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A STEFAN-LIKE PROBLEM IN BIOLOGY

Masayasu Mimura

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 bioilogical species in ecological systems. Following his line, many differential equation models have been proposed so far. In particular, for the situation where each individuals randomely migrates, reaction-diffusion (RD) systems have been often used. One general form of the equations for the population density $u = (u_1, u_2 \dots u_N)$ is given by

$$u_{it} = d_i \Delta u + f_i(u) u_i \tag{1.1}$$

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 ($i = 1, 2, \dots, N$) .

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:

$$\begin{aligned} u_{1t} &= d_1 \Delta u_1 + f_1(u) u_1 \\ & \qquad\qquad\qquad t > 0,\ x \in \Omega \\ u_{2t} &= d_2 \Delta u_2 + f_2(u) u_2 \end{aligned} \tag{1.2}$$

The result shown here has been obtained by the joint wolrk with D. Hilhorst and L. A. Peletier[1].

with $f_1 = r_1 - a_1u_1 - b_1u_2$ and $f_2 = r_2 - b_2u_1 - a_2u_2$ where r_i is the intrinsic growth rate, a_i is the intraspecific competition rate and b_i is the interspecific competiton rate which are all positive constants[2]. Ω is a bounded domain in R^n. For (1.2), we impose the zero-flux boundary conditions on the boundary $\partial\Omega$

$$u_{1\nu} = 0 = u_{2\nu}, \tag{1.3}$$

where ν is the outerward normal unit vector on $\partial\Omega$. We define here *strong competition for two species* by the following inequalies

$$a_1/b_2 < r_1/r_2 < b_1/a_2. \tag{1.4}$$

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), $(r_1/a_1, 0)$, $(0, r_2/a_2)$ and (u^*, v^*). The fourth solution is given by the intersection point of two lines $r_1 - a_1u_1 - b_1u_2 = 0$ and $r_2 - b_2u_1 - a_2u_2 = 0$, and that (0, 0) and (u^*, v^*) are unstable, while $(r_1/a_1, 0)$ and $(0, r_2/a_2)$ are stable. Therefore, we find that the solution $(u_1(t), u_2(t))$ tends generically to either $(r_1/a_1, 0)$ 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 exisitence and stability of equilibrium solutions of (1.2)- (1,4) are different from the ODE version. If the domain Ω 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 $(r_1/a_1, 0)$ and $(0, r_2/a_2)$ only, that is, the competitive exclusion principle still holds. On the other hand, If the domain Ω is not convex, the solution structure is more complicated, depending on the shape of Ω [3]. If Ω 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 $(r_1/a_1, 0)$ 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 Ω.

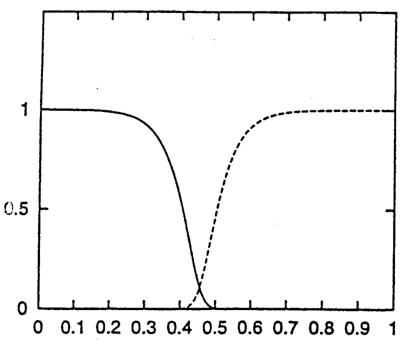
From the ecological view point on regional segregating problem for competing species, it is interesting to know how the time-evolution of segregting regions of two species is.

Our aim is to derive the evolutional 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

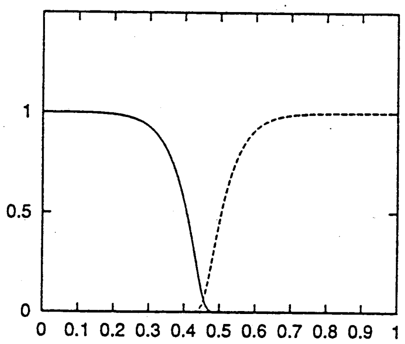
$$u_{1t} = d_1 \Delta u_1 + r_1(1-u_1)u_1 - bu_1u_2$$
$$t > 0,\ x \in \Omega \tag{1.5}$$
$$u_{2t} = d_2 \Delta u_2 + r_2(1-u_2)u_2 - \alpha bu_1u_2$$

where b and α 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 $\alpha < 1$.

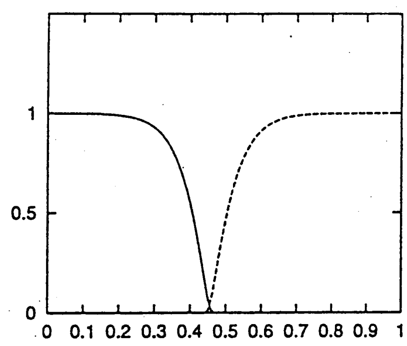
We first demonstrate some numerical simulations of the 1-dimensional problem of (1.2)-(1.4) for different values of b. For not large (but not small) b, it is shown that u_1 and u_2 exhibit spatial segregation with an overlapped zone, because of strong competition. When the value of b increases, the overlapped zone becomes narrower (see Fig. 1). Thus, taking the limit $b \uparrow\infty$, one can expect thst u_1 and u_2 possess disjoint supports (habitats) with only one common point, which seperates 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 differency is that no latent heat effect is included in the problem.



$b = 1000$



$b = 5000$



$b = 30000$

$r_1 = r_2 = 20 \quad d_1 = d_2 = 0.05 \quad \alpha = 1$

Fig. 1

Let $\Gamma(t)$ be an interface which seperates 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 Ω (see Fig.2).

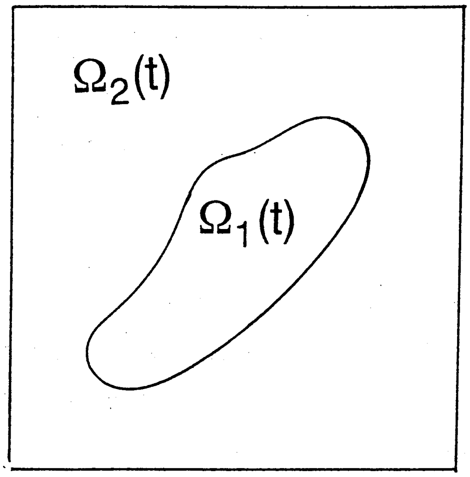


Fig. 2

Then u_1 and u_2 are described by

$$\begin{aligned} u_{1t} &= d_1 \Delta u_1 + r_1(1 - u_1)u_1 \qquad && t > 0,\ x \in \Omega_1(t) \\ u_{2t} &= d_2 \Delta u_2 + r_2(1 - u_2)u_2 \qquad && t > 0,\ x \in \Omega_2(t) \end{aligned} \tag{1.5}$$

$$u_{1\nu} = 0 = u_{2\nu} \qquad t > 0, \quad x \in \partial\Omega. \tag{1.6}$$

On the interface,

$$u_1 = u_2 = 0 \qquad t > 0, \quad x \in \Gamma(t) \tag{1.7}$$

and

$$0 = -\alpha d_1 u_{1\nu} - d_2 u_{2\nu} \qquad t > 0, \quad x \in \Gamma(t), \tag{1.8}$$

where ν is the outerward unit vector. The initial conditions are given by

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

which is seperated 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 α 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

$$\left.\begin{array}{l} u_t = d_1\Delta u + \{f(u) - kv\}u \\ \\ v_t = d_2\Delta v + \{g(v) - \alpha ku\}v. \end{array}\right. \quad \text{in } Q = \Omega \times R^+ \tag{2.1}$$

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

$$u_\nu = 0 = v_\nu \qquad \text{on } S = \partial\Omega \times R^+ \tag{2.2}$$

and

$$u(0,x) = u_0(x), \quad v(0,x) = v_0(x) \qquad x \in \Omega \tag{2.3}$$

where

(H_0) $$u_0, v_0 \in C^{2+\gamma}(\Omega) \quad \text{and} \quad 0 \le u_0 \le 1, \;\; 0 \le v_0 \le 1$$

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 $\{u_k\}$ 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 $\{u_k\}$ and functions $u^*, v^* \in L^2(0,T; H^1(\Omega))$ such that $0 \le u^* \le 1$, $0 \le v^* \le 1$ and

$$u_k \to u^* \quad \text{and} \quad v_k \to v^* \quad \text{as } k \to \infty \quad \text{in } L^1(Q_T) \tag{3.1a}$$

and

$$u_k \to u^* \quad \text{and} \quad v_k \to v^* \quad \text{as } k \to \infty \quad \text{in } L^2(0,T; H^1(\Omega)). \tag{3.1b}$$

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

$$w_t = d_1 \Delta u - \alpha^{-1} d_2 \Delta v + uf(u) - \alpha^{-1} vg(v) \qquad \text{in } Q_T \tag{3.2}$$

$$w_\nu = 0 \qquad \text{on } S_T, \tag{3.3}$$

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

$$(u^* - \alpha^{-1}v^*)_t = \Delta(d_1u^* - \alpha^{-1}d_2v^*) + u^*f(u^*) - \alpha^{-1}v^*g(v^*). \qquad (3.4)$$

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

$$w_t = \operatorname{div}(d(w)w) + F(w) \qquad \text{in } Q \qquad (3.5)$$

$$w_\nu = 0 \qquad \text{on } \partial\Omega \times R^+ \qquad (3.6)$$

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

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

(ii) $\int_\Omega w(T)\phi(T) - \iint_{Q_T}\{w\phi_t - d(w)\,\nabla w \nabla\phi + F(w)\phi\} = \int_\Omega w_0\phi(0)$

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 $\Gamma = \{\cup\Gamma(t),\ t \in (0,T]\}$ such that $\Gamma(t)$ in Ω for all $t \in (0,T]$, $w(t) > 0$ in side $\Gamma(t)$, say in Ω_t^{int} and $w(t) < 0$ outside $\Gamma(t)$, say in Ω_t^{ext} for each $t \in (0,T]$. Then if Γ is smooth enough and if the functions

$$u^* = w_+ \qquad \text{and} \qquad v^* = -\alpha w_- \ (s_- = \min(0,s))$$

are smooth up to Γ_t, u* and v* satisfy

$$u^*_t = d_1 \Delta u^* + f(u^*)u^* \quad \text{in} \quad \cup\{\ \Omega_t^{int},\ t \in (0,T]\}$$

$$v^*_t = d_2 \Delta v^* + g(v^*)v^* \quad \text{in} \quad \cup\{\ \Omega_t^{ext},\ t \in (0,T]\} \tag{3.8}$$

$$u^* = v^* = 0 \quad \text{on} \quad \Gamma \tag{3.9}$$

$$0 = -\alpha d_1 u^*_\nu - d_2 u^*_\nu \quad \text{on} \quad \Gamma \tag{3.10}$$

$$v^*_\nu = 0 \quad \text{on} \quad \partial\Omega \in (0,T]. \tag{3.11}$$

$$u^*(x,0) = u_0(x), \quad v^*(x,0) = v_0(x) \quad x \in \Omega \tag{3.12}$$

where we suppose that $u_0 > 0$, $v_0 = 0$ in Ω_0^{int} and $u_0 = 0$, $v_0 > 0$ in Ω_0^{ext}.

4. Cocluding 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 takes 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)-(3.12) where (3.10) is replaced by

$$\varepsilon V = -\alpha d_1 u^*_\nu - d_2 u^*_\nu \quad \text{on} \quad \Gamma \tag{4.1}$$

where V is the normal velocity of the interface Γ with a sufficiently small positive paraemeter ε, and let $(u^*_\varepsilon, v^*_\varepsilon)$ and Γ_ε be a solution of this problem. This impies that the latent heat effect is included in the system. With (4.1), we address the following question: How is the relation between $\{(u^*, v^*), \Gamma\}$ and $\{(u^*_\varepsilon, v^*_\varepsilon), \Gamma_\varepsilon\}$? More definitely, how is the convergence of $\{(u^*_\varepsilon, v^*_\varepsilon), \Gamma_\varepsilon\}$ to $\{(u^*, v^*), \Gamma\}$ as ε 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 e and large b, 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

$$u_{1t} = d_1\Delta u_1 + r_1(1 - u_1)u_1 - bu_1u_2 - \beta cu_1u_3$$

$$u_{2t} = d_2\Delta u_2 + r_2(1 - u_2)u_2 - \alpha bu_1u_2 - eu_2u_3 \qquad t > 0,\ x \in \Omega \tag{4.2}$$

$$u_{3t} = d_3\Delta u_3 + r_3(1 - u_3)u_3 - cu_1u_3 - \gamma eu_2u_3$$

where d_i, r_i, b, c, e, α, β, and γ 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 seperates two subregions

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

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 $\Omega_{23}(t)$:

$$u_{1t} = d_1\Delta u_1 + r_1(1 - u_1)u_1 - \beta cu_1u_3 \qquad t > 0,\ x \in \Omega_{13}(t)$$

$$\tag{4.3}$$

$$u_{3t} = d_3\Delta u_3 + r_3(1 - u_3)u_3 - cu_1u_3 \qquad t > 0,\ x \in \Omega_{13}(t)$$

and

$$u_{2t} = d_2\Delta u_2 + r_2(1 - u_2)u_2 - eu_2u_3 \qquad t > 0,\ x \in \Omega_{23}(t)$$

(4.4)

$$u_{3t} = d_3\Delta u_3 + r_3(1 - u_3)u_3 - \gamma e u_2 u_3 \qquad t > 0,\ x \in \Omega_{23}(t).$$

The interface euqation is

$$u_1 = 0 = u_2 \qquad u_3 \in C^1 \qquad t > 0,\ x \in \Gamma_{12}(t) \tag{4.5}$$

and

$$0 = -\alpha d_1 u_{1\nu} - d_2 u_{2\nu} \qquad t > 0, \quad x \in \Gamma_{12}(t), \tag{4.6}$$

where ν is the outerward unit vector on the interface. The initial conditions are given by

$$u_i(0,x) = u_{i0}(x) \qquad x \in \Omega_{i3}(0)\ (i = 1,2) \qquad \text{and} \qquad u_3(0,x) = u_{30}(x) \qquad x \in \Omega \tag{4.7}$$

$$\Gamma_{12}(0) = \Gamma_{012}. \tag{4.8}$$

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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Masayasu Mimura
Graduate School of Mathematical Sciences,
The University of Tokyo
3-8-1 Komaba, Meguro-ku, Tokyo 153
JAPAN
email mimura@ms. u-tokyo. ac. jp