SOME MATHEMATICAL REMARKS ON POPULATION PERSISTENCE IN A MULTI-PATCH SYSTEM

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ABSTRACT. The effects of a singular (different kind of) patch on the persistence of a population distributed over patches in one-dimensional environment is studied by the eigenvalue estimation. The eigenvalue analysis quantitatively shows how population persistence is influenced by a) the location of the singular patch, b) the difference in the growth and emigration rates from the corresponding rates in the other patches, and by c) the total number of patches in the system.

1. Introduction

Various theoretical studies on the effect of the patchy environment on population have been developed (see Levin, 1976a, b, for review). Kierstead and Slobodkin (1953) and Okubo (1982) studied the population persistence within an isolated patch and established a critical patch size below which the population becomes extinct (see also Skellam, 1951; Okubo, 1980). DeAngelis *et al.* (1979), Vance (1984), and Allen (1983a, b, 1987) analysed the population dynamics in a patchy environment, making use of "multi-patch" (spatially discrete) systems. With the same type of a system, May (1974) and Levin (1976b), Zeigler (1977), Travis and Post (1979), Hirata (1980), and Post *et al.* (1983) studied the community dynamics.

Cohen (1972) studied a general linear multi-patch system involving a continuously time-varying rate of leakage from each patch. He showed that the leakage from each patch has no influence on the distribution of substance in the system, if and only if the rate of leakage is the same in all the patches. We shall investigate a system of ordinary differential equations in order to consider an aspect of population persistence in a multi-patch system containing a "singular" patch within which the emigration and growth rates are different from the corresponding rates within the other patches. As a consequence of Cohen's result, the existence of a singular patch in the system is expected to influence the distribution of population and its persistence. In this paper, we shall describe in detail the analysis of the parameter-dependency of the maximal eigenvalue of our model. As for the discussion on the biological viewpoint, see Seno (1987).

2. Statement of the Model

We shall focus our attention on a population dynamics modeled by the following system of ordinary differential equations:

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

where $\boldsymbol{n} = {}^{\mathrm{T}}(n_1, n_2, \dots, n_{N-1}, n_N)$, and n_i is the population density of the i-th patch at time t. $\boldsymbol{M}$ is an $N \times N$ matrix whose ij-element is m_{ij}, with

$$m_{ii} = R - P \;\; (i \neq k), \;\; m_{kk} = R' - P'$$

$$m_{i+1,i} = m_{i-1,i} = PS/2 \;\; (i \neq k), \;\; m_{k+1,k} = m_{k-1,k} = P'S'/2,$$

otherwise, $m_{ij} = 0$.

R, P, and S are the rate of population growth within a patch, of emigration from a patch, and of immigration into the nearest-neighbor patch, respectively. $1-S$ is the leakage rate of the migrants. The populations within all the patches, except for the k-th patch, have the same rates, whereas the population of the k-th patch is assumed to have the growth rate R', the emigration rate P', and the leakage rate $1-S'$.

If and only if all the eigenvalues of $\boldsymbol{M}$ have negative real parts, then the extinction of population occurs independently of the initial distribution of population, otherwise population increases infinitely. Thus we shall estimate the maximum real part of the eigenvalues of $\boldsymbol{M}$ in order to discuss the dependence of population persistence on parameters.

3. Some Mathematical Results

We shall solve the characteristic equation $G(\lambda) = \det(\boldsymbol{M} - \lambda \boldsymbol{E}) = 0$ for the eigenvalue estimation, where $\boldsymbol{E}$ is the unit matrix. We shall define the following matrices $\boldsymbol{D}_{n,k}$ and $\boldsymbol{I}_k$:

$$\boldsymbol{D}_{n,k} = \begin{pmatrix} \omega & 1 & 0 & \cdots & & & 0 \\ 1 & \omega & 1 & \ddots & & & \vdots \\ 0 & \ddots & \omega & \ddots & \ddots & & \vdots \\ \vdots & & \ddots & \omega' & \ddots & \ddots & \vdots \\ \vdots & & & \ddots & \omega & \ddots & 0 \\ \vdots & & & & \ddots & \ddots & 1 \\ 0 & \cdots & & & 0 & 1 & \omega \end{pmatrix}, \qquad \boldsymbol{I}_k = \begin{pmatrix} \omega & 1 & 0 & \cdots & & 0 \\ 1 & \omega & 1 & \ddots & & \vdots \\ 0 & \ddots & \ddots & \ddots & \ddots & \vdots \\ \vdots & & \ddots & \ddots & \ddots & 0 \\ \vdots & & & \ddots & \ddots & 1 \\ 0 & \cdots & & 0 & 1 & \omega \end{pmatrix}$$

Expansion of $\det(\boldsymbol{D}_{n,k})$ is corresponding to that of $G(\lambda)$, where $\omega = 2(R-P-\lambda)/SP$ and $\omega' = 2(R'-P'-\lambda)/S'P'$. $\det(\boldsymbol{I}_k)$ will correspond to $G(\lambda)$ when $R'=R$, $P'=P$, and $S'=S$. May (1973) applied a useful technique to expand $\det(\boldsymbol{I}_k)$:

$$\det(\boldsymbol{I}_k) = \sin\{(k+1)\theta\}/\sin\theta, \qquad (1)$$

where the parameter ω is related to θ through $\omega = 2\cos\theta$, where θ is a complex value in general. The condition that all the eigenvalues of $\boldsymbol{I}_k$ have negative real parts will be given by $\cos\{\pi/(N+1)\} < (P-R)/SP$ (see May, 1973, Appendix II). We can use the same technique and expand $G(\lambda)$ for arbitrary R', P' and S'. We shall expand $\det(\boldsymbol{D}_{n,k})$ at first by the k-th column. Then, by some column or row expansions of determinant, $\det(\boldsymbol{D}_{n,k})$ can be calculated as a sum of three determinants including diagonally two blocks of the form of $\boldsymbol{I}_k$. We shall use the well-known result that the determinant of a diagonal block matrix is equal to the product of determinants of each block (Bellman, 1970):

$$\det(D_{n,k}) = \omega' \cdot \det(I_{k-1})\det(I_{N-k}) - \det(I_{k-1})\det(I_{N-k-1}) - \det(I_{k-2})\det(I_{N-k})$$

Then, using equation (1), we obtain the following expansions:

$$G(\lambda) = (PS/2)^{N-1} \cdot (P'S'/2) \cdot g(\theta)/\sin^2\theta \tag{2}$$

$$g(\theta) = \omega' \cdot \sin(k\theta)\sin\{(N-k+1)\theta\} - \sin\{(k-1)\theta\}\sin\{(N-k+1)\theta\} - \\ - \sin(k\theta)\sin\{(N-k)\theta\} \tag{3}$$

$$2(R - P - \lambda)/SP = 2\cos\theta \tag{4}$$

$$2(R' - P' - \lambda)/S'P' = \omega' . \tag{5}$$

The eigenvalue estimation using this general result is a complicated procedure, and in order to present its basics we shall study two special cases; a) the central patch is singular, and b) the edge patch is singular. In both cases, we shall assume that $R \le P$ and $R' \le P'$. The reason for this assumption is as follows. If $R > P$ or $R' > P'$ holds at least in one patch, then the population of any patch will finally increase --- no extinction occurs. This is because the population of a patch overcompensates for the loss due to the emigration.

3.1. SINGULAR CENTRAL PATCH CASE

Let $N = 2m + 1$ and $k = m + 1$ in (3):

$$g(\theta) = \sin\{(m+1)\theta\} \cdot [\omega' \cdot \sin\{(m+1)\theta\} - 2\sin(m\theta)] .$$

We shall begin by solving the equation $g(\theta)=0$, $\theta \in [0, \pi]$. In case of real θ, it is sufficient to solve $g(\theta)=0$ on $[0, \pi]$, because the eigenvalue λ depends on θ only through the cosine function symmetric with respect to π (see equation (4)). From $\sin\{(m+1)\theta\}=0$, m distinct roots are easily obtained: $\theta_j = j\pi/(m+1)$ ($j = 1, 2, \dots, m$). Using equations (4) and (5), the equation $\omega' \cdot \sin\{(m+1)\theta\} - 2\sin(m\theta)=0$ can be rewritten as:

$$\alpha = 2\sin(m\theta)/\sin\{(m+1)\theta\} - 2SP \cdot \cos\theta/S'P'. \tag{6}$$

where $\alpha = 2\{R' - P' - (R - P)\}/S'P'$. We shall denote the righthand side of (6) by $f_c(\theta)$. In Fig. 1, the graph of $f_c(\theta)$ on $[0, \pi]$ is shown. It is easy to see that equation (6) has $m-1$ distinct roots. For convenience, hereafter we shall set $\gamma = SP/S'P' - m/(m+1)$. When $\gamma < 0$, the graph of $f_c(\theta)$ becomes as in Fig. 1(a). It is clear from the graph that equation (6) has another root when $|2\gamma| < \alpha$, or does not have any other real root when $\alpha \le |2\gamma|$. On the contrary, when $0 \le \gamma$, the graph is as in Fig. 1(b). Equation (6) has two other roots when $\alpha \le |2\gamma|$, or it has only one other root when $|2\gamma| < \alpha$. Now, m distinct roots of (6) on $[0, \pi]$ can be obtained:

$$j\pi/(m+1) < \theta_j < (j+1)\pi/(m+1) \quad (j = 1, 2, \dots, m-1) \tag{7}$$

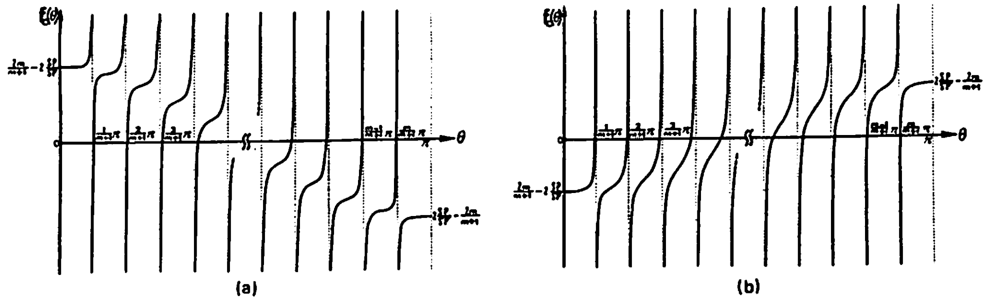

Fig. 1. The graph of $f_c(\theta)$ on $[0, \pi]$ for (a) $\gamma < 0$, and for (b) $0 < \gamma$.

$$\begin{cases} 0 < \theta_0 < \pi/(m+1) & \text{when } -2\gamma < \alpha, \quad (8a) \\ m\pi/(m+1) < \theta_m \leq \pi & \text{when } \alpha \leq -2\gamma. \quad (8b) \end{cases}$$

There are $2m+1$ roots, since M is the irreducible $(2m+1)\times(2m+1)$ matrix. The remaining roots are obtained from the following two equations:

$$\alpha = f_c(\pi + i\varphi), \quad \alpha = f_c(i\varphi), \tag{9}$$

where i is the imaginary unit. Note that both $f_c(\pi+i\varphi)$ and $f_c(i\varphi)$ are real, because $\cos i\varphi = \cosh\varphi$ and $\sin i\varphi = i\cdot\sin\varphi$. The graphs of $f_c(\pi+i\varphi)$ and $f_c(i\varphi)$ are shown in Fig. 2. It is sufficient to find the positive root φ because the eigenvalue λ depends on φ only through the hyperbolic cosine function symmetric with respect to zero. From Fig. 2(a), it can be seen that both equations (9) have the positive root when $\gamma < 0$ and $\alpha \leq |2\gamma|$, while only one of them has the root when $|2\gamma| < \alpha$.

In such a way, we have obtained all eigenvalues of M. From equation (4), $\lambda = R-P-SP\cos\theta$. Since $\cos\theta$ is monotone decreasing on $[0, \pi]$ and $\cos\theta \leq 1 \leq \cosh\varphi$, the maximum eigenvalue λ_{max} is given by

$$\lambda_{max} = \begin{cases} R - P + SP \cdot\cosh\varphi^* & \text{when } 2\gamma < \alpha \quad (10a) \\ R - P - SP \cdot\cos\theta^* & \text{when } \alpha < 2\gamma, \quad (10b) \end{cases}$$

where φ^* is the root of $\alpha = f_c(\pi + i\varphi)$ and θ^* is equal to θ_m given by (8b).

We shall now establish the condition which assures that all the eigenvalues are negative, in other words, $\lambda_{max} < 0$. By equations (10a, b), the condition is interpreted as:

$$\begin{cases} \cosh\varphi^* < \beta & \text{when } \beta' < (\beta - 1)\cdot SP/S'P' + m/(m+1) \quad (11a) \\ -\cos\theta^* < \beta & \text{when } (\beta - 1)\cdot SP/S'P' + m/(m+1) \leq \beta', \quad (11b) \end{cases}$$

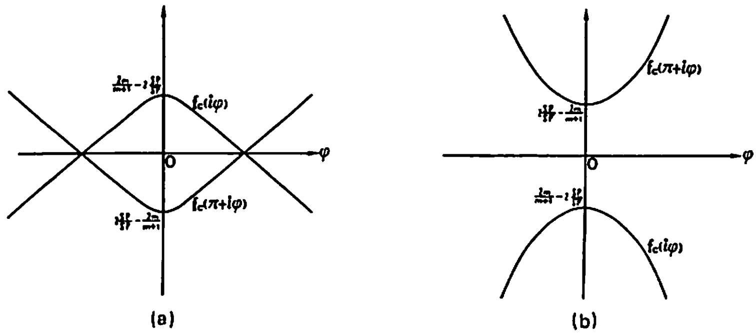

Fig. 2. The graphs of $f_c(i\varphi)$ and $f_c(\pi + i\varphi)$: (a) $\gamma < 0$, and (b) $0 < \gamma$.

where $\beta = (P-R)/SP$, $\beta' = (P'-R')/S\mathcal{P}'$. Both β and β' are not negative, since $R \le P$ and $R' \le P'$. In case of $(\beta - 1)\cdot SP/S\mathcal{P}' + m/(m+1) \le \beta'$, we can define such a $\theta^{\bullet}$ that $\cos\theta^{\bullet} = -\beta$ when $0 < \beta \le 1$. Then the condition (11b) is rewritten as:

$$m\pi/(m+1) < \theta^* < \theta^{\bullet} \le \pi, \tag{12}$$

where we used the decreasing monotonicity of the cosine function on $[0, \pi]$. Since $f_c(\theta)$ is monotone increasing on $(m\pi/(m+1), \pi]$ (see Fig. 1), the conditon (12) becomes $f_c(\theta^*) < f_c(\theta^{\bullet})$. Note that $f_c(\theta^*) = \alpha = 2\beta\, SP/S\mathcal{P}' - 2\beta'$ and $f_c(\theta^{\bullet}) = 2\beta\, SP/S\mathcal{P}' - 2h_c(\theta^{\bullet})$, where we shall define $h_c(\theta) = -\sin(m\theta)/\sin\{(m+1)\theta\}$. In the contrary case, $\beta' < (\beta - 1)\cdot SP/S\mathcal{P}' + m/(m+1)$, we can define such a positive $\varphi^{\bullet}$ that $\cosh\varphi^* = \beta$ when $1 \le \beta$. The condition (11a) becomes

$$0 < \varphi^* < \varphi^{\bullet}, \tag{13}$$

where we used the increasing monotonicity of the hyperbolic cosine function on $[0, +\infty)$. $f_c(\pi + i\varphi)$ is monotone increasing on $[0, +\infty)$ (Fig.2). Thus, the condition (13) leads to $f_c(\pi + i\varphi^*) < f_c(\pi + i\varphi^{\bullet})$. Here $f_c(\pi + i\varphi^{\bullet}) = 2\beta\, SP/S'P' - 2h_c(\pi + i\varphi^{\bullet})$. Consequently, the conditon searched becomes

$$h_c(\theta^{\bullet}) < \beta' \quad (0 \le \beta \le 1), \qquad h_c(\pi + i\varphi^{\bullet}) < \beta' \quad (1 < \beta). \tag{14}$$

3.2. SINGULAR EDGE PATCH CASE

By the symmetric nature of the system, we shall assume that the 1-st patch is singular. In this case, let $k = 1$ in (3):

$$g(\theta) = \sin\theta \cdot [\omega' \cdot \sin(N\theta) - \sin\{(N-1)\theta\}] .$$

We shall solve

$$\alpha = \sin\{(N-1)\theta\}/\sin(N\theta) - 2SP \cdot \cos\theta / S\mathcal{P}'. \tag{15}$$

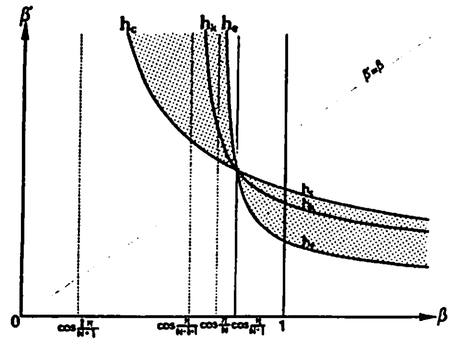

Fig. 3. The critical curves in β-β' plane for the persistence of population. The region above each curve is that of the extinction and the below region is that of the persistence. For β and β' in the dark region, there exists a critical location of the singular patch (see following sections).

Equation (15) corresponds to $g(\theta) = 0$. Hereafter we shall denote the righthand side of (15) as $f_e(\theta)$.

In a similar way as before, N distinct real eigenvalues can be obtained, and

$$\lambda_{max} = \begin{cases} R - P + SP\cdot\cosh\varphi^{**} & \text{when } 2SP/S'P' - (N-1)/N < \alpha \\ R - P - SP\cdot\cos\theta^{**} & \text{when } \alpha \le 2SP/S'P' - (N-1)/N, \end{cases}$$

where φ^{**} is the root of $\alpha = f_e(\pi + i\varphi)$ and θ^{**} is the root of $\alpha = f_e(\theta)$ on $((N-1)\pi/N, \pi]$. The condition for $\lambda_{max} < 0$ is

$$h_e(\theta^*) < \beta' \quad (0 \le \beta \le 1), \qquad h_e(\pi + i\varphi^*) < \beta' \quad (1 < \beta),$$

where $h_e(\theta) = -\sin\{(N-1)\theta\}/\sin(N\theta)$. θ^* and φ^* are the same as before.

3.3. GENERAL CASE

Because of the symmetric nature of system, we shall consider the case when $1 \le k \le (N+1)/2$. The equation corresponding to $g(\theta) = 0$ is

$$\alpha = \sin\{(k-1)\theta\}/\sin(k\theta) + \sin\{(N-k)\theta\}/\sin\{(N-k+1)\theta\} - 2SP\cdot\cos\theta/S'P'. \tag{16}$$

The roots of (16) can be investigated by a procedure similar to those used in the two special cases. The resulting condition which assures that all the eigenvalues are negative is

$$h_k(\theta^*) < \beta' \quad (0 \le \beta \le 1), \qquad h_k(\pi + i\varphi^*) < \beta' \quad (1 < \beta), \tag{17}$$

where $h_k(\theta) = -\sin\{(k-1)\theta\}/\sin(k\theta) - \sin\{(N-k)\theta\}/\sin\{(N-k+1)\theta\}$. Note that, for a fixed β, $h_k(\theta)$ is a monotonic function of k: increasing when $\beta < \cos\{\pi/(N+1)\}$ and decreasing when $\cos\{\pi/(N+1)\} < \beta$. Considering this monotonicity, the parameter region

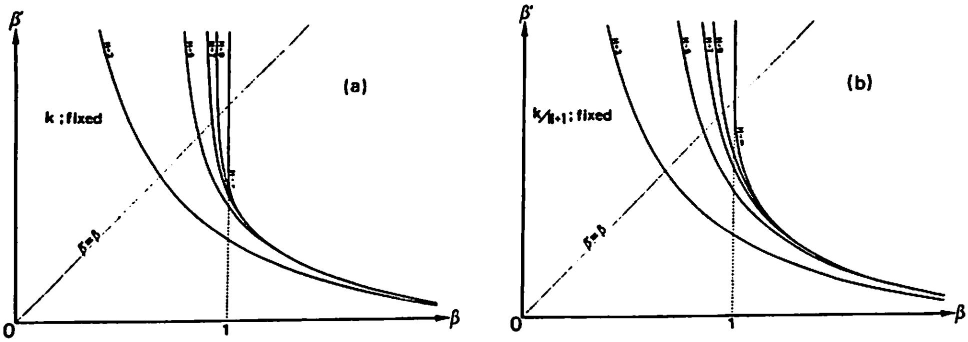

Fig. 4. The critical curves for different total numbers of patches in case of (a) the location of a singular patch $k = 2$ fixed, and (b) the ratio $k/(N+1) = 1/2$ fixed. For a fixed k, the limit curve approaches $(2k-1)/2k$ at $\beta = 1$. For a fixed k/N, it approaches 1 at $\beta = 1$. The region above each curve is that of the extincion and the region below it is that of the persistence.

can be divided into the following four sets (see Fig. 3):

i) The region where at least one positive eigenvalue exists independent of any k,

ii) The region where all the eigenvalues are negative, independent of k,

iii) The region where all the eigenvalues are negative when $^{\exists}k^* < k$, and at least one positive eigenvalue exists when $k < k^*$,

iv) The region where at least one positive eigenvalue exists when $^{\exists}k^{**} < k$, and all the eigenvalues are negative when $k < k^{**}$.

Next we turn our attention to the dependence of conditon (17) on the total number of patches. In Fig.3, the asymptotic line $\beta = \cos\{\pi/(N-k+1)\}$ comes closer to $\beta=1$ as the number N increases. If we let $N \to \infty$, with fixed k, the asymptotic line monotonically approaches $\beta=1$ and the critical curve $\beta' = h_k(\pi + i\varphi^*)$ monotonically converges to $2\beta' = \sinh\{(k-1)\varphi^*\}/\sinh(k\varphi^*) + \exp(-\varphi^*)$. See Fig. 4(a). On the other hand, if we let the ratio k/N be constant (for example, 1/2), then $\beta' = h_k(\pi + i\varphi^*)$ monotonically converges to $2\beta' = \exp(-\varphi^*)$ as $N \to \infty$ (Fig. 4(b)). This indicates that when the parameters β and β' lie between two critical curves of the total patch number $N_c - 1$ and N_c, then either all the eigenvalues are negative if the total patch number N satisfies $N < N_c$, or at least one positive eigenvalue appears if $N_c \le N$ (see Fig. 4).

4. Conclusions

1) The more centrally located a singular patch is, the greater is its effect on the maximal eigenvalue, especially in the parameter regions iii) and iv) mentioned above. The persistence of population seriously depends on the location of a singular patch.

2) In some cases, there exists a critical total number of patches. If the actual number is below it, all the eigenvalues are negative. In the other cases, there is no such a critical total number of patches and there is at least one positive eigenvalue independently of the system size, even if there are only negative eigenvalues when every patch is identical (see Fig. 3). The effect of a singular patch may stabilize the persistence of population.

The technique and results of our analysis may be profitably applied to other models in various contexts: for example, multi-membrane system, information flow in a cellular network, seed dispersal, plankton dispersal, desease epidemic (see also Seno, 1987).

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