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The Invadability of a Host in Host-parasitoid Systems*

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Abstract

In this paper, we consider a system of difference equations which describes host-parasitoid interactions in ecosystems. We obtain the criterion for the invadability of a host to the resident host-parasitoid system with a stable periodic orbit. The criterion is useful to investigate the effect of evolution of a host on host-parasitoid systems. Moreover we obtain the necessary condition for the coexistence of an invader host with a resident host and parasitoid. Although two hosts cannot coexist without a parasitoid, there is a possibility that two hosts coexist with the help of a parasitoid.

1 Introduction

The question about the possibility of the coexistence for the interacting species in a community is one of the most important problems in popu-

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lation ecology. The species composing a community can be replaced by the other species, because of the appearance of a mutant species in the community and the invasion of a different species from distant habitats. Therefore, it is necessary not only to investigate the population dynamics of the community composed of fixed member of species, but also to investigate the dynamics involving the effect of evolution. The dynamics of the population model involving the effect of evolution has been investigated (e.g. Godfray *et al.* [5], Metz *et al.* [9], Gatto [4], Hochberg and Holt [6], Abrams and Matsuda [1]).

By analyzing the invadability of the species, Gatto [4] specified the dynamics favored by natural selection. Gatto [4] investigated a single-species population dynamics. But there are many types of interactions between species in natural ecosystem. One of the most popular types is a host-parasitoid interaction. In this paper, we focus on host-parasitoid systems. The purpose of this paper is to obtain the criterion for the invadability of a host to a host-parasitoid system and the condition for the coexistence of the invader host with the resident host and parasitoid. The criterion for the invadability and the condition for the coexistence are useful to investigate the effect of evolution of a host on host-parasitoid systems.

This paper is composed as follows. In Section 2, we give the definition of the invadability and the model used in this paper. In Section 3, we summarize some known results on the invadability of an invader host to a resident host population and on the dynamics after the successful invasion. Further, in Section 4, we investigate the invadability of an invader host to the resident host-parasitoid system and the condition for the coexistence of the invader with the resident host and parasitoid. The final section includes conclusion and contains some future problems.

2 Preliminaries and Model

The model investigated in this paper is described by difference equations, which are used to model the population dynamics with non-overlapping generations such as insects . The dynamics of the system with (resident) k-species is generally given as follows:

$$x_i(n+1) = f_i(x_1(n), \dots, x_k(n)) \quad i = 1, \dots, k, \tag{1}$$

where $x_i(n)$ is the population density at generation n of the i-th species for $i = 1, \ldots, k$. To consider the case where an invader species appears in the resident system (1), the following $(k+1)$-dimensional difference equations are used:

$$x_i(n+1) = g_i(x_1(n), \ldots, x_k(n), x_{k+1}(n)) \quad i = 1, \ldots, k+1, \tag{2}$$

where x_{k+1} is the population density of the invader species, $g_i(x_1(n), \ldots, x_k(n), 0) = f_i(x_1(n), \ldots, x_k(n))$ for $i = 1, \ldots, k$ and $g_{k+1}(x_1(n), \ldots, x_k(n), 0) = 0$, that is, system (2) is reduced to system (1) if the invader x_{k+1} is absent. Hereafter a system without an invader (e.g. Eq.(1)) is called a resident system and one with an invader (e.g. Eq.(2)) is called a full system.

In general, the resident system is said to be invadable by an invader if there is a possibility that the density of the invader which is initially rare can increase. But in this paper we confine ourselves to the resident system which has a stable orbit and define the invadability to such a resident system as follows.

Definition 1. Suppose that the resident system has a stable periodic orbit. Let $\{(x_1(i), \ldots, x_k(i))\}_{i=0,\ldots m-1}$ be a stable orbit of period m. The resident system is said to be invadable by an invader if $\{(x_1(i), \ldots, x_k(i), 0)\}_{i=0,\ldots m-1}$ is unstable with respect to $\mathrm{int}\mathbf{R}_+^{k+1}$.

Note that the invadability does not depend on whether the invader survives after the invasion.

The following is a full system investigated in this paper:

$$\begin{cases} H_1(n+1) &=& r_1 H_1(n) \exp[-\mu_1(H_1(n) + H_2(n))] \exp[-a_1 P(n)] \\ P(n+1) &=& \sum_{i=1}^{2} b_i H_i(n)(1 - \exp[-a_i P(n)]) \\ H_2(n+1) &=& r_2 H_2(n) \exp[-\mu_2(H_1(n) + H_2(n))] \exp[-a_2 P(n)], \end{cases} \tag{3}$$

where $H_1(n)$ and $H_2(n)$ are the population densities of two hosts (one is a resident and the other is an invader), $P(n)$ is the density of the resident parasitoid, r_i is the intrinsic rate of increase of H_i, μ_i is the self-regulation parameter of H_i, a_i is the per capita parasitoid attack rate for H_i and b_i is the number of the parasitoid which develops per H_i. The competitive ability of each type of the hosts is identified by the pair

(μ, r, a, b). Model (3), which is an exploitative competitive model, is the special case of the model which was investigated by Comins and Hassell [3]. They considered the effect of a top predator on the stability of the system composed of competing prey species and showed that predators enhance prey species diversity.

As described above, the resident system is system (3) with $H_1(n) = 0$ or $H_2(n) = 0$. Beddington *et al.* [2] carried out a local stability analysis of a positive equilibrium of the resident system, and showed that its dynamics indicates chaotic oscillations depending on the values of the parameters.

Now we introduce the nondimensional quantities by

$$u_1 = \mu_1 H_1,\ u_2 = \mu_1 H_2,\quad v = a_1 P,\ \alpha = \frac{a_2}{a_1},\ \beta = \frac{\mu_2}{\mu_1},\ c_1 = \frac{b_1}{\mu_1},\ c_2 = \frac{b_2}{\mu_1}.$$

By substituting these quantities, system (3) becomes

$$\begin{cases} u_1(n+1) &= r_1 u_1(n) \exp[-(u_1(n) + u_2(n))] \exp[-v(n)] \\ v(n+1) &= c_1 u_1(n)(1 - \exp[-v(n)]) \\ &\quad + c_2 u_2(n)(1 - \exp[-\alpha v(n)]) \\ u_2(n+1) &= r_2 u_2(n) \exp[-\beta(u_1(n) + u_2(n))] \exp[-\alpha v(n)]. \end{cases} \tag{4}$$

This model contains six positive parameters. In the following section, we investigate the dynamics of this nondimensionalized system. To simplify descriptions, we introduce the following notations : $(4)_{Hoo}$ (or $(4)_{ooH}$) is model (4) with $v(n) = 0$ and $u_2(n) = 0$ (or $u_1(n) = 0$), $(4)_{HoH}$ is one with $v(n) = 0$, $(4)_{HPo}$ (or $(4)_{oPH}$) is one with $u_2(n) = 0$ (or $u_1(n) = 0$).

Before investigating the detailed dynamics of (4), we show that the solution of (4) is bounded. The boundedness is used in the following section.

Theorem 2. The solution of system (4) with $(u_1(0), v(0), u_2(0))^T \in \mathbf{R}^3_+$ is bounded.

Proof. Let $(u_1(n), v(n), u_2(n))^T \in \mathbf{R}^3_+$.
Then $(u_1(n+1), v(n+1), u_2(n+1))^T \in \mathbf{R}^3_+$. We obtain the following inequalities by using the first and third equations of (4):

$$\begin{aligned} u_1(n+1) + u_2(n+1) &\le r_1 u_1(n) \exp[-(u_1(n) + u_2(n))] \\ &\quad + r_2 u_2(n) \exp[-\beta(u_1(n) + u_2(n))] \\ &\le r_M (u_1(n) + u_2(n)) \exp[-\beta_m (u_1(n) + u_2(n))], \end{aligned}$$

where $r_M = \max\{r_1, r_2\}$ and $\beta_m = \min\{1, \beta\}$. Since the function $r_M x \exp[-\beta_m x]$ has a maximum value, $r_M/(\beta_m e)$, we obtain the following inequality:

$$u_1(n+1) + u_2(n+1) \leq \frac{r_M}{\beta_m e}.$$

Since $(u_1(n+1), v(n+1), u_2(n+1))^T \in \mathbf{R}^3_+$, we have $u_1(n+1) \leq r_M/(\beta_m e)$ and $u_2(n+1) \leq r_M/(\beta_m e)$. This shows the boundedness of $u_1(n)$ and $u_2(n)$. We obtain the following inequalities by using the second equation of (4):

$$\begin{aligned} v(n+1) &= c_1 u_1(n)(1 - \exp[-v(n)]) + c_2 u_2(1 - \exp[-\alpha v(n)]) \\ &\leq \sum_{i=1}^{2} c_i u_i(n) \\ &\leq 2c_M \frac{r_M}{\beta_m e}, \end{aligned}$$

where $c_M = \max\{c_1, c_2\}$. This shows the boundedness of $v(n)$.

3 Host-Host System

In this section, we describe some known results on the dynamics of system (4) without a parasitoid, that is $(4)_{HoH}$. Because of the absence of the parasitoid, the resident system is model $(4)_{Hoo}$ or $(4)_{ooH}$, and the full system is $(4)_{HoH}$. Systems $(4)_{Hoo}$ and $(4)_{ooH}$ are called the Ricker model. May and Oster [8] showed that its dynamics indicates stable cycles and chaotic oscillations depending on the values of the parameters.

The following theorems are known results on systems $(4)_{Hoo}$, $(4)_{ooH}$ and $(4)_{HoH}$ (see May and Oster [8], Gatto [4], Kocic and Ladas [7]).

Theorem 3. Let $\{u_i(n)\}$ $(i = 1, 2)$ be solutions of system $(4)_{Hoo}$ and $(4)_{ooH}$, respectively. If $\ln r_i > 0$, then $\lim_{n\to\infty} \inf u_i(n) > 0$ for any $u_i(0) > 0$ $(i = 1, 2)$.

From this theorem, we can see that the host u_1 and u_2, when they are isolated from each other, do not go to extinction if $\ln r_1 > 0$ and $\ln r_2 > 0$ respectively.

Theorem 4. Let $\{(u_1(n), u_2(n))\}$ be a solution of system $(4)_{HoH}$ and assume that $\ln r_1 > 0$ and $\ln r_2 > 0$.

(i) If $\ln r_2/(\beta \ln r_1) > 1$, then $\lim_{n\to\infty} u_1(n) = 0$ and $\lim_{n\to\infty} \inf u_2(n) > 0$ for any $(u_1(0), u_2(0))^T \in \text{int}\mathbf{R}^2_+$.

(ii) If $\ln r_2/(\beta \ln r_1) < 1$, then $\lim_{n\to\infty} u_2(n) = 0$ and $\lim_{n\to\infty} \inf u_1(n) > 0$ for any $(u_1(0), u_2(0))^T \in \text{int}\mathbf{R}^2_+$.

Theorem 4 gives the dynamics of system $(4)_{HoH}$ in the case where each host does not go to extinction when two hosts are isolated. In this case, we can see that if the invader host u_2 with the parameters satisfying $\ln r_2/(\beta \ln r_1) > 1$ appears in the resident system, the resident host u_1 goes to extinction and the invader host u_2 can survive. This shows that the resident system is replaced by u_2. Since $\lim_{n\to\infty} \inf u_2(n) > 0$ for any $(u_1(0), u_2(0))^T \in \text{int}\mathbf{R}^2_+$, the condition $\ln r_2/(\beta \ln r_1) > 1$ makes a stable periodic orbit of system $(4)_{Hoo}$ to be unstable with respect to $\text{int}\mathbf{R}^2_+$. According to Definition 1, the condition $\ln r_2/(\beta \ln r_1) > 1$ is the criterion for the invadability to the resident system $(4)_{Hoo}$ with a stable periodic orbit. In Definition 1, we did not define the invadability to the resident system with a non-periodic orbit. But the non-periodic orbit of $(4)_{Hoo}$ is shown to be unstable with respect to $\text{int}\mathbf{R}^2_+$ and $(4)_{HoH}$, if $\ln r_2/(\beta \ln r_1) > 1$. Under this extended sense of the invadability, system $(4)_{Hoo}$ with a non-periodic orbit is also invadable if $\ln r_2/(\beta \ln r_1) > 1$. The invadable set of the parameters in this sense is shown in Fig.1. The resident host u_1 and the invader host u_2 cannot coexist, except for the special case where the parameters satisfy $\ln r_2/(\beta \ln r_1) = 1$. We can see that to invade the resident system without the parasitoid the invader must be superior to the resident host at least in either the ability on the intrinsic rate of increase or on the self-regulation, that is $\ln r_2 > \ln r_1$ or $\beta < 1$. Fig.2 shows an example of the temporal fluctuation of the population density for $(4)_{HoH}$ satisfying $\ln r_1 > 0$, $\ln r_2 > 0$ and $\ln r_2/(\beta \ln r_1) > 1$.

4 Host-Parasitoid-Host System

In this section, we consider the case where the resident system is composed of a host and a parasitoid. Then the resident system is $(4)_{HPo}$ or $(4)_{oPH}$, and the full system is (4).

Numerical investigations show that the resident system $(4)_{HPo}$ and system $(4)_{oPH}$ have stable cycles depending on the parameters (see Beddington *et al.* [2]). The following theorem describes the necessary and sufficient condition for the resident system to have a periodic orbit of period m.

Theorem 5. (i) The system $(4)_{HPo}$ has a periodic orbit of period m if and only if there exists an orbit $\{u_1(i), v(i)\}_{i=0,\dots,m-1}$ $((u_1(i), v(i)) \neq (u_1(j), v(j)); i, j \in \{0, \dots m-1\}, i \neq j)$ satisfying the following equations:

$$\ln r_1 = \frac{\sum_{i=0}^{m-1} u_1(i)}{m} + \frac{\sum_{i=0}^{m-1} v(i)}{m} \quad \text{and} \quad v(0) = v(m). \tag{5}$$

(ii) The system $(4)_{oPH}$ has a periodic orbit of period m if and only if there exists an orbit $\{v(i), u_2(i)\}_{i=0,\dots,m-1}$ $((v(i), u_2(i)) \neq (v(j), u_2(j)); i, j \in \{0, \dots m-1\}, i \neq j)$ satisfying the following equations:

$$\ln r_2 = \beta\frac{\sum_{i=0}^{m-1} u_2(i)}{m} + \alpha\frac{\sum_{i=0}^{m-1} v(i)}{m} \quad \text{and} \quad v(0) = v(m). \tag{6}$$

Proof. (i) First, let $\{(u_1(i), v(i))\}_{i=0,\cdots,m-1}$ be a periodic orbit of period m of $(4)_{HPo}$. Then we can obtain the following equations by using the first equation of (4).

$$\begin{aligned}
u_1(1) &= r_1 u_1(0) \exp[-u_1(0)] \exp[-v(0)] \\
u_1(2) &= r_1 u_1(1) \exp[-u_1(1)] \exp[-v(1)] \\
&= r_1\{r_1 u_1(0) \exp[-v(0)] \exp[-u_1(0)]\} \exp[-u_1(1)] \exp[-v(1)] \\
&= r_1^2 u_1(0) \prod_{i=0}^{1} \exp[-u_1(i)] \exp[-v(i)] \\
&\vdots \\
u_1(m) &= r_1^m u_1(0) \prod_{i=0}^{m-1} \exp[-u_1(i)] \exp[-v(i)].
\end{aligned} \tag{7}$$

Using $u_1(m) = u_1(0)$ in the above, we obtain (5).

Conversely, from (5) and (7), we have $u_1(m) = u_1(0)$. Then we can see with the assumption $v(m) = v(0)$ that the orbit is periodic with period m.

(ii) It can be proved in similar way as (i).

These conditions (5) and (6) are used to obtain the invadable set of the parameters.

4.1 Invadability

Theorem 6. (i) Let $\{(u_1(i), v(i))\}_{i=0,\dots,m-1}$ be a stable periodic orbit of period m of the resident system $(4)_{HPo}$. If the parameters satisfy the following condition:

$$\ln r_2 > \beta \frac{\sum_{i=0}^{m-1} u_1(i)}{m} + \alpha \frac{\sum_{i=0}^{m-1} v(i)}{m}, \tag{8}$$

then the resident system $(4)_{HPo}$ is invadable by the invader u_2.

(ii) Let $\{(v(i), u_2(i))\}_{i=0,\dots,m-1}$ be a stable periodic orbit of period m of the resident system $(4)_{oPH}$. If the parameters satisfy the following condition:

$$\ln r_1 > \frac{\sum_{i=0}^{m-1} u_2(i)}{m} + \frac{\sum_{i=0}^{m-1} v(i)}{m},$$

then the resident system $(4)_{oPH}$ is invadable by the invader u_1.

Proof. To prove this theorem, we investigate the stability of the periodic orbit $\{\mathbf{p}(i)\}_{i=0,\dots,m-1} = \{(u_1(i), v(i), 0)\}_{i=0,\dots,m-1}$ of system (4). The Jacobian matrix J of (4) evaluated at the periodic orbit $\{\mathbf{p}(i)\}_{i=0,\dots,m-1}$ is given by

$$J = D\mathbf{F}^m(\mathbf{p}(0)) = D\mathbf{F}(\mathbf{p}(m-1)) \cdots D\mathbf{F}(\mathbf{p}(1)) D\mathbf{F}(\mathbf{p}(0))$$

where

$$\begin{aligned}
\mathbf{F}(x,y,z) &= \begin{pmatrix} F_1(x,y,z) \\ F_2(x,y,z) \\ F_3(x,y,z) \end{pmatrix} \\
&= \begin{pmatrix} r_1 x \exp[-(x+z)] \exp[-y] \\ c_1 x(1-\exp[-y]) + c_2 z(1-\exp[-\alpha y]) \\ r_2 z \exp[-\beta(x+z)] \exp[-\alpha y] \end{pmatrix} \\
\mathbf{F}^m(\mathbf{p}(i)) &= \mathbf{F}(\mathbf{F}(\cdots \mathbf{F}(\mathbf{p}(i)))) \\
D\mathbf{F}(\mathbf{p}(i)) &= \begin{pmatrix} \left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{p}(i)} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{p}(i)} & \left.\frac{\partial F_1}{\partial z}\right|_{\mathbf{p}(i)} \\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{p}(i)} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{p}(i)} & \left.\frac{\partial F_2}{\partial z}\right|_{\mathbf{p}(i)} \\ \left.\frac{\partial F_3}{\partial x}\right|_{\mathbf{p}(i)} & \left.\frac{\partial F_3}{\partial y}\right|_{\mathbf{p}(i)} & \left.\frac{\partial F_3}{\partial z}\right|_{\mathbf{p}(i)} \end{pmatrix}.
\end{aligned}$$

Then J is written as

$$J = \begin{pmatrix} \prod_{i=0}^{m-1} A_i & B \\ 0 & \prod_{i=0}^{m-1} C_i \end{pmatrix}$$

where

$$A_i = \begin{pmatrix} \left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{p}(i)} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{p}(i)} \\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{p}(i)} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{p}(i)} \end{pmatrix}, \quad C_i = \left.\frac{\partial F_3}{\partial z}\right|_{\mathbf{p}(i)},$$

B is a suitable 2×1 matrix and 0 is a 1×2 zero matrix. Then the stability of the periodic orbit $\{\mathbf{p}(i)\}_{i=0,\ldots,m-1}$ depends only on the value of $\prod_{i=0}^{m-1} C_i$, because the periodic orbit $\{(u_1(i), v(i))\}_{i=0,\ldots,m-1}$ of system $(4)_{HPo}$ is assumed to be stable (the absolute value of eigenvalues of the matrix $\prod_{i=0}^{m-1} A_i$ is smaller than unity). If

$$\left| \prod_{i=0}^{m-1} \left.\frac{\partial F_3}{\partial z}\right|_{\mathbf{p}(i)} \right| = \prod_{i=0}^{m-1} r_2 \exp[-\beta u_1(i)] \exp[-\alpha v(i)] > 1,$$

that is, if

$$\sum_{i=0}^{m-1} (\ln r_2 - \beta u_1(i) - \alpha v(i)) > 0,$$

the periodic orbit $\{\mathbf{p}(i)\}_{i=0,\ldots,m-1}$ is unstable with respect to u_2-direction and the resident system is invadable by the invader u_2.

(ii) It can be proved in similar way as (i).

The boundary for the invadability to the resident system $(4)_{HPo}$ with a stable periodic orbit of period m is given by (8) with an equality instead of an inequality. The boundary is rewritten as follows by using the necessary condition for the resident system to have a periodic orbit (see Theorem 5 (i)):

$$\frac{1}{\beta}\frac{\ln r_2}{\ln r_1} = \frac{\bar{v}_m}{\bar{u}_m + \bar{v}_m}\frac{\alpha}{\beta} + \frac{\bar{u}_m}{\bar{u}_m + \bar{v}_m}, \tag{9}$$

where $\bar{u}_m = \sum_{i=0}^{m-1} u_1(i)/m$ and $\bar{v}_m = \sum_{i=0}^{m-1} v(i)/m$. The boundary (9), which is the straight line passing through the point $(1, 1)$ with the intercept $\bar{u}_m/(\bar{u}_m + \bar{v}_m)$ and the positive slope $\bar{v}_m/(\bar{u}_m + \bar{v}_m)$ in the $\alpha/\beta - \ln r_2/(\beta \ln r_1)$ parameter space, is shown in Fig.3. From Fig.3, we can see that the superiority of the invader u_2 in the two-host system without a parasitoid (that is, $\ln r_2/(\beta \ln r_1) > 1$, see Theorem 4 (i)) is not sufficient for u_2 to invade the resident system $(4)_{HPo}$.

To obtain the criterion for invadability to the resident system with a non-periodic orbit is a future problem.

4.2 Non-coexistence

Now we examine the condition for the coexistence of three species. From the following theorem, we obtain the necessary condition.

Theorem 7. Let $\{(u_1(n), v(n), u_2(n))\}$ be a solution of system (4).
(i) If $\ln r_2/(\beta \ln r_1) > 1$ and $\alpha/\beta < 1$, then $\lim_{n\to\infty} u_1(n) = 0$ for any $(u_1(0), v(0), u_2(0))^T \in \mathrm{int}\mathbf{R}^3_+$.

(ii) If $\ln r_2/(\beta \ln r_1) < 1$ and $\alpha/\beta > 1$, then $\lim_{n\to\infty} u_2(n) = 0$ for any $(u_1(0), v(0), u_2(0))^T \in \mathrm{int}\mathbf{R}^3_+$.

Proof. To prove that $\lim_{n\to\infty} u_1(n) = 0$ globally in case (i), consider the dynamics of the ratio $u_1(n)/u_2(n)^{1/\beta}$. We can obtain the following equation by using the first and third equations of (4):

$$\begin{aligned}\frac{u_1(n+1)}{u_2(n+1)^{1/\beta}} &= \frac{r_1}{r_2^{1/\beta}}\frac{u_1(n)}{u_2(n)^{1/\beta}}\exp[-(1-\frac{\alpha}{\beta})v(n)]\\ &= \exp[\ln r_1 - \frac{\ln r_2}{\beta}]\exp[-(1-\frac{\alpha}{\beta})v(n)]\frac{u_1(n)}{u_2(n)^{1/\beta}}.\end{aligned}$$

Using the condition on the parameters ($\ln r_2/(\beta \ln r_1) > 1$ and $\alpha/\beta < 1$), we can see that the following equation holds:

$$\lim_{n\to\infty}\frac{u_1(n)}{u_2(n)^{1/\beta}} = 0.$$

By Theorem 2 (the boundedness of $u_2(n)$), we have

$$\lim_{n\to\infty} u_1(n) = 0.$$

We can similarly prove that $\lim_{n\to\infty} u_2(n) = 0$ globally in case (ii).

From this theorem and Theorem 6, we see that if u_2 with the parameters satisfying the condition (i) appears in the resident system $(4)_{HPo}$ with a stable periodic orbit, u_2 can invade and the resident host u_1 goes to extinction.

Theorem 8. Suppose systems $(4)_{HPo}$ and $(4)_{oPH}$ have stable periodic orbits $\{(u_1(i), v_1(i))\}_{i=0,\dots,m_1-1}$ and $\{(v_2(i), u_2(i))\}_{i=0,\dots,m_2-1}$ respectively, where m_1 and m_2 are periods of each orbit.

(i) If $\alpha/\beta > 1$ and $\ln r_2/(\alpha \ln r_1) > 1$, then the periodic orbit $\{(u_1(i), v_1(i), 0)\}_{i=0,\dots,m_1-1}$ is unstable and $\{(0, v_2(i), u_2(i))\}_{i=0,\dots,m_2-1}$ is stable in system (4).

(ii) If $\alpha/\beta < 1$ and $\ln r_2/(\alpha \ln r_1) < 1$, then the periodic orbit $\{(u_1(i), v_1(i), 0)\}_{i=0,\dots,m_1-1}$ is stable and $\{(0, v_2(i), u_2(i))\}_{i=0,\dots,m_2-1}$ is unstable in system (4).

Proof. (i) From the necessary condition for system $(4)_{HPo}$ to have a periodic orbit of period m_1 (see Theorem 5), the following equation holds:

$$\ln r_1 = \frac{\sum_{i=1}^{m_1-1} u_1(i)}{m_1} + \frac{\sum_{i=1}^{m_1-1} v_1(i)}{m_1}. \tag{10}$$

Then

$$\begin{aligned} &\ln r_2 - \beta\frac{\sum_{i=1}^{m_1-1} u_1(i)}{m_1} - \alpha\frac{\sum_{i=1}^{m_1-1} v_1(i)}{m_1} \\ > \;& \ln r_2 - \alpha(\frac{\sum_{i=1}^{m_1-1} u_1(i)}{m_1} + \frac{\sum_{i=1}^{m_1-1} v_1(i)}{m_1} \\ = \;& \ln r_2 - \alpha \ln r_1 > 0, \end{aligned} \tag{11}$$

where (10) and the assumptions $\alpha/\beta > 1$ and $\ln r_2/(\alpha \ln r_1) > 1$ are used. From Theorem 6, this shows that $\{(u_1(i), v_1(i), 0)\}_{i=0,\dots,m_1-1}$ is unstable in system (4).

Now, we investigate the invadability of u_1 to system $(4)_{oPH}$. From the necessary condition for system $(4)_{oPH}$ to have a periodic orbit of period m_2 (see Eq.(6)), the following equation holds:

$$\ln r_2 = \beta\frac{\sum_{i=1}^{m_2-1} u_2(i)}{m_2} + \alpha\frac{\sum_{i=1}^{m_2-1} v_2(i)}{m_2}.$$

Using the above equation, we can obtain the following inequalities:

$$\ln r_1 - \frac{\sum_{i=0}^{m_2-1} v_2(i)}{m_2} - \frac{\sum_{i=0}^{m_2-1} u_2(i)}{m_2}$$

$$= \ln r_1 - \frac{1}{\alpha}(\ln r_2 - \beta\frac{\sum_{i=0}^{m_2-1} u_2(i)}{m_2}) - \frac{\sum_{i=0}^{m_2-1} u_2(i)}{m_2}$$

$$= (\ln r_1 - \frac{\ln r_2}{\alpha}) + (\frac{\beta}{\alpha} - 1)\frac{\sum_{i=0}^{m_2-1} u_2(i)}{m_2} < 0.$$

where the assumptions $\alpha/\beta > 1$ and $\ln r_2/(\alpha \ln r_1) > 1$ are also used. This result shows that $\{(0, v_2(i), u_2(i))\}_{i=0,\ldots,m_2-1}$ is stable in system (4).

(ii) It can be proved in similar way as (i).

Although the above theorem gives the local dynamical properties of system (4), it is expected by numerical investigations that the properties are global. Fig.4 shows an example that the resident host goes to extinction and the $(v(n), u_2(n))$ converges to the equilibrium point of system $(4)_{oPH}$. Moreover it is expected by numerical investigations that the following statement is true: if condition (i) in Theorem 8 holds, system $(4)_{HPo}$ has a stable equilibrium (u_1, v_1) with respect to $\mathrm{int}\mathbf{R}^2_+$ and system $(4)_{oPH}$ has a strange attractor, then the orbit with $(u_1(0), v(0), u_2(0)) \in \mathrm{int}\mathbf{R}^3_+$ converges to the strange attractor of $(4)_{oPH}$ (see an example given in Fig.5).

Summarizing the results in the above theorems leads to Fig.6. From Fig.6, we see that the parameters must belong to the region (R3)-i or (R4)-i for three species in system (4) to coexist when systems $(4)_{HPo}$ and $(4)_{oPH}$ have a stable periodic orbit. Fig.7 shows an example of the coexistence of three species. In the case where three species coexist, the replacement of the host does not result from the invasion of a host, but the enhancement of the species diversity results from the invasion. Note that the coexistence of two hosts does not occur without the parasitoid. If the parameters belong to the region (R3)-ii or (R4)-ii in Fig.6, there is a possibility that system (4) is bistable (see Fig.8). The bistability means that two hosts are mutually non-invadable. That is, the system with the host which coexists with the parasitoid is not invadable by the other host.

5 Conclusion

We have investigated the invadability of the host in the resident host-parasitoid system with a stable periodic orbit and obtained the criterion for the invadability. The criterion for the invadability obtained in this paper can be applied only when the resident system has a stable periodic orbit. To obtain the criterion for the resident system containing a non-periodic orbit is a future problem.

In Theorem 7, the sufficient conditions for the non-coexistence of three species (two hosts and one parasitoid) are obtained. Theorem 8 and numerical investigations also give the sufficient condition for non-coexistence of three species in the case where system $(4)_{HPo}$ and $(4)_{oPH}$ have stable periodic orbits. We see that if the parameters do not satisfy these conditions, there is a possibility that two hosts coexist with the help of a parasitoid. Note that the two host cannot coexist without a parasitoid (Gatto [4], Kocic and Ladas [7]).

We cannot know from these theorems whether the remaining host and parasitoid coexist or not, after the resident host goes to extinction. But numerical investigations suggest that if the invader host and the parasitoid coexist in system $(4)_{oPH}$, they also coexist after the resident host goes to extinction.

By using the results obtained in this paper, we can investigate the effect of evolution of the host on host-parasitoid systems as follows. First, we check if the resident host-parasitoid system has a stable positive equilibrium. Second, we obtain the host which can invade the resident system by using the criterion for the invadability. Third, if the parameters satisfy the sufficient condition for the non-coexistence of three species, which was obtained in this paper, we see that the resident host goes to extinction. Hence, the effect of evolution of host on host-parasitoid system is examined by investigating the dynamics of the system composed of the invader host and the parasitoid. If three species coexist, we should further investigate the invadability of a host to the resident system composed of two hosts and a parasitoid. It is a future problem.

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Figure legends:

Figure 1: The $\beta - \frac{\ln r_2}{\ln r_1}$ parameter space. Here $\ln r_1 > 0$ and $\ln r_2 > 0$. The straight line is the boundary of the invadability, $\frac{\ln r_2}{\ln r_1 = \beta.}$ The hatched region is the invadable set of the parameters. if the parameters belong to

the invadable set, the resident system $(4)_{Hoo}$ is invadable by the invader u_2 and $\lim_{n\to+\infty} u_1(n) = 0$. if the parameters belong to the region which is not hatched, the resident system $(4)_{Hoo}$ is not invadable by the invader u_2 and $\lim_{n\to+\infty} u_2(n) = 0$.

Figure 2: An example of the temporal fluctuations of the population density of system $(4)_{HoH}$ with the parameters belonging to hatched region in Fig.1. The resident system $(4)_{Hoo}$ and system $(4)_{HoH}$ have a stable equilibrium, respectively. The parameters are $\ln r_1 = 1, \ln r_2 = 1.23$ and $\beta = 1$. The initial condition is $(u_1(0), u_2(0)) = (1, 0.000001)$. After the invasion of $u_2, \lim_{n\to+\infty} u_1(n) = 0$ and $u_2(n)$ converges to the equilibrium of system $(4)_{ooH}$.

Figure 3: The $\frac{\alpha}{\beta} - \frac{\ln r_2}{(\beta \ln r_1)}$ parameter space. The straight line is the boundary of the invadability to the resident system $(4)_{HPo}$ with a stable periodic orbit of period m (Eq.(9)). The hatched region is the invadable set of the parameters. If the parameters belong to the invadable set, the resident system $(4)_{HPo}$ is invadable by u_2. If not, $(4)_{HPo}$ is not invadable by u_2.

Figure 4: An example of the temporal fluctuations of the population density of system (4). The resident system $(4)_{HPo}$ has a stable equilibrium $(u_1, v_1) = (0.605183, 0.394817)$. System $(4)_{oPH}$ also has a stable equilibrium $(u_2, v_2) = (0.563833, 0.573400)$. The parameters satisfy $\frac{\alpha}{\beta} > 1$ and $\frac{\ln r_2}{(\alpha \ln r_1)} > 1$. After the invasion of $u_2, \lim_{n\to+\infty} u_1(n) = 0$ and $(v(n), u_2(n))$ converges to the equilibrium of system $(4)_{oPH}$. The parameters are $\ln r_1 = 1, \ln r_2 = 1.25, \beta = 1, \alpha = 1.2, c_1 = 2$ and $c_2 = 2$. The initial condition is $(u_1(0), v(0), u_2(0)) = (0.605183, 0.394817, 0.000001)$.

Figure 5: An example of the temporal fluctuations of the population density of system (4). The resident system $(4)_{HPo}$ has a stable equilibrium $(u_1, v_1) = (0.605183, 0.394817)$. System $(4)_{oPH}$ has a strange attractor. The parameters satisfy $\frac{\alpha}{\beta} > 1$ and $\frac{\ln r_2}{(\alpha \ln r_1)} > 1$. After the invasion of $u_2, \lim_{n\to+\infty} u_1(n) = 0$ and $(v(n), u_2(n))$ tends to the strange attractor of system $(4)_{oPH}$. The parameters are $\ln r_1 = 1, \ln r_2 = 2.1, \beta = 1, \alpha = 1.5, c_1 = 2$ and $c_2 = 2$. The initial condition is $(u_1(0), v(0), u_2(0)) = (0.605183, 0.394817, 0.000001)$.

Figure 6: The $\frac{\alpha}{\beta}-\frac{\ln r_2}{(\beta \ln r_1)}$ parameter space. The straight line is the boundary of the invadability to the resident system $(4)_{HPo}$ with a periodic orbit of period m (Eq.(9)). The sufficient condition for the non-coexistence of three species given in Theorem 7, $\{\frac{\ln r_2}{(\beta \ln r_1)} > 1$ and $\frac{\alpha}{\beta} < 1\}$ or $\{\frac{\ln r_2}{(\beta \ln r_1)} < 1$ and $\frac{\alpha}{\beta} > 1\}$ corresponds to the regions (R_1) and (R_6) respectively. The sufficient condition for the non-coexistence of three species given in Theorem 8, $\{\frac{\alpha}{\beta} > 1$ and $\frac{\ln r_2}{(\alpha \ln r_1)} > 1\}$ or $\{\frac{\alpha}{\beta} < 1$ and $\frac{\ln r_2}{(\alpha \ln r_1)} < 1\}$ corresponds to the regions (R_2) and (R_5) respectively. Hence the coexistence of three species is possible only for the parameters belonging to the regions $(R_3)-i$ and $(R_4)-i$. By numerical investigations we see that three species coexist if the parameters belong to the hatched region in the regions $(R_3)-i$ and $(R_4)-i$. The coexistence is determined by the criterion that all species have average population densities during 100 iterations after 10^4 initial iterations greater than 10^-4 when the initial condition is $(u_1(0), v(0), u_2(0)) = (0.1, 0.1, 0.1)$. The parameters are $\ln r_1 = 1, \beta = 1, c_1 = 2$ and $c_2 = 2$. The resident system $(4)_{HPo}$ has an equilibrium $(0.605183, 0.394817)$.

Figure 7: An example of the temporal fluctuations of the population density of system (4) with the parameters belonging to the hatched region in Fig.6. Three species coexist with a stable equilibrium. The parameters are $\ln r_1 = 1, \ln r_2 = 1.23\beta = 1, \alpha = 1.5, c_1 = 2$ and $c_2 = 2$. The initial condition is $(u_1(0), v(0), u_2(0)) = (0.605183, 0.394817, 0.000001)$.

Figure 8: The temporal fluctuations in the phase space (u_1, v, u_2) for (4) with the parameter belonging to $(R_4)-ii$. The orbits $\{u_1(i), v(i), u_2(i)\}_{i=0,\cdots,1000}$ with the initial condition $(u_1(0), v(0), u_2(0)) = (1, 1, 0.01)$ and $\{u_1(i), v(i), u_2(i)\}_{i=1000,\cdots,2000}$ with the initial condition $(u_1(0), v(0), u_2(0)) = (0.01, 1, 1)$ are shown. The former, of which points are connected with lines, converges to a positive equilibrium of system $(4)_{HPo}$ and the latter tends to an attractor of system $(4)_oPH$. The system (4) is bistable. The parameters are $\ln r_1 = 1, \ln r_2 = 1.35\beta = 1, \alpha = 1.89, c_1 = 2$ and $c_2 = 2$.

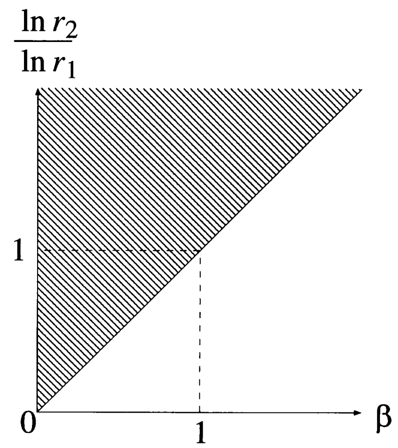
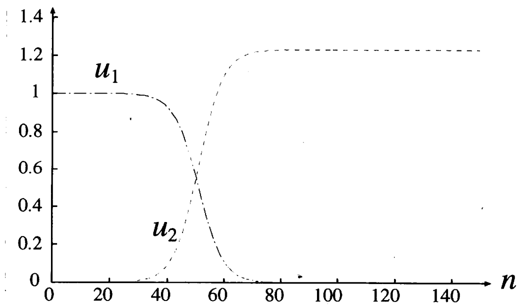


Fig. No. 1



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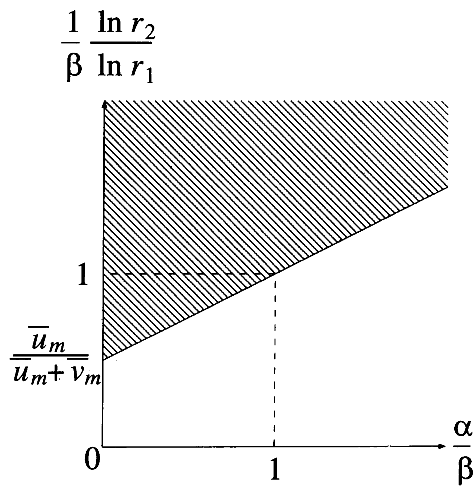

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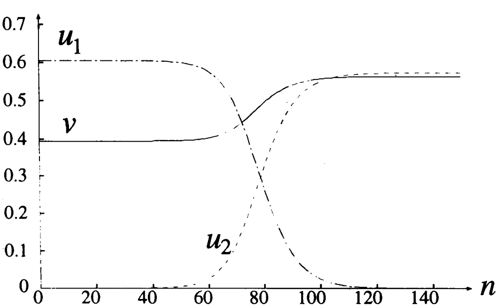

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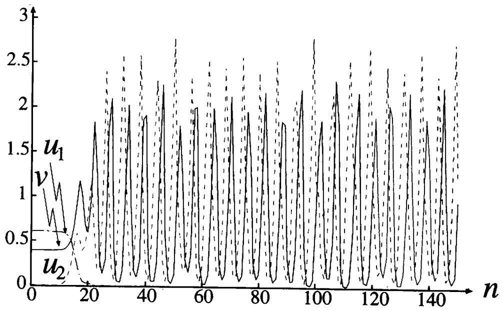

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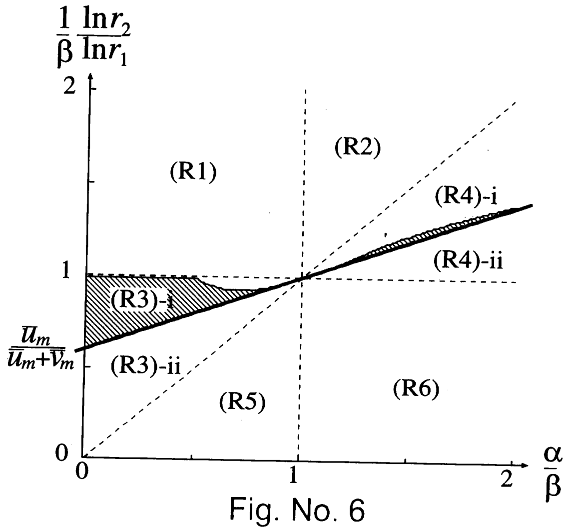

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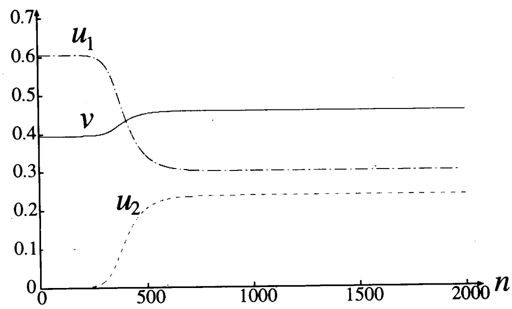

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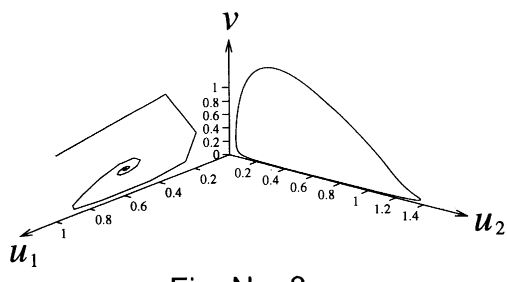

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