Competition for space in a heterogeneous environment

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Abstract. We consider effects of competition for space in a heterogeneous environment, making use of nonlinear interaction-diffusion equations. Competition for space is assumed to mean mutual repulsive interactions that force other individuals to disperse from a crowded region. In other words, we are concerned with density-dependent dispersal forced by population pressures. Spatial heterogeneity is incorporated in the growth rates, and the environment is assumed to have a favorable habitat for two populations surrounded by largely hostile regions. Space-independent migration rates are assumed. We ignore the usual density-dependence in the growth rates to focus our attention on density-dependence in the migration rates. Our main conclusion is that two populations can coexist if the interspecific repulsive forces are weaker than the intraspecific ones. It is also emphasized that density-dependent dispersal in a heterogeneous environment is not always a stabilizing agent, and that either of two populations may become extinct by competition for space. Finally, the resemblance of our results to those from Lotka–Volterra competition equations is suggested.

Key words: Competition for space — Heterogeneous environment — Density-dependent dispersal — Nonlinear diffusion — Repulsive forces

1. Introduction

Animal migration and non-uniform spatial distribution patterns of populations, together with interactions between populations, are important factors in regulating populations. Taylor and Taylor [31] emphasized the role of density dependence in migration as a behavioral response to avoid competition. Congestion of a population may result in severe competition between individuals. However, the degree of crowding is not only a product of multiplication, but also of movement (Taylor and Taylor [31]); and some populations disperse to avoid crowding. When an environment is crowded and space itself is a limited resource, it will be of profound value for an individual to occupy, more or less exclusively, some portion of space, thereby repulsing other individuals (Yodzis [33]). Therefore, although resource depression might be relieved by migration, there may arise competition for space instead of exploitation competition.

Some models considering density-dependent migration or dispersal enforced by population pressures have been proposed (see Okubo [20] and Levin [13] for

reviews). Shigesada et al. [28] have proposed a model that incorporates both random and density-dependent dispersal. They also considered a directed movement toward favorable places through the gradient of the environmental potential. Furthermore, in their model, competitive dynamics of the Lotka–Volterra type are taken into consideration. They have shown that two populations that cannot coexist locally may do well through spatial segregation by density-dependent dispersal and directed movement to a favorable place. The connection between their model and field or experimental observations demonstrating population pressure effects is discussed in detail by Shigesada et al. [28], Shigesada [26] and Okubo [20]. Mimura and Kawasaki [15], Mimura [14] and Mimura et al. [16] gave further mathematical analyses to a somewhat simplified version of the model. Hosono ([9, 10]) analyzed related problems from the standpoint of existence of traveling wave solutions.

On the other hand, many populations appear to be regulated at levels well below the apparent carrying capacities of their habitats. This provides a possibility which cannot be explained by models that do not incorporate spatial heterogeneity (Nisbet and Gurney [19]). Population models which include effects of environmental heterogeneity have recently been given a good deal of attention. Gurney and Nisbet [6] and Namba [17] have studied single species models with nonlinear diffusion and have demonstrated that the spatial distribution patterns formed through density-dependent dispersal in a heterogeneous environment play an effective role in regulating the population. Shigesada [27] and Shigesada et al. [29] have considered models taking effects of spatial heterogeneity in both dispersal and growth processes for single species models. Recently, Teramoto and Seno [32] have studied aggregated distribution patterns formed through density-dependent dispersal and heterogeneity determined by the environmental potential field for a single species and two species systems. Effects of environmental heterogeneities for prey-predator and competitive systems have also been studied (Kawasaki and Teramoto [11]; Shigesada et al. [28]; Pacala and Roughgarden [21]; Shigesada and Roughgarden [30], Pozio and Tesei [23, 25]).

However, in these models, effects of interspecific repulsive forces that cause movements to avoid crowding are not considered explicitly, except for Shigesada et al. [28] and Teramoto and Seno [32]. In this paper, we will investigate the combined effects of density-dependent dispersal and spatially variable growth on distributions of competing populations. However, we will not consider the usual competitive dynamics, which are expressed through decrease of growth rates in the presence of competing populations. It is suggested that "extrinsic population control by Malthusian killing agencies is partly an illusion borne of man's obsession with mortality" (Taylor and Taylor [31]). Thus, it may be more rational to expect migration before population densities rise so high as to cause severe competition, unless migration brings a great risk. Therefore, we ignore density dependence in growth rates, to focus our attention on density dependence in dispersal rates, or competition for space.

In the next section, we precisely state our model. Then, we analytically search for stationary spatial distributions of two populations. Then we will numerically solve the system to examine stability of stationary solutions and reveal the

condition for coexistence of two species. Finally, we will discuss some points regarding our results on competition for space.

2. Model

We consider the following system of equations as a model of competition for space in a heterogeneous environment;

$$\frac{\partial u_1}{\partial t} = d_1 \frac{\partial^2}{\partial x^2} [(u_1 + \alpha_1 u_2) u_1] + g_1(x) u_1,$$

$$\frac{\partial u_2}{\partial t} = d_2 \frac{\partial^2}{\partial x^2} [(u_2 + \alpha_2 u_1) u_2] + g_2(x) u_2,$$

(1)

where u_1 and u_2 are population densities of two species, and t and x respectively represent time and the coordinate of one-dimensional space. In the interaction-diffusion equations (1), nonlinear diffusion terms are the same as in Shigesada et al. [28], although we neglect random diffusion effects and leave only purely density-dependent terms. The expression implies the repulsive transition in Okubo's [20] classification, in which the transition probabilities depend only on conditions at the point of departure. That is, movement is determined by the state of the point of departure and individuals are compelled to migrate to avoid crowding, by both intraspecific and interspecific repulsive forces. α_1 and α_2 are parameters that measure the strengths of interspecific repulsive forces in comparison with those of intraspecific ones, and d_1 and d_2 are coefficients of diffusivity. Alternative models also are proposed for density-dependent dispersal (Busenberg and Travis [5] and Gurtin and Pipkin [8]), and a simplified version has been studied in detail from the standpoint of spatial segregation of competing populations (Bertsch et al. [3, 4]). However, we choose the system (1) in this paper, since effects of interspecific exclusion can be clearly appreciated in (1).

We assume that the growth rates of two populations do not depend on population densities, although they depend on the spatial position, reflecting environmental heterogeneity. It may be interpreted as an approximation when the population densities are far below the carrying capacities of the environment because of movements to avoid crowding. We consider a heterogeneous environment in which a favorable habitat for growth of the populations is surrounded by a hostile universe. Thus, we assume that the continuous function $g_i(x)$ is positive in the neighborhood of $x = 0$ and that it decreases monotonically to $-\infty$ as $|x|$ goes to infinity (Gurney and Nisbet [6]).

If $\alpha_i = 0$ or $u_j(t, x) \equiv 0$, then each of the two equations in system (1) reduces to

$$\frac{\partial u_i}{\partial t} = d_i \frac{\partial^2}{\partial x^2} (u_i)^2 + g_i(x) u_i,$$

(2)

which is the Directed Motion Model by Gurney and Nisbet [6] (see also, Gurtin and MacCamy [7]). If $g_i(x) \equiv 0$, then Eq. (2) becomes

$$\frac{\partial u_i}{\partial t} = d_i \frac{\partial^2}{\partial x^2} (u_i)^m,$$

(3)

with $m = 2$, which is known as the porous medium equation that describes a gas flow in a porous medium. A solution of Eq. (3) with $m > 1$ has a finite speed of propagation if it has an initial distribution vanishing outside a finite region, which is an important difference from the case of a solution of the linear diffusion equation with $m = 1$; and it has a bounded support for any $t > 0$ if the property is satisfied at $t = 0$ (see, for example, Aronson [1]). With respect to Eq. (2), it has been shown that it has a stable equilibrium solution with free boundaries whose support is bounded (see Aronson [2] for an introduction to the problem). That is, if a population is dispersing in a density-dependent manner, its distribution approaches a stable configuration with a finite range, and it never goes to extinction regardless of the surrounding hostile region.

The above property was discussed orginally by Namba [17]. Particularly, when the growth rate $g_i(x)$ takes a specific quadratic form,

$$g_i(x) = r_i \left[1 - \left(\frac{x}{x_i} \right)^2 \right], \tag{4}$$

he found a simple expression for the stationary solution, in terms of a fourth-order polynomial (Fig. 1);

$$u_i^*(x) = c_i \left(1 - \frac{x}{x_i^*} \right)^2 \left(1 + \frac{x}{x_i^*} \right)^2, \quad \text{if } |x| < x_i^*,$$
$$= 0 \qquad\qquad\qquad\qquad \text{if } |x| \geq x_i^*. \tag{5}$$

The boundaries $x = \pm x_i^*$ divide the environment into the populated and unpopulated regions and the solution satisfies both $u_i^*(x) = 0$ and $\nabla u_i^*(x) = 0$ at the free boundaries $x = \pm x_i^*$, where $x_i^* = \sqrt{7} x_i$ and $c_i = 7 r_i x_i^2 / (8 d_i)$. We will also use the specific form (4) later for numerical calculations. Equation (2) and some extended systems have been studied by Peletier and Tesei [22] and Pozio and Tesei [23, 24, 25].
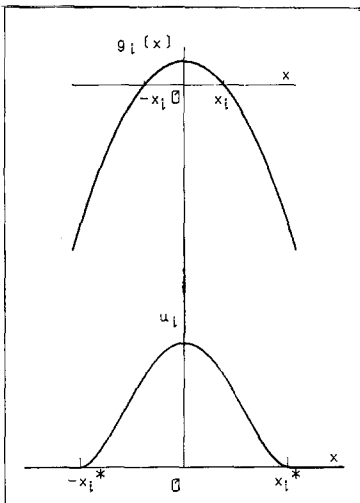

Fig. 1. An example of the growth rate $g_i(x)$ and the stationary solution $u_i^*(x)$ of Eq. (2), where $x = \pm x_i^*$ are free boundaries

3. Existence of coexistent stationary solutions

The above considerations show that the system (1) has two stationary solutions $(u_1^*(x), 0)$ and $(0, u_2^*(x))$. Needless to say, $(0, 0)$ is also a stationary solution of the system (1). However, it does not attract our attention, since it corresponds to the state in which nothing is alive. Hereafter, we will ignore it. Our main interest is whether or not coexistence of two species is possible in the presence of competition for space. We must search for a non-negative and non-zero solution in which both $u_1(t, x)$ and $u_2(t, x)$ are positive for some x. We call this solution a coexistent solution, or simply a positive solution. It is very difficult to solve generally the correspondent stationary problem to the system (1). Therefore, we impose another assumption,

$$g_2(x) = \beta g_1(x), \tag{6}$$

that is, $g_2(x)$ and $g_1(x)$ are proportional to each other. This means ecologically that the favorable habitats for two populations coincide and that the hostile regions are also the same for both species. It may be a reasonable assumption, if two competing species are ecologically similar.

By virtue of the additional assumption, we can obtain a positive stationary solution in some cases. First, we assume that a positive stationary solution $(\tilde{u}_1(x), \tilde{u}_2(x))$ satisfies

$$\tilde{u}_2(x) = \gamma \tilde{u}_1(x); \tag{7}$$

that is, the solution $\tilde{u}_2(x)$ itself is in proportion to $\tilde{u}_1(x)$. Note that this is only a convenient assumption, and there is no reason to assume (7). Then the stationary problem corresponding to the system (1) can be written, making use of only $g_1(x)$ and $\tilde{u}_1(x)$;

$$0 = d_1(1 + \alpha_1\gamma)\frac{\partial^2}{\partial x^2}(\tilde{u}_1)^2 + g_1(x)\tilde{u}_1,$$

$$0 = d_2\gamma(\gamma + \alpha_2)\frac{\partial^2}{\partial x^2}(\tilde{u}_1)^2 + \beta\gamma g_1(x)\tilde{u}_1. \tag{8}$$

From the previous consideration, we know that each equation of the system (8) has a solution with free boundaries. However, these two solutions must coincide with one another in order that they comprise a solution of the stationary problem of the system (1). Thus a compatibility condition can be obtained as a condition on the ratio of coefficients of the system (8);

$$\frac{d_2\gamma(\gamma + \alpha_2)}{d_1(1 + \alpha_1\gamma)} = \frac{\beta\gamma}{1}. \tag{9}$$

Then, we can determine γ from the above condition;

$$\gamma = \frac{d_1\beta - d_2\alpha_2}{d_2 - d_1\alpha_1\beta}. \tag{10}$$

In order that u_1 and u_2 are non-negative, γ must be positive. Therefore, we can obtain a sufficient condition for existence of a positive stationary solution of the system (1).

Theorem 1. *Suppose that $g_1(x)$ and $g_2(x)$ are chosen so that the reduced eq. (2) has a positive stationary solution with free boundaries. Further assume that $g_1(x)$ and $g_2(x)$ satisfy the relation (6). Then the system (1) has a positive stationary solution with free boundaries,*

$$(i) \quad if \alpha_1\alpha_2 > 1 \quad and \quad \frac{d_2}{d_1}\frac{1}{\alpha_1} < \beta < \frac{d_2}{d_1}\alpha_2,$$

or $\hspace{11cm}$ (11)

$$(ii) \quad if \alpha_1\alpha_2 < 1 \quad and \quad \frac{d_2}{d_1}\alpha_2 < \beta < \frac{d_2}{d_1}\frac{1}{\alpha_1}.$$

If $g_1(x)$ and $g_2(x)$ specifically satisfy (4), then β equals r_2/r_1. However, note that the sufficient conditions (11) for existence of a positive stationary solution do not depend on the specific forms of the functions $g_1(x)$ and $g_2(x)$ so long as the reduced Eq. (2) has a positive stationary solution. Hitherto, it is found that when either of conditions (11) is satisfied, system (1) has three stationary solutions $(u_1^*(x), 0)$, $(0, u_2^*(x))$ and $(\tilde{u}_1(x), \tilde{u}_2(x))$ (see Fig. 2). However, the stability of these solutions is not yet known. Moreover, we have not determined whether a positive solution may exist or not when conditions (11) are not satisfied. Even if conditions (11) are satisfied, we have not determined whether or not the stationary solution is uniquely determined. In other words, it is not certain whether there exists another positive stationary solution of system (1) in which $u_2(x)$ and $u_1(x)$ are not proportional. These questions will not be dealt with in this paper and remain to be solved.

However, it is certain that there always exist two stationary solutions $(u_1^*(x), 0)$ and $(0, u_2^*(x))$. If β becomes large enough to satisfy either of conditions (11), then a positive stationary solution $(\tilde{u}_1(x), \tilde{u}_2(x))$ appears. If β increases further to violate the upper condition, then the solution disappears (see Fig. 3). If the positive stationary solution is stable and a solution with positive initial data approaches it, then two populations can coexist permanently. However, if it is unstable and a solution approaches either of two solutions $(u_1^*(x), 0)$ and $(0, u_2^*(x))$, one population must go to extinction. Since it is also a difficult problem to examine stability of these stationary solutions analytically, we will solve numerically the system (1) to investigate stability and reveal the conditions for

$d_1 = 1.00 \qquad \alpha_1 = 0.25 \qquad r_1 = 1.00 \qquad x_1 = 1.00$
$d_2 = 1.00 \qquad \alpha_2 = 2.00 \qquad r_2 = 3.00 \qquad x_2 = 1.00$
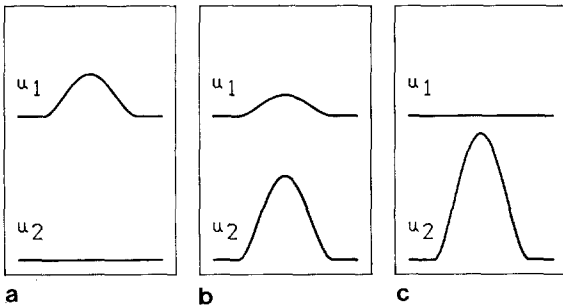
Fig. 2a–c. Examples of stationary solutions of system (1). **a** $(u_1^*(x), 0)$; **b** the positive stationary solution $(\tilde{u}_1(x), \tilde{u}_2(x))$; **c** $(0, u_2^*(x))$. Note that they have same free boundaries $x = \pm x_i^*$
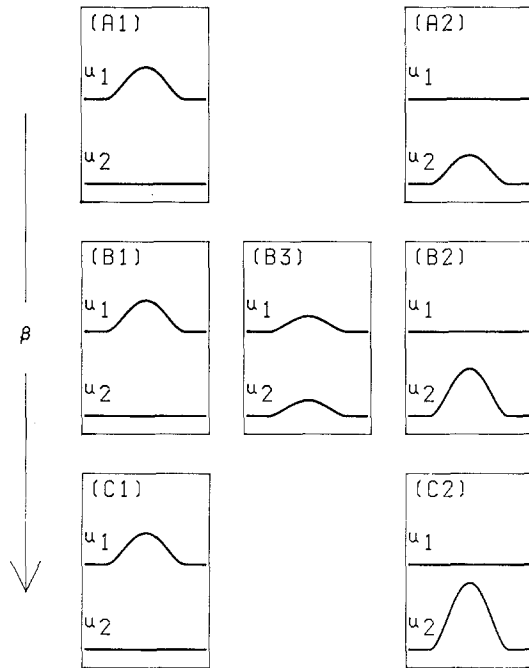
Fig. 3. The relation between the value of β and the number of stationary solutions. In case (B), there exist three stationary solutions including a positive one since β satisfies conditions (11)

coexistence. This will also provide a partial answer to the questions mentioned above.

4. Stability of stationary solutions

In this section, we solve numerically the system (1) by an explicit method, assuming the specific quadratic form (4) for $g_i(x)$. We use $r_2(=r_1\beta)$ as a parameter, fixing other parameters. Two cases should be distinguished depending on whether $\alpha_1\alpha_2$ is larger than 1 or not. Although an extensive repetition of numerical calculations cannot substitute for an analytical proof, we should perform these as systematically as possible to avoid bias. Thus, we prepare a set of 12 initial data (Fig. 4). In (U1A), (U1B), (U1C), (U1D), (U1E) and (U1F), the population u_1 is more abundant than u_2, and *vice versa* in (U2A), (U2B), (U2C), (U2D), (U2E) and (U2F). If solutions with initial data from (U1A) to (U1F) approach $(0, u_2^*(x))$, this implies that the population u_1 goes to extinction regardless of initial superiority to u_2. Then, we may well suppose that only $(0, u_2^*(x))$ is stable, and that the species 1 always becomes extinct. On the other hand, if solutions with initial data from (U2A) to (U2F) approach $(u_1^*(x), 0)$, we can expect that only $(u_1^*(x), 0)$ is a stable stationary solution and that species 2 must perish in the long run. If every solution with one of 12 initial data in the set approaches the positive stationary solution $(\tilde{u}_1(x), \tilde{u}_2(x))$, we may expect that the solution is stable for a larger class of initial data and that two populations can permanently coexist, since none of two populations becomes extinct, regardless of the initial

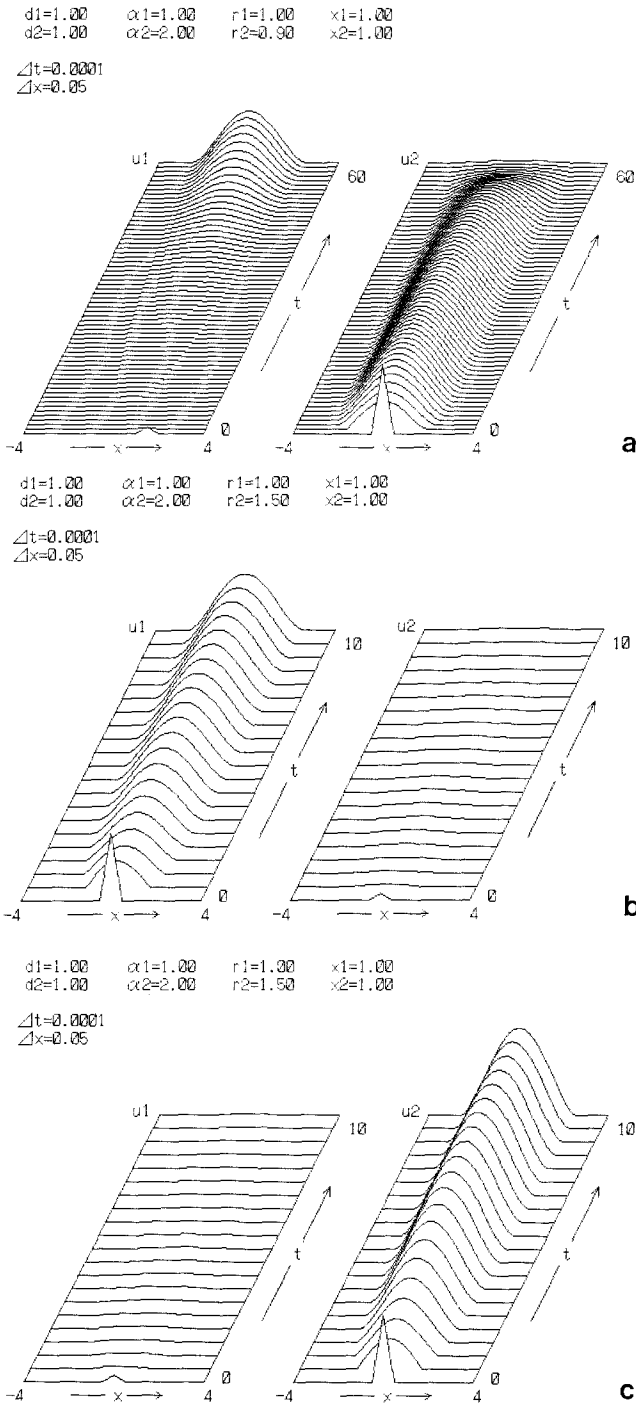INITIAL DATA   INITIAL DATA
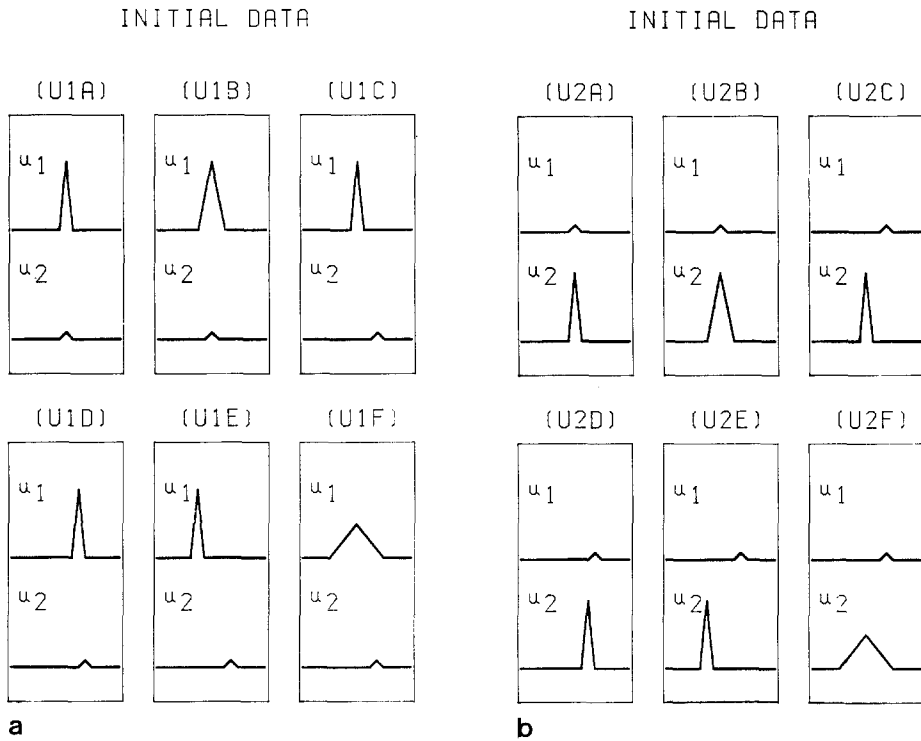
Fig. 4a, b. The set of 12 initial data used to calculate numerical solutions of system (1). **a** In (U1A), (U1B), (U1C), (U1D), (U1E) and (U1F), the population u_1 is abundant, and **b** *vice versa* in (U2A), (U2B), (U2C), (U2D), (U2E) and (U2F)

disparity in abundance. However, even in this case, we cannot assume that any solution with non-negative initial data approaches the positive solution; for if the intial support is confined to a border region, it may vanish because of the finite speed of propagation. This means ecologically that a population may become extinct before it can reach a favorable habitat if the intial distribution ranges within a severely harsh region.

Then, we will exhibit some examples of numerical solutions. First, we show the cases in which the condition $\alpha_1\alpha_2 > 1$ is satisfied (Fig. 5), or the interspecific repulsive effects are stronger than the intraspecific ones. In Fig. 5a, $r_2(=r_1\beta)$ is too small to satisfy conditions (11), and we have only two stationary solutions $(u_1^*(x), 0)$ and $(0, u_2^*(x))$. We can demonstrate that u_2 vanishes as time goes on. This is true for all six initial data from (U2A) to (U2F). We may suppose that only $(u_1^*(x), 0)$ is stable and that the species 2 definitely become extinct because of the relative smallness of r_2 as compared with r_1. Furthermore, we can expect that there exists no stable positive stationary solution. Thus, when two populations are competing for space through repulsive forces to enforce migration, one of them may be extinct because of harshness of the border environment, although it never goes to extinction in the absence of the rival species. In Fig. 5b and c, the cases with $r_2(=r_1\beta)$ sufficiently large to satisfy the first condition of (11) are

d1=1.00   α1=1.00   r1=1.00   x1=1.00
d2=1.00   α2=2.00   r2=0.90   x2=1.00

△t=0.0001
△x=0.05

a

d1=1.00   α1=1.00   r1=1.00   x1=1.00
d2=1.00   α2=2.00   r2=1.50   x2=1.00

△t=0.0001
△x=0.05

b

d1=1.00   α1=1.00   r1=1.00   x1=1.00
d2=1.00   α2=2.00   r2=1.50   x2=1.00

△t=0.0001
△x=0.05

c

Fig. 5a–d. Examples of numerical solutions of system (1), in case of $\alpha_1\alpha_2 > 1$. The parameter r_2 becomes larger and larger from **a** to **d**. However, in **b** and **c**, nothing other than the initial data differs. The first of conditions (11) is satisfied in **b** and **c**
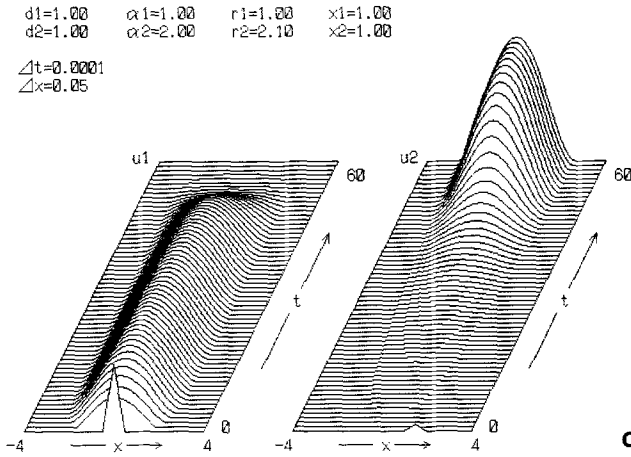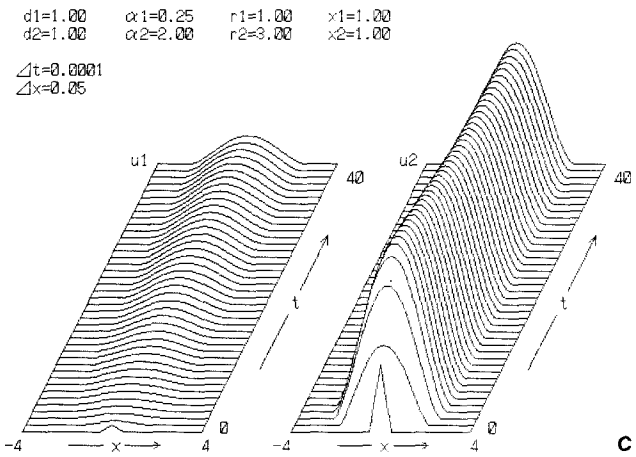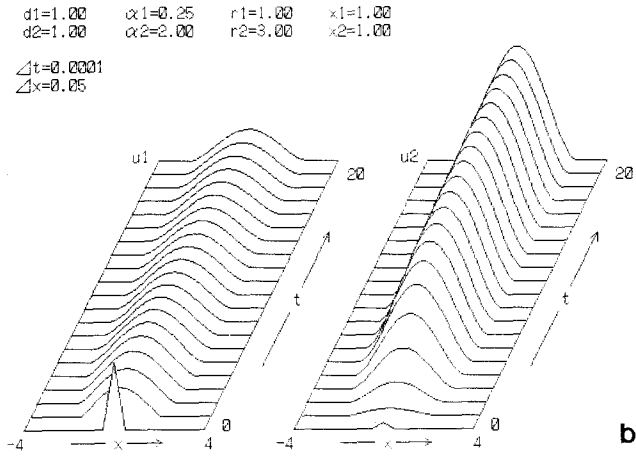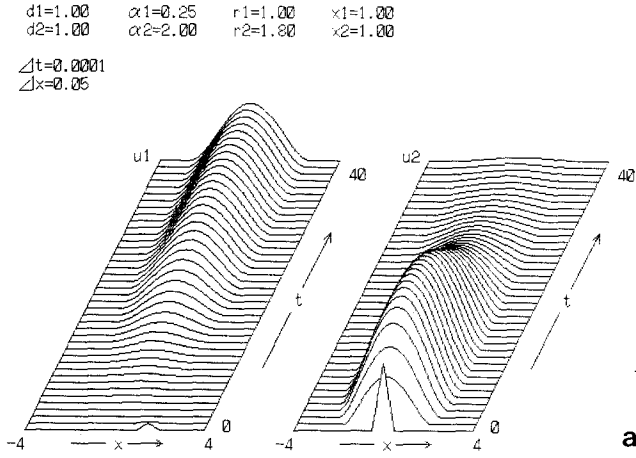
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d1=1.00    α1=1.00    r1=1.00    x1=1.00
d2=1.00    α2=2.00    r2=2.10    x2=1.00

⊿t=0.0001
⊿x=0.05
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Fig. 5 (continued)

shown. No differences other than the initial data exist between them. In Fig. 5b, the population u_1, which has a large initial population, forces u_2 to extinction. On the contrary, in Fig. 5c the initially superior population u_2 survives and u_1 becomes extinct. This implies that the results of competition depend on initial conditions and that the initially superior species eventually excludes the other. In this case, every solution with the initial data chosen from the set in Fig. 4 approaches either of $(u_1^*(x), 0)$ and $(0, u_2^*(x))$. Furthermore, we have examined some other cases with initial data that are not shown in Fig. 4. We have also confirmed convergence to $(u_1^*(x), 0)$ or $(0, u_2^*(x))$, even when u_1 and u_2 have similar initial abundances. Therefore, we can expect that the positive stationary solution $(\tilde{u}_1(x), \tilde{u}_2(x))$ is unstable and also that there exists no other stable positive stationary solution. If $r_2(= r_1\beta)$ increases further and the conditions (11) are not fulfilled, any solution approaches $(0, u_2^*(x))$ irrespective of the initial superiority of u_1 (Fig. 5d). Thus, we may suppose that only $(0, u_2^*(x))$ may be stable and that the species 1 may definitely go to extinction due to the relative largeness of r_2 compared with r_1. The cause of extinction can be attributed to competition for space because it never goes to extinction in the absence of the rival species, however harsh the surrounding environment may be. In summary, in case of competition for space, two populations cannot coexist if interspecific competitive effects are severer than intraspecific ones, which is a familiar conclusion from the Lotka–Volterra competition equations.

Second, we deal with the case in which $\alpha_1\alpha_2 < 1$, or the interspecific repulsive forces are weaker than the intraspecific ones (Fig. 6). If $r_2(= r_1\beta)$ is too small or too large and the second condition of (11) is not satisfied, the result is the same as before (Fig. 6a, d). If r_2 is too small, then we may suppose that only the stationary solution $(u_1^*(x), 0)$ is stable, and that u_2 definitely goes to zero (Fig. 6a) even if it is initially superior in number. When r_2 is too large, or r_1 is relatively small compared with r_2, then it can be expected that the only stable stationary solution is $(0, u_2^*(x))$, and that the survivor is species 2 (Fig. 6d).

d1=1.00   α1=0.25   r1=1.00   x1=1.00
d2=1.00   α2=2.00   r2=1.80   x2=1.00

△t=0.0001
△x=0.05

d1=1.00   α1=0.25   r1=1.00   x1=1.00
d2=1.00   α2=2.00   r2=3.00   x2=1.00

△t=0.0001
△x=0.05

d1=1.00   α1=0.25   r1=1.00   x1=1.00
d2=1.00   α2=2.00   r2=3.00   x2=1.00

△t=0.0001
△x=0.05

Fig. 6a–d. Examples of numerical solutions of system (1) in case of $\alpha_1 \alpha_2 < 1$. r_2 is increasing from **a** to **d**. In **b** and **c**, in which only the initial data differ, the second of conditions (11) is satisfied

d1=1.00   α1=0.25   r1=1.00   x1=1.00
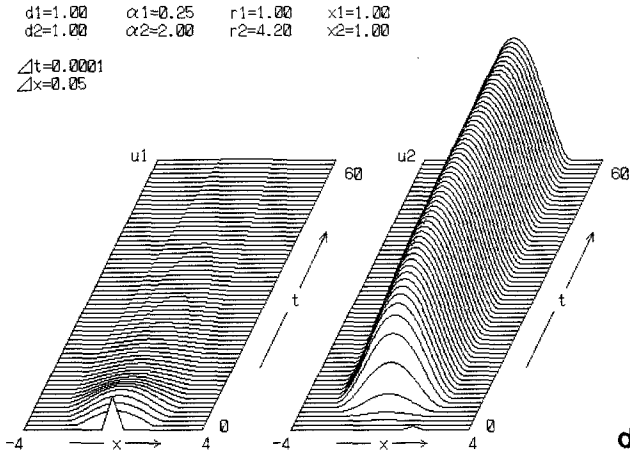d2=1.00   α2=2.00   r2=4.20   x2=1.00

△t=0.0001
△x=0.05

Fig. 6 (continued)

Finally, we investigate the case in which the second condition of (11) is satisfied, or the positive stationary solution $(\tilde{u}_1(x), \tilde{u}_2(x))$ exists (Fig. 6b, c). It can be appreciated that a solution approaches the coexistent solution both in Fig. 6b and c. This is also confirmed for the other ten initial data in Fig. 4. Therefore, we may suppose that the coexistent solution is stable for a large class of initial data, and that permanent coexistence is possible irrespective of which species is initially superior. An analogous statement to the case of the Lotka-Volterra model can again be made in terms of competition for space. If interspecific repulsive forces are weaker than intraspecific ones, coexistence of two species is possible, so far as their growth rates are balanced.

Results of numerical simulations can be easily summed up in the form of a bifurcation diagram, with r_2 being a parameter (Fig. 7). In the diagrams, the peak
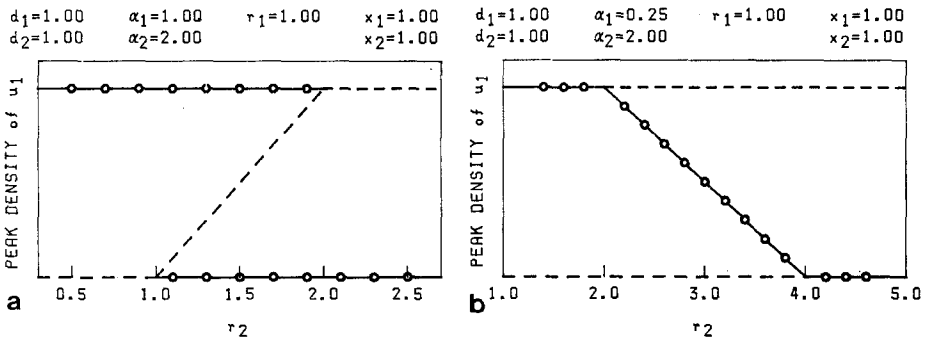
$d_1=1.00$ $\alpha_1=1.00$ $r_1=1.00$ $x_1=1.00$ $d_1=1.00$ $\alpha_1=0.25$ $r_1=1.00$ $x_1=1.00$
$d_2=1.00$ $\alpha_2=2.00$ $x_2=1.00$ $d_2=1.00$ $\alpha_2=2.00$ $x_2=1.00$

Fig. 7a, b. Bifurcation diagrams of system (1) as r_2 being a parameter in case of **a** $\alpha_1\alpha_2 > 1$ and **b** $\alpha_1\alpha_2 < 1$. The peak density of u_1 at $x = 0$ is used as a representative of a stationary solution

density of u_1 at $x = 0$ in a stationary solution is used as a representative of the solution. Therefore, three branches arranged in the order from top to bottom in Fig. 7a and b respectively express the stationary solutions $(u_1^*(x), 0)$, $(\tilde{u}_1(x), \tilde{u}_2(x))$ and $(0, u_2^*(x))$. A circle in these figures means that convergence of some solutions to the stationary solution corresponding to the circle is numerically verified. A solid line expresses a stable branch, and a broken line denotes an unstable branch. If r_2 is sufficiently small, only the branch $(u_1^*(x), 0)$ is stable in both figures and species 2 will go to extinction. On the other hand, if r_2 is sufficiently large, only the branch $(0, u_2^*(x))$ is stable and species 1 will become extinct. When r_2 takes an intermediate value, two alternative possibilities arise depending on the values of α_1 and α_2. If $\alpha_1 \alpha_2$ is larger than 1, then the branch of the positive solution is unstable and two branches of $(u_1^*(x), 0)$ and $(0, u_2^*(x))$ are both stable (Fig. 7a). This means that a solution approaches either of two stable solutions, depending on the initial conditions. On the contrary, the branch of positive solutions is stable when $\alpha_1 \alpha_2$ is smaller than 1 (Fig. 7b). Therefore, though the branch of positive stationary solutions bifurates from those of trivial solutions $(u_1^*(x), 0)$ and $(0, u_2^*(x))$ in both cases, stability of the branch depends on the direction of bifurcation.

5. Discussion

We have considered effects of competition for space in a heterogeneous environment. It is assumed that competition for space means mutual repulsive interactions that force other individuals to disperse from a crowded region, and that it does not imply decrease of the growth rates. The latter assumption may be rational when those repulsive forces are effective in decreasing population densities sufficiently below the carrying capacities so as to reduce competition for resources other than space. Spatial heterogeneity has been incorporated in the growth rates, and space-independent migration rates are assumed. The environment is assumed to have a favorable habitat surrounded by largely hostile regions. This assumption may be ecologically reasonable: the border of a habitat must be hostile for many populations since, or else the population can further extend its range. From these assumptions, we have considered a kind of nonlinear interaction-diffusion model that is similar to the models of Shigesada et al. [28] and Gurney and Nisbet [6]. Our main conclusion is that if the interspecific repulsive interactions are weaker than the intraspecific ones and the growth rates of two populations are balanced, then they can coexist permanently.

Previously, it has been emphasized that two competing populations can coexist by virtue of dispersal and environmental heterogeneity, even if local coexistence is impossible when no migration occurs (see for example Levin [12]; Shigesada et al. [28]; Namba and Mimura [18]). However, we have shown that density dependent dispersal in a heterogeneous environment sometimes results in extinction of one of two populations, although none of them become extinct in the absence of the other population however hard the environmental condition might be. Therefore, mutual repulsive interactions that exclude other individuals may

cause an inevitable damage if the effects are too strong, and migration in a heterogeneous environment is not always a stabilizing agent.

Another striking fact is the resemblance of our results to those from the Lotka-Volterra competition equations. The usual statement that two populations can coexist if interspecific competition is weaker than intraspecific competition holds without any modification, even if we interpret the term competition as competition for space in the sense of our model. The correspondence may become clearer if we consider the Lotka-Volterra competition equations in the following form;

$$\frac{du_1}{dt} = r_1 \left[1 - \frac{u_1 + \alpha_1 u_2}{K_1} \right] u_1,$$

$$\frac{du_2}{dt} = r_2 \left[1 - \frac{u_2 + \alpha_2 u_1}{K_2} \right] u_2,$$

(12)

where r_i is the intrinsic growth rate and K_i is the carrying capacity ($i = 1, 2$). α_i ($i = 1, 2$) measures the strength of interspecific competition as compared with that of intraspecific competition. There will not arise any confusion although we have used the same symbols in the system (12) as in (1). As is well-known, the ordinary differential equations (12) have at most three non-negative steady-state solutions except for $(0, 0)$. Two bifurcation diagrams that illustrate stability of these steady state solutions are shown in Fig. 8, with the carrying capacity K_2 being a parameter. Complete coincidence of them with those in Fig. 7 can be clearly understood. We might expect that these simple structures are to some extent reflecting true processes in the natural environment.

There remain some unresolved problems. The first is the question of uniqueness of the positive stationary solution. The second is to prove that a stable positive stationary solution does not exist when conditions (11) are violated. A final problem is an analytical proof of stability of stationary solutions. These problems may be tough. However, simple results confirmed by our numerical
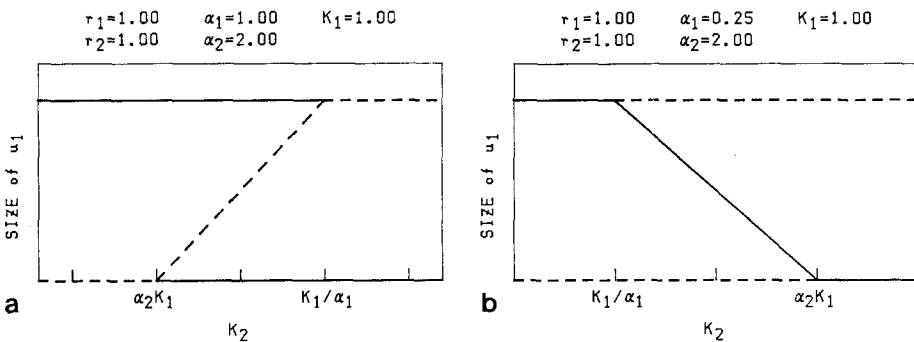

Fig. 8a, b. Bifurcation diagrams of the Lotka-Volterra equations (12) as the carrying capacity K_2 being a parameter, in case of **a** $\alpha_1 \alpha_2 > 1$ and **b** $\alpha_1 \alpha_2 < 1$. The size of u_1 is used as a representative of a steady state solution

simulations seem to assert the necessity of resolving these problems in the near future.

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