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EDGE EFFECT CAUSED
BY
COMPETITION-DIFFUSION MECHANISMS

by

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ABSTRACT

This paper points out that the spatially heterogeneous competition diffusion model on one dimensional line segment can have stable coexistent equilibrium solutions with any number of species even if their local dynamics without diffusion assures the competitive exclusion principle at each location. This solution may explain edge effect--relative abundance of species on the overlapping zone of two neighboring communities.

KEY WORDS: Competition -- Competitive Exclusion Principle --
Edge Effect -- Reaction-Diffusion

1. Introduction

Many ecological observations indicate relative abundance of species on overlapping zones of two neighboring communities. (See, e.g., Forman and Codron, 1986, pp.108-109 and 144-146; Odum, 1983, pp.429-437.) This phenomenon, called edge effect, is usually ascribed to the diversity of the microenvironment along the border of the zones. The purpose of this paper is to provide another view for this phenomenon by pointing out that the interspecific competition between major species tends to cause decrease of their densities around their overlapping zone, which makes it possible for minor species to invade there. Thus, even if only one species persists in the interior of each community, our results predict that any number of minor species may stably persist around the ecotone area.

This idea was suggested in Kishimoto(in press) from the behavior of the solutions of a two patch model of the Lotka-Volterra competitive system. However, dynamical behavior of a two patch system is sometimes substantially different from that of its continuous version. For example, Kishimoto(1980) and Kishimoto and Weinberger(1985) proved that Levin's result(1974) on the existence of stable coexistent equilibria over two identical patches cannot be extended to the case of spatially uniform continuous convex habitats. This paper shows that edge

effect phenomenon over two different patches is naturally extensible to the case of continuous one dimensional habitats.

2. THE MODEL SYSTEM

We assume that species S_1, S_2, \dots, S_J spread over a one dimensional line segment $[-L^-, L^+]$, which is composed of three subhabitats $D^- = \{x: -L^- < x < -\delta^-\}$, $D^0 = \{x: -\delta^+ < x < \delta^+\}$ and $D^+ = \{x: \delta^+ < x < L^+\}$ and their boundaries. We also introduce a symbol $D = D^- \cup \bar{D}^0 \cup D^+$, where the symbol " $\bar{}$ " over the domain symbol indicates the closure operation.

We consider location dependent population dynamics which is described by the competition diffusion equations of the following form:

$$\begin{aligned} \partial u_i(t, x) / \partial t = \sigma_i \partial^2 u_i(t, x) / \partial x^2 + f_i(u(t, x), x) u_i(t, x), \quad (1) \\ x \in D, t > 0, \quad i = 1, 2, \dots, J, \end{aligned}$$

$$\partial u_i(t, x) / \partial x = 0, \quad x = \partial D, t > 0, \quad i = 1, 2, \dots, J, \quad (2)$$

$$u_i(0, x) = u_{0i}(x), \quad x \in \bar{D}, \quad i = 1, 2, \dots, J, \quad (3)$$

where σ_i are the constants denoting the diffusion coefficients of S_i , $u_i(t, x)$ are the population densities of S_i at time t and at location x , and $f_i(u, x)$ are the smooth functions of $u = (u_1, u_2, \dots, u_J)$ and of x . We assume that the species compete for the same limited resources, so that

$$\partial f_i / \partial u_j < 0, \quad x \in \bar{D}, \quad i \text{ and } j = 1, 2, \dots, J, \quad (4)$$

hold for any u . We also assume that, in \bar{D}^- and in \bar{D}^+ , f_i are independent of x :

$$f(u, x) = \begin{cases} g_i^-(u), & \text{in } \bar{D}^-, \\ g_i^0(u, x), & \text{in } D^0, \\ g_i^+(u), & \text{in } \bar{D}^+. \end{cases} \quad (5)$$

($i = 1, 2, \dots, J$)

Suppose that we have reduced (1) into a system of ordinary differential equations of two components (u_i, u_j) parametrized by x , by putting $\sigma_k = 0$ ($k = i, j$) and $u_k(t, x) = 0$ ($k \neq i, j$). Its solutions provide us with the relations between S_i and S_j at location x in the absence of their spatial migration and in

the absence of the other species. If S_i always defeats S_j ($i \neq j$) in this system, i.e., both $\lim_{t \rightarrow \infty} u_i(t, x) > 0$ and $\lim_{t \rightarrow \infty} u_j(t, x) = 0$ hold irrespective of their initial state, we denote their relation by $S_i(x) > S_j(x)$ or simply by $S_i > S_j$, where ">" is a relation symbol. Field observations (Buss and Jackson, 1979, and the references therein) have shown that the relation ">" very often satisfies transitivity:

$$S_i > S_j \text{ and } S_j > S_k \text{ imply } S_i > S_k,$$

which will be also assumed hereafter. We take up S_1 and S_2 as the strongest species in D^+ and in D^- :

$$\begin{aligned} \text{[A]} \quad S_1 > S_i, \quad i = 2, 3, \dots, J, \quad \text{in } \bar{D}^-, \\ S_2 > S_i, \quad i = 1, 3, \dots, J, \quad \text{in } \bar{D}^+. \end{aligned}$$

Then, S_1 and S_2 are the interior species in \bar{D}^- and in \bar{D}^+ , respectively.

At least at some point (or generically, in some area) in D^0 where the competitive power of S_1 and S_2 crosses over, existence of the most powerful species is inevitably violated,

because of the continuity of f_i . Fortunately, however, the tendency for macroscopic coexistence of the species is strong enough not to be affected by the behavior of f_i in D^0 as we will see. That is why the conditions in D^0 do not appear in [A].

We notice that the densities of the species never diverge to infinity, because of the finiteness of resources. On the other hand, we are not interested in the species which cannot persist even in the absence of the other species. Thus, we assume that

$$f_i^{(1)}(0, \dots, 0, \bar{u}_i(x), 0, \dots, 0, x) = 0, \quad \bar{u}_i(x) > 0$$

$$x \in \bar{D}, \quad i = 1, 2, \dots, J, \quad (6)$$

hold for some $\bar{u}_i(x)$. From (4), such $\bar{u}_i(x)$ are uniquely determined. Under (4) and (6), one sees that [A] holds if and only if the following inequalities are satisfied:

$$\left\{ \begin{array}{l}
g_1^- \equiv \min_{x \in \bar{D}^-} g_1^-(0, \dots, 0, \bar{u}_j(x), 0, \dots, 0) > 0, \\
j = 2, \dots, J, \\
g_2^+ \equiv \min_{x \in \bar{D}^+} g_2^+(0, \dots, 0, \bar{u}_j(x), 0, \dots, 0) > 0, \\
j = 1, 3, 4, \dots, J, \\
g_i^- \equiv \max_{x \in \bar{D}^-} g_i^-(\bar{u}_1(x), 0, \dots, 0) \leq 0, \quad i = 2, 3, \dots, J, \\
g_i^+ \equiv \max_{x \in \bar{D}^+} g_i^+(0, \bar{u}_2(x), 0, \dots, 0) \leq 0.
\end{array} \right. \tag{7}$$

We need stronger assumptions for S_1 and S_2 ,

$$\left\{ \begin{array}{l}
g_1^- \equiv g_1^-(0, \max_{x \in \bar{D}} \bar{u}_2(x), 0, \dots, 0) > 0, \\
g_2^+ \equiv g_2^+(\max_{x \in \bar{D}} u_1(x), 0, \dots, 0) > 0, \\
i = 1, 3, 4, \dots, J,
\end{array} \right. \tag{8}$$

which assure that the interior species are not defeated by the other interior species in their home habitats even in the presence of diffusion.

We say that an equilibrium \bar{u} of (1) with (2) and (3) is coexistent if it satisfies the inequalities:

$$\bar{u}_i(x) > 0, \quad x \in \bar{D}, \quad i = 1, 2, \dots, J. \quad (9)$$

Existence of coexistent stable equilibrium solutions satisfying [A] is the subject of the following sections.

3. COEXISTENCE OF TWO SPECIES

As is noticed in Kishimoto(1981), the comparison theorem holds true in system (1) with (2)-(4) and $J = 2$, (rewrite (1) by putting $u_1 = y_1$ and $u_2 = -y_2$, and use (4)) and we can define its super- and sub-solutions. We say that $w(x) = (w_1(x), w_2(x))$ is a strict super- (resp. sub-) solution of (1) with (2)-(4) and $J = 2$ if w is not an equilibrium, and if the solution u with the initial condition $u_0 = w$ satisfies

$$u_1(t, x) \geq w_1(x), \quad u_2(t, x) \leq w_2(x),$$

(resp. $u_1(t, x) \leq w_1(x), \quad u_2(t, x) \geq w_2(x),$)

for any $t > 0$, where $u_0 = (u_{01}, u_{02})$. The result by Matano(1984) is arranged in the following form in our case:

LEMMA 1. If (1) with (2)-(4) and $J = 2$ has both super- and sub-solutions $w^U(x) = (w_1^U(x), w_2^U(x))$ and $w^L(x) = (w_1^L(x), w_2^L(x))$, there is a stable equilibrium solution $\bar{w}(x) = (\bar{w}_1(x), \bar{w}_2(x))$ satisfying both $w_1^L(x) \leq \bar{w}_1(x) \leq w_1^U(x)$ and $w_2^L(x) \geq \bar{w}_2(x) \geq w_2^U(x)$. □

If the diffusion coefficients are very large, the population dynamics behaves as if the species were to live in a habitat of one point, so that [A] assures that coexistence is never realized. Coexistence is possible only when the diffusion coefficients are not so large, or equivalently, their habitat is large compared with their migration speed. The following conditions are sufficient for describing our results:

$$\sigma_1\{(\pi/2)/(L^-\delta^-)\}^2 < g^-, \quad \sigma_2\{(\pi/2)/(L^+\delta^+)\}^2 < g^+. \quad (10)$$

The following theorem does not contain [A] in its premise, so that it holds when [A] is assumed.

Theorem 2. System (1) with (2)-(6), (8), (10) and $J = 2$ has a stable equilibrium solution $\bar{u}(x) = (\bar{u}_1(x), \bar{u}_2(x))$ satisfying (9).

(Proof) Let us define the following functions:

$$\begin{aligned}
 w_1^U(x) &= \begin{cases} -\varepsilon \sin((\pi/2)(x + \delta^-)/(L^- - \delta^-)), & x \in \bar{D}^-, \\ 0, & x \in \bar{D} \setminus \bar{D}^-, \end{cases} \\
 w_2^U(x) &= g_1^-, & x \in \bar{D}, \\
 w_1^L(x) &= g_2^+, & x \in \bar{D}, \\
 w_2^U(x) &= \begin{cases} 0, & x \in \bar{D} \setminus \bar{D}^+, \\ \varepsilon \sin(\pi/2)(x - \delta^+)/(L^+ - \delta^+), & x \in \bar{D}^+. \end{cases}
 \end{aligned}$$

Then, from (8) and (9), we see that $(w_1^U(x), w_2^U(x))$ and $(w_1^L(x), w_2^L(x))$ are, respectively, the super- and the sub-solutions of (1) with (2)-(4) for sufficiently small ε . Thus, the theorem follows from Lemma 1. □

4. ABUNDANCE OF SPECIES AROUND THE BORDER

It seems to be difficult to give ecologically transparent conditions for persistence of any number of edge species in a general nonlinear framework. Here, we confine our attention to the classic Lotka-Volterra-Gause dynamics, and impose several symmetric conditions on the species and on domains, so that the conditions may provide us with an intuitive interpretation of the results. Thus, the following conditions are imposed on (1) with (5):

$$\begin{cases} g_i^-(u, x) = 1 - \sum_{j=1}^J a_{ij}^- u_j(t, x), & \text{in } D^-, \\ g_i^+(u, x) = 1 - \sum_{j=1}^J a_{ij}^+ u_j(t, x). & \text{in } D^+, \end{cases} \quad (11)$$

$$i = 1, 2, \dots, J,$$

$$\sigma_i = \sigma, \quad i = 1, 2, \dots, J, \quad (12)$$

$a_{ii}^+ = a_{ii}^- = 1$ ($i = 1, 2, \dots, J$), $L^+ = L^- = L$, and $\delta^+ = \delta^- = \delta$.

We also assume that the competitive power of weaker species to the stronger species is so negligible that $a_{ij}^+ = a_{ij}^- = 0$ hold for any pair (i, j) , with $i < j$ except for $(i, j) = (1, 2)$.

Furthermore, we assume that the i strongest species S_1, S_2, \dots, S_i exercise equal effects on the weaker species $S_j (j > i)$ over both patches, so that $a_{ij}^+ = a_{ij}^- = \gamma_i$ hold for $i (\geq 3)$ and $j (\leq i-1)$. Then, a_{ij}^+ (resp. a_{ij}^-) are given as follows if disposed in a matrix form:

$$\begin{pmatrix} 1 & \alpha \text{ (resp. } \beta) & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ \beta \text{ (resp. } \alpha) & 1 & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ \gamma_3 & \gamma_3 & 1 & 0 & 0 & \dots & 0 & 0 & 0 \\ \gamma_4 & \gamma_4 & \gamma_4 & 1 & 0 & \dots & 0 & 0 & 0 \\ \gamma_5 & \gamma_5 & \gamma_5 & \gamma_5 & 1 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ \gamma_{J-1} & \gamma_{J-1} & \gamma_{J-1} & \gamma_{J-1} & \gamma_{J-1} & \dots & \gamma_{J-1} & 1 & 0 \\ \gamma_J & \gamma_J & \gamma_J & \gamma_J & \gamma_J & \dots & \gamma_J & \gamma_J & 1 \end{pmatrix}.$$

(13)

Then, (7) is satisfied if and only if

$$\alpha < 1 < \beta, \tag{8'a}$$

$$\gamma_i > 1 \quad (i = 3, 4, \dots, J), \tag{8'b}$$

hold, and (8) follows from (8'a) and (8'b). In this special case, our system is a hierarchical system satisfying the following properties:

$$\begin{aligned} S_1 > S_2 > S_3 > S_4 > \dots > S_J, & \text{ in } \bar{D}^-, \\ S_2 > S_1 > S_3 > S_4 > \dots > S_J, & \text{ in } \bar{D}^+. \end{aligned}$$

We notice that these assumptions naturally imply the competitive exclusion principle. We need to impose a further condition that the competition between S_1 and S_2 is strong enough to satisfy

$$\alpha + \beta > 2. \tag{14}$$

Notice that, under our symmetric assumptions on the domains and the species, the sum $z^{(J)}(x) = \sum_{j=1}^J \bar{u}_j(x)$ of the densities of all the species also indicates the measure of the total amount of resources consumed at location x in J species systems. Thus, our main result is stated as follows.

Theorem 3. For any integer $J (\geq 2)$ and for any pair of real numbers α and β with (8'a) and (14), there exists a $(J-2)$ -tuple $(\gamma_3, \gamma_4, \dots, \gamma_J)$ of real numbers for (13), such that system (1) with (2)-(5) and (10)-(13) satisfies (8'b) (and hence [A]),

and at the same time it has a stable equilibrium solution $\bar{u} = (\bar{u}_1, \bar{u}_2, \dots, \bar{u}_J)$ satisfying both (9) and

$$z^{(J)}(x) \leq \zeta^{(J)} < 1, \quad x \in \bar{D}. \quad (14)$$

(Proof) We take to the mathematical induction on the number J of species.

Since (6) and (8) follow from (11) and (13), Theorem 2 assures that the system with $J = 2$ has a stable equilibrium $\bar{u}^{(2)} = (\bar{u}_1^{(2)}, \bar{u}_2^{(2)})$ satisfying (9). Condition (8'b) is trivially satisfied for $J = 2$. Notice that $\bar{z}^{(2)} = \bar{u}_1^{(2)} + \bar{u}_2^{(2)}$ satisfies

$$\sigma \partial^2 \bar{z}^{(2)} / \partial x^2 + (1 - \bar{z}^{(2)}) \bar{z}^{(2)} + (2 - \alpha - \beta) \bar{u}_1^{(2)} \bar{u}_2^{(2)} = 0.$$

Compactness of \bar{D} and continuity of $\bar{z}^{(2)}(x)$ assure that $\bar{z}^{(2)}(x)$ takes its maximum value $\zeta^{(2)}$ in \bar{D} . Since (14) assures that the last term of the above equality is negative, we have $\zeta^{(2)} \in (0, 1)$. Thus, (14) is satisfied for $J = 2$.

Suppose that the existence of a stable equilibrium $\bar{u}^{(J-1)} = (\bar{u}_1^{(J-1)}, \bar{u}_2^{(J-1)}, \dots, \bar{u}_{J-1}^{(J-1)})$ with (9) and (14) for J species

systems has been established for $\gamma_i = \gamma_i^{(J-1)}$ ($i = 3, 4, \dots, J$). We put the first $J-3$ parameters $\gamma_i^{(J)}$ ($i = 3, 4, \dots, J-1$) for the J species system by $\gamma_i^{(J)} = \gamma_i^{(J-1)}$. We then determine $\gamma_J^{(J)}$ from the considerations on J th equation of (1):

$$\partial u_J / \partial t = \sigma \partial^2 u_J / \partial x^2 + (1 - \gamma_J^{(J)} \sum_{j=1}^{J-1} u_j - u_J) u_J, \quad x \in D, t > 0. \quad (16)$$

Since the dynamics of u_i ($1 \leq i \leq J-1$) are not affected by the value of u_J , we can find an equilibrium for (16) by finding an equilibrium of the scalar equation:

$$\partial u_J / \partial t = \sigma \partial^2 u_J / \partial x^2 + (1 - \gamma_J^{(J)} z^{(J-1)} - u_J) u_J, \quad x \in D, t > 0, \quad (17)$$

From (14) we can choose $\gamma_J^{(J)}$ satisfying $1 < \gamma_J^{(J)} < 1/\epsilon^{(J-1)}$, which assures (8'b) for the J species case. Then, $1 - \gamma_J^{(J)} z^{(J-1)} > 0$ ($x \in \bar{D}$) holds, so that we can apply Lemma 1 to (17) by putting $\bar{u}_2(x) = 0$ to show the existence of a stable equilibrium solution \bar{u}_J^* of (17) satisfying (9). Noticing that $1 -$

$\gamma_J^{(J)} z^{(J-1)} - \bar{u}_J^* > 0$ holds for any $x \in \bar{D}$ in (17), we see that $\bar{u}^{(J)} = (\bar{u}_1^{(J-1)}, \bar{u}_2^{(J-1)}, \dots, \bar{u}_{J-1}^{(J-1)}, \bar{u}_J^*)$ is an equilibrium solution of (1) with (2) satisfying (14). Since the dynamics of the first $J-1$ species is not affected by that of u_J , the stability of $\bar{u}^{(J-1)}$ in the $J-1$ species and that of $u^{(J)}$ in (17) imply the stability of $u^{(J)}$ in the J species system. \square

4. DISCUSSIONS

Except for the symmetric conditions on species and on domains, the essential assumptions for Theorem 3 are (14) and the zero value assumptions in the upper triangular part in (13). The former means that the interspecific competition between the interior species is strong, and is ecologically plausible. The latter can be slightly relaxed, because our result is valid if these zero components are slightly perturbed. We expect that this robustness obtains in much larger class of systems though we can give no theoretical proof here.

One may be afraid that we have laid too restrictive conditions in selecting γ_i in (13) in the process of constructing the stable equilibrium in the proof. Indeed, it is true that, if one arbitrarily selects a species from the real world, and tests whether the conditions of the theorem are

satisfied, then it may not be very probable that it can invade our system. One should remember, however, that there are so many species in the world. It is not very unpalausible that the some of them satisfy our requirements, and successfully invade our habitat. Thus, we add species one by one until we failed to find the species which meets our conditions. The number of present species at this point determines the number of edge species.

Thus, our mechanisms may play certain roles in the real world. It might be interesting to seek for actual examples.

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