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On predator invasion into a multi-patchy environment of two kinds of patches

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Abstract

We consider a Lotka–Volterra prey–predator two-species system in a n-patchy environment, assuming that predator can migrate among patches, while prey cannot. Those n patches are categorized into two groups, group 1 and group 2, according to the parameters determining the prey–predator relation and the predator's migration process. Prey population in a patch of group 1 has parameters different from those for prey population in a patch of group 2. Predator population inhabiting and emigrating from a patch of group 1 has parameters different from those for predator population inhabiting and emigrating from a patch of group 2. Local stability of equilibrium states are analyzed, and the condition for the predator's invasion success is derived to discuss the effect of environmentally heterogeneous patchiness on the coexistence of prey and predator.

Keywords: Coexistence; Heterogeneous environment; Invasion; Migration; Prey–predator relationships

1. Introduction

Population persistence is influenced by biotic and abiotic environmental heterogeneity: resource distribution, temperature, humidity, stochastic disturbance, etc. Some effect of local environmental heterogeneity is transferred through population migration processes and affects the whole population to affect population persistence. Especially populations in nature are influenced by environmental patchiness (Wiens, 1976). Various theoretical studies on the effect of environmental patchiness on population dynamics have been developed, following a great deal of field research. For well-known examples, Kierstead and Slobodkin (1953) and Okubo (1982) studied plankton patchiness, using diffusion equations (see also Okubo, 1980). They studied the population persistence within an isolated patch and established a critical patch size below which the population becomes extinct (see also Skellam, 1951). DeAngelis et al. (1979), Kawasaki and Teramoto (1979), Vance (1984), Allen (1983a,b, 1987), and Seno (1988) analyzed population dynamics in a patchy environment, making use of "multi-patch" (spatially discrete) systems. Allen (1987) and Seno (1988) discussed the critical patch number with a spatially discretized re-

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action–diffusion model. On the other hand, with the same type of system, May (1974) and Levin (1976), Zeigler (1977), Travis and Post (1979), Hirata (1980), and Post et al. (1983) studied community dynamics. The system corresponding to the case when patches have generally different parameters, has been mathematically investigated by many researchers, for example by Chau (1985). Further, DeAngelis et al. (1979) studied the general conditions for population persistence in the context of "M-matrix". However, their results are either too complicated or too general to be used practically for a detailed analysis of dependency of population persistence on parameters in a multi-patchy system.

Seno (1988) studied a single-species population persistence in a multi-patch system containing a patch within which emigration and growth rates are different from those within the other patches. Such a patch was called "singular". The singularity of a patch is regarded as an effect of disturbance in an ecological system, as was discussed by DeAngelis et al. (1985), or of constant harvest or of some artificial environmental change. Seno (1988) discussed the influence of a singular patch on the persistence of a single-species population migrating over N patches, and arrived at the following results: (a) population persistence depends on the location of a singular patch in the whole system; (b) in some cases, population can persist independently of a singular patch; (c) in some cases, there exists a critical total number of patches: if the total number of patches is below the critical number, population cannot persist; (d) there are the other cases in which there is not any critical total number of patches so that population can persist independently of the number of patches ($\geqslant 3$) even though it could not persist if all patches were identical or isolated. Some discussions in Seno (1988), as well as that in Allen (1987), shed some light on the effect of environmental patchiness on population persistence within it. An experimental study by Fahrig and Merriam (1985) clearly indicates the importance of such aspects for population dynamics.

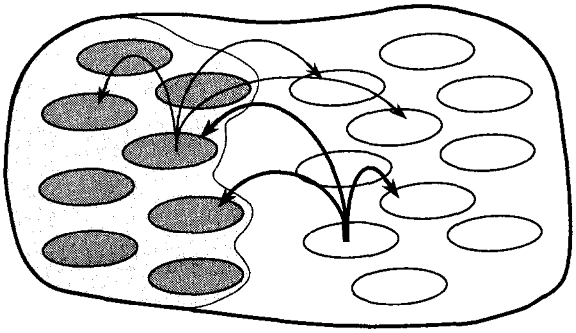

Fig. 1. Predator migrates among n patches categorized into two groups, group 1 (dark) and group 2 (white). For detail explanation, see text.

In this paper, we consider a Lotka–Volterra prey–predator two-species system (Volterra, 1926) in a n-patchy environment, corresponding to the system analyzed by Seno (1988). It is assumed that predator can migrate among patches, while prey cannot. Those n patches are categorized into two groups, group 1 and group 2, according to the environmental parameters determining the prey–predator relation and the predator's migration process (Fig. 1). Prey population in a patch of group 1 has parameters different from those for prey population in a patch of group 2. Predator population inhabiting and emigrating from a patch of group 1 has parameters different from those for predator population inhabiting and emigrating from a patch of group 2. Local stability of equilibrium states is analyzed, and the condition for the predator's invasion success is derived to discuss the effect of environmentally heterogeneous patchiness on the coexistence of prey and predator.

2. Statement of model

Consider the environment consisting of n patches. A prey–predator relation of the Lotka–Volterra type is present in each of patches. Predator can migrate among patches, while prey can not. Emigrating predator immigrates evenly into all other patches. Those n patches are assumed to be categorized into two groups, group 1 and group 2, according to the environmental parameters determining the prey–predator relation. Prey population in a patch of group 1 has parameters different from those for prey population in a patch of group 2. Predator population inhabiting and emigrating from a patch of group 1 has different parameters from those for predator population inhabiting and emigrating from a patch of group 2. Our model corresponds to the system analyzed by Seno (1988) and is expressed as follows (Fig. 2):

$$\begin{cases} \dfrac{\mathrm{d}X_i(t)}{\mathrm{d}t} = r_1\left(1 - \dfrac{X_i(t)}{K_1}\right)X_i(t) - b_1X_i(t)Y_i(t) \\ \dfrac{\mathrm{d}Y_i(t)}{\mathrm{d}t} = -\delta_1Y_i(t) + c_1X_i(t)Y_i(t) - P_1Y_i(t) \\ \qquad + \displaystyle\sum_{\substack{j=1 \\ j\neq i}}^{k} \frac{S_1P_1}{n-1}Y_j(t) + \sum_{j=k+1}^{n} \frac{S_2P_2}{n-1}Y_j(t) \end{cases} \tag{1}$$

for $i = 1, 2, \ldots, k$

$$\begin{cases} \dfrac{\mathrm{d}X_i(t)}{\mathrm{d}t} = r_2\left(1 - \dfrac{X_i(t)}{K_2}\right)X_i(t) - b_2X_i(t)Y_i(t) \\ \dfrac{\mathrm{d}Y_i(t)}{\mathrm{d}t} = -\delta_2Y_i(t) + c_2X_i(t)Y_i(t) - P_2Y_i(t) \\ \qquad + \displaystyle\sum_{j=1}^{k} \frac{S_1P_1}{n-1}Y_j(t) + \sum_{\substack{j=k+1 \\ j\neq i}}^{n} \frac{S_2P_2}{n-1}Y_j(t) \end{cases} \tag{2}$$

for $i = k+1,\ k+2, \ldots, n$, where $X_i(t)$ and $Y_i(t)$ are, respectively, prey density and predator density in patch i. r_1 and r_2 are the prey's intrinsic growth rates, respectively, in the patch of group 1 and in that of group 2. K_1 and K_2 are carrying capacities, b_1 and b_2 prey's predated rates, δ_1 and δ_2 the predator's death rates, c_1 and c_2 predation rates, P_1 and P_2 emigration rates, S_1 and S_2 success rates of migration. It is assumed that the predator's emigration rate and its success rate of migration are determined by the environment of the patch from which the predator emigrates. The first term for prey in the righthand side of Eqs. 1 and 2 expresses prey's logistic growth, and the second the decrease by predation. Next, the first term for predator in the righthand side of Eqs. 1 and 2 expresses the decrease of predator density by death, and the second the increase by predation. And the third term expresses predator's emigration process, and the fourth and the fifth the predator's immigration process from the other patches of group 1 and group 2, respectively, expected for the patch i.

3. Analysis

3.1. Linearized system

Consider the equilibrium state (X^*, Y^*) on $\mathbb{R}^{2n}$ for the system of Eqs. 1 and 2, where X^* and Y^* are vectors on $\mathbb{R}^n$ given by

$$X^* = \Big(\underbrace{X_1^*, X_1^*, \ldots, X_1^*}_{k}\ \underbrace{X_2^*, X_2^*, \ldots, X_2^*}_{n-k}\Big)$$

$$Y^* = \Big(\underbrace{Y_1^*, Y_1^*, \ldots, Y_1^*}_{k}\ \underbrace{Y_2^*, Y_2^*, \ldots, Y_2^*}_{n-k}\Big)$$

Now, we linearize the system of Eqs. 1 and 2

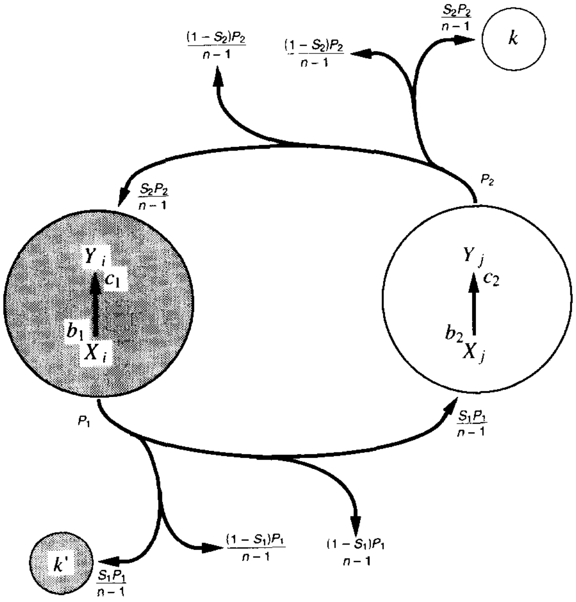

Fig. 2. Schematic description for the model system. For detailed explanation, see text.

around the equilibrium state $(\boldsymbol{X}^*,\boldsymbol{Y}^*)$. We substitute the following into Eqs. 1 and 2:

$$
\begin{aligned}
X_i(t) &= X_1^* + x_i(t) && \text{for } i = 1, 2, \ldots, k\\
X_i(t) &= X_2^* + x_i(t) && \text{for } i = k+1,\ k+2, \ldots, n\\
Y_i(t) &= Y_1^* + y_i(t) && \text{for } i = 1, 2, \ldots, k\\
Y_i(t) &= Y_2^* + y_i(t) && \text{for } i = k+1,\ k+2, \ldots, n
\end{aligned}
$$

where $(x_i(t),\ y_i(t))$ $(i = 1,2,\ldots,n)$ is the perturbation from the equilibrium state $(\boldsymbol{X}^*,\boldsymbol{Y}^*)$. Then, we obtain the following linearized system:

$$
\begin{cases}
\dfrac{\mathrm{d}x_i(t)}{\mathrm{d}t} = \left(r_1 - \dfrac{2r_1X_1^*}{K_1} - b_1Y_1^*\right)x_i(t)\\
\qquad - b_1X_1^*y_i(t)\\
\dfrac{\mathrm{d}y_i(t)}{\mathrm{d}t} = c_1Y_1^*x_i(t) + (c_1X_1^* - \delta_1 - P_1)y_i(t)\\
\qquad + \dfrac{S_1P_1}{n-1}\displaystyle\sum_{\substack{j=1\\ j\neq i}}^{k} y_j(t) + \dfrac{S_2P_2}{n-1}\displaystyle\sum_{j=k+1}^{n} y_j(t)
\end{cases}
\tag{3}
$$

for $i = 1, 2, \ldots, k$

$$
\begin{cases}
\dfrac{\mathrm{d}x_i(t)}{\mathrm{d}t} = \left(r_2 - \dfrac{2r_2X_2^*}{K_2} - b_2Y_2^*\right)x_i(t)\\
\qquad - b_2X_2^*y_i(t)\\
\dfrac{\mathrm{d}y_i(t)}{\mathrm{d}t} = c_2Y_2^*x_i(t) + (c_2X_2^* - \delta_2 - P_2)y_i(t)\\
\qquad + \dfrac{S_1P_1}{n-1}\displaystyle\sum_{j=1}^{k} y_j(t) + \dfrac{S_2P_2}{n-1}\displaystyle\sum_{\substack{j=k+1\\ j\neq i}}^{n} y_j(t)
\end{cases}
\tag{4}
$$

for $i = k+1,\ k+2, \ldots, n$. The system of Eqs. 3 and 4 can be expressed with $2n$-dimensional vector $\boldsymbol{n}$ and $2n \times 2n$ matrix $\boldsymbol{M}$ as follows:

$$\frac{\mathrm{d}\boldsymbol{n}}{\mathrm{d}t} = \boldsymbol{M}\cdot\boldsymbol{n},$$

where $\boldsymbol{n} = {}^{\mathrm{T}}(\boldsymbol{x},\boldsymbol{y})$. $\boldsymbol{x}$ and $\boldsymbol{y}$ are n-dimensional vectors respectively for prey and predator densities in the linearized system of Eqs. 3 and 4:

$$
\begin{aligned}
\boldsymbol{x} &= (x_1(t),\ x_2(t), \ldots, x_n(t))\\
\boldsymbol{y} &= (y_1(t),\ y_2(t), \ldots, y_n(t))
\end{aligned}
$$

As for the expression of $\boldsymbol{M}$, see Appendix A. If the real parts of all eigenvalues for $\boldsymbol{M}$ are negative, the equilibrium state $(\boldsymbol{X}^*,\boldsymbol{Y}^*)$ is locally stable.

3.2. *Equilibrium state with predator's extinction*

Consider the equilibrium state $\boldsymbol{Y}^* = \boldsymbol{O} \equiv (0,0,\ldots,0)$ such that any predator is to go extinct. In such case, the characteristic equation, $\det(\boldsymbol{M} - \lambda\boldsymbol{I}) = 0$, which determines the eigenvalue λ for $\boldsymbol{M}$, is obtained as follows (Appendix A):

$$
\begin{aligned}
&(H_1 - \lambda)^k(H_2 - \lambda)^{n-k}(L_1 - J_1 - \lambda)^{k-1}\\
&\quad\times(L_2 - J_2 - \lambda)^{n-k-1}(\lambda^2 - Q_1\lambda + Q_2) = 0,
\end{aligned}
\tag{5}
$$

where

$$
\begin{aligned}
H_1 &= r_1 - \frac{2r_1X_1^*}{K_1}\\
H_2 &= r_2 - \frac{2r_2X_2^*}{K_2}\\
L_1 &= c_1X_1^* - \delta_1 - P_1\\
L_2 &= c_2X_2^* - \delta_2 - P_2\\
J_1 &= \frac{S_1P_1}{n-1}\\
J_2 &= \frac{S_2P_2}{n-1}\\
Q_1 &= L_1 + L_2 + (k-1)J_1 + (n-k-1)J_2\\
Q_2 &= L_1L_2 + (k-1)L_2J_1 + (n-k-1)L_1J_2\\
&\quad - (n-1)J_1J_2.
\end{aligned}
$$

As easily seen from Eq. 5, all eigenvalues are real. Now, from Eq. 5, the condition with which each eigenvalue is negative, that is, the local stability condition for the equilibrium state $(\boldsymbol{X}^*,\boldsymbol{O})$ can be obtained as follows:

$$H_1 < 0 \tag{6}$$

$$H_2 < 0 \tag{7}$$

$$L_1 - J_1 < 0 \tag{8}$$

$$L_2 - J_2 < 0 \tag{9}$$

$$Q_1 < 0 \tag{10}$$

$$Q_2 > 0. \tag{11}$$

Let us consider four possible equilibrium states for $(\boldsymbol{X}^*, \boldsymbol{O})$ with the predator's extinction: $(\boldsymbol{O}, \boldsymbol{O})$; $(\boldsymbol{K}_1, \boldsymbol{O})$; $(\boldsymbol{K}_2, \boldsymbol{O})$; $(\boldsymbol{K}_{12}, \boldsymbol{O})$, where

$$\boldsymbol{K}_1 \equiv \Big(\underbrace{K_1, K_1, \ldots, K_1}_{k} \underbrace{0, 0, \ldots, 0}_{n-k}\Big)$$

$$\boldsymbol{K}_2 \equiv \Big(\underbrace{0, 0, \ldots, 0,}_{k} \underbrace{K_2, K_2, \ldots, K_2}_{n-k}\Big)$$

$$\boldsymbol{K}_{12} \equiv \Big(\underbrace{K_1, K_1, \ldots, K_1}_{k} \underbrace{K_2, K_2, \ldots, K_2}_{n-k}\Big)$$

The equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$ expresses such state that only the prey in the patch of group 1 persists, while the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$ expresses such state that only the prey in the patch of group 2 persists. The equilibrium state $(\boldsymbol{K}_{12}, \boldsymbol{O})$ expresses such state that the prey persists in any patch. These three equilibrium states are exclusive each other, that is, any two of them cannot be contemporally stable for any parameters, which will be shown in the following analysis.

Local stability for $(\boldsymbol{O}, \boldsymbol{O})$

The condition for local stability of $(\boldsymbol{O},\boldsymbol{O})$ is that $r_1 < 0$ and $r_2 < 0$. Those conditions given by Eqs. 8, 9, 10, and 11 are always satisfied, which is proved in Appendix B. Since this is the case when the intrinsic growth rate of prey is everywhere negative, prey population monotonically decreases to become extinct. Without prey, predator cannot survive.

Local stability for $(\boldsymbol{K}_1, \boldsymbol{O})$

For $(\boldsymbol{X}^*, \boldsymbol{Y}^*) = (\boldsymbol{K}_1, \boldsymbol{O})$, the condition for local stability is to satisfy the following:

$$r_1 > 0, \tag{12}$$

$$r_2 < 0, \tag{13}$$

$$D_1 > \frac{k(n-k)/(n-1)^2}{D_2 - (n-k-1)/(n-1)} + \sigma_1 + \frac{k-1}{n-1}, \tag{14}$$

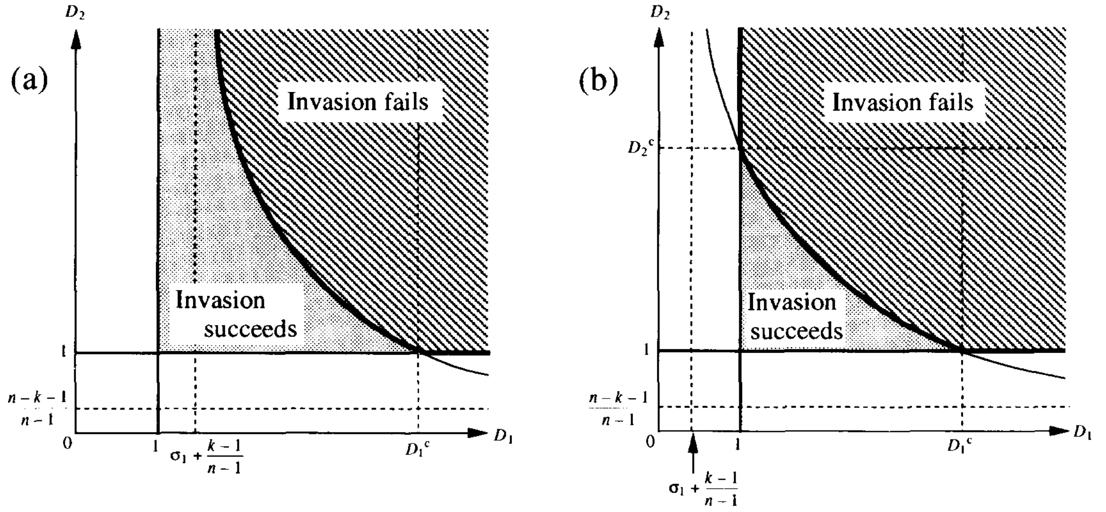

Fig. 3. (D_1, D_2)-dependence of the local stability for the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$, given by Eqs. 12, 13, and 14: (a) when $\sigma_1 + (k-1)/(n-1) \geqslant 1$; (b) when $\sigma_1 + (k-1)/(n-1) < 1$. Since $1 \leqslant D_1$ and $1 \leqslant D_2$, the white region is not considered. The shaded region indicates the parameter region for the unstability of $(\boldsymbol{K}_1, \boldsymbol{O})$, that is, for the predator's invasion success, while the striped region is for the local stability, that is, for the predator's invasion failure. The boundary curve between the invasion success and the failure regions is given by Eq. 14. D_1^c and D_2^c are given by Eqs. 15 and 17.

where, for convenience, we use the following parameters:

$$D_1 \equiv \frac{\delta_1 + P_1}{S_1 P_1}, \qquad D_2 \equiv \frac{\delta_2 + P_2}{S_2 P_2},$$

$$\sigma_1 \equiv \frac{c_1 K_1}{S_1 P_1}, \qquad \sigma_2 \equiv \frac{c_2 K_2}{S_2 P_2}.$$

Conditions 8, 9, and 10 are always satisfied if condition 11 is, which is proved in Appendix B. Note that, since $\delta_i \geqslant 0$ and $0 \leqslant S_i \leqslant 1$ $(i = 1, 2)$, it is satisfied that $D_i \geqslant 1$ $(i = 1, 2)$, where $D_i = 1$ only when $\delta_i = 0$ and $S_i = 1$.

The parameter D_i can be regarded as representing the environmental favorability of patches of group i for the predator, by which the predator population is *directly* affected through the migration process. As the environment is more favorable, the value of D_i becomes smaller. The parameter D_i does not depend on any parameter related to the predation process, while the parameter σ_i does on those parameters representing the effectiveness of predation, c_i and K_i. σ_i can be regarded as representing the quality of the prey for the predator in patches of group i. As the quality of prey is richer, the value of σ_i becomes larger. Hereafter, we conventionally use these parameters.

The parameter region for the local stability is given in Fig. 3. As easily seen from Fig. 3, if D_1 is not less than D_1^c given by

$$D_1^c = 1 + \sigma_1, \tag{15}$$

the local stability of $(\boldsymbol{K}_1, \boldsymbol{O})$ is established for any value of D_2. The predator's invasion fails independently of the environment of patches of group 2. This means that the environment of patches of group 1 is not satisfactory for the predator's invasion.

In contrast, as seen from Fig. 3b, when

$$\alpha_1 + \frac{k-1}{n-1} < 1 \tag{16}$$

and D_2 is not less than D_2^c given by

$$D_2^c = \frac{(n-k) - (n-k-1)\sigma_1}{(n-k) - (n-1)\sigma_1}, \tag{17}$$

the local stability of $(\boldsymbol{K}_1, \boldsymbol{O})$ is established for any value of D_1. The invasion fails for predator with

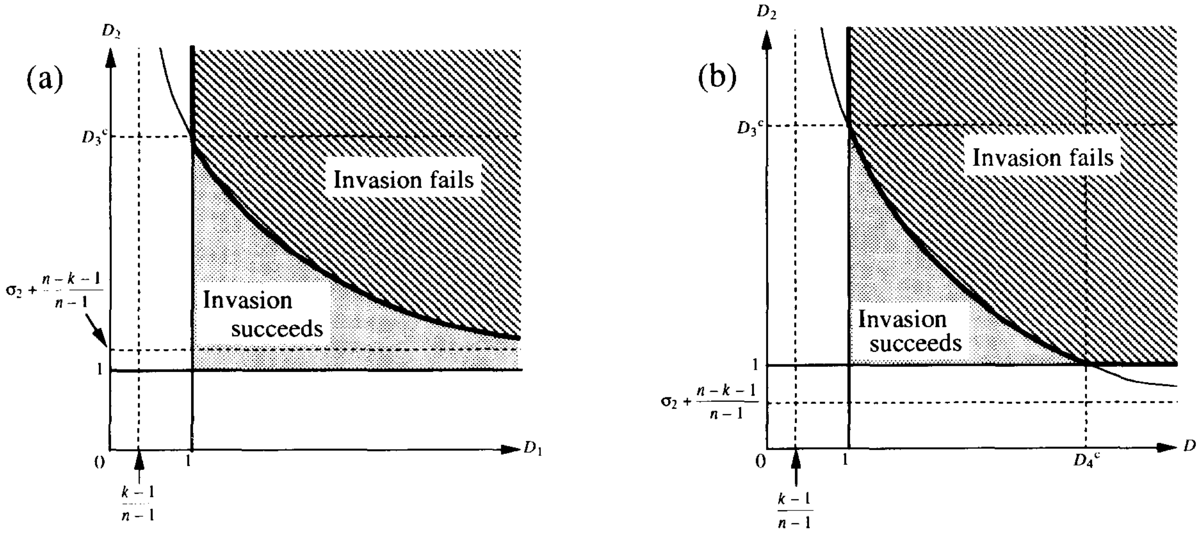

Fig. 4. (D_1, D_2)-dependence of the local stability for the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$, given by Eqs. 19, 20, and 21: (a) when $\sigma_2 + (n-k-1)/(n-1) \geqslant 1$; (b) when $\sigma_2 + (n-k-1)/(n-1) \geqslant 1$. Since $1 < D_1$ and $1 \leqslant D_2$, the white region is not considered. The shaded region indicates the parameter region for the unstability of $(\boldsymbol{K}_2, \boldsymbol{O})$, that is, for the predator's invasion success, while the striped region is for the local stability, that is, for the predator's invasion failure. The boundary curve between the invasion success and the failure regions is given by Eq. 21. D_3^c and D_4^c are given by Eqs. 22 and 24.

any death rate δ_1 in patches of group 1. This is the case when the environment of patches of group 2 is not favorable and the quality of prey in patches of group 1 is poor.

On the other hand, if

$$1 \leqslant D_1 \leqslant \sigma_1 + \frac{k-1}{n-1}, \tag{18}$$

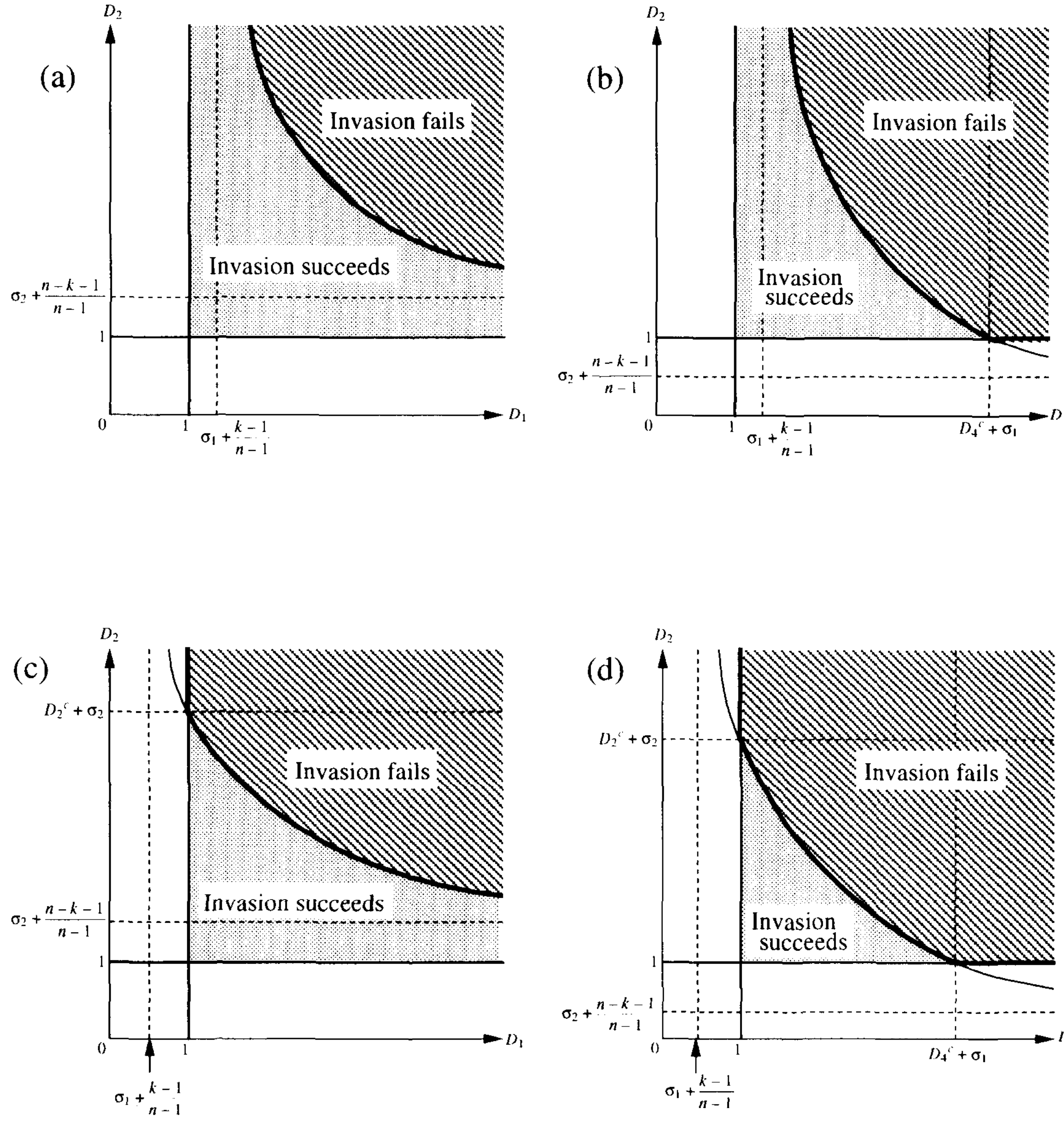

Fig. 5. (D_1, D_2)-dependence of the local stability for the equilibrium state (K_{12}, O) given by Eqs. 26, 27, and 28: (a) when $\sigma_1 + (k-1)/(n-1) \geqslant 1$ and $\sigma_2 + (n-k-1)/(n-1) \geqslant 1$; (b) when $\sigma_1 + (k-1)/(n-1) < 1$ and $\sigma_2 + (n-k-1)/(n-1) \geqslant 1$; (c) when $\sigma_1 + (k-1)/(n-1) < 1$ and $\sigma_2 + (n-k-1)/(n-1) \geqslant 1$; (d) when $\sigma_1 + (k-1)/(n-1) < 1$ and $\sigma_2 + (n-1)/(n-1) \geqslant 1$. Since $1 \leqslant D_1$ and $1 \leqslant D_2$, the white region is not considered. The shaded region indicates the parameter region for the unstability of (K_{12}, O), that is, for the predator's invasion success, while the striped region is for the local stability, that is, for the predator's invasion failure. The boundary curve between the invasion success and the failure regions is given by Eq. 28. D_2^c and D_4^c are given by Eqs. 17 and 24.

the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$ is unstable independently of the value of D_2 (Fig. 3a). The predator's invasion succeeds independently of the environment of patches of group 2. This means that the environment of patches of group 1 is favorable and the quality of prey in patches of group 1 is rich enough to complement the decrease of the predator population in patches of group 2 due to the unfavorable environment.

Local stability for $(\boldsymbol{K}_2, \boldsymbol{O})$

For $(\boldsymbol{X}^*, \boldsymbol{Y}^*) = (\boldsymbol{K}_2, \boldsymbol{O})$, the condition for local stability is to satisfy the following:

$$r_1 < 0 \tag{19}$$

$$r_2 > 0 \tag{20}$$

$$D_1 > \frac{k(n-k)/(n-1)^2}{D_2 - \{\sigma_2 + (n-k-1)/(n-1)\}} + \frac{k-1}{n-1}. \tag{21}$$

Conditions 8, 9, and 10 are always satisfied if condition 11 is, which is proved in Appendix B.

The parameter region for the local stability is given in Fig. 4. As easily seen from Fig. 4, if D_2 is not less than D_3^c given by

$$D_3^c = 1 + \sigma_2, \tag{22}$$

the local stability of $(\boldsymbol{K}_2, \boldsymbol{O})$ is established for any value of D_1. The predator's invasion fails independently of the environment of patches of group 1. The environment of patches of group 2 is not satisfactory for the predator's invasion.

In contrast, as seen from Fig. 4b, when

$$\sigma_2 + \frac{n-k-1}{n-1} < 1 \tag{23}$$

and D_1 is not less than D_4^c given by

$$D_4^c = \frac{k-(k-1)\sigma_2}{k-(n-1)\sigma_2}, \tag{24}$$

the local stability of $(\boldsymbol{K}_2, \boldsymbol{O})$ is established for any value of D_2. The invasion fails for predator with any death rate δ_2 in patches of group 2. On the other hand, if

$$1 \leqslant D_2 \leqslant \sigma_2 + \frac{n-k-1}{n-1}, \tag{25}$$

the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$ is unstable independently of the value of D_1 (Fig. 4a). The predator's invasion succeeds independently of the environment of patches of group 1. The environment of patches of group 2 is favorable and the quality of prey in patches of group 2 is rich enough to allow the predator's invasion into the whole system. These results are reciprocally corresponding to those for the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$.

Local stability for $(\boldsymbol{K}_{12}, \boldsymbol{O})$

For $(\boldsymbol{X}^*, \boldsymbol{Y}^*) = (\boldsymbol{K}_{12}, \boldsymbol{O})$, the condition for local stability is to satisfy the following:

$$r_1 > 0 \tag{26}$$

$$r_2 > 0 \tag{27}$$

$$D_1 > \frac{k(n-k)/(n-1)^2}{D_2 - \{\sigma_2 + (n-k-1)/(n-1)\}} + \sigma_1 + \frac{k-1}{n-1}. \tag{28}$$

Conditions 8, 9, and 10 are always satisfied if the condition 11 is, which is proved in Appendix B.

The parameter region for the local stability is given in Fig. 5. As easily seen from Figs. 5c and d, when Eq. 16 is satisfied and $D_2 - \sigma_2$ is not less than D_2^c given by Eq. 17, the local stability of $(\boldsymbol{K}_{12}, \boldsymbol{O})$ is established for any value of D_1. In contrast, as seen from Figs. 5b and d, when Eq. 23 is satisfied and $D_1 - \sigma_1$ is not less than D_4^c given by Eq. 24, the local stability of $(\boldsymbol{K}_{12}, \boldsymbol{O})$ is established for any value of D_2. In these cases, the environment in patches of group 1 or 2 is independent of the predator's invasion success. In these cases, the environment and the quality of prey in patches of one group is so poor that the predation in patches of another group does not work effective for the predator's invasion.

On the other hand, when Eq. 25 is satisfied, the equilibrium state $(\boldsymbol{K}_{12}, \boldsymbol{O})$ is unstable independently of the value of D_1 (see Figs. 5a and c). Moreover, when Eq. 18 is satisfied, the equilibrium state $(\boldsymbol{K}_{12}, \boldsymbol{O})$ is unstable independently of the value of D_2 (see Figs. 5a and b). There can exist the parameter region in which the predator's invasion succeeds independently of the environ-

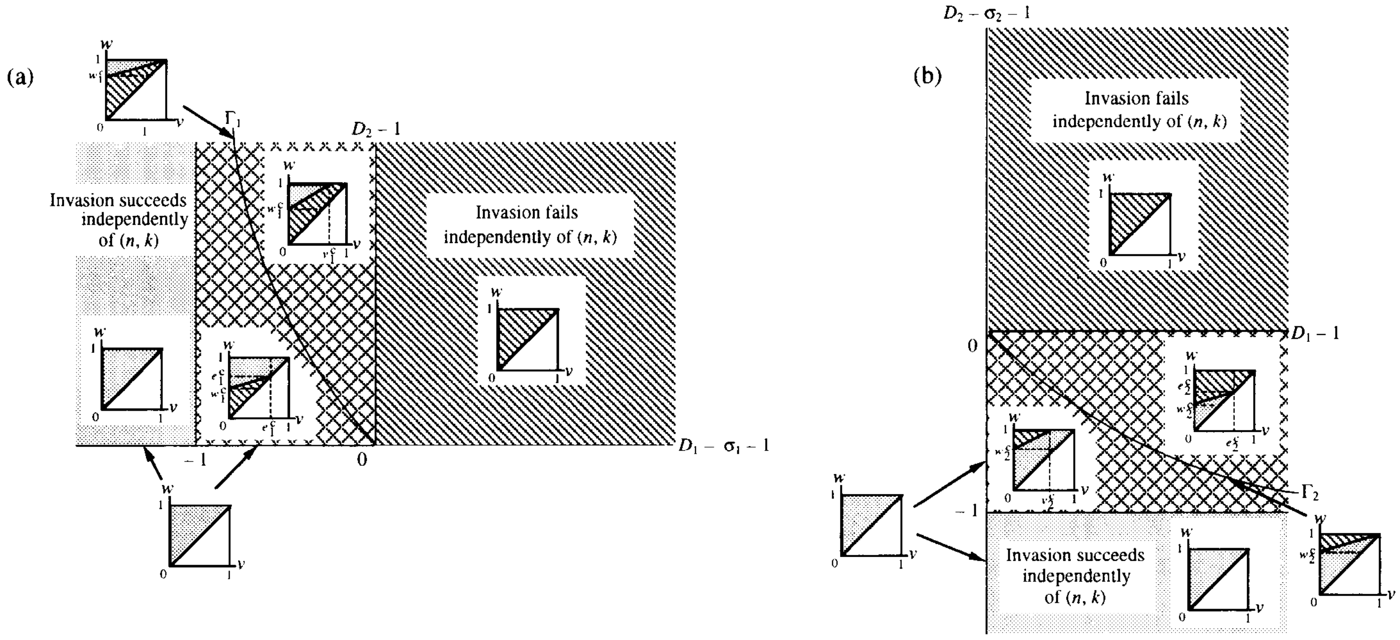

Fig. 6. Parameter dependence of the local stability for the equilibrium state: (a) $(\boldsymbol{K}_1, \boldsymbol{O})$; (b) $(\boldsymbol{K}_2, \boldsymbol{O})$. The shaded region is for the unstability, and the striped one is for the local stability, independent of the structure (n, k) of patchiness. In constrast, for the parameters in the cross-hatched region, the stability depends on the structural parameters (n, k) of patchiness. The curves Γ_i $(i = 1, 2)$ are respectively given by Eqs. 30 and 32. w_i^c, v_i^c, and e_i^c $(i = 1, 2)$ are respectively given by Eqs. 29, 31, 33, 34, 35, and 36, for the parameters $w = k/(n-1)$ and $v = 1/(n-1)$. In each region of parameters $(D_1 - \sigma_1 - 1, D_2 - 1)$ or $(D_1 - 1; D_2 - \sigma_2 - 1)$, the (v, w)-dependence of the local stability is shown by the configure of how the (v, w)-parameter space is categorized in terms of the local stability.

ment of patches of group 1 or 2. When the environment of patches of the better group is sufficiently favorable for predator's invasion, it allows the predator's invasion into the whole system, independently of the environment of patches of another group.

4. Effect of the structure of patchiness

In this section we focus on the effect of the structure of environmental patchiness, that is, the effect of the total number n of patches and the ratio k/n of patches of group 1, on the stability for the equilibrium state. For analytical convenience, we use the following parameters w and v for the structure of patchiness:

$$w \equiv \frac{k}{n-1}; \qquad v \equiv \frac{1}{n-1},$$

where $v \leqslant w \leqslant 1$. Parameter v expresses the effect of the total number of patches, and w that of the ratio of the number of patches of group 1 to the whole patches.

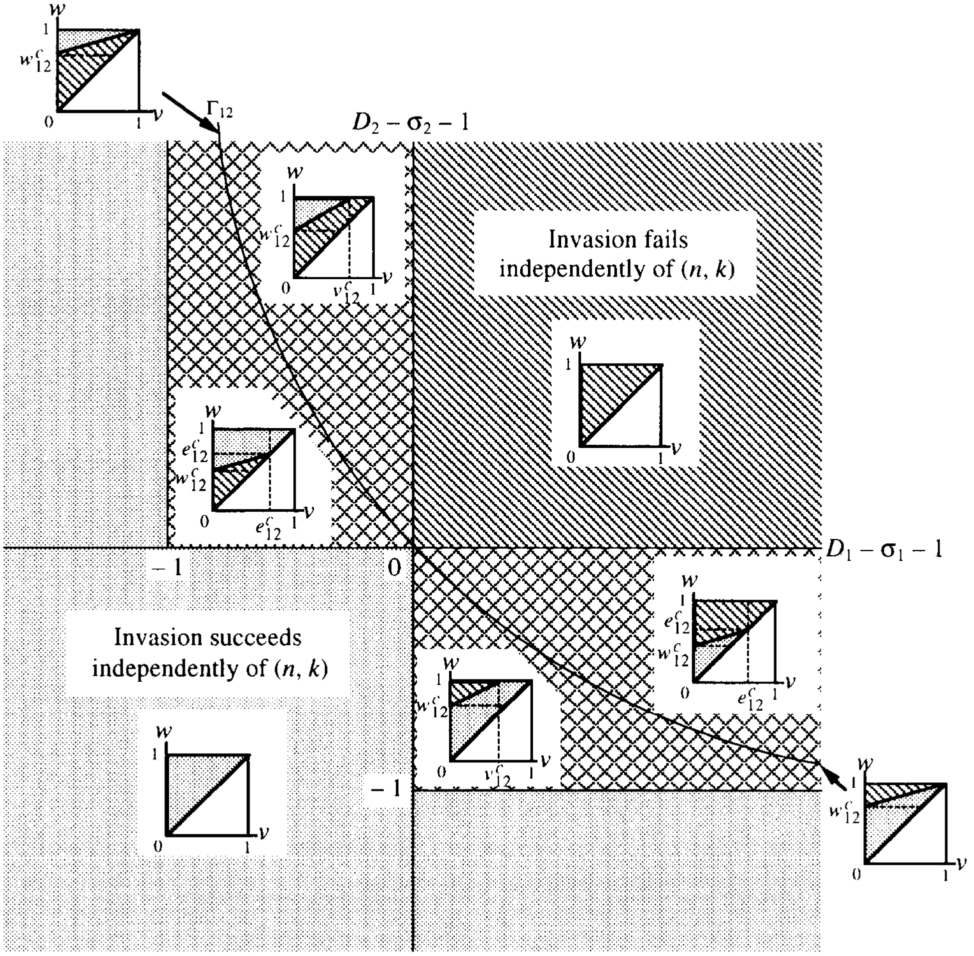

Fig. 7. Parameter dependence of the local stability for the equilibrium state (K_{12}, O). The shaded region is for the unstability, and the striped one is for the local stability, independent of the structure (n, k) of patchiness. In contrast, for the parameters in the cross-hatched region, the stability depends on the structural parameters (n, k) of patchiness. The curve Γ_{12} is given by Eq. 40. w^c_{12}, v^c_{12}, and e^c_{12} are respectively given by Eqs. 37, 38, and 39, for the parameters $w = k/(n-1)$ and $v = 1/(n-1)$. In each region of parameters $(D_1 - \sigma_1 - 1, D_2 - \sigma_2 - 1)$, the (v, w)-dependence of the local stability is shown by the configure of how the (v, w)-parameter space is categorized in terms of the local stability.

As for the equilibrium states, $(\boldsymbol{K}_1, \boldsymbol{O})$ and $(\boldsymbol{K}_2, \boldsymbol{O})$, the (v, w)-dependence of the local stability is shown in Fig. 6. The (v, w)-dependence appears only in the region of the other parameters such that $-1 < D_i - \sigma_i - 1 < 0$ $(i = 1, 2)$. For the parameters of the other region, the local stability is determined independently of (n, k). Therefore, the structure of environmental patchiness is significant only when the environment and the quality of prey in patches of the group richer than another is moderately favorable for the predator's invasion success.

As seen in Fig. 6a, when $-1 < D_1 - \sigma_1 - 1 < 0$, if w is not more than w_1^c given by

$$w_1^c = \frac{(D_1 - \sigma_1)(D_2 - 1)}{D_1 - \sigma_1 - D_2}, \tag{29}$$

the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$ is locally stable independently of the value of v. That is, independently of the total number of patches, if the ratio of patches of group 1 is sufficiently low, the predator's invasion fails. In contrast, when $-1 < D_1 - \sigma_1 - 1 < 0$ and the following is satisfied,

$$\frac{1}{D_1 - \sigma_1 - 1} + \frac{1}{D_2 - 1} + 1 > 0, \tag{30}$$

that is, when $0 < D_1 - \sigma_1 - 1 < -1 + 1/D_2$, if w is not less than e_1^c given by

$$e_1^c = -\frac{(D_1 - \sigma_1)(D_2 - 1)}{D_1 - \sigma_1 - 1}, \tag{31}$$

the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$ is unstable independently of the value of v. That is, independently of the total number of patches, if the ratio of patches of group 1 is sufficiently high, the predator's invasion succeeds.

Similarly, for the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$, as seen in Fig. 6b, when $-1 < D_2 - \sigma_2 - 1 < 0$ and the following is satisfied,

$$\frac{1}{D_2 - \sigma_2 - 1} + \frac{1}{D_1 - 1} + 1 < 0, \tag{32}$$

that is, when $-1 + 1/D_1 < D_2 - \sigma_2 - 1 < 0$, if w is not less than e_2^c given by

$$e_2^c = -\frac{D_1(D_2 - \sigma_2 - 1)}{D_1 - 1}, \tag{33}$$

the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$ is locally stable independently of the value of v. And, as seen in Fig. 6b, when $-D_2 - \sigma_2 - 1 < 0$, if w is not more than w_2^c given by

$$w_2^c = \frac{D_1(D_2 - \sigma_2 - 1)}{D_1 - D_2 + \sigma_2}, \tag{34}$$

the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$ is unstable independently of the value of v.

The predator's invasion success requires a sufficient ratio of the environmentally richer patches in the whole environment. In other words, there exists a critical value for the ratio of the number of patches of the richer group to the total of patches, below which the predator's invasion always fails. Further, there exists another critical value for the ratio of the number of patches of the richer group to the whole patches, beyond which the predator's invasion always succeeds.

On the other hand, as seen in Fig. 6, there exists a critical number for the total number of patches according to the predator's invasion failure. For the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$, when $-1 < D_1 - \sigma_1 - 1 < 0$ and the lefthand side of Eq. 30 is negative, that is, when $-1 + 1/D_2 < D_1 - \sigma_1 - 1 < 0$, if v is not less than v_1^c given by

$$v_1^c = -\frac{(D_1 - \sigma_1 - 1)D_2}{D_2 - 1}, \tag{35}$$

the predator's invasion fails independently of the value of w. Similarly, as for the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$, when $-1 < D_2 - \sigma_2 - 1 < 0$ and the lefthand side of Eq. 32 is negative, that is, when $-1 + 1/D_1 < D_2 - \sigma_2 - 1 < 0$, if v is not less than e_2^c given by Eq. 33, the predator's invasion fails independently of the value of w. Further, there exists another critical number for the total number of patches according to the predator's invasion success. For the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$, when $-1 < D_1 - \sigma_1 - 1 < 1 + 1/D_2$, if v is not less than e_1^c given by Eq. 31, the predator's invasion succeeds independently of the value of w, while for the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$, when $-1 < D_2 - \sigma_2 - 1 < -1 + 1/D_1$, if v is not less than v_2^c given by

$$v_2^c = -\frac{(D_1 - 1)(D_2 - \sigma_2)}{D_2 - \sigma_2 - 1}, \tag{36}$$

the predator's invasion succeeds independently of the value of w.

When the favorability of the richer patches is unsatisfactory for the predator's invasion success, the decrease of predator population due to the leakage in the migration process and the death in the poorer patches cannot be compensate by the growth of predator population in the richer ones. In contrast, if the richness of the environmentally richer patches is satisfactory for the predator's invasion success, even when the richer patch is only one in the whole system, the predator's invasion succeeds.

Also as for the equilibrium state $(\boldsymbol{K}_{12}, \boldsymbol{O})$, the analogous argument can be carried out. As easily seen in Fig. 7, this case can be discussed as case combined those for equilibrium states $(\boldsymbol{K}_1, \boldsymbol{O})$ and $(\boldsymbol{K}_2, \boldsymbol{O})$. Corresponding critical values for w and v are given in this case as follows:

$$w_{12}^c = \frac{(D_1 - \sigma_1)(D_2 - \sigma_2 - 1)}{D_1 - \sigma_1 - D_2 + \sigma_2} \tag{37}$$

$$v_{12}^c = -\frac{(D_1 - \sigma_1 - 1)(D_2 - \sigma_2)}{D_2 - \sigma_2 - 1} \tag{38}$$

$$e_{12}^c = -\frac{(D_1 - \sigma_1)(D_2 - \sigma_2 - 1)}{D_1 - \sigma_1 - 1}, \tag{39}$$

and the boundary curve Γ_{12} in the parameter region in which the (v, w)-dependence appears, that is, in the region such that $-1 < D_1 - \sigma_1 - 1 < 0$ and $0 < D_2 - \sigma_2 - 1$, or such that $0 < D_1 - \sigma_1 - 1$ and $-1 < D_2 - \sigma_2 - 1 < 0$, is given by

$$\frac{1}{D_1 - \sigma_1 - 1} + \frac{1}{D_2 - \sigma_2 - 1} + 1 = 0. \tag{40}$$

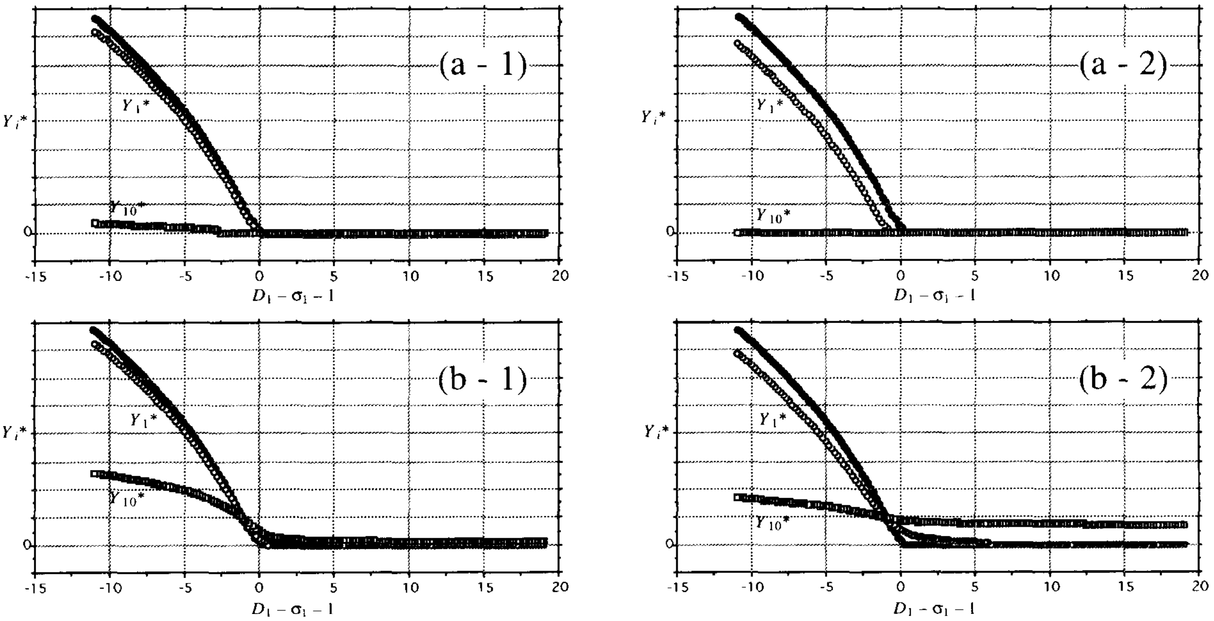

Fig. 8. Numerically calculated Y_1^* (○) and Y_{10}^* (□) at the stationary state of the system given by Eqs. 1 and 2 with $n = 10$; $b_1 = b_2 = b$; $r_1/b = r_2/b = 1.0$;$S_1 P_1/b = S_2 P_2/b = 0.1$;$(\delta_1 + P_1)/b = (\delta_2 + P)/b = 2.0$. (a-1) $k = 2$; $c_2 K_2/b = 0.0$ and $D_2 - \sigma_2 - 1 = 19.0$. (a-2) $k = 8$; $c_2 K_2/b = 0.0$ and $D_2 - \sigma_2 - 1 = 19.0$. (b-1) $k = 2$; $c_2 K_2/b = 1.999$ and $D_2 - \sigma_2 - 1 = -0.99$. (b-2) $k = 8$; $c_2 K_2/b = 1.999$ and $D_2 - \sigma_2 - 1 = -0.99$. The former k patches $(1, 2, \ldots, k)$ are of group 1, and the rest is of group 2. Only the equilibrium state $(\boldsymbol{K}_{12}, \boldsymbol{O})$ may become stable. The cases (a-1, 2) are for positive $D_2 - \sigma_2 - 1$, while (b-1, 2) are for the negative, referring to Fig. 7. Solid disks (●) are for the case when $c_2 K_2/b = c_1 K_1/b$, that is, $D_2 - \sigma_2 - 1 = D_1 - \sigma_1 - 1$, which corresponds to the case when the predator's invasion is independent of the structural parameters (v, w), as shown in Fig. 7.

5. Conclusion

Analyzing the local stability of equilibria with the predator's extinction, it is discussed how the predator's invasion is affected by the structure of environmental patchiness. Considered multi-patchy environment is categorized into two groups of patches. Every patches of each group have common environmental parameters which determine the relation between prey and predator, the growth of prey population, and the migration process of predator population. For the predator's invasion success, it is necessary that at least one of the two groups provides an environment satisfactory for predator population growth.

Although our mathematical analysis is focused the local stability of equilibria with the predator's extinction, some numerical calculations show the correspondence between the result by the local analysis and the global structure of stationary state (see Fig. 8, referring to Fig. 7). In addition, as the favorability of patches of one group becomes higher, the stationary predator population, that is, the predator population coexisting with prey gets larger. Further, we could not numerically find any dynamic stationary state, that is, periodically variational stationary coexistence. Therefore, as the environmental favorability for predator, which is measured by the parameter $D_i - \sigma_i - 1$ $(i = 1, 2)$ for our model, gets larger, the coexistence is promoted and the predator's stationary population becomes larger while the prey's stationary population becomes smaller (see Fig. 8).

Independently of the structural factors of environmental patchiness, that is, the total number of patches and the ratio of two groups, in some cases, it is determined whether the predator's invasion is successful or not. When one of groups provides sufficiently rich environment or high-quality prey, the predator's invasion succeeds even when the number of the more favorable patches is only one, while, when both groups provides too poor environment, it fails independently of the numbers of patches of each group.

In the other cases when the provided environment is moderate for the predator's population growth, the structural factors of environmental patchiness crucially determine whether predator can invade or not. In such case, there exist critical values for the total number of patches and for the ratio of two groups. If the more favorable group provides sufficiently satisfactory environment for the predator population, predator can invade independently of the total number of patches or of the ratio of two groups, while, if the more favorable group provides so unsatisfactory environment, predator fails to invade independently of them.

This result can be regarded as implying that the environmental fragmentation can become a cause for an outbreak or for an extinction of insects, etc. Even in the case when the area summed up all over fragmented zone is equal between two multi-patchy environments different from each other in terms of the structural factors of environmental patchiness, the structure of ecological community in each environment can be drastically different from each other, which is the case corresponding to that mentioned above. Spatial structure of environment could be crucial for the stability of ecological community.

In some parts of our analyses, the correspondence between our model and two-patch prey–predator system can be identified. As for the stationary state, group 1 and 2 in our model respectively correspond to two patches, in the other words, each of group 1 and 2 can be regarded as a meta-grouped patch. Those results for two-patch prey–predator system are applicable for our model, although some translation of parameters is required including the total number n of patches and the number k of group 1. This is because, at any stationary state of our model, every patch in each group reaches the same state, and patches in each group cannot be distinguished from each other. As long as they are at the stationary state, each group of patches can be treated as a group, that is, the stationary state for two-patch prey–predator system can be usefully applied with some translation of parameters. In contrast, in the stability analysis, since each group of patches has the larger degree of freedom of the perturbation around the equilibrium state than that for two-patch system, the analysis on two-patch system can provide results only for some specific cases for our model.

It should be remarked that, in our model, any locational structure of patches is not taken into account, because emigrating predator population is assumed to immigrate evenly into all the other patches, independently of which patch is the destination. In this reason, some results for our model would be vulnerable for the case when the mobility of predator is not high compared to its population growth. The model with a locational structure of patches, for example, like that in Seno (1988), would frequently bring some analytical difficulties, though it will be an interesting modelling analysis.

It is expected that our analysis will give some stimuli for mathematical modelling researches or for ecological researches.

Appendix A

For the equilibrium state $(\boldsymbol{X}^*, \boldsymbol{Y}^*)$, $\boldsymbol{M}$ is expressed with some block matrices as follows:

$$\boldsymbol{M} = \begin{pmatrix} H_1 \cdot \boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} & -b_1 X_1^* \cdot \boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} \\ \boldsymbol{O}_{n-k,k} & H_2 \cdot \boldsymbol{I}_{n-k} & \boldsymbol{O}_{n-k,k} & -b_2 X_2^* \cdot \boldsymbol{I}_{n-k} \\ c_1 Y_1^* \cdot \boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} & \boldsymbol{L}_1 & \boldsymbol{J}_2 \\ \boldsymbol{O}_{n-k,k} & c_2 Y_2^* \cdot \boldsymbol{I}_{n-k} & \boldsymbol{J}_1 & \boldsymbol{L}_2 \end{pmatrix} \quad \text{on } \mathbb{R}^{2n} \times \mathbb{R}^{2n},$$

where $\boldsymbol{I}_j$ is defined as $j \times j$ matrix whose elements are zero except for the diagonal elements which are all 1, $\boldsymbol{O}_{i,j}$ is defined as $i \times j$ matrix whose every elements are zero, and the other block matrices are defined as follows:

$$\boldsymbol{L}_1 = \begin{pmatrix} L_1 & & J_1 \cdots & J_1 \\ J_1 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & J_1 \\ J_1 & \cdots & J_1 & L_1 \end{pmatrix} \text{ on } \mathbb{R}^k \times \mathbb{R}^k \quad \boldsymbol{L}_2 = \begin{pmatrix} L_2 & & J_2 \cdots & J_2 \\ J_2 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & J_2 \\ J_2 & \cdots & J_2 & L_2 \end{pmatrix} \text{ on } \mathbb{R}^{n-k} \times \mathbb{R}^{n-k}$$

$$\boldsymbol{J}_1 = \begin{pmatrix} J_1 & \cdots & J_1 \\ \vdots & \ddots & \vdots \\ J_1 & \cdots & J_1 \end{pmatrix} \text{ on } \mathbb{R}^k \times \mathbb{R}^k \quad \boldsymbol{J}_2 = \begin{pmatrix} J_2 & \cdots & J_2 \\ \vdots & \ddots & \vdots \\ J_2 & \cdots & J_2 \end{pmatrix} \text{ on } \mathbb{R}^{n-k} \times \mathbb{R}^{n-k},$$

where H_1, H_2, L_1, L_2, J_1 and J_2 are the same as given in the main text. The characteristic equation for $\boldsymbol{M}$ is expressed as follows:

$$\det(\boldsymbol{M} - \lambda \boldsymbol{I}) = \begin{vmatrix} (H_1 - \lambda)\boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} & -b_1 X_1^* \cdot \boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} \\ \boldsymbol{O}_{n-k,k} & (H_2 - \lambda)\boldsymbol{I}_{n-k} & \boldsymbol{O}_{n-k,k} & -b_2 X_2^* \cdot \boldsymbol{I}_{n-k} \\ c_1 Y_1^* \cdot \boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} & (\boldsymbol{L}_1 - \lambda)\boldsymbol{I}_k & \boldsymbol{J}_2 \\ \boldsymbol{O}_{n-k,k} & c_2 Y_2^* \cdot \boldsymbol{I}_{n-k} & \boldsymbol{J}_1 & (\boldsymbol{L}_2 - \lambda)\boldsymbol{I}_{n-k} \end{vmatrix} = 0. \qquad \text{(A1)}$$

For the equilibrium state when $\boldsymbol{Y}^* = \boldsymbol{O}$, the determinant A1 becomes

$$\det(\boldsymbol{M} - \lambda \boldsymbol{I}) = \begin{vmatrix} (H_1 - \lambda)\boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} & -b_1 X_1^* \cdot \boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} \\ \boldsymbol{O}_{n-k,k} & (H_2 - \lambda)\boldsymbol{I}_{n-k} & \boldsymbol{O}_{n-k,k} & -b_2 X_2^* \cdot \boldsymbol{I}_{n-k} \\ \boldsymbol{O}_{k,k} & \boldsymbol{O}_{k,n-k} & (\boldsymbol{L}_1 - \lambda)\boldsymbol{I}_k & \boldsymbol{J}_2 \\ \boldsymbol{O}_{n-k,k} & \boldsymbol{O}_{n-k,n-k} & \boldsymbol{J}_1 & (\boldsymbol{L}_2 - \lambda)\boldsymbol{I}_{n-k} \end{vmatrix}$$

$$= \begin{vmatrix} (H_1 - \lambda)\boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} \\ \boldsymbol{O}_{n-k,k} & (H_1 - \lambda)\boldsymbol{I}_k \end{vmatrix} \cdot \begin{vmatrix} (\boldsymbol{L}_1 - \lambda)\boldsymbol{I}_k & \boldsymbol{J}_2 \\ \boldsymbol{J}_1 & (\boldsymbol{L}_2 - \lambda)\boldsymbol{I}_{n-k} \end{vmatrix} \qquad \text{(A2)}$$

The first determinant of Eq. A2 is expanded as follows:

$$\det\begin{pmatrix} (H_1-\lambda)\boldsymbol{I}_k & \boldsymbol{O}_{k,n-k} \\ \boldsymbol{O}_{n-k,k} & (H_2-\lambda)\boldsymbol{I}_{n-k} \end{pmatrix} = (H_1-\lambda)^k\cdot(H_2-\lambda)^{n-k}.$$

As for expanding the second determinant of Eq. A2, some tactical transformations are used. First, its first column is subtracted from every column over the second to the kth, and then the nth column is subtracted from every column over the $k+1$th to the $n-1$th. Next, those rows over the second to the kth are added to the first row, and those over the $k+1$th to the $n-1$th are to the nth. Then, expand it in terms of the first row. These steps carry the following determinants:

$$\det\begin{pmatrix} \boldsymbol{L}_1-\lambda\boldsymbol{I}_k & \boldsymbol{J}_2 \\ \boldsymbol{J}_1 & \boldsymbol{L}_2-\lambda\boldsymbol{I}_{n-k} \end{pmatrix}$$

$$=\{L_1-\lambda+(k-1)J_1\}\cdot\left|\begin{array}{c|c|c} (L_1-\lambda-J_1)\boldsymbol{I}_{k-1} & \boldsymbol{O}_{k-1,n-k-1} & \begin{matrix} J_2\\ \vdots\\ J_2\end{matrix} \\ \hline \boldsymbol{O}_{n-k-1,k-1} & (L_2-\lambda-J_2)\boldsymbol{I}_{n-k-1} & \begin{matrix} J_2\\ \vdots\\ J_2\end{matrix} \\ \hline 0\cdots\cdots\cdots0 & 0\cdots\cdots\cdots0 & L_2-\lambda+(n-k-1)J_2 \end{array}\right|$$

$$+(-1)^{n+1}kJ_2\cdot\left|\begin{array}{c|c|c} \begin{matrix} J_1\\ \vdots\\ J_1\end{matrix} & (L_1-\lambda-J_1)\boldsymbol{I}_{k-1} & \boldsymbol{O}_{k-1,n-k-1} \\ \hline \begin{matrix} J_1\\ \vdots\\ J_1\end{matrix} & \boldsymbol{O}_{n-k-1,k-1} & (L_2-\lambda-J_2)\boldsymbol{I}_{n-k-1} \\ \hline (n-k)J_1 & 0\cdots\cdots\cdots0 & 0\cdots\cdots\cdots0 \end{array}\right|.$$

Now, we expand the second determinant above in terms of the nth column:

$$(\text{The second determinant}) = (-1)^n\cdot(n-k)J_1\cdot\begin{vmatrix} (L_1-\lambda-J_1)\boldsymbol{I}_{k-1} & \boldsymbol{O}_{k-1,n-k-1} \\ \boldsymbol{O}_{n-k-1,k-1} & (L_2-\lambda-J_2)\boldsymbol{I}_{n-k-1} \end{vmatrix}.$$

Lastly, all determinants become triangular as seen above. For the expansion of triangular determinant, it is just necessary to multiplying the diagonal elements. Therefore, consequently, the characteristic equation 5 is obtained.

Appendix B

As for the condition for the local stability of the equilibrium state $(\boldsymbol{O},\boldsymbol{O})$, it is shown that those conditions 8, 9, 10, and 11 are satisfied. First, the conditions 8 and 9, $D_i > -1/(n-1)$ $(i=1,2)$, are clearly always satisfied since $D_i \geqslant 1$ ($i = 1, 2$). Next, since $D_i \geqslant 1$ ($i = 1, 2$), the following inequality for Eq. 10 can be estimated:

$$D_1 - \frac{k-1}{n-1} + \rho\left(D_2 - \frac{n-k-1}{n-1}\right) \geqslant \frac{n-k}{n-1} + \rho\frac{k}{n-1} > 0,$$

where

$$\rho \equiv \frac{S_2 P_2}{S_1 P_1}.$$

Thus, condition 10 is always satisfied. Next, since $D_i \geqslant 1$ ($i = 1, 2$), the following inequality for Eq. 11 can be estimated:

$$D_1 D_2 - \frac{k-1}{n-1} D_2 - \frac{n-k-1}{n-1} D_1 - \frac{1}{n-1} \geqslant D_1 D_2 - \frac{n-2}{n-1} D_1 - \frac{1}{n-1}$$
$$= D_1(D_2 - 1) + \frac{1}{n-1}\left(D_1 - \frac{1}{n-1}\right) > 0,$$

where $D_1 \geqslant D_2$ is assumed. For the case when $D_1 < D_2$, the similar estimation can be carried out. Therefore, the condition 11 is always satisfied, too.

As for the condition for the local stability of the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$, in the same way as the above, it can be shown that the condition 9 is always satisfied. The conditions 8 and 11 are compared with each other. The condition 11 is given by Eq. 14, and the conditions 8 is explicitly as follows:

$$D_1 > \sigma_1 - \frac{1}{n-1}. \tag{B1}$$

Since

$$D_2 - \frac{n-k-1}{n-1} \geqslant 1 - \frac{n-k-1}{n-1} > 0, \tag{B2}$$

the following inequality is obtained for Eq. 14:

$$D_1 > \frac{k(n-k)/(n-1)^2}{D_2 - (n-k-1)/(n-1)} + \sigma_1 + \frac{k-1}{n-1} > \sigma_1 + \frac{k-1}{n-1} > \sigma_1 - \frac{1}{n-1}. \tag{B3}$$

Thus, the condition 8 is satisfied if the condition 11 is. The condition 10 is given by

$$D_1 > -\rho D_2 + \sigma_1 + \frac{k-1}{n-1} + \rho\frac{n-k-1}{n-1}. \tag{B4}$$

If the righthand side of Eq. B4 is subtracted from that of Eq. 14:

$$\left\{\frac{k(n-k)/(n-1)^2}{D_2 - (n-k-1)/(n-1)} + \sigma_1 + \frac{k-1}{n-1}\right\} - \left\{-\rho D_2 + \sigma_1 + \frac{k-1}{n-1} + \rho\frac{n-k-1}{n-1}\right\}$$
$$= \frac{k(n-k)/(n-1)^2}{D_2 - (n-k-1)/(n-1)} + \rho\left(D_2 - \frac{n-k-1}{n-1}\right) > 0. \tag{B5}$$

where Eq. B2 is used. Therefore, the condition 10 is satisfied if the condition 11 is. Lastly, the conditions for the local stability of the equilibrium state $(\boldsymbol{K}_1, \boldsymbol{O})$ are obtained by Eqs. 6, 7, and 11 as indicated in the main text.

As for the condition for the local stability of the equilibrium state $(\boldsymbol{K}_2, \boldsymbol{O})$, it can be shown that the condition 8 is always satisfied. The condition 11 is given by Eq. 21, and the conditions 9 and 10 are by

$$D_2 > \sigma_2 - \frac{1}{n-1} \tag{B6}$$

$$D_1 > -\rho D_2 + \frac{k-1}{n-1} + \rho\left(\sigma_2 + \frac{n-k-1}{n-1}\right). \tag{B7}$$

In the similar way as for $(\boldsymbol{K}_1, \boldsymbol{O})$, it can be proved that those conditions 9 and 10 are satisfied if the condition 11 is.

As for the condition for the local stability of the equilibrium state $(\boldsymbol{K}_{12}, \boldsymbol{O})$, by the same steps as the above, it can be proved that the conditions 8, 9, and 10 are always satisfied if the condition 11 is.

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References

Allen, L.J.S., 1983a. Persistence and extinction in Lotka–Volterra reaction–diffusion equations. Math. Biosci., 65: 1–12.

Allen, L.J.S., 1983b. Persistence and extinction in single-species reaction–diffusion models. Bull. Math. Biol., 45: 209–227.

Allen, L.J.S., 1987. Persistence, extinction, and critical patch number for island populations. J. Math. Biol., 24: 617–625.

Chau, N.P., 1985. Linear *n*-compartment catenary models: Formulas to describe tracer amount in any compartment and identification of parameters from a concentration-time curve. Math. Biosci., 76: 185–206.

DeAngelis, D.L., Travis, C.C. and Post, W.M., 1979. Persistence and stability of seed-dispersed species in a patchy environment. Theor. Popul. Biol., 16: 107–125.

DeAngelis, D.L., Waterhouse, J.C., Post, W.M. and O'Neill, R.V., 1985. Ecological modelling and disturbance evaluation. Ecol. Model., 29: 399–419.

Fahrig, L. and Merriam, G., 1985. Habitat patch connectivity and population survival. Ecology, 66: 1762–1768.

Hirata, H., 1980. A model of hierarchical ecosystems with migration. Bull. Math. Biol., 42: 119–130.

Kawasaki, K. and Teramoto, E., 1979. Spatial pattern formation of prey–predator populations. J. Math. Biol., 8: 33–46.

Kierstead, H. and Slobodkin, L.B., 1953. The size of water masses containing plankton blooms. J. Mar. Res., 12: 141–147.

Levin, S.A., 1976. Spatial patterning and the structure of ecological communities. In: S.A. Levin (Editor), Some Mathematical Questions in Biology, Vol. 7, Lectures on Mathematics in the Life Sciences Vol. 8. Ann. Math. Soc., Providence, RI.

May, R.M., 1974. On the theory of niche overlap. Theor. Popul. Biol., 5: 297–332.

Okubo, A., 1980. Diffusion and Ecological Problems: Mathematical Models. Springer-Verlag, New York.

Okubo, A., 1982. Critical patch size for plankton and patchiness. In: S.A. Levin (Editor), Lecture Notes in Biomathematics, 54. Springer-Verlag, Berlin.

Post, W.M., DeAngelis, D.L. and Travis, C.C., 1983. Endemic disease in environments with spatially heterogeneous host populations. Math. Biosci., 63: 289–302.

Seno, H., 1988. Effect of a singular patch on population persistence in a multi-patch system. Ecol. Model., 43: 271–286.

Skellam, J.G., 1951. Random dispersal in theoretical populations. Biometrika, 38: 196–218.

Travis, C.C. and Post, W.M., 1979. Dynamics and comparative statics of mutualistic communities. J. Theor. Biol., 78: 553–571.

Vance, R.R., 1984. The effect of dispersal on population stability in one-species, discrete-space population growth models. Am. Nat., 123: 230–254.

Volterra, V., 1926. Variazione e fluttuazioni del numero d'individui in specie animali conviventi. Mem. Acad. Lincei., 6: 31–113.

Wiens, J.A., 1976. Population responses to patchy environments. Annu. Rev. Ecol. Syst., 7: 81–120.

Zeigler, B.P., 1977. Persistence and patchiness of predator–prey systems induced by discrete event population exchange mechanisms. J. Theor. Biol., 67: 687–713.