Thresholds of Survival for an $n$-Dimensional Volterra Mutualistic System in a Polluted Environment

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The effects of toxicants on the population for an $n$-dimensional Volterra mutualistic system in a polluted environment have been studied. The thresholds between persistence and extinction for each population have been obtained.

Key Words: population; persistence; extinction; toxicant; threshold.

1. INTRODUCTION

The rapid development of modern industry and agriculture has brought great benefit to mankind. But then follows pollution of the environment which becomes rather serious day by day. This situation is seriously imperiling the survival of the populations. Therefore, the study of the effects of toxicants on the ecosystem and the assessment of the risks taken by the populations is more and more important.

In the early 1980s, T. G. Hallam and his colleagues put forward an idea to use the method of dynamics to investigate the ecotoxicology [1, 2]. They proposed a toxicant-populations model and investigated the persistence and extinction of the populations invaded by a toxicant. The threshold of a population’s survival has been obtained under the assumption that the
capacity of the environment is very large relative to the population biomass and that the limit of exogenous input of toxicant exists [2]. In 1986, T. G. Hallam and Z. Ma found the threshold under the assumption that the exogenous input of toxicant is periodic and bounded [3]. In 1989, Z. Ma et al. proved that the threshold is also available under the assumption of arbitrary bounded exogenous input of toxicant [4]. In 1991, H. Liu and Z. Ma extended the methods to find the survival threshold of the Volterra model consisting of two populations in a polluted environment [5]. In 1995, Z. Ma et al. found the survival threshold of some Volterra food web models consisting of three species in a polluted environment [6]. In this article, we extend the method used in [5, 6] to a Volterra mutualistic model consisting of $n$ species in a polluted environment and obtain the threshold of survival for each population.

2. MODEL AND NOTATIONS

Consider the following food web models consisting of $n$ species with toxicant stress:

$$\begin{align*}
\frac{dx_1}{dt} &= x_1 \left[ r_{11} - a_{11} x_1(t) - a_{12} x_2(t) - \cdots - a_{1n} x_n(t) \right] \\
\frac{dx_2}{dt} &= x_2 \left[ r_{21} - a_{21} x_1(t) - a_{22} x_2(t) - \cdots - a_{2n} x_n(t) \right] \\
&\quad \quad \quad \cdots \quad \cdots \quad \cdots \\
\frac{dx_n}{dt} &= x_n \left[ r_{n1} - a_{n1} x_1(t) - a_{n2} x_2(t) - \cdots - a_{nn} x_n(t) \right] \\
\frac{dC_0}{dt} &= a_1 C_E + \frac{d_1 \theta \beta}{a_1} - (l_1 + l_2) C_0(t) \\
\frac{dC_E}{dt} &= -h C_E + u(t) \\
x_j(0) &= x_{j0} > 0 \ (j = 1, 2, \ldots, n), \ C_0(0) \geq 0, \ C_E \geq 0, \\
(M)
\end{align*}$$

where $x_i(t)$ represents density of the $i$th population; $C_0(t)$ is the concentration of toxicant in the organism at time $t$, supposing that the concentration of toxicant contained in each species at time $t$ is the same; $C_E(t)$ is the concentration of toxicant in the environment at time $t$; the parameters $a_1$, $\theta$, $\beta$, $d_1$, $l_1$, and $l_2$ are positive constants; $a_1$ denotes the environmental
toxicant uptake rate per unit mass organism; $d_i$ is the uptake rate of toxicant in food per unit mass organism; $\theta$ is the concentration of toxicant in the resources; $\beta$ is the average rate of food intake per unit mass organism; $l_1$ and $l_2$ are organismal net ingestion and deputation rates of toxicant, respectively; and constant $h$ represents the loss rate of toxicant from the environment. The exogenous rate of input of toxicant into the environment is represented by $u(t)$, which is restricted by $0 \leq u(t) \leq u_i < +\infty$, $0 \leq t < +\infty$; $a_i$ $(i = 1, 2, \ldots, n)$ is a positive constant, which represents the density dependence of the $i$th population; constant $a_{ij}$ $(i \neq j)$ is the interspecific interrupted coefficient; $r_{i1}$ $(i = 1, 2, \ldots, n)$ is the dose-response of species $i$ to the organismal toxicant concentration; $r_{i0}$ $(i = 1, 2, \ldots, n)$ is the intrinsic growth rate or death rate of the $i$th population.

The purpose of this paper is to find the threshold on $u(t)$ between the persistence and extinction of each population.

Model $(M)$ is an $(n + 2)$ dimensional system. Since the latter two equations in model $(M)$ are linear in $C$ and $C$, respectively, $C$ can be found by solving the last equation and then $C(t)$ can be found also by solving the $(n + 1)$st equation. Thus we need actually only to consider the first $n$ equations in model $(M)$ as long as we regard $C$ as a known function of $u(t)$ and put the threshold on $C(t)$.

For convenience of statement later, we introduce the notations

$$A = \begin{vmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{vmatrix}$$

$A_k$ is a $k$-order leading principal minor of the determinant $A$ and $(A_k)_{ij}$ is the complement minor of the element $a_{ij}$ in the determinant $A_k$. $A^i_k$ is a $k$-order determinant obtained by changing the $i$th column of determinant $A_k$ to $(r_{i0}, r_{i2}, \ldots, r_{ik})^T$. $\bar{A}^i_k$ is a $k$-order determinant obtained by changing the $i$th column of $A_k$ to $(r_{1i}, r_{2i}, \ldots, r_{ki})^T$. Denoting

$$A^k_k = B_k, \quad \bar{A}^i_k = \bar{B}_k,$$

$A^{(i)}_k$ is a $(k - 1)$-order determinant obtained by removing the $i$th row and the $i$th column of $A_k$. $B^{(i)}_k$ is a $(k - 1)$-order determinant obtained by removing the $i$th row and the $i$th column of $B_k$. $R^{(i)}_k$ is a $k$-order determinant obtained by changing the $i$th column of $A_k$ to
Let \((r_{10}, r_{20}, \ldots, r_{k0})^T\) and the \(j\)th column to \((r_{11}, r_{21}, \ldots, r_{k1})^T\). Furthermore we define
\[
\langle f \rangle = \frac{\int_0^t f(s) \, ds}{t}, \quad \langle f \rangle^* = \limsup_{t \to +\infty} \frac{\int_0^t f(s) \, ds}{t},
\]
\[
\langle f \rangle_* = \liminf_{t \to +\infty} \frac{\int_0^t f(s) \, ds}{t}.
\]

In this paper, we will investigate a type of model \((M)\) as
\[
\begin{aligned}
\frac{dx_1}{dt} &= x_1 \left[ r_{10} - r_{11} C_0(t) - a_{11} x_1(t) - a_{12} x_2(t) - \cdots - a_{1n} x_n(t) \right], \\
\frac{dx_2}{dt} &= x_2 \left[ r_{20} - r_{21} C_0(t) - a_{21} x_1(t) - a_{22} x_2(t) - \cdots - a_{2n} x_n(t) \right], \\
\vdots & \quad \vdots \quad \vdots \\
\frac{dx_n}{dt} &= x_n \left[ r_{n0} - r_{n1} C_0(t) - a_{n1} x_1(t) - a_{n2} x_2(t) - \cdots - a_{nn} x_n(t) \right],
\end{aligned}
\]

\((M_1)\)

where \(r_{ij}\) and \(a_{ij}\) \((i = 1, 2, \ldots, n)\) are positive constants, while all other coefficients of \((M_1)\) are negative.

On system \((M_1)\) we assume:

\((H_t)\) The system \((M)\) has a positive equilibrium when it is not invaded by a toxicant and the system \((M)\) has also a positive equilibrium if some populations and toxicant are absent, that is, \(A_i > 0\) \(A_k > 0\) \((k = 1, 2, \ldots, n; i = 1, 2, \ldots, k)\);

\((H_2)\) \(A_i > 0\) \(R_k^i > 0\) \((i, j = 1, 2, \ldots, k; k = 1, 2, \ldots, n)\).

Without loss of generality we also assume that
\((H_3)\) \(r_{10}/r_{11} > r_{20}/r_{21} > \cdots > r_{n0}/r_{n1}\),

which means that the order of antitoxic ability of populations (from strongest to weakest) is
\[x_1, x_2, \ldots, x_n.\]

**DEFINITION.** Population \(x(t)\) is called weakly persistent in the mean if \(\langle x \rangle^* > 0\); \(x(t)\) is called going to extinction if \(\lim_{t \to +\infty} x(t) = 0\).

**Lemma 1** [5]. *Let* \(f \in C([R_+, R_+ - \{0\}])\), \(\lim_{t \to +\infty} e(t) = 0\). *If there exist positive constants* \(\lambda_0\) *and* \(T\) *such that*
\[
\frac{1}{2} \ln \frac{f(t)}{f(0)} \leq \lambda + e(t) - \lambda_0 \langle f \rangle
\]
for all \( t \geq T \), then
\[
\begin{align*}
\lim_{t \to +\infty} f(t) &= 0, & \text{if } \lambda < 0 \\
\langle f \rangle^* &= 0, & \text{if } \lambda = 0 \\
\langle f \rangle^* &\leq \frac{\lambda}{\lambda_0}, & \text{if } \lambda > 0.
\end{align*}
\]

**Lemma 2.** Under the assumptions \((H_1), (H_2), \text{ and } (H_3)\), we can obtain
\[
\begin{align*}
(1) & 
\quad (-1)^{i+j}(A_k)_{ij} > 0; \\
(2) & 
\quad \frac{B_k}{B_k} > \frac{r_{k0}}{r_{k1}}.
\end{align*}
\]

**Proof.** (1) Let \((a_{ij})_{k}\) be a \( k \)-order matrix corresponding to the leading principal minor \( A_k \). According to the assumption \((H_1)\), we know that \((a_{ij})_{k}\) is an \( M \)-matrix; this means that \((-1)^{i+j}(A_k)_{ij} \geq 0\) (see [7]). An application of the Laplace theorem on determinant \( A_k \) gives the expansion
\[
(-1)^{i+j}(A_k)_{ij} = a_{11}(A_k)_{11} + a_{12}(A_k)_{12} + \cdots + a_{ij}(A_k)_{ij} + \cdots + a_{jk}(A_k)_{jk} = 0 \quad (i \neq j).
\]
Notice that \( a_{ij} > 0, a_{jl} < 0 \) \((j \neq l)\) and \((-1)^{i+j}(A_k)_{ij} \geq 0;\) we obtain \((-1)^{i+j}(A_k)_{ij} > 0\).

(2) For \( k = 1, 2, \ldots, n \), we have
\[
r_{k1}B_k - r_{k0}\tilde{B}_k = (-1)^{k-1}
\begin{bmatrix}
r_{k1} & r_{k0} & 0 & 0 & \cdots & 0 \\
r_{11} & r_{10} & a_{11} & a_{12} & \cdots & a_{1(k-1)} \\
r_{21} & r_{20} & a_{21} & a_{22} & \cdots & a_{2(k-1)} \\
\vdots & \vdots & \ddots & \ddots & \cdots & \ddots \\
r_{k1} & r_{k0} & a_{k1} & a_{k2} & \cdots & a_{k(k-1)}
\end{bmatrix}
= (-1)^k
\begin{bmatrix}
0 & 0 & a_{k1} & a_{k2} & \cdots & a_{k(k-1)} \\
r_{11} & r_{10} & a_{11} & a_{12} & \cdots & a_{1(k-1)} \\
r_{21} & r_{20} & a_{21} & a_{22} & \cdots & a_{2(k-1)} \\
\vdots & \vdots & \ddots & \ddots & \cdots & \ddots \\
r_{k1} & r_{k0} & a_{k1} & a_{k2} & \cdots & a_{k(k-1)}
\end{bmatrix}
= (-1)^k \left[ a_{k1}(-1)^{k-1}R_{k}^{1} - a_{k2}(-1)^{k}R_{k}^{2} \right. \\
\left. + \cdots + a_{k(k-1)}(-1)^{k-1}R_{k}^{(k-1)k} \right] \\
= -a_{k1}R_{k}^{1} - a_{k2}R_{k}^{2} - \cdots - a_{k(k-1)}R_{k}^{(k-1)k}.
\]
Since $a_{ki} < 0$, $R_k^i > 0$ ($i = 1, 2, \ldots, k - 1$), the right-hand side of above equality is positive. This completes the proof of Lemma 2.

**Lemma 3.** Every solution $x_i(t)$ of system $(M_i)$ with the initial conditions exists in the interval $[0, +\infty)$ and always remains positive for all $t \geq 0$.

We omit the proof since it is easy to prove.

3. MAIN RESULTS

Under the assumptions $(H_1)$, $(H_2)$, and $(H_3)$ above, we can obtain the following theorem.

**Theorem 4.** For the system $(M_i)$, let $\mu_k = B_k/\tilde{B}_k$, then

1. $\mu_k$ is a decreasing sequence of numbers with increasing of $k$.
2. Population $x_k(t)$ is weakly persistent in the mean if $\langle C_0 \rangle_* < \mu_k$ ($k = 1, 2, \ldots, n$).
3. Population $x_k(t)$ goes to extinction if $\langle C_0 \rangle_* > \mu_k$ ($k = 1, 2, \ldots, n$).

**Proof.** (1) Let

$$
F = \begin{vmatrix}
 a_{11} & a_{22} & \cdots & a_{1k} & r_{11} & r_{10} & 0 & 0 & \cdots & 0 \\
 a_{21} & a_{22} & \cdots & a_{2k} & r_{21} & r_{20} & 0 & 0 & \cdots & 0 \\
 \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\
 a_{k1} & a_{k2} & \cdots & a_{kk} & r_{k1} & r_{k0} & 0 & 0 & \cdots & 0 \\
 a_{(k+1)1} & a_{(k+1)2} & \cdots & a_{(k+1)k} & r_{(k+1)1} & r_{(k+1)0} & 0 & 0 & \cdots & 0 \\
 0 & 0 & \cdots & 0 & r_{11} & r_{10} & a_{11} & a_{12} & \cdots & a_{1(k-1)} \\
 0 & 0 & \cdots & 0 & r_{21} & r_{20} & a_{21} & a_{22} & \cdots & a_{2(k-1)} \\
 0 & 0 & \cdots & 0 & r_{k1} & r_{k0} & a_{k1} & a_{k2} & \cdots & a_{k(k-1)} \\
\end{vmatrix}.
$$

According to the Laplace Theorem, expanding determinant $F$ by its first $(k + 1)$ rows we get

$$
F = (-1)^{k-1} B_k \tilde{B}_{k+1} - (-1)^{k-1} \tilde{B}_k B_{k+1},
$$

(3.1)
Make an elementary transformation to the determinant $F$.

\[
F = \begin{vmatrix}
    a_{11} & a_{12} & \ldots & a_{1k} & 0 & 0 & -a_{11} & -a_{12} & \ldots & -a_{1(k-1)} \\
    a_{21} & a_{22} & \ldots & a_{2k} & 0 & 0 & -a_{21} & -a_{22} & \ldots & -a_{2(k-1)} \\
    \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\
    a_{k1} & a_{k2} & \ldots & a_{kk} & 0 & 0 & -a_{k1} & -a_{k2} & \ldots & -a_{k(k-1)} \\
    0 & 0 & \ldots & 0 & r_{11} & r_{10} & a_{11} & a_{12} & \ldots & a_{1(k-1)} \\
    0 & 0 & \ldots & 0 & r_{21} & r_{20} & a_{21} & a_{22} & \ldots & a_{2(k-1)} \\
    \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\
    0 & 0 & \ldots & 0 & r_{k1} & r_{k0} & a_{k1} & a_{k2} & \ldots & a_{k(k-1)}
\end{vmatrix}
\]

According to the Laplace Theorem, expanding determinant $F$ by its first $k$ rows, we obtain

\[
F = A_k \begin{vmatrix}
    r_{(k+1)1} & r_{(k+1)0} & 0 & 0 & \ldots & 0 \\
    r_{11} & r_{10} & a_{11} & a_{12} & \ldots & a_{1(k-1)} \\
    r_{21} & r_{20} & a_{21} & a_{22} & \ldots & a_{2(k-1)} \\
    \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\
    r_{k1} & r_{k0} & a_{k1} & a_{k2} & \ldots & a_{k(k-1)}
\end{vmatrix}
= (-1)^{k-1} A_k \left[ r_{(k+1)1} B_k - r_{(k+1)0} \tilde{B}_k \right].
\]  

Combining inequalities (2) in Lemma 2 and the fundamental assumption $(H_3)$ with equalities (3.1), (3.2), we obtain

\[
B_k \tilde{B}_{k+1} - \tilde{B}_k B_{k+1} > 0.
\]

Namely,

\[
\frac{B_k}{\tilde{B}_k} > \frac{B_{k+1}}{\tilde{B}_{k+1}}.
\]  

Thus $\mu_k$ is a decreasing sequence of numbers with increasing of $k$.

(2) When $\langle C_0 \rangle_* < \mu_k \ (k = 1, 2, \ldots, n)$, by using an integration, the system $(M_i)$ can be rewritten as

\[
\begin{align*}
1 - \frac{1}{t} \ln x_1 &= r_{10} - r_{11} \langle C_0 \rangle - a_{11} \langle x_1 \rangle - a_{12} \langle x_2 \rangle - \cdots - a_{1n} \langle x_n \rangle \\
1 - \frac{1}{t} \ln x_2 &= r_{20} - r_{21} \langle C_0 \rangle - a_{21} \langle x_1 \rangle - a_{22} \langle x_2 \rangle - \cdots - a_{2n} \langle x_n \rangle \\
\vdots & \vdots \vdots \vdots \vdots \\
1 - \frac{1}{t} \ln x_n &= r_{n0} - r_{n1} \langle C_0 \rangle - a_{n1} \langle x_1 \rangle - a_{n2} \langle x_2 \rangle - \cdots - a_{nn} \langle x_n \rangle.
\end{align*}
\]
Notice that \( a_{kj} < 0 \) and \( \langle x_j \rangle \geq 0 \) \((k < j \leq n)\); it is easily obtained that

\[
\begin{align*}
\frac{1}{t} \ln x_{i} & \geq r_{10} - r_{11} \langle C_0 \rangle - a_{11} \langle x_1 \rangle - a_{12} \langle x_2 \rangle - \cdots - a_{1k} \langle x_k \rangle \\
\frac{1}{t} \ln x_{20} & \geq r_{20} - r_{21} \langle C_0 \rangle - a_{21} \langle x_1 \rangle - a_{22} \langle x_2 \rangle - \cdots - a_{2k} \langle x_k \rangle \\
& \quad \vdots \\
\frac{1}{t} \ln x_{k0} & \geq r_{k0} - r_{k1} \langle C_0 \rangle - a_{k1} \langle x_1 \rangle - a_{k2} \langle x_2 \rangle - \cdots - a_{kk} \langle x_k \rangle.
\end{align*}
\]  
(3.5)

Let \( m_1, m_2, \ldots, m_{k-1} \) satisfy the equations

\[
\begin{align*}
a_{11}m_1 + a_{12}m_2 + \cdots + a_{(k-1)1}m_{k-1} &= a_{k1} \\
a_{12}m_1 + a_{22}m_2 + \cdots + a_{(k-1)2}m_{k-1} &= a_{k2} \\
& \quad \vdots \\
a_{(k-1)1}m_1 + a_{(k-1)2}m_2 + \cdots + a_{(k-1)(k-1)}m_{k-1} &= a_{k(k-1)}.
\end{align*}
\]  
(3.6)

Solving Eqs. (3.6), we get

\[
m_i = \frac{(-1)^{k+i+1} (A_k)_{ik}}{A_{k-1}}.
\]

Since \((-1)^{k+i}(A_k)_{ik} > 0\), we have \( m_i < 0 \) \((i = 1, 2, \ldots, k-1)\).

Multiplying both sides of each inequality (3.5) by \(-m_1, -m_2, \ldots, -m_{k-1}, 1\), respectively, and then adding these \( k \) inequalities, we obtain

\[
\begin{align*}
\frac{1}{t} \ln x_k & \geq \frac{m_1}{t} \ln x_1 + \frac{m_2}{t} \ln x_2 + \cdots + \frac{m_{k-1}}{t} \ln x_{k-1} \\
& \quad + \frac{B_k - \tilde{B}_k \langle C_0 \rangle}{A_{k-1}} - \frac{A_k}{A_{k-1}} \langle x_k \rangle.
\end{align*}
\]

From Lemma 3, we have \( \limsup_{t \to +\infty} (1/t) \ln(x_j/x_{j0}) \leq 0 \) \((j = 1, 2, \ldots, k)\). Notice \( m_i < 0 \); taking limit superior on both sides of the inequality and using the properties of superior limit and inferior limit, we obtain

\[
0 \geq \limsup_{t \to +\infty} \frac{1}{t} \ln x_k \geq \frac{B_k - \tilde{B}_k \langle C_0 \rangle}{A_{k-1}} - \frac{A_k}{A_{k-1}} \langle x_k \rangle^*.
\]  
(3.7)
Note \( B_k > 0, \bar{B}_k > 0, A_k > 0, A_{k-1} > 0; \) therefore \( \langle x_k \rangle^* > 0 \) if \( \langle C_0 \rangle^*_\neq \mu_k = B_k/\bar{B}_k. \)

(3) At first, we prove that population \( x_n(t) \) goes to extinction if \( \langle C_0 \rangle^*_\neq \mu_n. \)

From (3.4), we can see that

\[
\begin{align*}
\frac{1}{t} \ln \frac{x_1}{x_{10}} & \leq r_{10} - r_{11} \langle C_0 \rangle^*_\neq \alpha_{11} \langle x_1 \rangle^* - \alpha_{12} \langle x_2 \rangle^* - \cdots - \alpha_{1n} \langle x_n \rangle^* \\
\frac{1}{t} \ln \frac{x_2}{x_{20}} & \leq r_{20} - r_{21} \alpha_{21} \langle x_1 \rangle^* - \alpha_{22} \langle x_2 \rangle^* - \cdots - \alpha_{2n} \langle x_n \rangle^* \\
\cdots & \cdots \cdots \cdots \\
\frac{1}{t} \ln \frac{x_n}{x_{n0}} & \leq r_{n0} - r_{n1} \alpha_{n1} \langle x_1 \rangle^* - \alpha_{n2} \langle x_2 \rangle^* - \cdots - \alpha_{nn} \langle x_n \rangle^*,
\end{align*}
\]

which is shown as

\[
\begin{align*}
\frac{1}{t} \ln \frac{x_1}{x_{10}} & \leq \lambda_1 - \alpha_{11} \langle x_1 \rangle^* \\
\frac{1}{t} \ln \frac{x_2}{x_{20}} & \leq \lambda_2 - \alpha_{22} \langle x_2 \rangle^* \\
\cdots & \cdots \cdots \cdots \\
\frac{1}{t} \ln \frac{x_n}{x_{n0}} & \leq \lambda_n - \alpha_{nn} \langle x_n \rangle^*,
\end{align*}
\]

where

\[
\lambda_i = r_{i0} - r_{i1} \langle C_0 \rangle^*_\neq \alpha_{i1} \langle x_1 \rangle^* - \alpha_{i2} \langle x_2 \rangle^* - \cdots - \alpha_{i(i-1)} \langle x_{i-1} \rangle^* \\
- \alpha_{i(i+1)} \langle x_{i+1} \rangle^* - \cdots - \alpha_{in} \langle x_n \rangle^*.
\]

Next, we show the proof process in three steps.

(i) If \( \langle x_i \rangle^* > 0 \) for all \( i (i = 1, 2, \ldots, n - 1), \) then we have \( \lambda_i > 0 \) (otherwise, inequalities (3.9) and Lemma 1 would lead to \( \langle x_i \rangle^* = 0, \) which is a contradiction with \( \langle x_i \rangle^* > 0 \)). An application of Lemma 1 to the first \( n - 1 \) inequalities of (3.9) shows

\[
\langle x_i \rangle^* \leq \frac{\lambda_i}{\alpha_{ii}}.
\]
Namely,
\[
\begin{align*}
&\left\{ \begin{array}{l}
\langle a_{11}x_1 \rangle^* + \cdots + a_{1(n-1)}\langle x_{n-1} \rangle^* \leq r_{10} - r_{11}\langle C_0 \rangle^* - a_{1n}\langle x_n \rangle^* \\
\langle a_{21}x_1 \rangle^* + \cdots + a_{2(n-1)}\langle x_{n-1} \rangle^* \leq r_{20} - r_{21}\langle C_0 \rangle^* - a_{2n}\langle x_n \rangle^* \\
\vdots \\
\langle a_{(n-1)1}x_1 \rangle^* + \cdots + a_{(n-1)(n-1)}\langle x_{n-1} \rangle^* \leq r_{(n-1)0} - r_{(n-1)1}\langle C_0 \rangle^* - a_{(n-1)n}\langle x_n \rangle^* \\
\end{array} \right. \\
\leq r_{(n-1)0} - r_{(n-1)1}\langle C_0 \rangle^* - a_{(n-1)n}\langle x_n \rangle^*.
\end{align*}
\]  
(3.10)

Solving the inequalities (3.10), we get
\[
\langle x_n \rangle^* \leq \frac{A_{n-1}^{-1} - A_{n-1}^{-i}\langle C_0 \rangle^*}{A_{n-1}} - \frac{(-1)^{n+i+1}(A_n)_{ni}\langle x_n \rangle^*}{A_{n-1}},
\]
\[
i = 1, 2, \ldots, n-1.
\]  
(3.11)

In this case, it has to be \(\langle x_n \rangle^* = 0\). If it is not zero, then \(\langle x_n \rangle^* > 0\). An application of Lemma 1 to the last inequality of (3.9) shows
\[
\langle x_n \rangle^* \leq \frac{\lambda_n}{a_{nn}}
\]
\[
= \frac{r_{n0} - r_{n1}\langle C_0 \rangle^* - a_{n1}\langle x_1 \rangle^* - \cdots - a_{n(n-1)}\langle x_{n-1} \rangle^*}{a_{nn}}.
\]

Substituting (3.11) into the above inequality, we obtain
\[
\frac{B_n - \tilde{B}_n\langle C_0 \rangle^*}{A_{n-1}} - \frac{A}{A_{n-1}}\langle x_n \rangle^* \geq 0,
\]
which is a contradiction with \(\langle C_0 \rangle^* > \mu_\eta\). Therefore, \(\langle x_n \rangle^* = 0\).

Substituting inequalities (3.11) into the last inequality of (3.8), we obtain
\[
1 - \ln \frac{x_n}{x_{n0}} \leq r_{n0} - r_{n1}\langle C_0 \rangle^* \\
- \sum_{i=1}^{n-1} a_{ni} \left[ \frac{A_{n-1} - A_{n-1}^{-i}\langle C_0 \rangle^*}{A_{n-1}} - \frac{(-1)^{n+i+1}(A_n)_{ni}\langle x_n \rangle^*}{A_{n-1}} \right] \\
- a_{nn}\langle x_n \rangle^* \\
= \frac{B_n - \tilde{B}_n\langle C_0 \rangle^*}{A_{n-1}} - \frac{A}{A_{n-1}}\langle x_n \rangle + \varepsilon_1(t),
\]  
(3.12)

where \(\varepsilon_1(t) = a_{nn}(\langle x_n \rangle^*\langle x_n \rangle)\). Because \(\langle x_n \rangle^* = 0\), we have \(\lim_{t \to +\infty} \varepsilon_1(t) = 0\).
From Lemma 1, we obtain $\lim_{t \to +\infty} x_n(t) = 0$, namely, population $x_n(t)$ goes to extinction if $\langle C_0 \rangle_\ast > \mu_n$; $\langle x_n \rangle^* = 0$ if $\langle C_0 \rangle_\ast = \mu_n$.

(ii) If there exists one $i$ ($i = 1, 2, \ldots, n - 1$) such that $\langle x_i \rangle^* = 0$, then it corresponds to removing the $i$th row and $i$th column of the coefficient determinant $A_{n-1}$ of inequalities (3.10). The same argument as in case (i) also shows that

$$\frac{1}{t} \ln \frac{x_n(t)}{x_{n0}} \leq \frac{B^{(i)}_n - \tilde{B}^{(i)}_n \langle C_0 \rangle_\ast}{A^{(i)}_{n-1}} - \frac{A^{(i)}_{n-1}}{A^{(i)}_{n-1}} \langle x_n \rangle^* + \varepsilon(t)$$

(3.13)

where $\lim_{t \to +\infty} \varepsilon(t) = 0$. From Lemma 1, we have $\langle x_n \rangle^* = 0$ if $\langle C_0 \rangle_\ast \geq B^{(i)}_n / B^{(i)}_n$.

Let

$$G = \begin{vmatrix}
  a_{11} & \cdots & a_{1(i-1)} & a_{1(i+1)} & \cdots & a_{1(k-1)} & r_{10} & r_{11} & 0 & \cdots & 0 \\
  a_{21} & \cdots & a_{2(i-1)} & a_{2(i+1)} & \cdots & a_{2(k-1)} & r_{20} & r_{21} & 0 & \cdots & 0 \\
  \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
  a_{(i-1)1} & \cdots & a_{(i-1)(i-1)} & a_{(i-1)(i+1)} & \cdots & a_{(i-1)(k-1)} & r_{(i-1)0} & r_{(i-1)1} & 0 & \cdots & 0 \\
  a_{(i+1)1} & \cdots & a_{(i+1)(i-1)} & a_{(i+1)(i+1)} & \cdots & a_{(i+1)(k-1)} & r_{(i+1)0} & r_{(i+1)1} & 0 & \cdots & 0 \\
  \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
  a_{k1} & \cdots & a_{k(i-1)} & a_{k(i+1)} & \cdots & a_{k(k-1)} & r_{k0} & r_{k1} & 0 & \cdots & 0 \\
  0 & \cdots & 0 & 0 & \cdots & 0 & r_{00} & r_{11} & a_{11} & \cdots & a_{1(k-1)} \\
  0 & \cdots & 0 & 0 & \cdots & 0 & r_{20} & r_{21} & a_{21} & \cdots & a_{2(k-1)} \\
  \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
  0 & \cdots & 0 & 0 & \cdots & 0 & r_{k0} & r_{k1} & a_{k1} & \cdots & a_{k(k-1)}
\end{vmatrix}$$

According to the Laplace Theorem, expanding determinant $G$ by its first $(k - 1)$ rows, we obtain

$$G = (-1)^{n-1} \left[ B^{(i)}_k \tilde{B}^{(i)}_k - \tilde{B}^{(i)}_k B^{(i)}_k \right]$$

(3.14)

and make an elementary transformation to determinant $G$.

$$G = \begin{vmatrix}
  a_{11} & \cdots & a_{1(i-1)} & a_{1(i+1)} & \cdots & a_{1(k-1)} & 0 & 0 & -a_{11} & \cdots & -a_{1(k-1)} \\
  a_{21} & \cdots & a_{2(i-1)} & a_{2(i+1)} & \cdots & a_{2(k-1)} & 0 & 0 & -a_{21} & \cdots & -a_{2(k-1)} \\
  \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
  a_{(i-1)1} & \cdots & a_{(i-1)(i-1)} & a_{(i-1)(i+1)} & \cdots & a_{(i-1)(k-1)} & 0 & 0 & -a_{(i-1)1} & \cdots & -a_{(i-1)(k-1)} \\
  a_{(i+1)1} & \cdots & a_{(i+1)(i-1)} & a_{(i+1)(i+1)} & \cdots & a_{(i+1)(k-1)} & 0 & 0 & -a_{(i+1)1} & \cdots & -a_{(i+1)(k-1)} \\
  \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
  a_{k1} & \cdots & a_{k(i-1)} & a_{k(i+1)} & \cdots & a_{k(k-1)} & r_{k0} & r_{k1} & 0 & \cdots & 0 \\
  0 & \cdots & 0 & 0 & \cdots & 0 & r_{00} & r_{11} & a_{11} & \cdots & a_{1(k-1)} \\
  0 & \cdots & 0 & 0 & \cdots & 0 & r_{20} & r_{21} & a_{21} & \cdots & a_{2(k-1)} \\
  \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
  0 & \cdots & 0 & 0 & \cdots & 0 & r_{k0} & r_{k1} & a_{k1} & \cdots & a_{k(k-1)}
\end{vmatrix}$$
According to the Laplace Theorem, expanding determinant $G$ by its first $(k - 2)$ rows, we obtain

$$G = (-1)^{n-1} A^{(i)}_{k-1} \left[ r_{k0} \bar{B}_k - r_{k1} B_k \right]. \quad (3.15)$$

Applying Lemma 2 to equalities (3.14) and (3.15), we get

$$B_k^{(i)} \bar{B}_k - \bar{B}_k^{(i)} B_k = A^{(i)}_{k-1} \left[ r_{k0} \bar{B}_k - r_{k1} B_k \right] < 0.$$ 

Namely,

$$\frac{B_k^{(i)}}{\bar{B}_k^{(i)}} < \frac{B_k}{\bar{B}_k}. \quad (3.16)$$

An application of Lemma 1 to inequality (3.13) gives $\langle x_n \rangle^* = 0$ if $\langle C_0 \rangle^*_n \geq B_n/\bar{B}_n$.

(iii) If there exist unequal $i_1, i_2, \ldots, i_l$ ($i_1, i_2, \ldots, i_l \in \{1, 2, \ldots, n-1\}$) such that $\langle x_{i_1} \rangle^* = 0, \langle x_{i_2} \rangle^* = 0, \ldots, \langle x_{i_l} \rangle^* = 0$, similarly, we can obtain the same conclusion as in case (ii).

Second, we prove that population $x_k(t)$ goes to extinction if $\langle C_0 \rangle^*_n \geq \mu_k$ ($k = 1, 2, \ldots, n - 1$).

When $k = n - 1$, the condition $\langle C_0 \rangle^*_n \geq \mu_{n-1}$ implies that $\langle C_0 \rangle^*_n \geq \mu_n$. From the above proof, we have $\langle x_n \rangle^* = 0$. So model $(M_i)$ becomes an $(n-1)$ dimensional system. Similarly, we obtain the corresponding conclusions, which are that $x_{n-1}(t)$ is weakly persistent in the mean if $\langle C_0 \rangle^*_n < \mu_{n-1}$, and population $x_{n-1}(t)$ goes to extinction if $\langle C_0 \rangle^*_n > \mu_{n-1}$.

In turn, we can also obtain the rest of the consequences.

Therefore, all the conclusions of the theorem have been proved.

Remark. It should be indicated that a similar conclusion of the theorem can be obtained if $R_k^0 < 0$.

REFERENCES


