

Spatial Segregation of Interacting Species

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(Received 16 August 1978, and in revised form 22 December 1978)

The distributional pattern formation of the populations of two competitive species in heterogeneous environments is analyzed. In the mathematical formulation, a non-linear dispersive force due to mutual interferences of individuals and an environmental potential function are introduced as a behavioral version of Morisita's phenomenological theory of "Environmental density". Mathematical analyses of effects of these forces give the result that the heterogeneity of the environment and the non-linear dispersive movements raise a spatial segregation of the populations of two similar and competing species and there is a possibility that this spatial segregation acts to stabilize the coexistence of two similar species, relaxing the interspecific competition.

1. Introduction

The spatial distribution pattern of an animal population in its natural environment may be realized as a result of various kinds of biological effects. For example, heterogeneity of environmental conditions, mutually attractive or repulsive interactions of individuals and localization of egg-laying processes may be principal causes of spatial pattern formation. The spatial pattern structure of biological community is a fundamental subject in the mathematical ecology as is the trophic level structure. Although the spatial patterns of living populations have been widely studied by statistical treatments as "statistical ecology", mathematical analysis of the process of spatial pattern formation has not been so much developed as "population dynamics", which has been developed since the pioneer work of Volterra and deals with temporal changes in the sizes of interacting populations in terms of ordinary differential equations.

However, several authors (Keller & Segel, 1970; Segel & Jackson, 1972; Montroll & West, 1973; Comins & Blatt, 1974; Levin, 1974, 1976, 1978; Gurney & Nisbet, 1975, 1976; Okubo, 1975; Rosen, 1977; Fife, 1978) have presented interesting works on the spatial distribution pattern formed by

dispersive motions of populations with intra- and inter-specific interactions. They are mainly interested in the possibility that the formation of spatial distribution pattern due to emigration or dispersion may play an important role in the regulation of the population of some species. Gurney and Nisbet have shown that the introduction of a suitable non-linearity into the dispersive behavior has the effect of stabilization under a wide range of conditions. In this paper we also discuss a similar problem and show that in heterogeneous environment two similar and competing species raise a spatial segregation through a non-linear dispersive force and this segregation of habitat really stabilizes the populations by relaxing the interspecific competitions. In the present discussion the non-linear dispersive force is deduced as a generalization of Morisita's phenomenological theory of "environmental density". Therefore we shall present here a brief survey of the idea of Morisita's environmental density (Morisita, 1952, 1971).

Observations on an ant-lion *Glenuroides japonicus* (Morisita, 1952) and aphids *Rhoparosiphum prunifoliae*, *Aphis maidis*, *Macrosiphum granarium* (Ito, 1952) showed that the individuals are found only in the most favorable spots when the mean population density in the whole area is low, but the distribution area of the population expands with increase of mean density, and at high density the density in less favorable regions also reaches the same high level as that in the favorable region. After a series of experimental studies using the ant-lion, Morisita presented an idea of "environmental density" by which the degree of preference for habitats can be quantitatively measured. The experiments were done using a box, just one half of which is filled with fine sand and the other half is filled with coarse sand. The ant-lions were put one by one on the border line of the two sands and the number of individuals settled in each sand was counted after their pit formation. He found that the ant lions have strong tendency to prefer fine sand to coarse sand for pit formation when the population density is low, but this tendency gradually falls with increasing density until an almost equal number of individuals settles in both sands, showing the existence of repulsive interference among the individuals. In order to explain quantitatively this experimental result, he assumed that the probability of settlement of an individual in fine sand area A (or coarse sand area B) is inversely proportional to the degree of "unfavorableness" of that habitat, and the degree of unfavorableness is given by the sum of the quantity $E_A(E_B)$ named "Environmental density" which is a measure of the intrinsic unfavorableness of the habitat itself and the number of individuals $n_A(n_B)$ already settled in the fine sand (coarse sand) area.

Then the probabilities that an individual settles its residence and forms a pit in fine sand area A or coarse sand area B when n_A and n_B individuals have

already settled in areas A and B respectively are given by

$$\begin{aligned} P_A &= (E_B + n_B)/(E_A + E_B + n_A + n_B) \\ P_B &= (E_A + n_A)/(E_A + E_B + n_A + n_B). \end{aligned} \quad (1)$$

Analyzing this Markov process, the average number of individuals found in fine sand area, after n individuals are introduced into the box, is obtained as

$$\frac{\langle n_A \rangle}{n} = \frac{E_B + (n-1)/2}{E_A + E_B + n - 1} \quad (2)$$

and it is seen that this ratio approaches a value, $1/2$, as n increases. The experimental results were satisfactorily interpreted by this theoretical formula not only for the ant-lion but also for the populations of other animal species (Kosaka, 1956; Kubo, 1957).

In order to deduce the non-linear dispersive force, we shall present a behavioral interpretation of Morisita's theory in the next section.

2. Behavioral Version of Morisita's Idea

Here we shall assume that the movement of an individual searching its residence is under influence of the following forces: (i) the dispersive force which is associated with random movement of individuals, (ii) the population pressure due to mutual interferences between individuals, (iii) the attractive force which induces directed movements of individuals toward favorable places.

The population pressure due to the mutual interferences among the individuals may be taken into account by considering that the dispersive force will be increased by repulsive interference with the increase of population density. Then we can assume the isotropic dispersive force to be given by a dispersion coefficient expressed as

$$\alpha + \beta n(x), \quad (3)$$

where $n(x)$ is the population density at the position x . As will be seen later, the linear dependence leads to a result consistent with that of Morisita's theory. Generally the intrinsic dispersion coefficient α and the coefficient of population pressure β may be also functions of position co-ordinate x .

Secondly, we shall introduce a quantity $-U(x)$ which represents the value or "favorableness" of habitat at the position x , where the negative sign is attached so as to regard the function $U(x)$ as an environmental potential. Each individual tends to move toward lower potential area where the environmental conditions are more favorable. Thus it may be plausible to

assume that the mean velocity of the movement caused by the favorableness of habitat is proportional to the force produced by the potential function $U(x)$, that is: $-\text{grad}_x U(x)$.

Now we shall consider again the experiment of ant-lions. When a new individual is put in and is searching the residence in the box in which n_A and n_B individuals have already settled in A and B areas respectively, the transition probability rate at which the added individual transfers from B area to A area is considered to be given by $\alpha_B + \beta_B n_B + \kappa/2$, where κ is proportional to the potential difference $U_B - U_A$ which is positive in this case since the value of potential in the fine sand area A is lower than that of the coarse sand area B . Similarly, the transition probability rate from A to B is given by $\alpha_A + \beta_A n_A - \kappa/2$. Then the probability that the newly-added individual will be settled in A area, P_A , becomes proportional to the transition probability rate from B to A . An analogous relation also holds for P_B . So we have

$$\begin{aligned} P_A &= (\alpha_B + \beta_B n_B + \kappa/2) / (\alpha_A + \alpha_B + \beta_A n_A + \beta_B n_B) \\ P_B &= (\alpha_A + \beta_A n_A - \kappa/2) / (\alpha_A + \alpha_B + \beta_A n_A + \beta_B n_B). \end{aligned} \quad (4)$$

Comparing this expression with equations (1) and if $\beta_A = \beta_B = \beta$, it is seen that the expression (4) becomes equivalent to the equation (1) by equating the environmental densities as

$$E_A = \left(\alpha_A - \frac{\kappa}{2} \right) / \beta, \quad E_B = \left(\alpha_B + \frac{\kappa}{2} \right) / \beta. \quad (5)$$

This expression can be regarded as a behavioral interpretation of Morisita's environmental density. Thus, by the equation (2) and putting $\alpha_A = \alpha_B = \alpha$, the average numbers of individuals found in A and B area, after n individuals are introduced into the box become,

$$\begin{aligned} \frac{\langle n_A \rangle}{n} &= \frac{(\alpha + \kappa/2)/\beta + (n-1)/2}{2\alpha/\beta + n - 1}, \\ \frac{\langle n_B \rangle}{n} &= \frac{(\alpha - \kappa/2)/\beta + (n-1)/2}{2\alpha/\beta + n - 1}. \end{aligned} \quad (6)$$

In the experiment on the ant-lion discussed above, the individuals are introduced successively one by one into the experimental box and the positions of the residents already settled in the box are fixed and not influenced by a newcomer. Now, we shall consider the case that n individuals of some animal species are simultaneously put in the box which similarly consists of two different areas A and B of the same size and they do not settle their nest at fixed positions but frequently change their positions due to the

transition probability rates described above. In this case the change of population in each area is given by, assuming $\alpha_A = \alpha_B = \alpha$ and $\beta_A = \beta_B = \beta$,

$$\begin{aligned} \frac{d}{dt} n_A &= - \left\{ \alpha + \beta(n_A - 1) - \frac{\kappa}{2} \right\} n_A + \left\{ \alpha + \beta(n_B - 1) + \frac{\kappa}{2} \right\} n_B, \\ \frac{d}{dt} n_B &= - \left\{ \alpha + \beta(n_B - 1) + \frac{\kappa}{2} \right\} n_B + \left\{ \alpha + \beta(n_A - 1) - \frac{\kappa}{2} \right\} n_A, \end{aligned} \quad (7)$$

where the population pressures for an individual in A and B area are exerted from remaining $n_A - 1$ and $n_B - 1$ individuals respectively. The solution of equation (7), with the initial conditions $n_A(0) = n_A^0$ and $n_B(0) = n_B^0 = n - n_A^0$, is obtained as

$$\begin{aligned} n_A(t) &= \frac{n\{\alpha + \beta(n-1) + \kappa/2\}}{2\alpha + 2\beta(n-1)} \\ &\quad + \frac{(n_A^0 - n_B^0)\{\alpha + \beta(n-1) + \kappa/2\} - \kappa n_A^0}{2\alpha + 2\beta(n-1)} \exp[-\{2\alpha + 2\beta(n-1)\}t], \end{aligned} \quad (8)$$

$$\begin{aligned} n_B(t) &= \frac{n\{\alpha + \beta(n-1) - \kappa/2\}}{2\alpha + 2\beta(n-1)} \\ &\quad - \frac{(n_A^0 - n_B^0)\{\alpha + \beta(n-1) - \kappa/2\} - \kappa n_B^0}{2\alpha + 2\beta(n-1)} \exp[-\{2\alpha + 2\beta(n-1)\}t], \end{aligned}$$

which approach stationary values, as t tends to infinity,

$$\begin{aligned} \frac{n_A}{n} &= \frac{(\alpha + \kappa/2)/2\beta + (n-1)/2}{\alpha/\beta + (n-1)}, \\ \frac{n_B}{n} &= \frac{(\alpha - \kappa/2)/2\beta + (n-1)/2}{\alpha/\beta + (n-1)}. \end{aligned} \quad (9)$$

If we compare the result (9) with that of the previous case (6), it is seen that β in the expression (6) is just replaced by 2β in (9). This fact may be understood, if we consider the fact that in the previous case individuals settled already in the box are not affected by newcomers but in the latter case all individuals are always under the influence of population pressure.

3. Continuously Varied Environment

We have discussed the motion of individuals due to the dispersive force including the population pressure and also the environmental potential force, based on which the distributions in a spatially discrete model are

analyzed. Here if we take the continuous limit of the discrete model, it can be easily shown that the flow of population at the position x is given by (Appendix)

$$J = -\text{grad}_x \{(\alpha + \beta n(x, t))n(x, t)\} - n(x, t) \text{grad}_x (U), \quad (10)$$

where $n(x, t)$ is the population density at the position x and time t . Then the change of the population is described by the equation of continuity

$$\frac{\partial}{\partial t} n(x, t) = -\text{div } J. \quad (11)$$

Now let us consider a one-dimensional space with boundaries at which $J = 0$. A stationary distribution $n^*(x)$ can be obtained as a solution of the equation $J = 0$, that is

$$(\alpha + 2\beta n^*) \frac{dn^*}{dx} + \frac{dU}{dx} n^* = 0. \quad (12)$$

The solution of this equation is given by

$$2\beta\{n^*(x) - n(0)\} + \alpha \ln \{n^*(x)/n(0)\} = -\{U(x) - U(0)\}, \quad (13)$$

where $n(0)$ and $U(0)$ are the values at an arbitrary chosen fixed point in the habitat area, where we can set the origin of co-ordinate.

Here we can show that the stationary solution (13) which satisfies the equation (12) is really a globally stable stationary solution of the equation (11), and if the solution $n(x, t)$ of equation (11) starting from an initial condition $n(x, 0)$ (> 0 for all x) is a smooth function of x and t , it approaches this stationary solution $n^*(x)$. Let us consider a function defined by

$$H = \int \{\alpha n \ln (n/n^*) - \alpha(n - n^*) + \beta(n - n^*)^2\} dx \geq 0, \quad (14)$$

where the equality holds only when $n(x, t) = n^*(x)$ for all x . The time derivative of this function (14) is calculated as, using the equation (11),

$$\begin{aligned} \frac{dH}{dt} &= \int \{\alpha \ln (n/n^*) + 2\beta(n - n^*)\} \frac{\partial n}{\partial t} dx \\ &= -\int \frac{\partial J}{\partial x} \{\alpha \ln (n/n^*) + 2\beta(n - n^*)\} dx \end{aligned}$$

and by partial integration with the boundary condition $J = 0$ we have

$$\begin{aligned} \frac{dH}{dt} &= \int J \left\{ \frac{\alpha}{n} \frac{\partial n}{\partial x} - \frac{\alpha}{n^*} \frac{\partial n^*}{\partial x} + 2\beta \left(\frac{\partial n}{\partial x} - \frac{\partial n^*}{\partial x} \right) \right\} dx \\ &= -\int \frac{J^2}{n} dx \leq 0, \end{aligned} \quad (15)$$

where equations (10) and (12) have been used. The equality of equation (15) holds again only when $J = 0$, that is, $n = n^*$. Therefore we can see that the solution of (11), $n(x, t)$, always approaches the stationary solution $n^*(x)$ given by the equation (13). The stationary solution (13) has a simple form

$$n^*(x) = n(0) \exp [-\{U(x) - U(0)\}/\alpha]$$

if $\beta = 0$. When there is the population pressure effect ($\beta \neq 0$), the stationary distribution shows such a tendency that the population density at areas with relatively low potential becomes lower than that of the case $\beta = 0$ and contrarily the population density at areas with relatively high potential becomes higher compared with the case $\beta = 0$. The population pressure has an effect to make even the population density and it is also seen from Fig. 1 that the distribution becomes flatter as the total number of individuals increases.

Here we shall present a method to determine the values of parameters α and β and also the potential function $U(x)$ from experimental data on laboratory systems. Since significant quantities are not their absolute values but their relative values, here we shall consider the value of α/β and the function $U(x)/\beta$. We use the data of two experiments in which the total number of individuals are N and N' . When we have observational data for stationary distributions $n(x)$ and $n'(x)$ achieved after sufficiently long time in

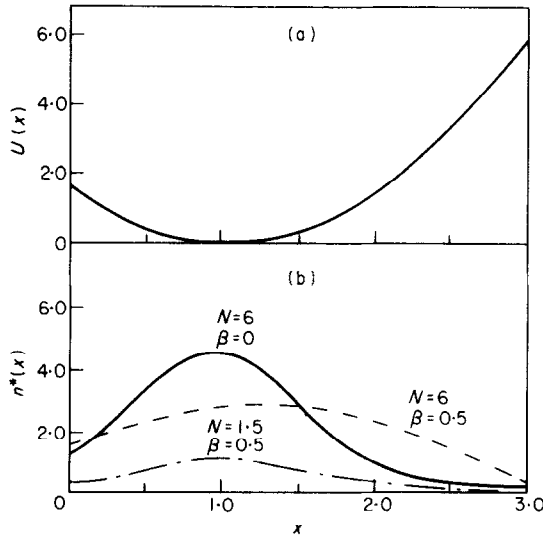


FIG. 1. (a) Environmental potential function $U(x) = 1.5(x-1)^2$. (b) Stational population densities. N is the total number of individuals.

these two experiments, we can expect from equation (13) that the relation

$$\frac{2\{n'(x) - n(x) + n(0) - n'(0)\}}{\ln \{n(x)n'(0)/n'(x)n(0)\}} = \frac{\alpha}{\beta} \quad (16)$$

will be satisfied. This relation can be also used for the purpose to check the validity of the present theory, since the expression (16) should give a constant value independent of x for any pair of observational data $n(x)$ and $n'(x)$. Using this value of α/β and observational data $n(x)$ in the equation (13), we can determine the environmental potential function $U(x)/\beta$ where we can choose the standard value as $U(0) = 0$.

4. Populations of Two Similar Species

Now let us consider the populations of two animal species which have almost the same favorableness for the environment and are under the influence of the population pressure due to intra- and inter-specific interferences. The changes of the population densities $n_1(x, t)$ and $n_2(x, t)$ are given by

$$\begin{aligned} \frac{\partial}{\partial t} n_1 &= -\frac{\partial}{\partial x} J_1 = \frac{\partial}{\partial x} \left[\frac{\partial}{\partial x} \{(\alpha_1 + \beta_{11}n_1 + \beta_{12}n_2)n_1\} + \gamma_1 \frac{dU}{dx} n_1 \right], \\ \frac{\partial}{\partial t} n_2 &= -\frac{\partial}{\partial x} J_2 = \frac{\partial}{\partial x} \left[\frac{\partial}{\partial x} \{(\alpha_2 + \beta_{21}n_1 + \beta_{22}n_2)n_2\} + \gamma_2 \frac{dU}{dx} n_2 \right] \end{aligned} \quad (17)$$

and we assume again that $J_1 = J_2 = 0$ at the boundaries. The stationary distributions are obtained from $J_1 = J_2 = 0$, then we have the differential equations

$$\begin{aligned} \frac{d}{dx} n_1^* &= -\gamma_1 \frac{dU}{dx} n_1^* \left\{ \alpha_2 + \beta_{21}n_1^* + \left(2\beta_{22} - \frac{\gamma_2}{\gamma_1} \beta_{12} \right) n_2^* \right\} / \Delta, \\ \frac{d}{dx} n_2^* &= -\gamma_2 \frac{dU}{dx} n_2^* \left\{ \alpha_1 + \beta_{12}n_2^* + \left(2\beta_{11} - \frac{\gamma_1}{\gamma_2} \beta_{21} \right) n_1^* \right\} / \Delta, \end{aligned} \quad (18)$$

where

$$\Delta = (\alpha_1 + 2\beta_{11}n_1^* + \beta_{12}n_2^*)(\alpha_2 + \beta_{21}n_1^* + 2\beta_{22}n_2^*) - \beta_{12}\beta_{21}n_1^*n_2^* > 0.$$

In order to look for qualitative properties of the solution of equation (18), we shall consider their isoclines as in the case of dynamical systems. The

isoclines given by $dn_1^*/dx = 0$ and $dn_2^*/dx = 0$ are

$$n_1^* = 0, \quad n_2^* = \frac{\alpha_2}{(\gamma_2/\gamma_1)\beta_{12} - 2\beta_{22}} + \frac{\beta_{21}}{(\gamma_2/\gamma_1)\beta_{12} - 2\beta_{22}} n_1^*, \quad (19)$$

$$n_2^* = 0, \quad n_1^* = -\frac{\alpha_1}{\beta_{12}} + \frac{(\gamma_1/\gamma_2)\beta_{21} - 2\beta_{11}}{\beta_{12}} n_2^*, \quad (20)$$

respectively, and the signs of gradients of the lines (19) and (20) are determined by those of the quantities

$$D_1 = (\gamma_2/\gamma_1)\beta_{12} - 2\beta_{22}, \quad D_2 = (\gamma_1/\gamma_2)\beta_{21} - 2\beta_{11}, \quad (21)$$

respectively, as shown in Fig. 2. Therefore we must consider four cases

$$(D_1, D_2) = (+, +), (+, -), (-, +), (-, -).$$

Furthermore, in the case (+, +) it can be easily shown that the gradients of two isoclines satisfy the relation $\beta_{21}/D_1 > D_2/\beta_{12}$, therefore two lines never intersect in the first quadrant.

The spatial change of the stationary population densities $n_1^*(x)$ and $n_2^*(x)$ in these four cases are schematically shown in Fig. 3, where $dU/dx > 0$ is assumed. Where $dU/dx < 0$, the directions of the vectors are just reversed.

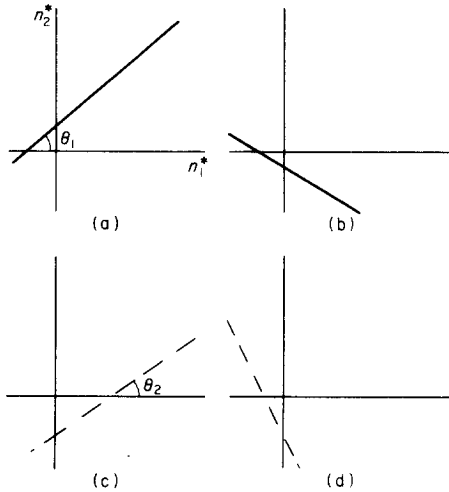


FIG. 2. Isoclines of $dn_1^*/dx = 0$ in the cases (a) $D_1 > 0$ and (b) $D_1 < 0$, and those of $dn_2^*/dx = 0$ in the cases (c) $D_2 > 0$ and (d) $D_2 < 0$. Gradients are given by $\tan \theta_1 = \beta_{21}/D_1$ and $\tan \theta_2 = D_2/\beta_{12}$.

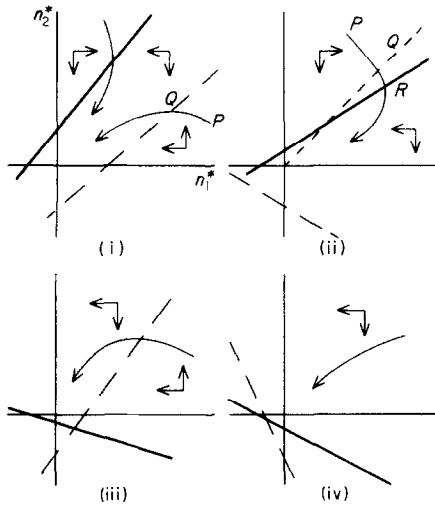


FIG. 3. Vector field in (n_1^*, n_2^*) space in the cases (i) $(D_1, D_2) = (+, +)$, (ii) $(+, -)$, (iii) $(-, +)$ and (iv) $(-, -)$.

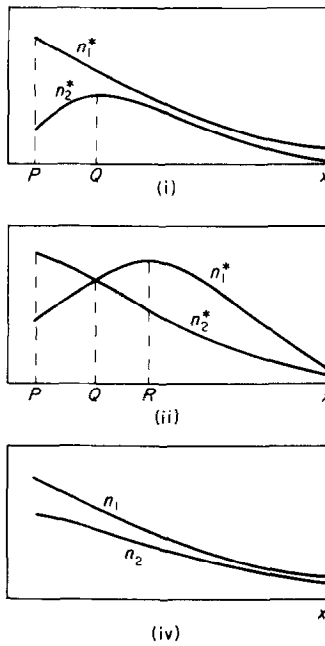


FIG. 4. Typical behavior of trajectories of population densities n_1^* and n_2^* with respect to an assumed time x in the cases of (i), (ii) and (iv) of Fig. 3. Here the condition $dU/dx > 0$ is assumed. The small arrows indicate the direction of the trajectories when x increases.

As we can see from these figures, the origin is always a unique stable stationary point in terms of dynamical systems and all trajectories approach the origin as x tends to infinity. It will be also obvious that: (1) at the point of intersection of the trajectory with the isocline $dn_1^*/dx = 0$, $n_1^*(x)$ becomes maximum and similarly at the point of intersection with the isocline $dn_2^*/dx = 0$, $n_2^*(x)$ becomes maximum; and (2) at the point where the trajectory crosses the line $n_1^* = n_2^*$, the population density curve $n_1^*(x)$ and $n_2^*(x)$ as functions of x cross one another. Taking into account these properties of x dependence of n_1^* and n_2^* , we have typical patterns of population densities in the cases (i), (ii) and (iv) as shown in Fig. 4. The case (iii) becomes equivalent to the case (ii), if we exchange the assignments of 1 and 2 to the species. It should be again noticed that in Fig. 4 $dU/dx > 0$ is assumed. Where $dU/dx < 0$, the x dependence is just reversed and the patterns become those of Fig. 4 with opposite direction of x co-ordinate. Here we take an interest especially in the pattern of Fig. 4-(ii) in which the gradients of two population density curves have opposite signs at the intersecting point. This type of pattern shows the possibility of the segregation of two species in the habitat or the allopatric distribution. It will be easily seen from Fig. 4 that this type of distribution is also possible in the case (i), but any way in order to have this type of pattern we need the condition

$$0 < \tan \theta_1 = \frac{\beta_{21}}{(\gamma_2/\gamma_1)\beta_{12} - 2\beta_{22}} < 1$$

or

$$\tan \theta_2 = \frac{(\gamma_1/\gamma_2)\beta_{21} - 2\beta_{11}}{\beta_{12}} > 1$$
(22)

to be satisfied, where θ_1 and θ_2 are the angles of the isoclines with the abscissa.

As an illustrative example of allopatric distribution, we shall consider populations of two species in which only the population pressure of the species 1 is exerted on the species 2 and raises its dispersive force, i.e. $\beta_{11} = \beta_{12} = \beta_{22} = 0$ and $\beta_{21} \neq 0$.

In this case the differential equations (18) become much simplified as

$$\frac{d}{dx} n_1^* = -\frac{\gamma_1}{\alpha_1} \frac{dU}{dx} n_1^*$$

$$\frac{d}{dx} n_2^* = -\frac{\gamma_2}{\alpha_1} \frac{dU}{dx} n_2^* \left(\alpha_1 - \frac{\gamma_1}{\gamma_2} \beta_{21} n_1^* \right) / (\alpha_2 + \beta_{21} n_1^*)$$
(23)

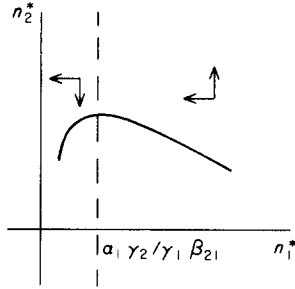


FIG. 5. Isoclines for the special case $\beta_{12} = \beta_{11} = \beta_{22} = 0$.

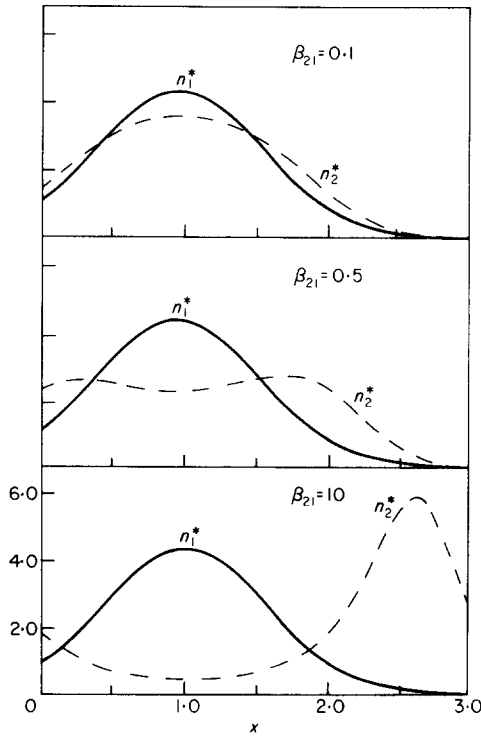


FIG. Stational population densities of two species. Potential function and parameters chosen are $U_1(x) = U_2(x) = 1.5(x-1)^2$; total numbers of individuals $N_1 = N_2 = 6$; $\alpha_1 = \alpha_2 = 1$, $\beta_{11} = \beta_{22} = \beta_{12} = 0$, $\beta_{21} = 0.1, 0.5$ and 10 .

and the solution is given by

$$\begin{aligned} n_1^* &= C_1 \exp \{-\gamma_1 U(x)/\alpha_1\}, \\ n_2^* &= C_2(\alpha_2 + \beta_{21}n_1^*)^{-1 - \alpha_1\gamma_2/\alpha_2\gamma_1} n_1^{*(\alpha_1\gamma_2/\alpha_2\gamma_1)}, \end{aligned} \tag{24}$$

where C_1 and C_2 are constants which are determined by the total population sizes N_1 and N_2 . Here if we consider the product $(dn_1^*/dx)(dn_2^*/dx)$, it is seen from equation (23) that the gradients of n_1^* and n_2^* have opposite signs when $n_1^*(x) > \alpha_1\gamma_2/\beta_{21}\gamma_1$. This may be also obvious from Fig. 5. Therefore, when the value of $\alpha_1\gamma_2/\beta_{21}\gamma_1$ is sufficiently small, for instance, the population pressure of the species 1 on the species 2 is very high or the population size of species 1 is sufficiently large, we can expect the allopatric distribution will appear. We show such examples in Fig. 6 and Fig. 7.

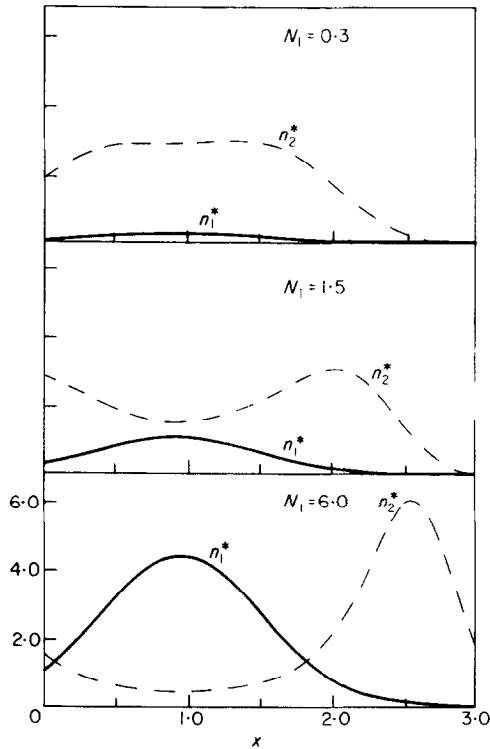


FIG. 7. Stational population densities of two species. Potential function and parameters chosen are $U_1(x) = U_2(x) = 1.5(x-1)^2$; $\alpha_1 = \alpha_2 = 1$; $\beta_{11} = \beta_{22} = \beta_{12} = 0$, $\beta_{21} = 10$; $N_2 = 6$, $N_1 = 0.3, 1.5$ and 6.0 .

5. Coexistence by Segregation of Habitat

Finally, based on the discussions given in the previous sections, we shall study the possibility that the spatial segregation of habitat which results from the mutual interferences and the heterogeneity of the environment has an effect to relax the interspecific competition, resulting in stabilization of the populations as a whole.

In order to study this problem, let us consider firstly spatially uniform populations of two competitive species. The Volterra type equations for this system are written as

$$\begin{aligned}\frac{d}{dt} n_1 &= (\varepsilon_1 - \mu_{11} n_1 - \mu_{12} n_2) n_1, \\ \frac{d}{dt} n_2 &= (\varepsilon_2 - \mu_{21} n_1 - \mu_{22} n_2) n_2,\end{aligned}\tag{25}$$

where ε_1 and ε_2 are the intrinsic growth rates of the populations of two species, μ_{11} and μ_{22} are the coefficients of intraspecific competitions and μ_{12} and μ_{21} are those of interspecific competitions. It is well known that the coexistence of these two species becomes possible only when the conditions

$$\mu_{11}/\varepsilon_1 > \mu_{21}/\varepsilon_2 \quad \text{and} \quad \mu_{22}/\varepsilon_2 > \mu_{12}/\varepsilon_1$$

are satisfied, otherwise only one of the species can survive and another species is led to extinction (Gause's competitive exclusion principle).

Now we shall take into account the heterogeneity of the environment and the non-linear dispersive movements of the individuals of these populations, then the equations of our system can be given by

$$\begin{aligned}\frac{\partial}{\partial t} n_1 &= -\frac{\partial}{\partial x} J_1 + (\varepsilon_1 - \mu_{11} n_1 - \mu_{12} n_2) n_1, \\ \frac{\partial}{\partial t} n_2 &= -\frac{\partial}{\partial x} J_2 + (\varepsilon_2 - \mu_{21} n_1 - \mu_{22} n_2) n_2,\end{aligned}\tag{26}$$

where J_1 and J_2 are the population flows given by the equations (17). The effect of the dispersive motion on the competitive species has been already investigated by Levin (1974, 1978). He showed that, in a patchy environment, linear diffusional flows have stabilizing effect on the coexistence of competitive species. However, it remained yet open to question whether or not such effects are realized also in the case of a continuous environment. The non-linear system (26) is actually difficult to deal with analytically. However, we can show by computer calculations that

the spatial segregation caused by the non-linear flows by (17) actually stabilizes the coexistence of two competitive species. For the numerical calculations, we assumed the conditions

$$\mu_{21}/\varepsilon_2 > \mu_{11}/\varepsilon_1 \quad \text{and} \quad \mu_{12}/\varepsilon_1 > \mu_{22}/\varepsilon_2.$$

Under these conditions, the spatially uniform system (25) leads to the stable critical state $(\varepsilon_1/\mu_{11}, 0)$ when it starts from a state in which the population density n_1 is relatively larger than n_2 , conversely the system approaches the state $(0, \varepsilon_2/\mu_{22})$ if it starts from a state in which n_2 is relatively larger than n_1 . In any way either of the species is destined to ruin.

As for the parameters of the dispersive forces and the environmental potential functions we used the same values and functions as those used in the previous section (Fig. 6), for which the system has shown a typical allopatric distribution. Figure 8 shows numerical results of the stationary distributions $n_1(x, \infty)$ and $n_2(x, \infty)$ which are established after a sufficiently long time starting from an initially uniform distribution.

Further computer simulations for this system with the parameter values of Fig. 8 have shown that this non-uniform stationary distribution is locally stable for small perturbations of population densities and is established starting from a wide variety of initial distributions. However, there remains a possibility that this pattern can not be reached by starting from some special type of distributions. The establishment of such a stable segregation of

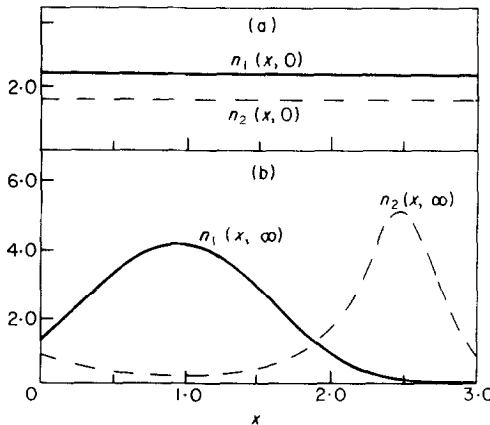


FIG. 8. Population densities of two similar and competing species. $U_1(x) = U_2(x) = 1.5(x-1)^2$; $\alpha_1 = \alpha_2 = 1$; $\beta_{11} = \beta_{22} = \beta_{12} = 0$, $\beta_{21} = 10$; $\varepsilon_1 = \varepsilon_2 = 6$; $\mu_{11} = \mu_{22} = 1.4$; $\mu_{21} = \mu_{12} = 2.8$. (a) Initial distributions, $n_1(x, 0)$ and $n_2(x, 0)$. (b) Finally attained stationary distributions, $n_1(x, \infty)$ and $n_2(x, \infty)$.

distribution pattern clearly depends also on the parameter values. For instance, the simulation has shown that such a pattern becomes unstable when

$$\varepsilon_1 = \varepsilon_2 = 18, \quad \mu_{11} = \mu_{22} = 4.2, \quad \mu_{12} = \mu_{21} = 8.4$$

(just three times the values used in Fig. 8 with the remaining parameter values and the initial uniform distribution unchanged).

Thus, from our computer simulations, it has been clarified that if we take into consideration the environmental heterogeneity and the non-linear dispersive forces, the coexistence of two similar and competing species can be realized at least under some conditions assumed in the present discussions, even if the two species have the same favorableness for the environment.

The authors would like to express their sincere thanks to Professor M. Morisita for valuable informations and comments concerning his elaborate works. Thanks are also due to Dr H. Nakajima and Dr N. Yamamura for their valuable discussion.

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APPENDIX

We shall consider the individuals (random walkers) in linearly connected boxes, each of which has the same width λ and has different environmental condition with one another. Between any adjacent boxes, walkers transfer due to the dispersive force including the population pressure and also the

environmental potential force as is explained in the text. Let us consider the flux at the boundary of the i th and $i+1$ th boxes. We denote the number of individuals in the i th box at time t by n_i and the environmental potential of the i th box by U_i . According to the basic mechanisms of movement considered in the text, the numbers of individuals moving across the boundary from the i th to the $i+1$ th box during time interval τ and those moving in the opposite direction are given, respectively, by the equations,

$$\begin{aligned} & \left\{ \alpha' + \beta' n_i + \frac{\gamma'}{2\lambda} (U_i - U_{i+1}) \right\} n_i, \\ & \left\{ \alpha' + \beta' n_{i+1} + \frac{\gamma'}{2\lambda} (U_{i+1} - U_i) \right\} n_{i+1}, \end{aligned} \quad (\text{A1})$$

where the coefficients α' , β' and γ' are dependent on λ and τ . Therefore the net flux at the boundary of the i th and $i+1$ th boxes is given by

$$\begin{aligned} J = \frac{1}{\tau} \{ (\alpha' + \beta' n_i) n_i - (\alpha' + \beta' n_{i+1}) n_{i+1} \} \\ + \frac{\gamma'}{2\tau\lambda} (U_i - U_{i+1}) (n_i + n_{i+1}). \end{aligned} \quad (\text{A2})$$

Here if both λ and τ tend to zero, we obtain the following expression for the flux in continuously changing environment as the limit:

$$J(x, t) = - \frac{\partial}{\partial x} \{ (\alpha + \beta n(x, t)) n(x, t) \} - n(x, t) \frac{d}{dx} U(x), \quad (\text{A3})$$

where we put

$$\begin{aligned} \lim_{\lambda, \tau \rightarrow 0} \frac{\alpha' \lambda^2}{\tau} &= \alpha, & \lim_{\lambda, \tau \rightarrow 0} \frac{\beta' \lambda^3}{\tau} &= \beta, \\ \lim_{\lambda, \tau \rightarrow 0} \frac{n_i}{\lambda} &= n(x, t), & \lim_{\lambda, \tau \rightarrow 0} \frac{\gamma' \lambda}{\tau} \frac{U_{i+1} - U_i}{\lambda} &= \frac{dU}{dx}. \end{aligned} \quad (\text{A4})$$

By similar procedures, we can obtain the flux in two-dimensional space as

$$J = - \text{grad}_x \{ (\alpha + \beta n) n \} - n \text{grad}_x U. \quad (\text{A5})$$