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Effect of a Parasitoid on Permanence of Competing Hosts*

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Abstract. In this paper we consider the permanence of the system composed of two hosts and one parasitoid focusing on dynamics of a subsystem, a two-host system. The subsystem is classified into four cases, namely, dominance, coexistence, bistability and special case. It is shown that the system with dominance or coexistence subsystem can be permanent by the introduction of a parasitoid. Sufficient conditions for the permanence are given with the forms which can be easily checked. It is also shown that the systems with bistability and special subsystems are difficult to be permanent.

1. Introduction

In this paper, we consider the dynamics of the following system:

$$\begin{cases} H_1(t+1) = & \lambda_1 H_1(t)\exp[-\sum_{j=1}^{2}\mu_{1j}H_j(t)]\exp[-a_1P(t)], \\ H_2(t+1) = & \lambda_2 H_2(t)\exp[-\sum_{j=1}^{2}\mu_{2j}H_j(t)]\exp[-a_2P(t)]. \\ P(t+1) = & \sum_{j=1}^{2} b_jH_j(t)(1-\exp[-a_jP(t)]), \end{cases} \tag{1}$$

where $\lambda_i > 1$, $\mu_{ij} > 0$, $a_i > 0$, $b_i > 0$ $(i, j \in \{1, 2\})$ and $(H_1(0), H_2(0), P(0)) \in \mathbb{R}^3_+ := \{(H_1, H_2, P) \in \mathbb{R}^3 : H_1 \geq 0, H_2 \geq 0, P \geq 0\}$, $t \in \mathbb{Z}_+ := \{0, 1, 2, \dots\}$. This system gives population dynamics of two hosts and one parasitoid which interact with each other. The population densities of the two hosts at generation t are denoted by $H_1(t)$ and $H_2(t)$. The population density of the parasitoid at generation t is denoted by $P(t)$. The system was proposed by Comins and

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Hassell [1] to investigate an effect of a parasitoid on the diversity of hosts. By examining stability of a positive fixed point, which stands for coexistence state of three species they showed that three species can coexist. However, it is known that even if a positive fixed point is stable, it is possible that population density converges to zero depending on initial population densities (see Neubert and Kot [9]). Therefore, we use permanence, which ensures that there are no initial population densities which result to extinction of species, as an evaluation for coexistence, and consider the effect of a parasitoid on the coexistence of two hosts.

This paper is organized as follows. In Sec. 2, some mathematical notations are introduced. In Sec. 3, the dynamics of a two-host system, which is a subsystem of (1), is investigated. The dynamics of the two-host system is classified into four types. Sec. 4 considers permanence of the full system (1) focusing on the dynamics of the two-host system. Sec. 5 contains future problems.

2. Preliminaries

We introduce some notations about a discrete dynamical system $f : X \to X$. The orbit starting at $\mathbf{x}$ is the set

$$\gamma_+(\mathbf{x}) = \{\mathbf{y} : \mathbf{y} = f^t(\mathbf{x}) \quad \text{for some} \quad t \in \mathbb{Z}_+\}.$$

The omega limit set is defined by

$$\Omega(\mathbf{x}) = \{\mathbf{y} : f^{t_j}(\mathbf{x}) \to \mathbf{y} \quad \text{for some sequence} \quad t_j \to \infty\}.$$

For a subset $X_0 \subset X$ put

$$\gamma_+(X_0) = \bigcup_{\mathbf{x}\in X_0} \gamma_+(\mathbf{x}), \quad \Omega(X_0) = \bigcup_{\mathbf{x}\in X_0} \Omega(\mathbf{x}).$$

X_0 is said to be *forward invariant* if $f(X_0) \subset X_0$ and *strictly forward invariant* if $f(\overline{X_0}) \subset \ \text{int}\, X_0$. The set M is *absorbing* for X_0 if it is forward invariant and $\gamma_+(\mathbf{x}) \cap M \neq \emptyset$ for every $\mathbf{x} \in X_0$. The system f is said to be dissipative if there exists a compact set $X_0 \subset X$ such that for all $\mathbf{x} \in X$ there exists a $T = T(\mathbf{x})$ satisfying $f^t(\mathbf{x}) \in X_0$ for all $t \geq T$. If the system f is still dissipative for a sufficiently small change in its parameters, then the system is said to be *robustly dissipative*. Permanence is defined as follows:

Definition 1. *Let $X = \mathbb{R}^n_+$. The system f is said to be permanent if there exists a compact absorbing set $M \subset \text{int}\mathbb{R}^n_+$ for $\text{int}\mathbb{R}^n_+$.*

If the system f is still permanent for a sufficiently small change in its parameters, then the system is said to be *robustly permanent*.

3. Tow-host Systems

The dynamics of System (1) without a parasitoid is given by the following two-species competitive system:

$$\begin{cases} H_1(t+1) = & \lambda_1 H_1(t)\exp[-\mu_{11}H_1(t) - \mu_{12}H_2(t)], \\ H_2(t+1) = & \lambda_2 H_2(t)\exp[-\mu_{21}H_1(t) - \mu_{22}H_2(t)]. \end{cases} \tag{2}$$

The system is a special case of the following generalized Lotka-Volterra type difference equation:

$$H_i(t+1) = \lambda_i H_i(t)\exp\big[-\sum_{j=1}^{n}\mu_{ij}H_j(t)\big], \quad i \in \{1,\dots,n\}, \tag{3}$$

where $\lambda_i > 0$ and $\mu_{ij} \in \mathbb{R}$ $(i, j \in \{1,\dots,n\})$. The dynamics of (3) has been investigated in several papers. By using the results in the papers, we classify the dynamics of System (2) as follows. The qualitative property of the dynamics of System (2) is divided into four cases according to the value of the parameters, $\lambda_i, \mu_{ij} (i, j \in \{1, 2\})$ (see Fig. 1). The first case is dominance, where the two hosts cannot coexist. A certain host goes to extinction irrespective of the initial population densities. The second case is coexistence, where two hosts coexist in the sense of permanence. The third case is bistability, where both of the hosts can go to extinction depending on the initial population densities. The final case is very special. In this case, the system has an infinite number of fixed points in $\operatorname{int}\mathbb{R}^2_+$. Hereafter we consider each case in detail.

3.1. Dominance

The case of dominance of System (3) with $\mu_{ij} > 0$ $(i, j \in \{1,\dots,n\})$ was investigated by Franke and Yakubu [2]. The dominance is defined as follows:

Definition 2. *In System* (3) *with* $\mu_{ij} > 0$ *(*$i, j \in \{1,\dots,n\}$*) , the host* H_i *is said to be dominated if there exists a* $k \in \{1,\dots,n\}\setminus\{i\}$ *such that* N_i *is a proper subset of* N_k*, where*

$$N_l := \{(H_1,\dots,H_n) \in \mathbb{R}^n_+ : \lambda_l \exp\big[-\sum_{j=1}^{n}\mu_{lj}H_j\big] \geq 1\}.$$

System (3) has the following dynamical property about the dominance:

Lemma 3. (Franke and Yakubu [2, Theorem 3.1]) *If in System* (3) *with* $\mu_{ij} > 0$ *(*$i, j \in \{1,\dots,n\}$*) the host* H_i *is dominated, then* $\Omega(\operatorname{int}\mathbb{R}^n_+) \subset \{(H_1,\dots,H_n) \in \mathbb{R}^n_+ : H_i = 0\}$.

By applying the lemma to (2), we obtain the following corollary:

Corollary 4. *Let* $\{(H_1(t), H_2(t))\}_{t\in\mathbb{Z}_+}$ *be a solution of System* (2). *Suppose that*

$$\frac{\ln\lambda_i}{\mu_{ii}} \leq \frac{\ln\lambda_j}{\mu_{ji}} \quad \textit{and} \quad \frac{\ln\lambda_j}{\mu_{jj}} \geq \frac{\ln\lambda_i}{\mu_{ij}} \tag{4}$$

with at least one strict inequality, where $i, j \in \{1, 2\}$ *and* $i \neq j$. *Then* $\lim_{t\to\infty} H_i(t) = 0$ *for every* $(H_1(0), H_2(0)) \in \operatorname{int}\mathbb{R}^2_+$.

Figure 1. The null clines for System (2). (a): The host H_i is dominated. (b): The two hosts coexist in the sense of permanence. (c): The system is bistable. (d): The system has an infinite number of fixed points.

3.2. Coexistence

Permanence of (3) was investigated by Hofbauer *et al.*[4] (see also Lu and Wang [8] for (3) with $n = 2$). The necessary and sufficient condition for permanence of (3) with $n = 2$ is given by

Lemma 5. (Hofbauer *et al.* [4, Theorem 5.1.]) *Suppose that System* (3) *with* $n = 2$ *is robustly dissipative. System* (3) *is permanent if and only if the interior fixed point exists and* $\det A = \mu_{11}\mu_{22} - \mu_{12}\mu_{21} > 0$.

The following lemma gives a sufficient condition for dissipation of (3):

Lemma 6. (Hofbauer *et al.* [4, Lemma 3.3]) *If the interaction matrix* $A = (\mu_{ij})$ *is hierarchically ordered, that is there exists a rearrangement of the indices such that* $\mu_{ij} \geq 0$ *whenever* $i \leq j$ *and additionally* $\mu_{ii} > 0$ *for every* i*, then System* (3) *is dissipative.*

By applying the lemmas to (2), we have the following corollary:

Corollary 7. *System* (2) *is permanent if and only if*

$$\frac{\ln\lambda_1}{\mu_{11}} < \frac{\ln\lambda_2}{\mu_{21}} \quad \textit{and} \quad \frac{\ln\lambda_2}{\mu_{22}} < \frac{\ln\lambda_1}{\mu_{12}}. \tag{5}$$

3.3. Bistability

Definition 8. *System* (2) *is said to be bistable if there exist compact sets* $M_i \subset \{(H_1, H_2) \in \mathbb{R}^2_+ : H_i = 0, H_j > 0\}$ *(*$i, j \in \{1, 2\}$, $i \neq j$*) which contain attractors, that is there is a neighborhood* U *of* M_i *in* $\mathbb{R}^2_+$ *such that* $\Omega(\mathbf{x}) \subset M_i$ *for every* $\mathbf{x} \in U$.

The bistability of (2) is investigated by using the following lemma:

Lemma 9. (Hofbauer *et al.* [4, Theorem 2.7]) *Suppose* (3) *is dissipative. Assume that there is a subset* M *of* $\operatorname{bd}\mathbb{R}^n_+$ *which is strictly forward invariant* (*for the system restricted to* $\operatorname{bd}\mathbb{R}^n_+$), *and that there are positive numbers* $p_1, \ldots, p_n > 0$ *such that* $\sum_{i=1}^n p_i(\ln\lambda_i - \sum_{j=1}^n \mu_{ij}H^*_j) < 0$ *for every fixed point* $(H^*_1, \ldots, H^*_n) \in M$. *Then* M *contains an attractor.*

Lemma 10. *System* (2) *is bistable if*

$$\frac{\ln\lambda_1}{\mu_{11}} > \frac{\ln\lambda_2}{\mu_{21}} \quad \textit{and} \quad \frac{\ln\lambda_2}{\mu_{22}} > \frac{\ln\lambda_1}{\mu_{12}}. \tag{6}$$

Proof. By Lemma 6, we can apply Lemma 9 to System (2). Since (2) is dissipative and the origin is a repellor, there exist $\delta > 0$ and $D > 0$ such that $M_1 = \{(H_1, H_2) \in \mathbb{R}^2_+ : H_1 = 0, \delta \leq H_2 \leq D\}$ is strictly forward invariant for (2) restricted to $\operatorname{bd}\mathbb{R}^2_+$. The point $(H^*_1, H^*_2) = (0, \ln\lambda_2/\mu_{22})$ is a unique fixed point in M_1. Then, for any $p_1 > 0$,

$$\begin{aligned}\sum_{i=1}^{2} p_i(\ln\lambda_i - \sum_{j=1}^{2}\mu_{ij}H^*_j) &= p_1(\ln\lambda_1 - \mu_{12}H^*_2) + p_2(\ln\lambda_2 - \mu_{22}H^*_2)\\ &= p_1\Big(\ln\lambda_1 - \mu_{12}\frac{\ln\lambda_2}{\mu_{22}}\Big) < 0.\end{aligned}$$

This and Lemma 6, imply the existence of the attractor in M_1. Similarly, we can prove that M_2 contains an attractor. ■

3.4. Special Case

Consider the special case where the parameters satisfy the following equations:

$$\frac{\ln\lambda_1}{\mu_{11}} = \frac{\ln\lambda_2}{\mu_{21}} \quad \text{and} \quad \frac{\ln\lambda_2}{\mu_{22}} = \frac{\ln\lambda_1}{\mu_{12}}. \tag{7}$$

The equations imply $\mu_{11}\mu_{22} = \mu_{12}\mu_{21}$.

Lemma 11. *If Eq.* (7) *holds, then the solution of System* (2), $\{(H_1(t), H_2(t))\}_{t\in\mathbb{Z}_+}$, *with* $(H_1(0), H_2(0)) \in \operatorname{int}\mathbb{R}^2_+$ *satisfies the following equation:*

$$\frac{H_1(t)^{1/\mu_{11}}}{H_2(t)^{1/\mu_{21}}} = \frac{H_1(0)^{1/\mu_{11}}}{H_2(0)^{1/\mu_{21}}} \quad \text{for all} \quad t \in \mathbb{Z}_+.$$

Proof. By (2), we have

$$\frac{H_1(t+1)^{p_1}}{H_2(t+1)^{p_2}} = \frac{H_1(t)^{p_1}\exp[p_1(\ln\lambda_1 - \mu_{11}H_1(t) - \mu_{12}H_2(t))]}{H_2(t)^{p_2}\exp[p_2(\ln\lambda_2 - \mu_{21}H_1(t) - \mu_{22}H_2(t))]}$$

for $p_1, p_2 > 0$. By putting $p_1 = 1/\mu_{11}$ and $p_2 = 1/\mu_{21}$, we obtain the following:

$$\frac{H_1(t+1)^{1/\mu_{11}}}{H_2(t+1)^{1/\mu_{21}}} = \frac{H_1(t)^{1/\mu_{11}}}{H_2(t)^{1/\mu_{21}}},$$

where $\mu_{11}\mu_{22} = \mu_{12}\mu_{21}$ is used. This completes the proof. ∎

It is clear that in this case each point (H_1, H_2) satisfying $\ln\lambda_1 - \mu_{11}H_1 - \mu_{12}H_2 = 0$ (or $\ln\lambda_2 - \mu_{21}H_1 - \mu_{22}H_2 = 0$) is a fixed point.

The above results give Fig. 2.

4. Permanence

In this section, we consider the permanence of System (1) focusing on the dynamics of the system in which the parasitoid is removed (System (2)). One of the successful approach to investigate the permanence is given by Hutson [5].

Lemma 12. (Hutson [5, Theorem 2.2]) *Let (X, d) be a metric space. Consider the system $f : X \to X$, where f is continuous. Assume that X is compact and that S is a compact subset of X with empty interior. Let S and $X \setminus S$ be forward invariant. Suppose that there is a continuous function $\Phi : X \to \mathbb{R}_+$, which is called an average Liapunov function, satisfying the following conditions:*

(a) $\Phi(\mathbf{x}) = 0 \Longleftrightarrow \mathbf{x} \in S$,

(b) $\sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to\mathbf{x} \\ \mathbf{y}\in X\setminus S}} \dfrac{\Phi(f^t(\mathbf{y}))}{\Phi(\mathbf{y})} > 1 \quad (\mathbf{x} \in S)$.

Then S is a repellor, that is, there is a compact absorbing set $M \subset X \setminus S$ for $X \setminus S$.

Lemma 13. (Hutson [5, Corollary 2.3]) *The conclusion of Lemma* 12 *remains true if instead of* (b) *it is assumed that*

$$\sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to\mathbf{x} \\ \mathbf{y}\in X\setminus S}} \frac{\Phi(f^t(\mathbf{y}))}{\Phi(\mathbf{y})} > \begin{cases} 1 & (\mathbf{x} \in \Omega(S)) \\ 0 & (\mathbf{x} \in S). \end{cases}$$

The following lemmas are used to apply the above lemmas to System (1):

Figure 2. The $\ln \lambda_1/\mu_{11} - \ln \lambda_2/\mu_{22}$ parameter space

Lemma 14. (Yakubu [11, Corollary 10]) *System* (1) *is dissipative.*

Lemma 15. (Hutson [5, Lemma 2.1] and Hofbauer *et al.* [4, Lemma 2.1]) *Consider the system* $f : X \to X$*, where* f *is a continuous function. Let* U *be open with compact closure, and suppose that* V *is open and forward invariant, where* $\overline{U} \subset V \subset X$*. Then if* $\gamma^+(\mathbf{x}) \cap U \neq \emptyset$ *for every* $\mathbf{x} \in V$*,* $\gamma^+(\overline{U})$ *is compact and absorbing for* V*.*

Since System (1) is dissipative, the lemma with $X = V = \mathbb{R}^3_+$ shows that System (1) has a compact absorbing set for $\mathbb{R}^3_+$. Therefore for considering the permanence of (1) it is enough to investigate the dynamics in such a compact absorbing set, which, hereafter, is denoted by X. We divide $X \cap \text{bd}\ \mathbb{R}^3_+$ into three faces as follows:

$$S_i := \{(H_1, H_2, P) \in X : H_i = 0\}, \quad i \in \{1, 2\}$$
$$S_3 := \{(H_1, H_2, P) \in X : P = 0\}.$$

Define the following continuous functions $\Phi_i : X \to \mathbb{R}_+$ $(i \in \{1, 2, 3\})$ by setting

$$\Phi_i(\mathbf{x}) = H_i \quad (i \in \{1, 2\}) \quad \text{and} \quad \Phi_3(\mathbf{x}) = P.$$

Put

$$\sigma_i(\mathbf{x}) = \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to\mathbf{x}\\ \mathbf{y}\in X\setminus S_i}} \frac{\Phi_i(f^t(\mathbf{y}))}{\Phi_i(\mathbf{y})}, \quad i \in \{1,2,3\},$$

where f is defined as the right-hand side of System (1). By using (1) and the notations $\overline{H}_i(t) = \sum_{k=0}^{t-1} H_i(k)/t$ $(i = 1,2)$ and $\overline{P}(t) = \sum_{k=0}^{t-1} P(k)/t$, we have:

$$\begin{aligned}
\sigma_i(\mathbf{x}) &= \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to\mathbf{x}\\ \mathbf{y}\in X\setminus S_i}} \frac{I_i(t)}{I_i(t-1)} \cdots \frac{I_i(1)}{I_i(0)} \\
&= \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to\mathbf{x}\\ \mathbf{y}\in X\setminus S_i}} \prod_{k=0}^{t-1} \frac{I_i(k)\exp\left[\ln\lambda_i - \sum_{j=1}^{2}\mu_{ij}I_j(k) - a_iQ(k)\right]}{I_i(k)} \\
&= \sup_{t\geq 0} \left(\exp\left[\ln\lambda_i - \mu_{ij}\overline{H}_j(t) - a_i\overline{P}(t)\right]\right)^t, \quad \mathbf{x}\in S_i \ (i,j\in\{1,2\}, j\neq i) \\
\sigma_3(\mathbf{x}) &= \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to\mathbf{x}\\ \mathbf{y}\in X\setminus S_3}} \frac{Q(t)}{Q(t-1)} \cdots \frac{Q(1)}{Q(0)} \\
&= \sup_{t\geq 0} \liminf_{\substack{\mathbf{y}\to\mathbf{x}\\ \mathbf{y}\in X\setminus S_3}} \prod_{k=0}^{t-1}\sum_{i=1}^{2}\left(b_iI_i(k)\frac{1-\exp[-a_iQ(k)]}{Q(k)}\right) \\
&= \sup_{t\geq 0} \prod_{k=0}^{t-1}\sum_{i=1}^{2} a_ib_iH_i(k), \quad \mathbf{x}\in S_3,
\end{aligned}$$

where $(H_1(t), H_2(t), P(t)) = f^t(\mathbf{x})$ for $\mathbf{x}\in S_i$ and $(I_1(t), I_2(t), Q(t)) = f^t(\mathbf{y})$ for $\mathbf{y}\in X\setminus S_i$, and the continuity of f is used. The $\sigma_i(\mathbf{x})$ is clearly positive for all $\mathbf{x}\in S_i$ $(i\in\{1,2\})$, and the $\sigma_3(\mathbf{x})$ is also positive for all $\mathbf{x}\in S_3\setminus S_i$ $(i\in\{1,2\})$.

4.1. Dominance

Permanence of System (1) with dominant subsystem (2) was investigated by Kon and Takeuchi [7]. They showed that under some conditions the system can be permanent (see Fig. 3 for an example of population dynamics of (1) satisfying the conditions):

Theorem 16. (Kon and Takeuchi [7, Theorem 15]) *If the following conditions hold, then System* (1) *is permanent:*

$$\frac{\ln\lambda_i}{\mu_{ii}} < \frac{\ln\lambda_j}{\mu_{ji}}, \quad \frac{\ln\lambda_i}{\mu_{ij}} = \frac{\ln\lambda_j}{\mu_{jj}}, \quad \frac{\ln\lambda_i}{a_i} > \frac{\ln\lambda_j}{a_j}$$

$$\left\{\left\{\frac{a_jb_j\ln\lambda_j}{\mu_{jj}} > 1, \quad 0<\ln\lambda_j\leq 2\right\} \ \textit{or}\ \left\{\frac{a_jb_j\exp[\xi_j\ln\lambda_j+\zeta_j]}{\mu_{jj}} > 1, \quad 2<\ln\lambda_j\right\}\right\},$$

$$\left\{\frac{a_ib_i\ln\lambda_i}{\mu_{ii}} < 1 \ \ \textit{or}\ \ \left\{\frac{a_ib_i\ln\lambda_i}{\mu_{ii}} \geq 1, \quad \frac{1}{a_ib_i} > \widehat{H}_i\right\}\right\}$$

where $i,j\in\{1,2\}$, $i\neq j$,

$$\eta_j := \exp[2\ln\lambda_j - 1 - \exp[\ln\lambda_j - 1]]$$
$$\xi_j := \frac{(\ln\lambda_j - 1) - \ln\eta_j}{\exp[\ln\lambda_j - 1] - \eta_j}$$
$$\zeta_j := \ln\eta_j - \xi_j\eta_j$$
$$\widehat{H}_i := \frac{a_j\ln\lambda_i - a_i\ln\lambda_j}{a_j\mu_{ii} - a_i\mu_{ji}} > 0.$$

Figure 3. An example of the population dynamics of System (1) with the parameters satisfying the conditions in Theorem 16. In this case the two-host system is dominance. The solid, broken and dotted lines indicate the population densities $H_1(t)$, $H_2(t)$ and $P(t)$, respectively. The parameters are set by $\ln\lambda_1 = 1$, $\ln\lambda_2 = 3$, $\mu_{11} = 1$, $\mu_{12} = 1/3$, $\mu_{21} = 1$, $\mu_{22} = 1$, $a_1 = 1$, $a_2 = 5$, $b_1 = 0.5$, $b_2 = 1$. The initial population density is $(H_1(0), H_2(0), P(0)) = (0.1, 0.1, 0.1)$.

4.2 Coexistence

The following lemmas are used to show the permanence condition for (1) with coexistence subsystem (2):

Lemma 17. (Wang and Lu [10, Theorem 2]) *Suppose that System* (2) *is permanent, that is Eq.* (5) *holds. If* $0 < \ln\lambda_i \le 1$ *for* $i = 1$ *and* 2*, then the positive fixed point* (H_1^*, H_2^*) *of System* (2) *is globally asymptotically stable, where*

$$H_1^* = \frac{\mu_{22}\ln\lambda_1 - \mu_{12}\ln\lambda_2}{\mu_{11}\mu_{22} - \mu_{12}\mu_{21}}, \quad H_2^* = \frac{\mu_{11}\ln\lambda_2 - \mu_{21}\ln\lambda_1}{\mu_{11}\mu_{22} - \mu_{12}\mu_{21}}.$$

Lemma 18. (Kon and Takeuchi [7, Lemma 4]) *Let* $\{(H_1(t), H_2(t), P(t))\}_{t\in\mathbb{Z}_+}$ *be a solution of System* (1) *with* $H_j(0) = 0$, $j \in \{1, 2\}$. *Suppose that there are real numbers* $h_m > 0$ *and* h_M, *and a sequence* $\{t_k\}$ *with* $t_k \to \infty$ *such that* $h_m \le H_i(t_k) \le h_M$, $0 \le P(t_k) \le h_M$, $i \in \{1, 2\}$, $i \ne j$. *Then there is a subsequence* $\{t_l\}$ *with* $t_l \to \infty$ *of* $\{t_k\}$ *such that*

$$\ln\lambda_i = \mu_{ii}\lim_{l\to\infty}\overline{H}_i(t_l) + a_i\lim_{l\to\infty}\overline{P}(t_l).$$

Lemma 19. (Kon and Takeuchi [7, Lemma 12]) *Let* $\{(H_1(t), H_2(t), P(t))\}_{t\in\mathbb{Z}_+}$ *be a solution of System* (1) *with* $H_i(0) > 0$, $P(0) > 0$ *and* $H_j(0) = 0$, $i, j \in \{1, 2\}$, $i \neq j$. *Suppose that there are real numbers* $h_m > 0$ *and* h_M, *and a sequence* $\{t_k\}$ *with* $t_k \to \infty$ *such that* $h_m \leq P(t_k) \leq h_M$. *Then there is a subsequence* $\{t_l\}$ *with* $t_l \to \infty$ *of* $\{t_k\}$ *such that*

$$\lim_{l\to\infty}\overline{H}_i(t_l) \geq \frac{1}{a_i b_i}.$$

Lemma 20. (Kon and Takeuchi 7, Lemma 13]) *Let* $\{(H_1(t), H_2(t), P(t))\}_{t\in\mathbb{Z}_+}$ *be a solution of System* (1) *with* $H_j(0) = 0$, $j \in \{1, 2\}$. *If* $(a_i b_i \ln\lambda_i)/\mu_{ii} < 1$ $(i \in \{1, 2\}, i \neq j)$, *then* $\lim_{t\to\infty} P(t) = 0$ *for every* $(H_i(0), P(0)) \in \mathbb{R}^2_+$.

Theorem 21. *Suppose that System* (2) *is permanent, that is Eq.* (5) *holds. If the following conditions hold, then System* (1) *is permanent:*

$$\frac{\ln\lambda_i}{a_i} \geq \frac{\ln\lambda_j}{a_j}, \left\{\frac{a_i b_i\ln\lambda_i}{\mu_{ii}} < 1 \quad or \quad \left\{\frac{a_i b_i\ln\lambda_i}{\mu_{ii}} \geq 1, \quad \frac{1}{a_i b_i} > \widehat{H}_i\right\}\right\}$$

$$\left\{\sum_{k=1}^{2} a_k b_k H_k^* > 1, \quad 0 < \ln\lambda_1 \leq 1, \quad 0 < \ln\lambda_2 \leq 1\right\},$$

where $i, j \in \{1, 2\}$, $i \neq j$.

Proof. We give the proof only for $i = 1$, $j = 2$. Before we show that each face S_i $(i \in \{1, 2, 3\})$ is a repellor by using the average Liapunov functions successively, we have to show that P-axis is a repellor for the system restricted to each face S_i $(i \in \{1, 2\})$. This property is proven by using the fact that the omega limit set on P-axis, $S_p := \{(H_1, H_2, P) \in \mathbb{R}^3_+ : H_1 = H_2 = 0\}$, is composed only of the origin, that is $\Omega(S_p) = \{(0, 0, 0)\}$, and $\sigma_i(0, 0, 0) = \sup_{t\geq 0}(\lambda_i)^t > 1$ $(i \in \{1, 2\})$. Hence, we can use Lemma 18 for the system restricted to each S_i $(i \in \{1, 2\})$.

Hereafter, we shall show that both S_1 and S_2 are repellor. For $\mathbf{x} \in S_i$, $i \in \{1, 2\}$

$$\begin{aligned}\sigma_i(\mathbf{x}) &= \sup_{t\geq 0}\left(\exp\left[\ln\lambda_i - \mu_{ij}\overline{H}_j(t) - a_i\overline{P}(t)\right]\right)^t \\ &= \sup_{t\geq 0}\Big(\exp\Big[\frac{1}{a_j}\{(a_i\mu_{jj} - a_j\mu_{ij})\overline{H}_j(t) - (a_i\ln\lambda_j - a_j\ln\lambda_i)\} \\ &+ \frac{a_i}{a_j}(\ln\lambda_j - \mu_{jj}\overline{H}_j(t) - a_j\overline{P}(t))\Big]\Big)^t.\end{aligned}$$

Let us consider the $\sigma_1(\mathbf{x})$. We claim that $\lim_{k\to\infty}(a_1\mu_{22} - a_2\mu_{12})\overline{H}_2(t_k) - (a_1\ln\lambda_2 - a_2\ln\lambda_1) > 0$ for some sequence $\{t_k\}$ with $t_k \to \infty$ and all $\mathbf{x} \in S_1 \setminus S_p$. If $a_1\mu_{22} - a_2\mu_{12} = 0$, then the claim is true since $a_1\ln\lambda_2 - a_2\ln\lambda_1$ is negative under the assumption (Eq. (5)). Therefore, we assume that $a_1\mu_{22} - a_2\mu_{12} \neq 0$. In this case

$$\sigma_1(\mathbf{x}) = \sup_{t\geq 0}\Big(\exp\Big[\frac{1}{a_2}\{(a_1\mu_{22}-a_2\mu_{12})(\overline{H}_2(t)-\widehat{H}_2)\} + \frac{a_1}{a_2}(\ln\lambda_2-\mu_{22}\overline{H}_2(t)-a_2\overline{P}(t))\Big]\Big)^t.$$

If $a_1\mu_{22}-a_2\mu_{12}>0$, then $\widehat{H}_2<0$. Moreover, $\overline{H}_2(t)\geq 0$ for all $t\geq 0$ since $\mathbb{R}^2_+$ is invariant. Therefore, in this case the claim is true. If $a_1\mu_{22}-a_2\mu_{12}<0$, then $\widehat{H}_2-\ln\lambda_2/\mu_{22}>0$. Moreover, Lemma 18 shows that $\ln\lambda_2/\mu_{22}\geq\lim_{k\to\infty}\overline{H}_2(t_k)$ for some sequence $\{t_k\}$ with $t_k\to\infty$ and for all $\mathbf{x}\in S_1\setminus S_p$. Therefore, the claim is true. By the above claim and Lemma 18, we see that $\sigma_1(\mathbf{x})>1$ for all $\mathbf{x}\in S_1\setminus S_p$. Moreover, since $\sigma_1(\mathbf{x})>1$ for $\mathbf{x}\in\Omega(S_p)$, then $\sigma_1(\mathbf{x})>1$ for $\mathbf{x}\in\Omega(S_1)$. This implies that S_1 is a repellor.

Let us consider the $\sigma_2(\mathbf{x})$. Since $\ln\lambda_1/a_1\geq\ln\lambda_2/a_2$ and $\ln\lambda_1/\mu_{11}<\ln\lambda_2/\mu_{21}$, we see that $a_2\mu_{11}-a_1\mu_{21}>0$. Then,

$$\sigma_2(\mathbf{x}) = \sup_{t\geq 0}\Big(\exp\Big[\frac{1}{a_1}\{(a_2\mu_{11}-a_1\mu_{21})(\overline{H}_1(t)-\widehat{H}_1)\} + \frac{a_2}{a_1}(\ln\lambda_1-\mu_{11}\overline{H}_1(t)-a_1\overline{P}(t))\Big]\Big)^t.$$

If $a_1b_1\ln\lambda_1/\mu_{11}<1$, then Lemmas 18 and 20 show that $\lim_{k\to\infty}\overline{H}_1(t_k)=\ln\lambda_1/\mu_{11}$ for some sequence $\{t_k\}$ with $t_k\to\infty$ and for all $\mathbf{x}\in S_2\setminus S_p$. Therefore, the fact that $\ln\lambda_1/\mu_{11}-\widehat{H}_1>0$ and Lemma 18 show that $\sigma_2(\mathbf{x})>1$ for all $\mathbf{x}\in S_2\setminus S_p$. If $a_1b_1\ln\lambda_1/\mu_{11}\geq 1$, then for all $\mathbf{x}\in S_2\setminus S_p$, $\lim_{t\to\infty}P(t)=0$ or there exist real numbers $h_m>0$ and h_M, and a sequence $\{t_k\}$ with $t_k\to\infty$ such that $h_m\leq P(t_k)\leq h_M$. In the former case, we see that $\sigma_2(\mathbf{x})>1$ for all $\mathbf{x}\in S_2\setminus S_p$ similarly to the case $a_1b_1\ln\lambda_1/\mu_{11}<1$. In the latter case, Lemma 19 shows that $\lim_{k\to\infty}\overline{H}_1(t_k)\geq 1/a_1b_1$ for some sequence $\{t_k\}$ with $t_k\to\infty$ and for all $\mathbf{x}\in S_2\setminus S_p$. Therefore, $\sigma_2(\mathbf{x})>1$ for all $\mathbf{x}\in S_2\setminus S_p$. Moreover, since $\sigma_2(\mathbf{x})>1$ for $\mathbf{x}\in\Omega(S_p)$, then $\sigma_1(\mathbf{x})>1$ for $\mathbf{x}\in\Omega(S_2)$. This implies that S_2 is a repellor.

Since both S_1 and S_2 are repellor, all solutions in $\operatorname{int}\mathbb{R}^3_+$ eventually enter a compact set $X_1\subset X$ with $X_1\subset X\setminus(S_1\cup S_2)$ and remain there.

Hereafter, we consider the dynamics in X_1 and show that $S_3\cap X_1$ is a repellor. By Lemma 17, $\Omega(S_3\cap X_1)=\{(H_1^*,H_2^*)\}$, where (H_1^*,H_2^*) is a positive fixed point of (2). Then,

$$\sigma_3(\mathbf{x}) = \sup_{t\geq 0}\prod_{k=0}^{t-1}\sum_{i=1}^{2}a_ib_iH_i^* > 1$$

for $\mathbf{x}\in\Omega(S_3\cap X_1)$. Lemma 13 completes the proof. ■

Fig. 4 shows an example of population dynamics of (1) with a permanent two-host system.

4.3. Bistability and Special Case

It is known that the system with a bistable subsystem is difficult to be permanent. For example, the following theorem shows that System (3) with $n=3$

cannot be robustly permanent if it has a bistable subsystem (see also Hofbauer and Sigmund [3, pp.206-207]):

Theorem 22. (Hofbauer *et al.* [4, Theorem 4.2]) *Suppose that* (3) *is robustly dissipative. Then the following conditions are necessary for* (3) *to be robustly permanent:*

(i) (3) *has an interior fixed point.*
(ii) $\det A > 0$, *where* $A = (\mu_{ij})$.
(iii) *If there exists a fixed point* $\mathbf{y}^*$ *with* $y_k^* = 0$ *and* $y_i^* \geq 0$ *for* $i \neq k$, *then the submatrix* $A^{(k)}$ *with* k -th *row and column deleted has a positive determinant.*

Figure 4. An example of the population dynamics of System (1) with the parameters satisfying the conditions in Theorem 21. In this case the two-host system is permanent. The solid, broken and dotted lines indicate the population densities $H_1(t)$, $H_2(t)$ and $P(t)$, respectively. The parameters are set by $\ln \lambda_1 = 1$, $\ln \lambda_2 = 1$, $\mu_{11} = 2$, $\mu_{12} = 1$, $\mu_{21} = 1$, $\mu_{22} = 2$, $a_1 = 1$, $a_2 = 5$, $b_1 = 1$, $b_2 = 5$. The initial population density is $(H_1(0), H_2(0), P(0)) = (0.1, 0.1, 0.1)$.

Suppose that System (3) with $n = 3$ is robustly permanent and it has a bistable subsystem. Then the parameters of the system satisfy Eq.(6). The condition (6) implies that the submatrix $A^{(k)}$ with respect to the subsystem has a negative determinant. This is a contradiction to (iii) in the theorem.

Under the strict assumption (the existence of the $\mathbf{x}^*$ defined below), we can show that System (1) has a similar property to (3) with $n = 3$.

Theorem 23. *Assume that* $\ln \lambda_i / a_i \geq \ln \lambda_j / a_j$ *and System* (1) *has a fixed point* $\mathbf{x}^* = (H_1^*, H_2^*, P^*)$ *with* $H_i^* > 0$, $H_j^* = 0$ *and* $P^* > 0$ $(i, j \in \{1, 2\},\ i \neq j)$. *Suppose that one of Eqs.*(6) *and* (7) *holds, then System* (1) *is not permanent.*

Proof. First, we assume that Eq. (6) and $\ln \lambda_i / a_i \geq \ln \lambda_j / a_j$ hold, or Eq.(7) and $\ln \lambda_i / a_i > \ln \lambda_j / a_j$ hold. We focus on the stability of the fixed point $\mathbf{x}^*$. It satisfies

$$\begin{aligned} &\ln \lambda_i - \mu_{ii} H_i^* - a_i P^* = 0 \\ &(\ln \lambda_i)/\mu_{ii} > H_i^* > 0, \quad P^* > 0. \end{aligned} \tag{8}$$

The stability of $\mathbf{x}^*$ with respect to the H_j-direction are determined by

$$\Lambda_j = \exp[\ln \lambda_j - \mu_{ji} H_i^* - a_j P^*],$$

which is an eigenvalue of the Jacobian matrix of (1) at $\mathbf{x}^*$ with respect to the H_j-direction. By (8),

$$\Lambda_j = \exp[-\frac{1}{a_i}(a_j\mu_{ii} - a_i\mu_{ji})(\widehat{H}_i - H_i^*)].$$

Note that $a_j\mu_{ii} - a_i\mu_{ji} \neq 0$. If $a_j\mu_{ii} - a_i\mu_{ji} < 0$, then the Λ_j is clearly less than one since $\widehat{H}_i < 0$. If $a_j\mu_{ii} - a_i\mu_{ji} > 0$, then $\widehat{H}_i - H_i^* > 0$ since $H_i^* < \ln \lambda_i/\mu_{ii}$. Hence $\Lambda_j < 1$. This implies that there exists an interior orbit which converges to the rest point on $\mathrm{bd}\mathbb{R}^3_+$.

Finally, we consider the case where Eq.(7) and $\ln \lambda_i/a_i = \ln \lambda_j/a_j$ $(i, j \in \{1, 2\}, i \neq j)$ hold. In this case, System (1) has a constant of motion, that is all solutions of (1) with $(H_1(0), H_2(0), P(0)) \in \mathrm{int}\,\mathbb{R}^3_+$ satisfy

$$\frac{H_1(t)^{1/\mu_{11}}}{H_2(t)^{1/\mu_{21}}} = \frac{H_1(0)^{1/\mu_{11}}}{H_2(0)^{1/\mu_{21}}}.$$

This property is proved similarly to Lemma 11. Then, it is clear that an eventual location of orbits depends on the initial condition $(H_1(0), H_2(0), P(0))$. This implies that there is no compact absorbing set $M \subset \mathrm{int}\,\mathbb{R}^3_+$ for $\mathrm{int}\mathbb{R}^3_+$.

5. Future Work

We considered the permanence of the system composed of two hosts and one parasitoid focusing on the dynamics of a two-host system. If one host is dominated in a two-host system, then the system with the parasitoid can be permanent. If a two-host system is permanent, then the system with the parasitoid can also be permanent. However, the sufficient conditions in Theorem 21 do not contain the case where $\ln \lambda_i > 1$ $(i = 1$ or $2)$. To consider the case is a future work. Under the strict assumption, we see that a bistable two-host system cannot be permanent even with the help of a parasitoid. To remove the strict assumption from Theorem 23 is also a future work.

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