数理解析研究所講究録 1372 巻 2004 年 128-134

Coexistent Steady State of Sessile Metapopulation Model: Case of Two Species and Two Habitats

(二種二生息域、固着性メタ個体群モデルの共存定常解)

Katumi, KAMIOKA (神岡 勝見)
Department of Mathematical Sciences, University of Tokyo
(東京大学大学院数理科学研究科)

1 Introduction

A metapopulation such as barnacles is composed of many habitats for sessile adults and the planktonic larvae. The larvae are produced from all the local habitats, which are mixed in a common larval pool. The larvae then return to settle on vacant space in a local habitat. The local population can be regulated by the density dependent death rate of adult population and the settlement rate of larval population, which is proportional to the amount of vacant space in the each habitat and the density of larval population.

Iwasa and Roughgarden [1, 2] have proposed the sessile metapopulation model with space-limited recruitment to investigate the regional competition community between species. They have shown that the existence of steady states of single species and its stabilities. And they have shown that at least n kinds of habitats are necesarry for n kinds of species to coexist. Then in order to investigate the competition community between species, they have treated the special case that numbers of both species and habitats are two. But they cannot obtain the sufficient condition for coexistence.

Here we also consider the basic model for two kinds of species and two kinds of hatitats, and show the sufficient condition for the existence of coexistent steady state. The basic tools to examine the above problem are the various kind of basic reproduction numbers.

The Iwasa-Roughgarden's basic model [2] is as follows:

$$\frac{d}{dt}P_{ij}(t) = -\mu_{ij}P_{ij}(t) + c_{ij}(Q_j - S_j(u(t)))L_i(t), \tag{1.1}$$

$$\frac{d}{dt}L_i(t) = -v_iL_i(t) - \sum_{j=1}^{2} c_{ij}(Q_j - S_j(u(t)))L_i(t) + \sum_{j=1}^{2} m_{ij}P_{ij}(t), \tag{1.2}$$

where $S_j(u) := \sum_{i=1}^{2}\gamma_{ij}P_{ij}$, $u := (P_{11}, P_{12}, P_{21}, P_{22}, L_1, L_2)^\tau$ and τ denotes the transpose of the vector. P_{ij} denotes the number of adult population of species i living in hatitat j and L_i does the number of larvae of species i in the larval pool. In the following we use the index i, j to indicate species i and habitat j. $\mu_{ij}, v_i, c_{ij}, \gamma_{ij}$ and m_{ij} represent death rate of adult population, larval death rate, accessibility to a local habitat and area occupied by a single individual and birth rate. $Q_j - S_j(u)$ denotes the vacant area of habitat j, respectively. The settlement rate may vary in time and that induces nonlinearity into this model.

2 Preliminary results

The steady states $u^* := (P_{11}^*, P_{12}^*, P_{21}^*, P_{22}^*, L_1^*, L_2^*)^T$ are given as the roots of the following system derived from (1.1)-(1.2):

$$0 = -\mu_{ij} P_{ij}^* + c_{ij}(Q_j - S_j(u^*))L_i^*, \tag{2.1}$$

$$0 = -v_i L_i^* - \sum_{j=1}^{2} c_{ij}(Q_j - S_j(u^*))L_i^* + \sum_{j=1}^{2} m_{ij} P_{ij}^*, \tag{2.2}$$

where $i, j = 1, 2$. Eliminating P_{ij}^* and $S_j(u^*)$, and replacing $(L_1^*, L_2^*)^T$ by $w = (x, y)^T$, we obtain

$$T(w) = w, \tag{2.3}$$

where

$$T(w) := (T_1(w), T_2(w))^T,$$

$$T_1(w) := \Psi_1\left(\frac{(\alpha_{11}x + \alpha_{21}y)Q_1}{1 + \alpha_{11}x + \alpha_{21}y}, \frac{(\alpha_{12}x + \alpha_{22}y)Q_2}{1 + \alpha_{12}x + \alpha_{22}y}\right)x,$$

$$T_2(w) := \Psi_2\left(\frac{(\alpha_{11}x + \alpha_{21}y)Q_1}{1 + \alpha_{11}x + \alpha_{21}y}, \frac{(\alpha_{12}x + \alpha_{22}y)Q_2}{1 + \alpha_{12}x + \alpha_{22}y}\right)y,$$

$$\alpha_{ij} := \frac{\gamma_{ij} c_{ij}}{\mu_{ij}},$$

$$\Psi_i(\xi_1, \xi_2) := \frac{\sum_{j=1}^{2} \frac{m_{ij} c_{ij}}{\mu_{ij}}(Q_j - \xi_j)}{v_i + \sum_{j=1}^{2} c_{ij}(Q_j - \xi_j)}.$$

Here we deifne the *basic reproduction number* as a threshold parameter which determines whether one of the species will succeed in invasion or not when a small number of larvae invade into the completely vacant habitats. We consider the initial invasion phase of the larvae. In the early stage of invasion, the dynamics of metapopulation can be described by the linearized equation at the trivial steady state as follows:

$$\frac{d}{dt} P_{ij}(t) = -\mu_{ij} P_{ij}(t) + c_{ij} Q_j L_i(t), \tag{2.4}$$

$$\frac{d}{dt} L_i(t) = -\left(v_i + \sum_{j=1}^{2} c_{ij} Q_j\right) L_i(t) + \sum_{j=1}^{2} m_{ij} P_{ij}(t). \tag{2.5}$$

By the variation of constants formula, (2.4)-(2.5) are reduced to

$$P_{ij}(t) = P_{ij}(0)e^{-\mu_{ij}t} + c_{ij} Q_j \int_0^t L_i(s) e^{-\mu_{ij}(t-s)} ds, \tag{2.6}$$

$$L_i(t) = L_i(0)e^{-(v_i + \sum_{j=1}^{2} c_{ij}Q_j)t} + \sum_{j=1}^{2} m_{ij} \int_0^t P_{ij}(s) e^{-(v_i + \sum_{j=1}^{2} c_{ij}Q_j)(t-s)} ds. \tag{2.7}$$

Substituting (2.6) into (2.7), we obtain the Volterra integral equation:

$$\mathbb{L} = \mathbb{F}(t) + \int_0^t \mathbb{G}(t-\xi)\mathbb{L}(\xi)d\xi, \tag{2.8}$$

where

$$\begin{aligned}
\mathbb{L}(t) :=& (L_1(t), L_2(t))^\tau,\ \mathbb{F}(t) := (F_1(t), F_2(t))^\tau,\\
F_i(t) :=& L_i(0)e^{-(v_i+\sum_{j=1}^2 c_{ij}Q_j)t}\\
&+ \sum_{j=1}^2 m_{ij}P_{ij}(0)\int_0^t e^{-\mu_{ij}s}e^{-(v_i+\sum_{j=1}^2 c_{ij}Q_j)(t-s)}ds,\\
\mathbb{G}(t) :=& \begin{pmatrix} G_1(t) & 0 \\ 0 & G_2(t) \end{pmatrix},\\
G_i(t) :=& \sum_{j=1}^2 m_{ij}c_{ij}Q_j\int_0^t e^{-\mu_{ij}s}e^{-(v_i+\sum_{j=1}^2 c_{ij}Q_j)(t-s)}ds.
\end{aligned}$$

It is well known in the Volterra integral equation theory that $\lim_{t\to\infty}\mathbb{L}(t) = 0$ if the spectral radius of the integral operator is less than one, whereas $\mathbb{L}(t)$ increases if it is more than one. Then we define the basic reproduction number R_0 (see Diekmann et al [3]) by the spectral radius of the integral operator as follows:

$$R_0 := \max_{i=1,2}\int_0^\infty G_i(t)dt = \max_{i=1,2}\frac{\sum_{j=1}^2 \frac{m_{ij}c_{ij}}{\mu_{ij}}Q_j}{v_i + \sum_{j=1}^2 c_{ij}Q_j}. \tag{2.9}$$

R_0 also means the number of secondary larvae released by one larva that has come in totally vacant habitats.

In the following Theorem 1-4, we state the preliminary results.

Letting $x > 0$ and $y = 0$, (2.3) is reduced to

$$\Psi_1\left(\frac{\alpha_{11}xQ_1}{1+\alpha_{11}x}, \frac{\alpha_{12}xQ_2}{1+\alpha_{12}x}\right) = 1. \tag{2.10}$$

We also define the basic reproduction number for species i by

$$R_{0i} := \frac{\sum_{j=1}^2 \frac{m_{ij}c_{ij}}{\mu_{ij}}Q_j}{v_i + \sum_{j=1}^2 c_{ij}Q_j}.$$

Since (2.10) is a single quadratic equation for x, we can immediately show

Theorem 1. *(i)If $R_{01} > 1$, then (2.10) has a unique positive root.*
(ii)If $R_{01} = 1$, then
(iia)(2.10) has a unique positive root provided $E_1 > 1$, where

$$E_i := \Psi_i(\alpha_{i1}Q_1/(\alpha_{i1}+\alpha_{i2}), \alpha_{i2}Q_2/(\alpha_{i1}+\alpha_{i2})),$$

while
(iib)no positive root provided $E_1 \leq 1$.
(iii)If $R_{01} < 1$, *then*
(iiia)(2.10) has two positive roots provided $E_1 > 1$ *and* $D_1 > 0$, *where*

$$D_1 := \{v_1(\alpha_{11}+\alpha_{12}) + c_{11}Q_1\alpha_{12} + c_{12}Q_2\alpha_{11}\}^2(1-E_1)^2 - 4v_1\alpha_{11}\alpha_{12}(v_1 + c_{11}Q_1 + c_{12}Q_2)(1-R_{01}),$$

(iiib)unique positive root provided $E_1 > 1$ *and* $D_1 = 0$, *and*
(iiic)no positive root provided $E_1 \leq 1$ *or* $D_1 < 0$.

Theorem 2. *If* $R_0 < 1$, *then the trivial steady state is locally asymptotically stable, whereas it is unstable if* $R_0 > 1$.

We introduce a threshold parameter R^*_{0i} defined by

$$R^*_{0i_1} := \Psi_{i_1}(S_1(u^*_{i_2}), S_2(u^*_{i_2})),\ i_1 \neq i_2,\ i_1, i_2 = 1, 2.$$

R^*_{0i} is the reproduction number for species i under the stationary occupation of the other species.

Theorem 3. *The (large) non-trivial single-species' steady state is locally asymptotically stable if* $R^*_{02} < 1$ *and it is unstable if* $R^*_{02} > 1$. *Furthermore the small non-trivial single-species' steady state (if it exist) is always unstable.*

The results similar to Theorem 1-3 hold for species 2 by replacing $i = 1$ by $i = 2$.

Moreover we define the basic reproduction number for species i in the case that only habitat j exists by R_{0ij}:

$$R_{0ij} := \frac{\frac{m_{ij}c_{ij}}{\mu_{ij}}Q_j}{v_i + c_{ij}Q_j}.$$

Theorem 4. *If* $R_{0ij} \leq 1, R_{0i} \leq 1, i, j = 1, 2$, *then the trivial steady state is globally asymptotically stable.*

Theorem 2, 3 are proved by the linearized stability argument and Theorem 4 is proved by using the Lyapunov function:

$$V(u) := \sum_{i,j=1,2} \frac{m_{ij}}{\mu_{ij}} P_{ij} + \sum_{i=1}^{2} L_i.$$

3 Coexistent Steady state

In this section, we consider the coexistent steady state, which corresponds to a fixed point of the mapping T in the interior of $\mathbb{R}^2_+$. We have the following existence theorem.

Theorem 5. *If $R_0 > 1, R_{01}^* > 1$ and $R_{02}^* > 1$, then T has at least one fixed point $w = (x, y)^\tau$ with both $x > 0$ and $y > 0$.*

Proof. Let us define the bounded, convex and closed domain U_B by

$$U_B := \{w = (x, y)^\tau \in \mathbb{R}_+^2; x \leq B, y \leq B\}.$$

and define the continuous mapping T^r with a positive number r ($r < B$) by

$$T^r(w) = (T_1^r(w), T_2^r(w))^\tau,$$

where

$$T_1^r(w) := \begin{cases} T_1(w), & x > r, \\ T_1(w) + r - x, & x \leq r, \end{cases} \tag{3.1}$$

$$T_2^r(w) := \begin{cases} T_2(w), & y > r, \\ T_2(w) + r - y, & y \leq r. \end{cases} \tag{3.2}$$

The continuous mapping T^r transforms U_B into itself if B is sufficiently large. Therefore by the Brouwer's fixed point theorem, T^r has a fixed point in U_B. We note that the fixed point of T^r is not on the boundary of U_B.

In the following, we shall show that these fixed points of T^r satisfies both $x > r$ and $y > r$ if r is sufficiently small.

We assume that every T^r has a fixed point which satisfies $\min\{x, y\} \leq r$ for all $r > 0$. Then we can construct a sequence $\{w_n\}_{n=1}^\infty = \{(x_n, y_n)^\tau\}_{n=1}^\infty \subset U_B$ which are fixed points of $T^{\frac{1}{n}}$ and satisfy

$$0 < \min\{x_n, y_n\} \leq \frac{1}{n}, \ n \in \mathbb{N}. \tag{3.3}$$

By the Bolzano-Weierstrass theorem, there exists a subsequence $\{w_{n_k}\}_{k=1}^\infty$ such that $w_\infty = (x_\infty, y_\infty)^\tau := \lim_{k\to\infty} w_{n_k} \in U_B$. From (3.3), we see that $x_\infty = 0$ or $y_\infty = 0$. If $x_\infty > 0, y_\infty = 0$, then from (3.1)-(3.2), we have

$$T_1(w_{n_k}) = x_{n_k}, \tag{3.4}$$

$$T_2(w_{n_k}) \leq y_{n_k} \tag{3.5}$$

for sufficiently large n_k. After dividing (3.4) by $x_{n_k} > 0$ and letting n_k go to infinity, then we obtain

$$\Psi_1\left(\frac{\alpha_{11}Q_1x_\infty}{1 + \alpha_{11}x_\infty}, \frac{\alpha_{12}Q_2x_\infty}{1 + \alpha_{12}x_\infty}\right) = 1,$$

which is equivalent to the equation (2.10). Therefore $x_\infty = L_1^*$ follows, where L_1^* is the fifth element of u_1^*. After dividing (3.5) by $y_{n_k} > 0$ and letting n_k go to infinity, we obtain

$$R_{02}^* = \Psi_2(S_1(u_1^*), S_2(u_1^*)) = \Psi_2\left(\frac{\alpha_{11}Q_1L_1^*}{1 + \alpha_{11}L_1^*}, \frac{\alpha_{12}Q_2L_1^*}{1 + \alpha_{12}L_1^*}\right)$$

$$= \Psi_2\left(\frac{\alpha_{11}Q_1x_\infty}{1 + \alpha_{11}x_\infty}, \frac{\alpha_{12}Q_2x_\infty}{1 + \alpha_{12}x_\infty}\right) \leq 1,$$

which contradicts $R_{02}^* > 1$.

Next if $x_\infty = 0, y_\infty > 0$. From the similar manner, we obtain $R_{01}^* \leq 1$, which also contradicts $R_{01}^* > 1$.

At last let $x_\infty = y_\infty = 0$. From (3.1)-(3.2), we have

$$T_1(w_{n_k}) \leq x_{n_k}, \tag{3.6}$$
$$T_2(w_{n_k}) \leq y_{n_k} \tag{3.7}$$

for sufficiently large $n_k \in \mathbb{N}$, again. Since $x_{n_k} > 0$ and $y_{n_k} > 0$, dividing (3.6)-(3.7) by x_{n_k}, y_{n_k} respectively, we have

$$\Psi_i\left(\frac{(\alpha_{11}x_{n_k} + \alpha_{21}y_{n_k})Q_1}{1 + \alpha_{11}x_{n_k} + \alpha_{21}y_{n_k}}, \frac{(\alpha_{12}x_{n_k} + \alpha_{22}y_{n_k})Q_2}{1 + \alpha_{12}x_{n_k} + \alpha_{22}y_{n_k}}\right) \leq 1, \ i = 1, 2.$$

Letting n_k go to infinity, it follows that

$$R_{0i} = \Psi_i(0, 0) \leq 1, \ i = 1, 2.$$

These inequalities contradict our assumption $R_0 = \max_{i=1,2} R_{0i} > 1$. Consequently we know that there does not exist such a sequence $\{w_n\}_{n=1}^{\infty}$. Hence the fixed point of T^r satisfies $x > r, y > r$ for sufficiently small r and it is a fixed point of T with $x > 0, y > 0$. This completes the proof. □

We remark that the conditions $R_{0i}^* > 1$ of Theorem 5 must hold for every single species' steady state if it exist.

We can show the following uniqueness theorem by means of matrix calculation.

Theorem 6. *Suppose the following four relations hold:*

$$\alpha := \alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} \neq 0, \ \beta := \beta_{11}\beta_{22} - \beta_{12}\beta_{21} \neq 0,$$
$$\beta_{11}v_2 \neq \beta_{21}v_1, \ \beta_{12}v_2 \neq \beta_{22}v_1,$$

where $\beta_{ij} := \left(\frac{m_{ij}}{\mu_{ij}} - 1\right) c_{ij}Q_j$. *Then* u_c^* *is uniquely explicitely determined if it exist.*

4 Discussion

In Theorem 5, we have obtained the sufficient condition for the existence of coexistent steady state. Theorem 5 tells us that even if $R_{02} \leq 1$, the coexistent steady state exists provided $R_{01} > 1, R_{01}^* > 1$ and $R_{02}^* > 1$ hold. $R_{02} \leq 1$ and $R_{02}^* > 1$ biologically means that species 2 seems to extinct if it solely exist, but it can maintain its numbers owing to the existence of species 1.

Then we think that even if each species cannot exist solely, two species may coexist owing to the presence of each competitors. Then we conjecture that the coexistent steady state exists if $R_0 \leq 1, R_{01}^* > 1$ and $R_{02}^* > 1$. In short, the

coexistent steady state may exist if all single species' steady states are unstable (i.e. $R_{01}^* > 1$ and $R_{02}^* > 1$).

Our several results of two species and two habitats model can be extended to understand the regional competition community of general number of species and habitats.

References

[1] Y. Iwasa, J. Roughgarden, Dynamics of a metapopulation with space-limited subpopulations, Theor. Popu. Bio. **29**(1986)235-261.

[2] Y. Iwasa, J. Roughgarden, Interspecific competition among metapopulations with space-limited subpopulations, Theor. Popu. Bio. **30**(1986)194-214.

[3] O. Diekmann and J.A.P. Heesterbeek, Mathematical Epidemiology of Infectious Diseases: Model Building, Analysis and Interpretation, John Wiley and Sons, Chichester, 2000.