] \} \\
\frac{\partial v^*}{\partial t} &= d_2 \Delta v^* + g(v^*)v^* \quad \text{in } \bigcup \{ \Omega^\text{ext}_t, t \in (0,T] \} \\
\frac{\partial u^*}{\partial v^*} &= \frac{\partial v^*}{\partial u^*} = 0 \quad \text{on } \Gamma \\
0 &= - \alpha d_1 u^* v^* - d_2 u^* v^* \quad \text{on } \Gamma \\
v^* &= 0 \quad \text{on } \partial \Omega \in (0,T],
\end{align*}
\]

(3.8) (3.9) (3.10)

$\{u^*, v^*\} = \{u_0(x), v_0(x)\}$ for $x \in \Omega$

(3.12)

where we suppose that $u_0 > 0$, $v_0 = 0$ in $\Omega^\text{int}_{0}$ and $u_0 = 0$, $v_0 > 0$ in $\Omega^\text{ext}_{0}$.

4. Concluding remarks

We have considered the 2-component RD system for strongly competing species. In order to study the dynamics of spatial segregation of two competing species, we have taken the spatial segregation limit in the system, and have derived the corresponding free boundary problem which is quite similar to the classical two phase Stefan problem. An essential difference with the classical Stefan problem is that the latent heat is zero. Consider the free boundary problem (3.8)-(3.11) where (3.10) is replaced by

\[
\epsilon V = - \alpha d_1 u^* v^* - d_2 u^* v^* \quad \text{on } \Gamma
\]

(4.1)

where $V$ is the normal velocity of the interface $\Gamma$ with a sufficiently small positive parameter $\epsilon$, and let $(u^*_\epsilon, v^*_\epsilon)$ and $\Gamma^*_\epsilon$ be a solution of this problem. This implies that the latent heat effect is included in the system.

With (4.1), we address the following question: How is the relation between $\{u^*, v^*\}$ and $\{u^*_\epsilon, v^*_\epsilon\}$? More definitely, how is the convergence of $\{u^*_\epsilon, v^*_\epsilon\}$ to $\{u^*, v^*\}$ as $\epsilon$ tends to zero? This convergence problem has not yet proved, though numerical computation suggests that is plausible. If this convergence holds, we find that for small $\epsilon$ and large $\beta$, the competition-diffusion system (2.1) can be approximated by the classical two phase Stefan problem with reaction terms.

In this paper, we have restricted our discussion to the Neumann boundary conditions but the result is valid
for other boundary conditions as well.

Our method can be extended to the similar problem for more number of competing species. Let us show one RD systems for three competing species which is described by

\[
\begin{align*}
    u_{1t} &= d_1 \Delta u_1 + r_1 (1 - u_1) u_1 - \beta c u_1 u_3 \\
    u_{2t} &= d_2 \Delta u_2 + r_2 (1 - u_2) u_2 - \alpha b u_1 u_2 - e u_2 u_3 \\
    u_{3t} &= d_3 \Delta u_3 + r_3 (1 - u_3) u_3 - \gamma e u_2 u_3 
\end{align*}
\]

(4.2)

where \( d_i, r_i, b, c, \alpha, \beta, \) and \( \gamma \) are positive constants. Of course, it is obvious that when \( u \) is identically zero, the system reduces to the (1.5). The resulting limiting systems are classified into three cases:

(i) Only \( b \) is sufficiently large and the other parameters are of order \( O(1) \);
(ii) Both \( b \) and \( c \) are sufficiently large and the other parameters are of order \( O(1) \);
(iii) All of \( b, c \) and \( e \) are sufficiently large and the other parameters are of order \( O(1) \).

Here we only demonstrate the limiting system of (4.2) for the case (i). One can expect that only \( u_1 \) and \( u_2 \) are very strongly competing so that they exhibit spatial segregation, while \( u_3 \) is smoothly distributed in the whole domain, though it competes with them. Let \( \Gamma_{12}(t) \) be an interface which separates two subregions

\[
\Omega_{13}(t) = \{ x \in \Omega, \ u_1, u_3 > 0 \text{ and } u_2 = 0 \} \quad \text{and} \quad \Omega_{23}(t) = \{ x \in \Omega, \ u_2, u_3 > 0 \text{ and } u_1 = 0 \}.
\]

Then \((u_1,u_3)\) and \((u_2,u_3)\) respectively satisfy the following RD systems for two competing species in \( \Omega_{13}(t) \) and \( \Omega_{23}(t) \):

\[
\begin{align*}
    u_{1t} &= d_1 \Delta u_1 + r_1 (1 - u_1) u_1 - \beta c u_1 u_3 \\
    u_{3t} &= d_3 \Delta u_3 + r_3 (1 - u_3) u_3 - \gamma e u_2 u_3 
\end{align*}
\]

(4.3)

and

\[
\begin{align*}
    u_{2t} &= d_2 \Delta u_2 + r_2 (1 - u_2) u_2 - e u_2 u_3 
\end{align*}
\]

(4.4)
The interface equation is

\[ u_1 = 0 = u_2 \quad \text{and} \quad u_3 \in C^1 \quad t > 0, \ x \in \Gamma_{12}(t) \]  

(4.5)

and

\[ 0 = -\alpha d_1 u_{1v} - d_2 u_{2v} \quad t > 0, \ x \in \Gamma_{12}(t). \]  

(4.6)

where \( v \) is the outerward unit vector on the interface. The initial conditions are given by

\[ u_i(0,x) = u_{i0}(x) \quad x \in \Omega_{13}(0) \quad i = 1,2 \quad \text{and} \quad u_3(0,x) = u_{30}(x) \quad x \in \Omega \]  

(4.7)

\[ \Gamma_{12}(0) = \Gamma_{012}. \]  

(4.8)

One finds that the free boundary problem derived from three species model is slightly different from the classical Stefan problem arising in solidification. This just appears as the consequence of biological problems. The analysis of a new Stefan problem (4.3)-(4.8) will be a future work for us.

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References


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