ON A DISCRETE THREE-DIMENSIONAL LESLIE-GOWER COMPETITION MODEL

YUNSHYONG CHOW
Institute of Mathematics
Academia Sinica
Taipei, Taiwan 106

KENNETH PALMER*
Department of Mathematics
National Taiwan University
Taipei, Taiwan 106

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Abstract. We consider a special discrete time Leslie-Gower competition models for three species: 

$$x_i(t+1) = \frac{a_i x_i(t)}{1 + x_i(t) + \sum_{j \neq i} c_{ij} x_j(t)},$$

for $1 \leq i \leq 3$ and $t \geq 0$. Here $c$ is the interspecific coefficient among different species. Assume $a_1 > a_2 > a_3 > 1$. It is shown that when $0 < c < c_0 := (a_3 - 1)/(a_1 + a_2 - a_3 - 1)$, a unique interior equilibrium $E^*$ exists and is locally stable. Then from a general theorem in Balreira, Elaydi and Luis (2017), it follows that $E^*$ is globally asymptotically stable. Using a result of Ruiz-Herrera [11], it is shown that the unique positive equilibrium in the $x_1x_2$-plane is globally asymptotically stable for $c_0 < c < \beta_{21} = (a_2 - 1)/(a_1 - 1)$. Then it is shown that $(a_1 - 1, 0, 0)$ is globally asymptotically stable for $\beta_{21} < c < \beta_{12} = (a_1 - 1)/(a_2 - 1)$. This partially generalizes a result in Chow and Hsieh (2013) and Ackleh, Sacker and Salceanu (2014). For $c > \beta_{12}$, it is shown that there are multiple asymptotically stable equilibria.

1. Introduction. Discrete time Leslie-Gower competition models for $n$ species can be described by the following system:

$$x_i(t+1) = \frac{a_i x_i(t)}{1 + \sum_{j=1}^{n} c_{ij} x_j(t)}, \quad 1 \leq i \leq n \text{ and } t \geq 0. \quad (1)$$

Here $c_{ij} > 0$ are the interspecific competition coefficients, $x_i(t)$ is the population size at time $t$ and $a_i > 1$ is the reproduction rate of the $i$-th species.

For $n = 2$, Cushing et al. [7] were able to determine the asymptotic fate of all solutions. For later use, we recall here their result.
Consider the system
\[ x_1(t+1) = \frac{a_1x_1(t)}{1 + c_{11}x_1(t) + c_{12}x_2(t)}, \quad x_2(t+1) = \frac{a_2x_2(t)}{1 + c_{21}x_1(t) + c_{22}x_2(t)}, \]
where \( a_i > 1 \) and \( c_{ij} > 0 \). Write \( a = \frac{a_2}{c_{22}}, b = \frac{a_1}{c_{21}} \) and \( \beta = \frac{a_1 - 1}{c_{11}} \).

(i) when \( a, b < \beta \), all positive solutions approach the boundary equilibria in Section 2.

(ii) when \( a, b > \beta \), all solutions approach \( E_1 = (0, (a_1 - 1)/c_{11}) \).

(iii) when \( a < \beta < b \), all positive solutions approach the interior fixed point \( E_{12} = \left( \frac{c_{22}(a_1 - 1) - c_{12}(a_2 - 1)}{c_{11}c_{22} - c_{12}c_{21}}, \frac{c_{21}(a_1 - 1) + c_{11}(a_2 - 1)}{c_{11}c_{22} - c_{12}c_{21}} \right) \).

(iv) when \( b < b_1 < a \), \( E_1 \) and \( E_2 \) are stable, \( E_{12} \) is a saddle and all positive solutions approach \( E_1 \) or \( E_2 \) except for those on the stable manifold \( M \) of \( E_{12} \).

The aim of this paper is to extend the results in [5] and [7] to (2), a somewhat restricted three dimensional situation. Notice that by rescaling if necessary, we may set all \( c_{ij} = 1 \) in (1). So (2) is obtained from (1) with \( c = 1 \) and all interspecific coefficients \( c_{ij} = c > 0 \) for all \( i \neq j \). We restrict to the situation where the \( a_i \)'s are distinct. Without loss of generality we may assume the capacities of the species in (2) satisfy
\[ b_1 > b_2 > b_3 > 0, \quad \text{where} \quad b_i = a_i - 1. \]  

Define \( \beta_{ij} = \frac{a_i - 1}{a_j - 1} = \frac{b_i}{b_j} \) for \( i \neq j \). Then \( \beta_{ij} = \frac{1}{\beta_{ji}} \) and for \( i < j \),
\[ \beta_{ij} > 1 > \beta_{ji} \text{ and } \beta_{13} > \max\{\beta_{23}, \beta_{12}\} > 1, \beta_{31} < \min\{\beta_{32}, \beta_{21}\} < 1. \]

Solutions of (2) are iterates of the map \( f(x_1, x_2, x_3) \) given by
\[ \left( \frac{a_1x_1}{1 + x_1 + c(x_2 + x_3)}, \frac{a_2x_2}{1 + x_2 + c(x_1 + x_3)}, \frac{a_3x_3}{1 + x_3 + c(x_1 + x_2)} \right). \]

When \( x_i \geq 0, i = 1, 2, 3 \), \( f \) is analytic, one to one and a local diffeomorphism. It is easy to find the equilibria by solving \( f(x_1, x_2, x_3) = (x_1, x_2, x_3) \). We first deal with the boundary equilibria in Section 2.
Proposition 1. Assume \( (3) \). Then for \( c > 0 \), system \((2)\) has the equilibria

\[
E_0 = (0, 0, 0), \quad E_1 = (b_1, 0, 0), \quad E_2 = (0, b_2, 0), \quad E_3 = (0, 0, b_3),
\]
on the coordinate axes and three equilibria on the coordinate planes

\[
E_{23} = \left(0, \frac{b_2 - cb_3}{1 - c^2}, \frac{b_3 - cb_2}{1 - c^2}\right), \quad E_{13} = \left(\frac{b_1 - cb_3}{1 - c^2}, 0, \frac{b_3 - cb_1}{1 - c^2}\right),
\]

\[
E_{12} = \left(\frac{b_1 - cb_2}{1 - c^2}, \frac{b_2 - cb_1}{1 - c^2}, 0\right),
\]

where \( E_{ij} \) exists for \( c < \beta_{ji} < 1 \) or \( c > \beta_{ij} > 1 \).

The stability at an equilibrium point \((x_1, x_2, x_3)\) depends on the eigenvalues of the Jacobian matrix \( J = \left[\frac{\partial f_i}{\partial x_j}\right] = [a_{ij}]\), where for \( i = 1, 2, 3, \)

\[
a_{ii} = a_i + c \sum_{i \neq j} x_j \] and \( a_{ij} = \frac{-c a_i x_i}{1 + x_i + c \sum_{j \neq i} x_j} \) for \( j \neq i \).

(6)

Using Theorem 1.1, it is a routine matter to determine local stability of the boundary equilibria in Proposition 1.

Interior equilibria for system \((2)\) must satisfy

\[
 x_i + c \sum_{j \neq i} x_j = a_i - 1 = b_i \text{ for } i = 1, 2, 3.
\]

(7)

A simple calculation shows equation \((7)\) has the following solution

\[
 E^* = \left(\frac{(1 + c)b_1 - c(b_2 + b_3)}{(1 - c)(2c + 1)}, \frac{(1 + c)b_2 - c(b_1 + b_3)}{(1 - c)(2c + 1)}, \frac{(1 + c)b_3 - c(b_1 + b_2)}{(1 - c)(2c + 1)}\right).
\]

(8)

Hence \( E^* \) is an interior equilibrium if \( 0 < c < c_0 \) or \( c > c_1 \). Here

\[
c_0 = \frac{1}{\beta_{13} + \beta_{24} - 1} \quad \text{and} \quad c_1 = \frac{1}{\beta_{21} + \beta_{31} - 1}.
\]

(9)

We take the convention that \( c_1 = \infty \) if \( \beta_{21} + \beta_{31} - 1 \leq 0 \). Note that by \((4)\), \( c_0 < \beta_{31} \) and \( c_1 > \beta_{13} \). Hence,

\[
c_0 < 1 < c_1 \quad \text{and} \quad c_0 < \beta_{ij} < c_1 \text{ for all } i, j = 1, 2, 3.
\]

(10)

It turns out that the determination of the local stability of \( E^* \) is rather more complicated. In particular, we will show in Section 3 that all eigenvalues of \( J|_{E^*} \) are real and have absolute value < 1 only if \( 0 < c < c_0 \). Therefore, we have the following result.

Proposition 2. Assume \((3)\). The interior equilibrium \( E^* \) of system \((2)\) is locally asymptotically stable if \( 0 < c < c_0 \) and is a saddle with one dimensional stable manifold when it exists for \( c > c_1 \).

Balreira et al. \([4]\) give some criteria for higher dimensional monotone maps to be globally attracting to the unique interior equilibrium. As examples, they demonstrate the global asymptotic stability of the unique interior equilibrium for both Leslie-Gower and Ricker competition population models of Kolmogorov form. Our system \((2)\), whose Kolmogorov form

\[
f(x) = (x_1 f_1(x), x_2 f_2(x), x_3 f_3(x))
\]

is shown in \((5)\), is covered in Section 5.1.2 of Balreira et al. \([4]\). For simplicity, they only worked out the detail for the case \( n = 3 \) and \( a_1 = a_2 = a_3 \) so that \( c_0 = c_1 = 1 \).
For completeness, we provide in Section 4 the detail for system (2). It is remarkable that Balreira et al. do not need to know that all eigenvalues of $J|_{E^*}$ have absolute value < 1 as we prove in Proposition 2.

**Theorem 1.2.** Assume (3). The interior equilibrium $E^*$ of system (2) is globally asymptotically stable if $0 < c < c_0$.

We are also interested in the global behavior of system (2) for $c > c_0$. Since there is no known analogue of the result of Liu and Elaydi for dimension higher than two, we are only able to obtain partial results concerning the global asymptotic behaviour. However the partial results we obtain do suggest that the result of Liu and Elaydi holds also for system (2). Chow [6] verifies that every solution to the $n$-dimensional version of system (2) converges to an equilibrium if $a_1 = a_2 = ... = a_n > 1$ and $c > 0$.

Using Corollary 2.1 in Ruiz-Herrera [11], we show in Section 5 that $E_{12}$ is globally asymptotically stable for $c \in (c_0, \beta_{21})$.

**Theorem 1.3.** Assume (3). For $c \in (c_0, \beta_{21})$, any solution $x(t)$ of (2) with all $x_i(0) > 0$ satisfies $\lim_{t \to \infty} x(t) = E_{12}$.

Next in Section 6, we use a comparison method to show

**Theorem 1.4.** Assume (3). For $c \in (\beta_{21}, \beta_{12})$, any solution $x(t)$ of (2) with $x_1(0) > 0$ satisfies $\lim_{t \to \infty} x(t) = E_1 = (a_1 - 1, 0, 0)$.

We observe that this result can also be proved using Corollary 2.1 in Ruiz-Herrera [11]. Note that for three species, this result extends that in Ackleh et al. [2] and Chow and Hsieh [5] as $1 \in (\beta_{21}, \beta_{12})$. Moreover, the interval $(\beta_{21}, \beta_{12})$ is maximal for $E_1$ to be globally asymptotically stable as we will see in Section 2 that $E_2$ is locally asymptotically stable for $c \in (\beta_{12}, \infty)$ and $E_{12}$ is locally asymptotically stable for $c \in (c_0, \beta_{21})$.

For the remaining case $c > \beta_{12}$, the result of Balreira et al. [4] is no longer applicable because Proposition 2 shows the unique interior equilibrium $E^*$ is not stable when it exists. However, Theorem 2.2 in Ruiz-Herrera [11] is applicable for $c < c_1$ and we conjecture that similar to Theorem 1.1(iv), all positive solutions converge to an equilibrium when $c > \beta_{12}$. We can show the partial result that in this case all solutions starting in a certain cone converge to one of the three equilibria $E_1, E_2$ and $E_{12}$.

### 2. Stability of the boundary equilibria

In this section we determine the stability of the boundary equilibria. The stability depends on the eigenvalues of the Jacobian matrix $J = \left[ \frac{\partial f_i}{\partial x_j} \right] = [a_{ij}]$ at the equilibrium point $(x_1, x_2, x_3)$, where for $i = 1, 2, 3$,

$$a_{ii} = \frac{a_i(1 + c \sum_{j \neq i} x_j)}{1 + x_i + c \sum_{j \neq i} x_j^2} \quad \text{and} \quad a_{ij} = \frac{-ca_i x_i}{1 + x_i + c \sum_{j \neq i} x_j^2} \quad \text{for} \quad j \neq i. \quad (12)$$

Note that an equilibrium $E$ is **locally asymptotically stable** if all eigenvalues of $J$ at $E$ lie inside the unit circle, a **repeller** if all the eigenvalues lie outside the unit circle and a **saddle** if no eigenvalue lies on the unit circle and there is at least one inside and at least one outside. First we consider the equilibria on the coordinate axes.
Proposition 3. Let $E_i$ be given in Proposition 1. Then
(i) $E_0$ is a repeller.
(ii) $E_1$ is locally asymptotically stable if $c > \beta_{21}$, it is a saddle with its two-dimensional stable manifold contained in the $x_1x_3$-plane if $\beta_{31} < c < \beta_{21}$, and it is a saddle with one-dimensional stable manifold along the $x_1$-axis if $c < \beta_{31}$.
(iii) $E_2$ is locally asymptotically stable if $c > \beta_{12}$, it is a saddle with its two-dimensional stable manifold contained in the $x_2x_3$-plane if $\beta_{32} < c < \beta_{12}$, and it is a saddle with one-dimensional stable manifold along the $x_2$-axis if $c < \beta_{32}$.
(iv) $E_3$ is locally asymptotically stable if $c > \beta_{13}$, it is a saddle with its two-dimensional stable manifold contained in the $x_2x_3$-plane if $\beta_{23} < c < \beta_{13}$, and it is a saddle with one-dimensional stable manifold along the $x_3$-axis if $c < \beta_{23}$.

Proof. At $E_0 = (0, 0, 0)$, $J = \text{diag}(a_1, a_2, a_3)$. By (3) $E_0$ is a repeller. At $E_1 = (b_1, 0, 0)$, we have

$$J = \begin{pmatrix}
1 & -\frac{cb_1}{a_1} & -\frac{cb_1}{a_1} \\
\frac{a_1}{b_1} & 0 & 0 \\
0 & 1 + \frac{cb_1}{a_1} & \frac{a_3}{1 + cb_1}
\end{pmatrix}.$$

Note that $\frac{1}{a_1} < 1$, $\frac{a_1}{1 + cb_1} < 1$ if and only if $c > \beta_{21}$ and $\frac{a_3}{1 + cb_1} < 1$ if and only if $c > \beta_{31}$. So $E_1$ is stable if $c > \beta_{21}$. If $\beta_{31} < c < \beta_{21}$, it is a saddle with two-dimensional stable manifold and if $c < \beta_{31}$, it is a saddle with one-dimensional stable manifold. Now for the system in the $x_1x_3$-plane,

$$x_1(t+1) = \frac{a_1x_1(t)}{1 + x_1(t) + cx_3(t)}$$

and

$$x_3(t+1) = \frac{a_3x_3(t)}{1 + cx_1(t) + x_3(t)}.$$

By Theorem 1.1, $(b_1, 0, 0)$ is globally stable when $c > \beta_{31}$. So when $\beta_{31} < c < \beta_{21}$, the stable manifold of $E_1$ must be contained in the $x_1x_3$-plane since its local stable manifold is therein and the positive quadrant in the $x_1x_3$-plane and the positive octant are invariant under the mapping. Next when $c < \beta_{31}$, the stable manifold of $E_1$ must be contained in the $x_1$-axis since its local stable manifold is therein and the positive $x_1$-axis and the positive octant are invariant under the mapping. The stability at $E_2$ and $E_3$ can be dealt with similarly. The detail is omitted.

Next we study the boundary equilibria on the coordinate planes.

Proposition 4. Let $E_{ij}$ be as given in Proposition 1. Then
(i) $E_{12}$ is a saddle with two-dimensional stable manifold consisting of the positive quadrant in the $x_1x_2$-plane when $0 < c < c_0$, locally asymptotically stable when $c_0 < c < \beta_{21}$ and a saddle with two-dimensional stable manifold intersecting the $x_1x_2$-plane in a curve, when $c > \beta_{12}$.
(ii) $E_{23}$ is a saddle with two-dimensional stable manifold consisting of the positive quadrant in the $x_2x_3$-plane when $c < \beta_{32}$, a saddle with one-dimensional stable manifold lying in the $x_2x_3$-plane when $\beta_{23} < c < c_1$ and a saddle with two-dimensional stable manifold intersecting the $x_2x_3$-plane in a curve when $c > c_1$, $c_1$ as defined in (9).
(iii) $E_{13}$ is always a saddle with two-dimensional stable manifold consisting of the positive quadrant in the $x_1x_3$-plane when $c < \beta_{31}$ and intersecting the $x_1x_3$-plane in a curve when $c > \beta_{13}$.
Proof. We just check (i). Stability of $E_{23}$ and $E_{13}$ can be treated in a similar way. Write $E_{12} = (x_1, x_2, 0)$. Then $(x_1, x_2)$ is determined by

$$x_1 + cx_2 = b_1 \quad \text{and} \quad cx_1 + x_2 = b_2. \tag{13}$$

and by (12), the Jacobian matrix $J = [a_{ij}]$ at $(x_1, x_2, 0)$ satisfies

$$a_{31} = a_{32} = 0 \quad \text{and} \quad a_{33} = \frac{a_3}{1 + cx_1 + cx_2} = \frac{(1 + c)a_3}{c(a_1 + a_2 - 1) + 1}. \tag{14}$$

Using (9), $J$ has one eigenvalue $\frac{a_3}{1 + cx_1 + cx_2}$ with

$$\frac{a_3}{1 + cx_1 + cx_2} < 1 \quad \text{iff} \quad c > \frac{a_3 - 1}{a_1 + a_2 - a_3 - 1} = \frac{1}{\beta_{13} - \beta_{23} - 1} = c_0. \tag{15}$$

By (14), the other two eigenvalues of $J$ coincide with those of $B = [a_{ij}]_{2 \times 2}$. By (13), $B$ is the Jacobian matrix at the interior equilibrium $(x_1, x_2)$ of the following system

$$x_1(t + 1) = \frac{a_1x_1(t)}{1 + x_1(t) + cx_2(t)} \quad \text{and} \quad x_2(t + 1) = \frac{a_2x_2(t)}{1 + cx_1(t) + x_2(t)}. \tag{16}$$

Since $c_0 < \beta_{31} < \beta_{21} < 1 < \beta_{12}$, (15) and Theorem 1.1(iii) shows that $E_{12}$ is stable when $c_0 < c < \beta_{21}$ and a saddle with two-dimensional stable manifold consisting of the positive quadrant in the $x_1x_2$-plane when $0 < c < c_0$. The claim for $c > \beta_{12}$ follows from Theorem 1.1(iv). \hfill \square

3. Proof of Proposition 2 on LAS of $E^*$. In this section we determine the local stability properties of the interior equilibrium $E^* = (x_1, x_2, x_3)$ defined in (7) and (8). By (12) we have

$$J = \begin{bmatrix} 
\frac{a_1 - x_1}{a_1} & -\frac{cx_1}{a_1} & -\frac{cx_1}{a_1} \\
-\frac{cx_2}{a_2} & \frac{a_2 - x_2}{a_2} & -\frac{cx_2}{a_2} \\
-\frac{cx_3}{a_3} & \frac{cx_3}{a_3} & \frac{a_3 - x_3}{a_3}
\end{bmatrix}. \tag{17}$$

Write $J = I - P$, where

$$P = \begin{bmatrix} 
x_1 & cx_1 & cx_1 \\
x_2 & x_2 & cx_2 \\
x_3 & cx_3 & x_3
\end{bmatrix}. \tag{18}$$

Define $X_i = \sqrt{\frac{x_i}{a_i}}$ and $Q = \text{Diag}(\frac{1}{X_1}, \frac{1}{X_2}, \frac{1}{X_3}) \cdot P \cdot \text{Diag}(X_1, X_2, X_3)$. Then $Q = (Q_{ij})$ is similar to $P$ and is a symmetric matrix as $Q_{ii} = X_i^2$ and $Q_{ij} = cx_iX_j$ for $i \neq j$. It follows that all eigenvalues of $Q$, and thus $P$, are real. Denote them by $\lambda_3 \leq \lambda_2 \leq \lambda_1$. Let $g(\lambda) = \det(\lambda I - P)$ be their common characteristic polynomial. By direct expansion,

$$\lambda_1\lambda_2\lambda_3 = \det(P) = (1 - c)^2(1 + 2c)\frac{x_1x_2x_3}{a_1a_2a_3} > 0. \tag{19}$$
First consider $0 \leq c < c_0$. What we need prove here is that the eigenvalues of $J$ lie inside the unit circle. Gershgorin’s theorem can be used to show this is certainly the case when $0 \leq c < 1/2$. However this leaves the interval $1/2 \leq c < c_0$ to be considered. One possibility would be to use Jury’s criterion. See, for instance, Allen [3]. However this turns out to be even more complicated than what we now do.

Since $\{1 - \lambda_i\}$ are the eigenvalues of $J$, the stability of $E^*$ will follow from

$$\text{all } |1 - \lambda_i| < 1, \text{or equivalently, } 0 < \lambda_3 \text{ and } \lambda_1 < 2. \quad (17)$$

For any nonzero vector $Y = (y_1, y_2, y_3)^T,$

$$Y^T QY = (1 - c)(X_1^2 y_1^2 + X_2^2 y_2^2 + X_3^2 y_3^2) + c(X_1 y_1 + X_2 y_2 + X_3 y_3)^2 \quad (18)$$

is positive for $0 \leq c < 1$. So $Q$ is positive definite and hence all $\lambda_i > 0$. It remains to check $\lambda_1 < 2$ in ($17$). When $c = 0$, it is easy to see from (2) that the eigenvalues of $Q$ are $\frac{1}{a_i} < 1$. By continuity, if $Q$ has an eigenvalue $\geq 2$ for some value of $c$ in $(0, c_0)$, then there must be a value of $c$ in $(0, c_0)$ at which one of the eigenvalues is 2. So we need only show that for all $c \in (0, c_0)$, 2 is not an eigenvalue of $Q$, or equivalently, $g(2) = \det(2I - P) \neq 0$.

Recall that $b_i = a_i - 1$ by (3). Define the positive quantities

$$\begin{cases}
S_1 = b_1^2 + b_2^2 + b_3^2, & S_2 = b_1 b_2 + b_2 b_3 + b_3 b_1, & S_3 = b_1^2 + b_2^2 + b_3^2, \\
S_4 = b_1^2 (b_2 + b_3) + b_2^2 (b_1 + b_3) + b_3^2 (b_1 + b_2), & S_5 = b_1 b_2 b_3.
\end{cases} \quad (19)$$

With $x_1, x_2, x_3$ as in (8), a careful calculation shows that

$$(1 - c)(1 + 2c)^2 a_1 a_2 a_3 g(2) = I_1 + I_2 + I_3, \quad (20)$$

where

$$I_1 = 4(1 - c)[2(1 + 2c)^2 + (1 + 2c)(1 + 4c)(b_1 + b_2 + b_3)] \geq 0 \text{ iff } c \leq 1, \quad (21)$$

$$I_2 = 2c(2 + 5c - c^2) S_1 + (2 + 10c + 4c^2 - 28c^3) S_2, \quad (22)$$

$$I_3 = c^2(1 + c) S_3 + c(1 + 3c - c^2) S_4 + (1 + 3c - 6c^2 - 22c^3) S_5. \quad (23)$$

For $c \in (0, 1)$ we use $2 + 5c - c^2 > 0$ and $S_1 \geq S_2$ to get

$$I_2 \geq 2(1 + 7c + 7c^2 - 15c^3) S_2 = 2(1 - c)(1 + 8c + 15c^2) S_2 > 0. \quad (24)$$

For $c \in (0, c_0)$ we have from (8) that

$$(1 + c) b_i > c \sum_{j \neq i} b_j \text{ for } i = 1, 2, 3. \quad (25)$$

Hence, $(1 + c) b_i > c b_j \sum_{j \neq i} b_j$ and $b_i \sum_{j \neq i} b_i^2 \geq 2b_1 b_2 b_3 = 2S_5$. Summing and using the definition in (19), these two inequalities imply respectively that

$$(1 + c) S_3 \geq c S_4 \text{ for } c \in (0, c_0) \text{ and } S_4 \geq 6S_5. \quad (25)$$

Hence for $c \in (0, c_0)$,

$$I_3 \geq c(1 + 3c) S_4 + (1 + 3c - 6c^2 - 22c^3) S_5 \geq (1 - c)(1 + 10c + 22c^3) S_5 > 0. \quad (26)$$

Combining (20), (21), (24) and (26), we get $g(2) = \det(2I - P) \neq 0$ as needed.

Now consider the stability of $E^* = (x_1, x_2, x_3)$ when $\beta_{21} + \beta_{31} > 1$ and $c > c_1 = (\beta_{21} + \beta_{31} - 1)^{-1} > 1$. As in (17), to prove the required properties of the eigenvalues of $J$, it suffices to show that

$$1 < 1 - \lambda_2 < 1 - \lambda_3 \text{ and } -1 < 1 - \lambda_1 < 1. \quad (27)$$
Since $P$ is a positive matrix, the Perron-Frobenius Theorem implies that $\lambda_1 = \max |\lambda_i| > 0$. If we take $X_1 y_1 = -X_2 y_2 = 1$ and $y_3 = 0$ in (18), we see that $Y^T Q Y = 2(1 - c) < 0$. Hence $\lambda_3 = \min \lambda_i < 0$. Moreover, $\lambda_2 < 0$ as well due to $\lambda_1 \lambda_2 \lambda_3 = \det(P) > 0$ by (16). It remains to check $-1 < 1 - \lambda_1$ in (27). That is $\lambda_1 < 2$. We will prove below that in (20) all $I_i < 0$. Then it will follow that $g(2) > 0$ since $c > 1$. Because $g(0) = -\det(P) < 0$ and $\lambda_2 < 0$ as just verified, we get $0 < \lambda_1 < 2$ by continuity and the proof is complete.

So we just need to prove that all $I_i < 0$. By (21), $I_1 < 0$. We treat $I_2$ now. Obviously, $2 + 10c + 4c^2 - 28c^3 < 0$ for $c > 1$. We may assume $2 + 5c - c^2 \geq 0$. Otherwise, $I_2 < 0$ as both terms in (22) are negative. Using $c > 1$ and $E^* > 0$ in (8), we have

$$(1 + c) S_1 - 2c S_2 = \sum_{i=1}^{3} \left( (1 + c) b_i - c \sum_{j \neq i} b_j \right) b_i < 0.$$

Then $(1 + c) 2c(2 + 5c - c^2) S_1 \leq 4c^2(2 + 5c - c^2) S_2$. Applying it to (22), we get $I_2 < 0$ as

$$(1 + c) I_2 \leq 2(1 - c)(1 + 7c + 18c^2 + 16c^3) S_2 < 0.$$

As for $I_3$, we define $C = (1 - c)^3(1 + 2c)^3 x_1 x_2 x_3$. We see that $C < 0$ since $c > 1$.

Also we can write $C = \prod_{i=1}^{3} ((1 + c) b_i - c \sum_{j \neq i} b_j)$ by (8) and a careful expansion shows that

$$0 > C = c^2 (1 + c) S_3 - c(1 + c + c^2) S_4 + (1 + 3c + 6c^2 + 2c^3) S_5.$$

Applying this equation to (23), we get easily that

$$I_3 = C + 2c(1 + 2c)(S_1 - 6c S_5) < 0,$$

since $S_1 - 6c S_5 = b_1 b_2 b_3 (\beta_{12} + \beta_{21} + \beta_{13} + \beta_{31} + \beta_{23} + \beta_{32} - 6c) < 0$ due to $c > c_1 > \beta_{ij}$ for all $i, j$ by (10). This completes the proof of Proposition 2.

4. Proof of Theorem 1.2 on GAS of $E^*$. In this section we prove that all positive solutions converge to the interior equilibrium $E^*$ when $0 < c < c_0$ by verifying the four hypotheses (H1)–(H4), which are described on page 2040 of [4]. Here $\Omega = \mathbb{R}^3_+$ and taking $R = \mathbb{R}^3_+$ also, it is immediate that $R$ is a monotone region and $f(\Omega \setminus R) = f(\mathbb{R}^3_+ \setminus R) = \phi \subset f(R)$. Also $f$ restricted to $R$ is an orientation preserving local homeomorphism because it is a local diffeomorphism and the determinant of $Df(x)$ at the point $(x_1, x_2, x_3)$ is

$$\frac{a_1 a_2 a_3 [1 + c(x_1 + x_2 + x_3)]^2}{[1 + x_1 + c(x_2 + x_3)]^2[1 + x_2 + c(x_1 + x_3)]^2[1 + x_3 + c(x_1 + x_2)]^2} > 0. \quad (28)$$

(H2) requires that $f$ restricted to $R = \mathbb{R}^3_+$ is a monotone map. Using Lemma 4.1 in [4], this holds since the transpose matrix of cofactors of $Df(x)$

$$\frac{T}{T_1 T_2 T_3} \begin{bmatrix} \alpha_{1x_1} T_1 & \alpha_{1x_2} T_2 & \alpha_{1x_3} T_3 \\ \alpha_{2x_1} T_1 & \alpha_{2x_2} T_2 & \alpha_{2x_3} T_3 \\ \alpha_{3x_1} T_1 & \alpha_{3x_2} T_2 & \alpha_{3x_3} T_3 \end{bmatrix}$$

is positive, where $T_i = \left(1 + x_1 + c \sum_{j \neq i} x_j \right)^2 a_i$ and $T = 1 + c(x_1 + x_2 + x_3)$.

(H3) is satisfied if each $E_{ij}$ is a saddle such that $E_{ij}$ is a global asymptotic equilibrium for $f$ restricted to the positive quadrant in the $x_i x_j$-plane. For our map, this follows from Proposition 4 and Theorem 1.1 as $c_0 < \beta_{ij}$ by (10).
(H4) requires that \( f \) have a carrying simplex. According to Corollary 6.1 in [11], this is satisfied if conditions (i), (ii) and (iii) of that corollary hold. Condition (i) requires that \( f \) have the property that if \( x \leq y \) but \( x \neq y \), then \( f_i(y) < f_i(x) \) for all \( i \), which clearly holds for our \( f \) (see (11) and (5)). (ii) requires the existence of the fixed points \( E_i \) and (iii) requires that \( f \) be retrotone and locally one to one in \( C = [0, a_1 - 1] \times [0, a_2 - 1] \times [0, a_3 - 1] \). This follows from Proposition 4.1 in [11] since \( f \) is \( C^1 \) on a neighbourhood of \( C \) and for all \( x \in C \setminus \{0\} \),
\[
[Df(x)]_{i,j}^{-1} > 0 \quad \text{for} \quad i, j \in I(x) = \{k : x_k \neq 0\},
\]
as we can see from the transpose matrix of cofactors above and (28).

Since the hypotheses (H1)-(H4) are satisfied and when \( 0 < c < c_0 \), the system has a unique interior equilibrium \( E^* \), it follows from Theorem 2.4 in [4] that \( E^* \) is globally asymptotically stable.

5. Proof of Theorem 1.3 on GAS of \( E_{12} \). By Propositions 3 and 4, the only stable equilibrium is \( E_{12} \) when \( c_0 < c < \beta_{21} \). Here we show all positive solutions of (2) tend to \( E_{12} \) when \( c_0 < c < \beta_{21} \).

We use Corollary 2.1 in Ruiz-Herrera [11]. Conditions (C1), (C2) and (C3) are just the conditions (i), (ii) and (iii) which we verified in connection with the verification of (H4) in the proof of Theorem 1.2. (C4) just requires that the number of fixed points on the boundary be finite, clearly satisfied here. Then condition (ii) of Corollary 2.1 requires that there is no interior fixed point and the stable manifolds of all the other fixed points on the boundary do not intersect the interior. For \( c_0 < c < \beta_{21} \), it follows from (8)-(10) that there is no interior fixed point. Also, in view of Propositions 3 and 4, the stable manifolds of all the other fixed points on the boundary do not intersect the interior when \( c_0 < c < \beta_{21} \). So Theorem 1.3 follows from Corollary 2.1 in Ruiz-Herrera [11]. The claim of the theorem is verified.

6. Proof of Theorem 1.4 on GAS of \( E_1 \). First we show the following comparison lemma.

Lemma 6.1. For \( t \geq 0 \), let \( f_1(t, x, y) \) be a continuous real function, nondecreasing in \( x \) and nonincreasing in \( y \) and let \( f_2(t, x, y) \) be a continuous real function, nondecreasing in \( y \) and nonincreasing in \( x \). Let \((x(t), y(t)), (u(t), v(t))\) be sequences such that for all \( t \geq t_0 \),
\[
x(t + 1) \leq f_1(t, x(t), y(t)), \quad y(t + 1) \geq f_2(t, x(t), y(t))
\]
and
\[
u(t + 1) = f_1(t, u(t), v(t)), \quad v(t + 1) = f_2(t, u(t), v(t)).
\]
Then \( x(t) \leq u(t), y(t) \geq v(t) \) for all \( t \geq t_0 \) if \( x(t_0) \leq u(t_0), y(t_0) \geq v(t_0) \).

Proof. Suppose \( x(t) \leq u(t), y(t) \geq v(t) \) for some \( t \geq t_0 \). Then
\[
x(t + 1) \leq f_1(t, x(t), y(t)) \leq f_1(t, u(t), y(t)) \leq f_1(t, u(t), v(t)) = u(t + 1)
\]
and
\[
y(t + 1) \geq f_2(t, x(t), y(t)) \geq f_2(t, u(t), y(t)) \geq f_2(t, u(t), v(t)) = v(t + 1).
\]
The lemma follows by induction on \( t \). \( \square \)
Now we are ready to prove the theorem. By (2),
\[
x_1(t+1) = \frac{a_1 x_1(t)}{1 + x_1(t) + c(x_2(t) + x_3(t))}
\]
and by increasing the denominators and using \(a_3 < a_2\), we find that
\[
x_2(t+1) + x_3(t+1) \leq \frac{a_2(x_2(t) + x_3(t))}{1 + cx_1(t) + \min(c, 1)(x_2(t) + x_3(t))}.
\]

Now consider the solution \((y(t), z(t))\) of the system
\[
y(t+1) = \frac{a_1 y(t)}{1 + y(t) + cz(t)} \quad \text{and} \quad z(t+1) = \frac{a_2 z(t)}{1 + cy(t) + \min(c, 1)z(t)}
\]
with \(y(0) = x_1(0)\) and \(z(0) = x_2(0) + x_3(0)\). It follows from Lemma 6.1 that \(x_1(t) \geq y(t)\) and \(x_2(t) + x_3(t) \leq z(t)\) for all \(t \geq 0\). Using Theorem 1.3(i), \(\lim_{t \to \infty} (y(t), z(t)) = (a_1 - 1, 0)\) under the present assumption \(\beta_{21} < c < \beta_{12}\).
Hence,
\[
\lim_{t \to \infty} x_2(t) + x_3(t) = 0 \quad \text{and} \quad \liminf_{t \to \infty} x_1(t) \geq a_1 - 1.
\]

We need the following simple lemma.

**Lemma 6.2.** For \(t \geq t_0\), let \(f(t, x)\) be a nondecreasing continuous real function of \(x\) and \(x(t)\) be sequences such that \(x(t+1) \leq f(t, x(t))\), \(y(t+1) \geq f(t, y(t))\). Then \(x(t) \leq y(t)\) for all \(t \geq t_0\) if \(x(t_0) \leq y(t_0)\).

**Proof.** Suppose \(x(t) \leq y(t)\) for some \(t \geq t_0\). Then \(x(t+1) \leq f(t, x(t)) \leq f(t, y(t)) \leq y(t+1)\). The lemma follows by induction on \(t\).

Obviously we have from (29) that
\[
x_1(t+1) \leq \frac{a_1 x_1(t)}{1 + x_1(t)}.
\]
Now if \(u(t)\) is the solution of \(u(t+1) = \frac{a_1 u(t)}{1 + u(t)}\) with \(u(0) = x_1(0)\), we know that \(\lim_{t \to \infty} u(t) = a_1 - 1\). By the lemma above, \(x_1(t) \leq u(t)\) for all \(t\) and thus \(\limsup_{t \to \infty} x_1(t) \leq a_1 - 1\). The conclusion that \(\lim_{t \to \infty} x(t) = (a_1 - 1, 0, 0) = E_1\) follows from (31).

**Remark.** By repeating the proof for Theorem 1.3, this theorem can also be shown by using Corollary 2.1 in Ruiz-Herrera [11].

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E-mail address: chow@math.sinica.edu.tw
E-mail address: palmer@math.ntu.edu.tw