Predator-Mediated Coexistence and Extinction*

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Received 2 December 1980

ABSTRACT

In this paper we analyze a mathematical model for a two-competing-prey, one-predator system and discuss the effect of predation on the two competing prey. Our basic assumption is that the predator can survive on either of the two competing prey in a one-predator, one-prey subcommunity. Conditions for the coexistence of the two competing prey and the extinction of either prey are completely determined and discussed. The conclusion is that the outcomes depend critically on the prey species' capability of invading the complementary subcommunity formed by predator species and other prey. Our mathematical analysis is rigorous and global.

1. INTRODUCTION

In this paper the following system of ordinary differential equations is considered which models the predation effect on two competing species

$$\frac{dN_1}{dt} = N_1\left[r_1\left(1 - \frac{N_1}{K_1}\right) - \alpha_{12}N_2 - \alpha_{13}P\right],$$

$$\frac{dN_2}{dt} = N_2\left[r_2\left(1 - \frac{N_2}{K_2}\right) - \alpha_{21}N_1 - \alpha_{23}P\right], \qquad (1.1)$$

$$\frac{dP}{dt} = P\left[\alpha_{31}N_1 + \alpha_{32}N_2 - D\right],$$

$$N_1(0)>0, \qquad N_2(0)>0, \qquad P(0)>0.$$

This is Lotka-Volterra-type model for a predator species P and two competing prey species N_1, N_2. The model (1.1) was developed by Parrish and Saila [11] and was actually motivated by the experiments of Paine [10] on some intertribal communities of marine invertebrates. Paine removed the

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major predator from an intertribal community and observed its change from 15 species to 8 species during a period of less than two years. Paine demonstrated clearly that a top predator could serve to increase diversity in this intertidal system. Porter [12, 13] showed that the diversity of coral reefs was increased by predation. Harper [7] discussed the role of an herbivore in increasing the diversity of grass species, and Conell [1] discussed the role of predators in preventing competitive exclusion in the rain forest and the intertidal zone.

In [3] Cramer and May gave a numerical example for the case of "equal predation," i.e., $\alpha_{13} = \alpha_{23}$, $\alpha_{32} = \alpha_{31}$, and demonstrated possible coexistence. Fujii [4] did some numerical analysis on (1.1) and showed that there exists a stable limit cycle in some range of parameters. Hallam [5] gave a more systematic local-stability analysis of this model. However, his biological interpretation is not clear, due to the complicated notation. Vance [14] also discusses this system, assuming the two competing prey identical in all respects except for the differences which evoke frequency-dependent predation and the difference in the species against which the prey direct their principal defense mechanisms. None of them gave satisfactory results for the model. In this paper we intend to give complete results for an important case: we shall assume species P can survive on either prey in the subcommunity.

In Sec. 2 we scale the system (1.1) into one easier to analyze. We briefly state the results on two-dimensional subcommunities in Sec. 3 and state our principal results in Sec. 4. Section 5 is the discussion section, and we give the proofs in Sec. 6.

2. SCALING

In this brief section we choose appropriate nondimensional variables. Hereafter we shall use bars over parameters and independent and dependent variables to signify that they appear in the original equations (1.1). Parameters and variables without bars will be used for the new nondimensional entities. Where no change is made in a parameter or variable, no bars will appear. Thus we let

$$t = \bar{D}\bar{t}, \quad N_1(t) = \frac{\bar{\alpha}_{31}}{\bar{D}}\bar{N}_1(t), \quad N_2(t) = \frac{\bar{\alpha}_{32}}{\bar{D}}\bar{N}_2(t), \quad P(t) = \frac{\bar{\alpha}_{13}}{\bar{D}}\bar{P}(t),$$

$$r_1 = \frac{\bar{r}_1}{\bar{D}}, \quad K_1 = \frac{\bar{K}_1\bar{\alpha}_{31}}{\bar{D}}, \quad \alpha_{12} = \frac{\bar{\alpha}_{12}}{\bar{\alpha}_{32}}, \quad r_2 = \frac{\bar{r}_2}{\bar{D}}, \quad K_2 = \frac{\bar{K}_2\bar{\alpha}_{32}}{\bar{D}},$$

$$\alpha_{21} = \frac{\bar{\alpha}_{21}}{\bar{\alpha}_{31}}, \qquad \alpha_{23} = \frac{\bar{\alpha}_{23}}{\bar{\alpha}_{13}}.$$

With this change (1.1) becomes

$$\frac{dN_1}{dt} = N_1\left[r_1\left(1-\frac{N_1}{K_1}\right) - \alpha_{12}N_2 - P\right],$$

$$\frac{dN_2}{dt} = N_2\left[r_2\left(1-\frac{N_2}{K_2}\right) - \alpha_{21}N_1 - \alpha_{23}P\right], \qquad (2.1)$$

$$\frac{dP}{dt} = P[N_1 + N_2 - 1],$$

$$N_1(0) > 0, \qquad N_2(0) > 0, \qquad P(0) > 0.$$

3. RESULTS ON TWO DIMENSIONAL SUBCOMMUNITIES OF (2.1)

First, we state the well-known results on the classical Lotka-Volterra competition model:

$$\dot{N}_1 = N_1\left[r_1\left(1-\frac{N_1}{K_1}\right) - \alpha_{12}N_2\right],$$

$$\dot{N}_2 = N_2\left[r_2\left(1-\frac{N_2}{K_2}\right) - \alpha_{21}N_1\right]. \qquad (3.1)$$

THEOREM 2.1

(i) *If $r_1/\alpha_{12} > K_2$ and $r_2/\alpha_{21} > K_1$ (denoted by $N_1 \underset{c}{\leftrightarrow} N_2$), then*

$$\lim_{t \to \infty}\left(N_1(t), N_2(t)\right) = \left(N_1^*, N_2^*\right)$$

$$= \left(\frac{1}{K_1} \cdot \frac{1}{K_2} - \frac{\alpha_{12}}{r_1}\frac{\alpha_{21}}{r_2}\right)^{-1}\left(\frac{1}{K_2} - \frac{\alpha_{12}}{r_1}, \frac{1}{K_1} - \frac{\alpha_{21}}{r_2}\right).$$

(ii) *If $K_2 > r_1/\alpha_{12}$ and $r_2/\alpha_{21} > K_1$ (denoted by $N_2 \gg N_1$), then*

$$\lim_{t \to \infty}\left(N_1(t), N_2(t)\right) = (0, K_2).$$

(iii) *If $K_1 > r_2/\alpha_{21}$ and $r_1/\alpha_{12} > K_2$ (denoted by $N_1 \gg N_2$), then*

$$\lim_{t \to \infty}\left(N_1(t), N_2(t)\right) = (K_1, 0).$$

(iv) *If $K_1 > r_2/\alpha_{21}$ and $K_2 > r_1/\alpha_{12}$ (denoted by $N_1 \Leftrightarrow N_2$), then $(K_1, 0), (0, K_2)$ are locally stable, and there exists a one-dimensional stable manifold through the saddle point (N_1^*, N_2^*).*

We note that we have adopted the notation $N_1 \gg N_2$, $N_2 \gg N_1$, $N_1 \underset{c}{\leftrightarrow} N_2$, $N_1 \oplus N_2$ from [5]. These outcomes are represented in Fig. 1.

Next, we consider the Lotka-Volterra predator-prey system

$$\frac{dN}{dt} = N\left[r\left(1 - \frac{N}{K} \right) - \alpha P \right],$$

$$\frac{dP}{dt} = P[\beta N - D]. \tag{3.2}$$

THEOREM 3.2 [8]

(i) *If* $K > D/\beta$, *then*

$$\lim_{t \to \infty} (N(t), P(t)) = \left(\frac{D}{\beta}, \frac{r}{\alpha}\left(1 - \frac{D}{K\beta} \right) \right).$$

(ii) *If* $K < D/\beta$, *then*

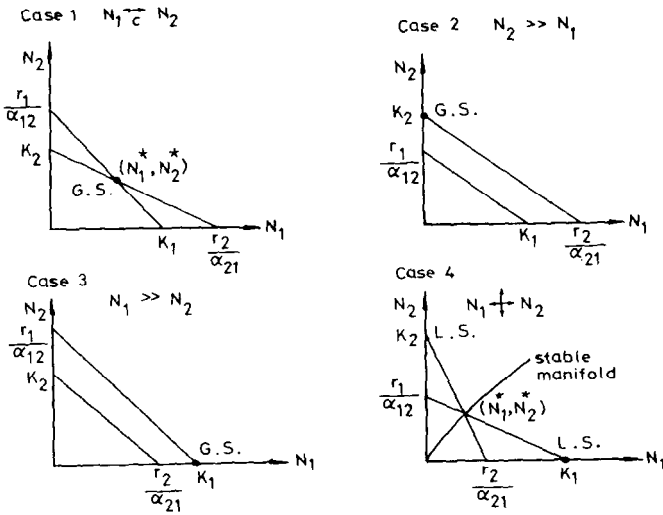$$\lim_{t \to \infty} (N(t), P(t)) = (K, 0).$$

FIG. 1.   G.S. = globally stable, L.S. = locally stable.

4. STATEMENTS OF RESULTS

In this section we state the principal results of this paper on the system (2.1). We shall reformulate these results in terms of the original parameters in the discussion section. The proofs and certain technical lemmas are deferred to Sec. 6. First we note the following lemma and omit the proof.

LEMMA 4.1

The solutions $N_1(t)$, $N_2(t)$, $P(t)$ of (2.1) are positive and bounded.

Our basic assumption on (2.1) is

$$K_1 > 1, \qquad K_2 > 1, \tag{H}$$

i.e., we assume the predator can survive on either prey in the predator-prey subcommunities. Under the assumption (H), we have two important equilibria of (2.1), namely,

$$(E_{1P}) = (1, 0, P_1), \qquad \text{where} \quad P_1 = r_1\left(1 - \frac{1}{K_1}\right),$$

$$(E_{2P}) = (0, 1, P_2), \qquad \text{where} \quad P_2 = \frac{r_2}{\alpha_{23}}\left(1 - \frac{1}{K_2}\right).$$

The following lemma can be obtained directly from linear stability analysis of (E_{1P}) and (E_{2P}), and we omit the proof.

LEMMA 4.2

(i) (E_{1P}) is asymptotically stable if

$$\frac{r_2 - \alpha_{21}}{r_1(1 - 1/K_1)} < \alpha_{23}, \tag{4.1}$$

and unstable when the reversed inequality holds.
(ii) (E_{2P}) is asymptotically stable if

$$\frac{r_1 - \alpha_{12}}{r_2(1 - 1/K_2)} < \frac{1}{\alpha_{23}}, \tag{4.2}$$

and unstable when the reversed inequality holds.
Now we state the main results of this paper.

THEOREM 4.3

Let (H) hold.

(i) If

$$\frac{r_2 - \alpha_{21}}{r_1(1 - 1/K_1)} < \alpha_{23} \quad and \quad \frac{r_1 - \alpha_{12}}{r_2(1 - 1/K_2)} > \frac{1}{\alpha_{23}},$$

then (E_{1P}) is globally stable.

(ii) If

$$\frac{r_1 - \alpha_{12}}{r_2(1 - 1/K_2)} < \frac{1}{\alpha_{23}} \quad and \quad \frac{r_2 - \alpha_{21}}{r_1(1 - 1/K_1)} > \alpha_{23},$$

then (E_{2P}) is globally stable.

The next theorem states the results in which the outcomes will depend on the initial populations.

THEOREM 4.4

Let (H) hold. If

$$\frac{r_2 - \alpha_{21}}{r_1(1 - 1/K_1)} < \alpha_{23} \quad and \quad \frac{r_1 - \alpha_{12}}{r_2(1 - 1/K_2)} < \frac{1}{\alpha_{23}},$$

then

(i) $(E_c) = (N_{1c}, N_{2c}, P_c)$ exists uniquely with $N_{ic} > 0$, $i = 1, 2$, $P_c > 0$ if and only if $r_1 r_2 (1 - 1/K_1)(1 - 1/K_2) > (r_1 - \alpha_{12})(r_2 - \alpha_{21})$.

(ii) If (E_c) exists, then (E_c) is a saddle point with two-dimensional stable manifold through (E_c). In this case, if $(E_{12}) = (N_1^*, N_2^*, 0)$ exists and $N_1 \Leftrightarrow N_2$, then (E_{12}) is a saddle point with one-dimensional stable manifold through (E_{12}) in the N_1-N_2 plane, while in the case $N_1 \underset{c}{\leftrightarrow} N_2$, (E_{12}) is a saddle point with two-dimensional stable manifold in the N_1-N_2 plane.

(iii) If (E_c) doesn't exist, then (E_{12}) exists with $N_1 \Leftrightarrow N_2$ and is a saddle point with two-dimensional stable manifold through it.

DEFINITION

If no solution $(N_1(t), N_2(t), P(t))$ has a component which approaches zero as t approaches infinity, then the system (2.1) is said to be persistent.

THEOREM 4.5

If

$$\frac{r_2 - \alpha_{21}}{r_1(1 - 1/K_1)} > \alpha_{23} \quad and \quad \frac{r_1 - \alpha_{12}}{r_2(1 - 1/K_2)} > \frac{1}{\alpha_{23}},$$

then (E_c) exists and the system (2.1) is persistent.

We note that in this paper we only consider the solutions whose initial values lie in the interior of the positive octant.

5. DISCUSSION

We now return to original equations (1.1) and original parameters, variables and independent variable. First of all, our basic assumption (H) becomes

$$K_1 > \bar{N}_1 = \frac{D}{\alpha_{31}}, \qquad K_2 > \bar{N}_2 = \frac{D}{\alpha_{32}}, \tag{5.1}$$

i.e., we assume the predator P can survive in the N_1-P and N_2-P subcommunities. The inequalities in (4.1) and (4.2) and their reversed inequalities are reformulated as

$$\frac{r_2 - \alpha_{21}\bar{N}_1}{r_1(1 - \bar{N}_1/K_1)} < \frac{\alpha_{23}}{\alpha_{13}}, \tag{5.2}$$

$$\frac{r_2 - \alpha_{21}\bar{N}_1}{r_1(1 - \bar{N}_1/K_1)} > \frac{\alpha_{23}}{\alpha_{13}}, \tag{5.3}$$

$$\frac{r_1 - \alpha_{12}\bar{N}_2}{r_2(1 - \bar{N}_2/K_2)} < \frac{\alpha_{13}}{\alpha_{23}}, \tag{5.4}$$

$$\frac{r_1 - \alpha_{12}\bar{N}_2}{r_2(1 - \bar{N}_2/K_2)} > \frac{\alpha_{13}}{\alpha_{23}}. \tag{5.5}$$

Next, we give the biological interpretations of (5.2), (5.3), (5.4), and (5.5). From Theorem 3.2 we assume predator species P and prey species N_1 are in the stable subcommunity with steady state $(\bar{N}_1, P_1^*)$, and let the prey species N_2 invade the N_1-P subcommunity. The specific growth rate of N_2 is $r_2 - \alpha_{21}\bar{N}_1$. If $r_2 - \alpha_{21}\bar{N}_1 \leq 0$, then obviously the prey species N_2 cannot even survive. On the other hand, if $r_2 - \alpha_{21}\bar{N}_1 > 0$, then we may rewrite (5.2) as

$$\frac{\alpha_{13}}{r_1(1 - \bar{N}_1/K_1)} < \frac{\alpha_{23}}{r_2 - \alpha_{21}\bar{N}_1}. \tag{5.6}$$

In (5.6), the left- and right-hand sides are the intensities of predation exerted by the predator species P on a per capita basis relative to the per capita power of prey species N_1, N_2, respectively, to multiply at steady state $(\bar{N}_1, P_1^*)$. Thus the inequality (5.6) says predator P exerts higher predation pressure on species N_2 than on species N_1. Hence (5.2) states that the prey species N_2 cannot invade the N_1-P subcommunity successfully. Similarly (5.3)

states that the prey species N_2 is a stronger competitor and can invade the N_1-P subcommunity successfully. The biological interpretation for (5.4), (5.5) follows similarly by interchanging the indices 1 and 2.

With these biological interpretations in mind, we are now in a position to explain Theorem 4.3, 4.4 and 4.5 and use the original parameter to state the results.

THEOREM 4.3

(i) *Let* (5.1), (5.2), *and* (5.5) *hold. Then*

$$\lim_{t \to \infty} \left(N_1(t), N_2(t), P(t) \right) = \left(\overline{N}_1, 0, P_1^* \right).$$

(ii) *Let* (5.1), (5.3), *and* (5.4) *hold. Then*

$$\lim_{t \to \infty} \left(N_1(t), N_2(t), P(t) \right) = \left(0, \overline{N}_2, P_2^* \right).$$

Part (i) states that the species N_1 can invade the N_2-P community, successfully and its rival N_2, a weaker competitor, can't invade the N_1-P community. Hence N_1 is always the winner. A similar interpretation follows for (ii).

THEOREM 4.4

Let (5.1), (5.2), (5.4) *hold. Then the competition outcomes depend on the initial populations.*

In this case, neither species N_i can invade the complementary subcommunity, so the result is expected.

THEOREM 4.5

Let (5.1), (5.3), (5.5) *hold. Then the system* (1.1) *is persistent.*

This case is the most important one. When either species N_i has the capability to invade the complementary subcommunity, the species N_1, N_2 persist. They may persist either in stable equilibrium or in a stable limit cycle [3, 4]. We note that the linear stability analysis about (E_c) is too complicated to determine the local stability of (E_c). In our numerical simulation, we chose $r_1 = 300$, $r_2 = 210$, $\alpha_{13} = 1 = \alpha_{31} = \alpha_{32}$, $D = 1$, $\alpha_{12} = \alpha_{21} = 60$, $K_1 = \frac{10}{6}$, $K_2 = \frac{35}{2}$, and let α_{23} be a parameter. By Theorem 4.6, if $\frac{33}{40} < \alpha_{23} < \frac{5}{4}$, the system (2.1) is persistent. Our numerical computation shows:

(i) If $\alpha_{23} = 0.830$, then $(E_c) = (0.232584 \times 10^{-1}, 0.976738, 0.237209 \times 10^3)$ is locally stable;
if $\alpha_{23} = 0.845$, then $(E_c) = (0.898849 \times 10^{-1}, 0.910119, 0.229214 \times 10^3)$ is locally stable;
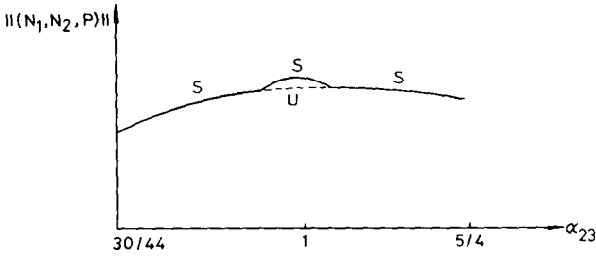
FIG. 2.

if $\alpha_{23} = 1.22$, then $(E_c) = (0.963565, 0.378924 \times 10^{-1}, 0.124287 \times 10^3)$ is locally stable.

(ii) If $\alpha_{23} = 1$, then $(E_c) = (\frac{2}{3}, \frac{5}{12}, 170)$ is unstable, and a limit cycle appears.

The bifurcation diagram is sketched in Fig. 2, where the lower branch corresponds to the steady state (E_c) and the upper branch corresponds to the stable limit cycle. Obviously we have two Hopf bifurcations.

Theorem 4.5 has some interesting implications. When two competitors can coexist without a predator, they can coexist with a predator provided that the ratio, α_{23}/α_{13}, of the predator's effect on N_2 to its effect on N_1 lies in a certain range (i.e., is neither too small nor too large—the predator should be "even-handed"). However, there are communities of two competing prey and a single predator for which the elimination of the predator will result in the extinction of one of the prey.

The competitive-exclusion principle [6] states that two competing species can coexist only if they exploit their environment differently. With the predation, Theorem 4.6 states that competing prey species can coexist even with exactly identical resource requirements if each prey species has invasion potential for the complementary predator-prey subcommunity.

For the three other cases concerning the system (2.1) (namely, $K_1 > 1$, $K_2 < 1$; $K_1 < 1$, $K_2 > 1$; $K_1 < 1$, $K_2 < 1$), it should be straightforward to classify and interpret the results. The rigorous mathematical proofs remain to be given.

6. PROOFS

Before we prove our main theorems, we state a theorem of Markus [9] and a theorem of Coppel [2] which will be used repeatedly.

DEFINITION

Let $A: x_i' = f_i(x, t)$ and $A: x_i' = f_i(x)$ $(i = 1, 2, \ldots, n)$ be a first-order system of ordinary differential equations. The real-valued functions $f_i(x, t)$ and $f_i(x)$

are continuous in (x, t) for $x \in G$, where G is an open subset of R^n, and for $t > t_0$, and they satisfy a local Lipschitz condition in x. A is said to be *asymptotic* to A_∞ $(A \to A_\infty)$ in G if for each compact set $K \subset G$ and for each $\varepsilon > 0$, there is a $T = T(K, \varepsilon) > t_0$ such that $|f_i(x, t) - f_i(x)| < \varepsilon$ for all $i = 1, 2, \ldots, n$, all $x \in K$, all $t > T$.

DEFINITION

The Ω-limit set for $\{\dot{x} = f(x, t), x(t_0) = x_0\}$ is the set of ω-limit points y, where $y = \lim_{n \to \infty} x(t_n)$ for some sequence $\{t_n\}$, $t_n \to \infty$.

THEOREM (MARKUS)

Let $A \to A_\infty$ in G, and let P be an asymptotically stable critical point of A_∞. Then there is a neighborhood N of P and time T such that the ω-limit set for every solution $x(t)$ of A which intersects N at a time later than T is equal to P.

THEOREM (COPPEL [2, p. 141])

If a real-valued function $f(t)$ has a finite limit as $t \to \infty$ and $f^{(n)}(t)$ (the nth derivative) is bounded for $t \geq t_0$, then $\lim_{t \to \infty} f^{(k)}(t) = 0$, $0 < k < n$.

Proof of Theorem 4.3. First we prove (i). The proof for (ii) follows similarly and we omit it. Let $\eta \in R$ be selected below and consider

$$
\begin{aligned}
\frac{\dot{N}_2}{N_2} + \eta \frac{\dot{P}}{P} - \alpha_{23} \frac{\dot{N}_1}{N_1} &= \left[r_2 \left(1 - \frac{N_2}{K_2} \right) - \alpha_{21} N_1 - \alpha_{23} P \right] + \eta [N_1 + N_2 - 1] \\
&\quad + \alpha_{23} \left[r_1 \left(1 - \frac{N_1}{K_1} \right) - \alpha_{12} N_2 - P \right] \\
&= (r_2 - \alpha_{23} r_1 - \eta) + N_1 \left(-\alpha_{21} + \eta + \frac{r_1}{K_1} \alpha_{23} \right) \\
&\quad + N_2 \left(-\frac{r_2}{K_2} + \alpha_{23} \alpha_{12} + \eta \right).
\end{aligned}
\tag{6.1}
$$

Since

$$
\frac{r_2 - \alpha_{21}}{r_1(1 - 1/K_1)} > \alpha_{23},
$$

i.e., $r_2 - \alpha_{21} < r_1 \alpha_{23}(1 - 1/K_1)$, we have

$$
r_2 - r_1 \alpha_{23} < \alpha_{21} - \frac{r_1}{K_1} \alpha_{23},
\tag{6.2}
$$

and since

$$
\frac{r_1 - \alpha_{12}}{r_2(1 - 1/K_2)} > \frac{1}{\alpha_{23}},
$$

i.e., $\alpha_{23}(r_1 - \alpha_{12}) > r_2(1 - 1/K_2)$, we have

$$r_2 - \alpha_{23}r_1 < \frac{r_2}{K_2} - \alpha_{12}\alpha_{23}. \tag{6.3}$$

From (6.2), (6.3) we can choose $\eta \in R$ such that $r_2 - \alpha_{23}r_1 - \eta < 0$, $-\alpha_{21} + \eta + (r_1/K_1)\alpha_{23} > 0$, and $-(r_2/K_2) + \alpha_{23} + \eta < 0$. Integrating from 0 to t and taking exponentials on both sides of (6.1) yields

$$\frac{N_2(t)}{N_2(0)} \cdot \left(\frac{P(t)}{P(0)}\right)^\eta \leqslant \left(\frac{N_1(t)}{N_1(0)}\right)^{\alpha_{23}} e^{\rho t},$$

where $\rho = r_2 - \alpha_{23}r_1 - \eta < 0$. If $\eta \leqslant 0$, then $\lim_{t \to \infty} N_2(t) = 0$. If $\eta > 0$, then $\lim_{t \to \infty} N_2(t)[P(t)]^\eta = 0$. We claim $\lim_{t \to \infty} N_2(t)P(t) = 0$. Let $u = \max(1, \eta)$; then

$$\left[N_2(t)P(t)\right]^u = N_2(t)\left[P(t)\right]^\eta \left[N_2(t)\right]^{u-1}\left[P(t)\right]^{u-\eta}$$

$$\leqslant N_2(t)\left[P(t)\right]^\eta \left(\sup_{0 \leqslant t \leqslant \infty} N_2(t)\right)^{u-1}\left(\sup_{0 \leqslant t \leqslant \infty} P(t)\right)^{u-\eta}.$$

From Lemma 4.1, it follows that $\lim_{t \to \infty} N_2(t)P(t) = 0$. In order to show that (E_{1P}) is globally stable, we have following possible cases.

Case 1: $\lim_{t \to \infty} P(t) = 0$. We intend to show this case is impossible by contradiction.

Subcase A: $\lim_{t \to \infty} N_2(t)$ exists.
A1: If $\lim_{t \to \infty} N_2(t) = 0$, then $\lim_{t \to \infty} N_1(t) = K_1$. It follows that $P(t)$ becomes unbounded as t large. This is a contradiction to Lemma 4.1.
A2: If $\lim_{t \to \infty} N_2(t) = C > 0$, by Coppel's theorem we have $C = K_2$ or $C = N_2^*$ and $\lim_{t \to \infty} N_1(t) = 0$ or N_1^*, since $K_1 > 1$, $K_2 > 1$, and $r_1 > \alpha_{12}$. From Fig. 1, cases 1, 4, it follows that $N_1^* + N_2^* > 1$ and $P(t)$ becomes unbounded for t large; again this is a contradiction.

Subcase B: $\lim_{t \to \infty} N_2(t)$ doesn't exist.
B1: $N_2 \gg N_1$. There exists $\varepsilon > 0$ and $\{t_n\}$ ($t_n \to \infty$ as $n \to \infty$) such that $\dot{N}_2(t_n) = 0$ and $N_2(t_n) > \varepsilon$ is a relative minimum. Choose a subsequence $\{t_{ni}\}$ of $\{t_n\}$ such that $\lim_{n_i \to \infty} N_2(t_{ni}) = N_{2\omega} \geqslant \varepsilon$. Since $\dot{N}_2(t_{ni}) = 0$, then $\lim_{n_i \to \infty} N_1(t_{ni}) = N_{1\omega} \geqslant 0$. Hence $(N_{1\omega}, N_{2\omega}, 0) \in \Omega$, the ω-limit set of the solution $(N_1(t), N_2(t), P(t))$. We note that $(N_{1\omega}, N_{2\omega})$ is on the line $r_2(1 - N_2/K_2) - \alpha_{21}N_1 = 0$. By the invariance property of the ω-limit set, it follows that $(0, K_2, 0) \in \Omega$. Compare the following asymptotic autonomous system

and its limiting equations:

$$\dot{N}_1 = N_1 \left[r_1 \left(1 - \frac{N_1}{K_1} \right) - \alpha_{12} N_2 \right] - N_1 P(t),$$

$$\dot{N}_2 = N_2 \left[r_2 \left(1 - \frac{N_2}{K_2} \right) - \alpha_{21} N_1 \right] - \alpha_{23} N_2 P(t)$$

and

$$\dot{N}_1 = N_1 \left[r_1 \left(1 - \frac{N_1}{K_1} \right) - \alpha_{12} N_2 \right],$$

$$\dot{N}_2 = N_2 \left[r_2 \left(1 - \frac{N_2}{K_2} \right) - \alpha_{21} N_1 \right].$$

From Markus's theorem, it follows that $\lim_{t \to \infty} N_1(t) = 0$ and $\lim_{t \to \infty} N_2(t) = K_2$. This contradicts the assumption that $\lim_{t \to \infty} N_2(t)$ doesn't exist.

B2: $N_1 \gg N_2$. Since $N_2(t)$ is bounded by K_2 for large t and $\lim_{t \to \infty} N_2(t) \neq K_2$, there exists $\varepsilon > 0$ and sequence $\{t_n\}$ such that $N_2(t_n) < K_2 - \varepsilon$ is a relative maximum. Using the arguments in B1 yields $(N_{1\omega}, N_{2\omega}, 0) \in \Omega$ for some $N_{2\omega} \leqslant K_2 - \varepsilon$, $N_{1\omega} > 0$. Hence we have $(K_1, 0, 0) \in \Omega$. Applying Markus's theorem yields $\lim_{t \to \infty} N_1(t) = K_1$ and $\lim_{t \to \infty} N_2(t) = 0$. Again this is a contradiction.

B3: $N_1 \leftrightarrow N_2$. *Case (a): There exists $t_0 \geqslant 0$ such that $N_2(t) \geqslant N_2^*$ for all $t \geqslant t_0$.* In this case, applying the arguments in B2 yields $(N_{1\omega}, N_{2\omega}, 0) \in \Omega$ for some $N_{1\omega}$, $N_{2\omega}$ satisfying $N_2^* \leqslant N_{2\omega} \leqslant K_2 - \varepsilon$ and $N_{1\omega} > 0$ and with $(N_{1\omega}, N_{2\omega})$ on the line $r_2(1 - N_2/K_2) - \alpha_{21} N_1 = 0$. Then $(N_1^*, N_2^*, 0) \in \Omega$. Applying Markus's theorem yields $\lim_{t \to \infty} N_1(t) = N_1^*$ and $\lim_{t \to \infty} N_2(t) = N_2^*$. Hence this is a contradiction. *Case (b): There exists $t_0 \geqslant 0$ such that $N_2(t) \leqslant N_2^*$ for all $t \geqslant t_0$.* In this case, applying the arguments in B1 yields $(N_{1\omega}, N_{2\omega}, 0) \in \Omega$ with $\varepsilon \leqslant N_{2\omega} \leqslant N_2^*$, $N_{1\omega} > 0$, and $(N_{1\omega}, N_{2\omega})$ on the line $r_2(1 - N_2/K_2) - \alpha_{21} N_1 = 0$. The arguments in case (a) yield a contradiction. *Case (c): $N_2(t)$ oscillates around $N_2 = N_2^*$.* In this case there exists $\{t_n\}$ such that $\dot{N}_2(t_n) < 0$, $N_2(t_n) = N_2^*$. Then $(N_{1\omega}, N_2^*, 0) \in \Omega$ for some $N_{1\omega} > 0$. The arguments in case (a) yield a contradiction.

B4: $N_1 \not\leftrightarrow N_2$. In this case, we again have three cases as we did in B3. In these three cases, there exists $\varepsilon > 0$ and a sequence $\{t_n\}$ ($t_n \to \infty$ as $n \to \infty$) such that either $N_2(t_n) > N_2^* + \varepsilon$ is a relative maximum for all n or $N_2(t_n) < N_2^* - \varepsilon$ is a relative minimum for all n. If $N_2(t_n) > N_2^* + \varepsilon$ is a relative maximum, then $(N_{1\omega}, N_{2\omega}, 0) \in \Omega$ with $N_{1\omega} \geqslant 0$, $N_{2\omega} \geqslant N_2^* + \varepsilon$, and $(N_{1\omega}, N_{2\omega})$ on the line $r_2(1 - N_2/K_2) - \alpha_{21} N_1 = 0$. It follows that $(0, K_2, 0) \in \Omega$. Applying Markus's theorem yields a contradiction. Similarly, if $N_2(t_n) < N_2^* - \varepsilon$ is a

relative maximum, then $(N_{1\omega}, N_{2\omega}, 0) \in \Omega$ with $N_{1\omega} > 0$, $N_{2\omega} \leqslant N_2^* - \varepsilon$, and $(N_{1\omega}, N_{2\omega})$ on the line $r_2(1 - N_2/K_2) - \alpha_{21}N_1 = 0$. It follows that $(K_1, 0, 0) \in \Omega$. Then Markus's theorem yields a contradiction.

Case 2. If $\limsup_{t \to \infty} P(t) > 0$, then there exist $\varepsilon > 0$ and a sequence $\{t_n\}$ such that $P(t_n) \geqslant \varepsilon$ and $\dot{P}(t_n) = 0$. Since $\lim_{t \to \infty} P(t) N_2(t) = 0$, it follows that $\lim_{n \to \infty} N_2(t_n) = 0$. From the third equation of (2.1) we have $\lim_{n \to \infty} N_1(t_n) = 1$. Hence there exists $P_\omega > 0$ such that $(1, 0, P_\omega) \in \Omega$. By the invariance property of ω-limit set and the asymptotic stability of (E_{1P}), we have that (E_{1P}) is globally stable.

Proof of Theorem 4.4. (i) Existence of E_c: From (2.1), we solve

$$N_1 + N_2 = 1,$$

$$r_1\left(1 - \frac{N_1}{K_1}\right) - \alpha_{12}N_2 = \frac{1}{\alpha_{23}}r_2\left(1 - \frac{N_2}{K_2}\right) - \alpha_{21}N_1.$$

Then

$$N_{1c} = \frac{(r_1 - \alpha_{12}) - \dfrac{1}{\alpha_{23}}r_2\left(1 - \dfrac{1}{K_2}\right)}{\left(\dfrac{r_1}{K_1} - \alpha_{12}\right) + \dfrac{1}{\alpha_{23}}\left(\dfrac{r_2}{K_2} - \alpha_{21}\right)}.$$

We need to show $0 < N_{1c} < 1$ and $P_c > 0$. From (6.2), (6.3), we have

$$\left(\frac{r_1}{K_1} - \alpha_{12}\right) + \frac{1}{\alpha_{23}}\left(\frac{r_2}{K_2} - \alpha_{21}\right)$$

$$= (r_1 - \alpha_{12}) - r_1\left(1 - \frac{1}{K_1}\right) + \frac{1}{\alpha_{23}}\left[(r_2 - \alpha_{21}) - r_2\left(1 - \frac{1}{K_2}\right)\right]$$

$$= \left[\frac{1}{\alpha_{23}}(r_2 - \alpha_{21}) - r_1\left(1 - \frac{1}{K_1}\right)\right] + \left[(r_1 - \alpha_{12}) - \frac{1}{\alpha_{23}}r_2\left(1 - \frac{1}{K_2}\right)\right] < 0.$$

Hence $N_{1c} > 0$. We still need to show that $N_{1c} < 1$, i.e.,

$$\frac{1}{\alpha_{23}}r_2\left(1 - \frac{1}{K_2}\right) - (r_1 - \alpha_{12}) < \left[r_1\left(1 - \frac{1}{K_1}\right) - \frac{1}{\alpha_{23}}(r_2 - \alpha_{21})\right]$$

$$+ \left[\frac{1}{\alpha_{23}}r_2\left(1 - \frac{1}{K_2}\right) - (r_1 - \alpha_{12})\right],$$

or

$$r_2 - \alpha_{23} < \alpha_{23} r_1 \left(1 - \frac{1}{K_1} \right).$$

It follows that $N_{1c} < 1$, and hence $N_{2c} = 1 - N_{1c} > 0$. From (2.1), we have

$$\left(1 - \frac{N_{1c}}{K_1} \right) - \alpha_{12} N_{2c} - P_c = 0;$$

hence

$$P_c = \frac{\left(\alpha_{21} - \frac{r_2}{K_2} \right)(r_1 - \alpha_{12}) + r_2 \left(1 - \frac{1}{K_2} \right)\left(\alpha_{12} - \frac{r_1}{K_1} \right)}{\alpha_{23}\left(\alpha_{12} - \frac{r_1}{K_1} \right) + \left(\alpha_{21} - \frac{r_2}{K_2} \right)}.$$

We wish to show $P_c > 0$, i.e.,

$$\left(\alpha_{21} - \frac{r_2}{K_2} \right)(r_1 - \alpha_{12}) + r_2 \left(1 - \frac{1}{K_2} \right)\left(\alpha_{12} - \frac{r_1}{K_1} \right) > 0,$$

or

$$\left[(\alpha_{21} - r_2) + r_2 \left(1 - \frac{1}{K_2} \right) \right](r_1 - \alpha_{12}) + r_2 \left(1 - \frac{1}{K_2} \right)$$
$$\times \left[(\alpha_{12} - r_1) + r_1 \left(1 - \frac{1}{K_2} \right) \right] > 0,$$

or

$$(\alpha_{21} - r_2)(r_1 - \alpha_{12}) + r_1 r_2 \left(1 - \frac{1}{K_1} \right)\left(1 - \frac{1}{K_2} \right) > 0,$$

or

$$r_1 r_2 \left(1 - \frac{1}{K_1} \right)\left(1 - \frac{1}{K_2} \right) > (r_1 - \alpha_{12})(r_2 - \alpha_{21}).$$

Hence we complete the proof for (i).

(ii): The characteristic polynomial of variation matrix at (E_c) is

$$f(\lambda) = \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3,$$

where

$$a_1 = \frac{r_1}{K_1} N_{1c} + \frac{r_2}{K_2} N_{2c},$$

$$a_2 = \left(\frac{r_1}{K_1} \frac{r_2}{K_2} - \alpha_{12}\alpha_{21} \right) N_{1c} N_{2c} + P_c (\alpha_{23} N_{2c} + N_{1c}),$$

$$a_3 = \left(\frac{r_1}{K_1} \alpha_{23} + \frac{r_2}{K_2} - \alpha_{12}\alpha_{23} - \alpha_{21} \right) N_{1c} N_{2c} P_c.$$

We note that

$$\frac{r_1}{K_1} \alpha_{23} + \frac{r_2}{K_2} - \alpha_{12}\alpha_{23} - \alpha_{21}$$

$$= \left(\frac{r_1}{K_1} - \alpha_{12} \right) \alpha_{23} + \left(\frac{r_2}{K_2} - \alpha_{21} \right)$$

$$= \left[(r_1 - \alpha_{12}) - r_1 \left(1 - \frac{1}{K_1} \right) \right] \alpha_{23} + \left[(r_2 - \alpha_{21}) - r_2 \left(1 - \frac{1}{K_2} \right) \right]$$

$$= \left[(r_2 - \alpha_{21}) - r_1 \left(1 - \frac{1}{K_1} \right) \alpha_{23} \right] + \left[(r_1 - \alpha_{12}) \alpha_{23} - r_2 \left(1 - \frac{1}{K_2} \right) \right]$$

$$\begin{cases} >0 & \text{if } (E_{1P}),(E_{2P}) \text{ both are unstable,} \\ <0 & \text{if } (E_{1P}),(E_{2P}) \text{ both are stable,} \end{cases}$$

since $a_1 > 0$ and $a_3 < 0$. From the Routhe-Hurwitz criterion, (E_c) is unstable. Furthermore $f(\lambda) = 0$ has two roots with negative real parts and one positive root; hence (E_c) is a saddle point and there exists a 2-dimensional stable manifold through (E_c).

Assume (E_{12}) exists and $N_1 \leftrightarrow N_2$; then we have $(r_1/K_1)(r_2/K_2) < \alpha_{12}\alpha_{21}$. The characteristic polynomial for the variation matrix at (E_{12}) is

$$f(\lambda) = \lambda^3 + \left(\frac{r_1}{K_1} N_1^* - \frac{r_2}{K_2} N_2^* + N_1^* + N_2^* - 1 \right) \lambda^2$$

$$+ \left[\left(\frac{r_1}{K_1} \frac{r_2}{K_2} - \alpha_{12}\alpha_{21} \right) N_1^* N_2^* - (N_1^* + N_2^* - 1) \left(\frac{r_2}{K_2} N_2^* + \frac{r_1}{K_1} N_1^* \right) \right] \lambda$$

$$- (N_1^* + N_2^* - 1) \left(\frac{r_1}{K_1} \frac{r_2}{K_2} - \alpha_{12}\alpha_{21} \right) N_1^* N_2^*$$

$$= \left[\lambda - (N_1^* + N_2^* - 1) \right] \left[\lambda^2 + \left(\frac{r_1}{K_1} N_1^* + \frac{r_2}{K_2} N_2^* \right) \lambda \right.$$

$$\left. + \left(\frac{r_1}{K_1} \frac{r_2}{K_2} - \alpha_{12}\alpha_{21} \right) N_1^* N_2^* \right],$$

where

$$N_1^* + N_2^* - 1 = \cfrac{\dfrac{\alpha_{12}}{r_1} + \dfrac{\alpha_{21}}{r_2} + \dfrac{1}{K_1}\dfrac{1}{K_2} - \dfrac{1}{K_1} - \dfrac{1}{K_2} - \dfrac{\alpha_{12}}{r_1}\dfrac{\alpha_{21}}{r_2}}{\dfrac{\alpha_{12}}{r_1}\dfrac{\alpha_{21}}{r_2} - \dfrac{1}{K_1}\dfrac{1}{K_2}}$$

$$= \cfrac{\alpha_{21}r_1 - \alpha_{12}\alpha_{21} - \dfrac{r_2}{K_2}r_1 + \dfrac{r_2}{K_2}\alpha_{12} - \dfrac{r_2}{K_2}\alpha_{12} + \alpha_{12}r_2 - \dfrac{r_1}{K_1}r_2 + \dfrac{r_2}{K_2}\dfrac{r_1}{K_1}}{\alpha_{12}\alpha_{21} - \dfrac{r_1}{K_1}\dfrac{r_2}{K_2}}$$

$$= \cfrac{\left(\alpha_{21} - \dfrac{r_2}{K_2}\right)(r_1 - \alpha_{12}) + r_2\left(1 - \dfrac{1}{K_2}\right)\left(\alpha_{12} - \dfrac{r_1}{K_1}\right)}{\alpha_{12}\alpha_{21} - \dfrac{r_1}{K_1}\dfrac{r_2}{K_2}} < 0,$$

or

$$r_1 r_2\left(1 - \frac{1}{K_1}\right)\left(1 - \frac{1}{K_2}\right) < (r_1 - \alpha_{12})(r_2 - \alpha_{21}).$$

Hence if (E_c) exists, then (E_{12}) is unstable with 1-dimensional manifold through (E_{12}) in the N_1-N_2 plane. The case $N_1 \overset{c}{\leftrightarrow} N_2$ follows similarly.

(iii): $r_1 r_2(1 - 1/K_1)(1 - 1/K_2) < (r_1 - \alpha_{12})(r_2 - \alpha_{21})$ if and only if (E_c) doesn't exist, since $r_2 - \alpha_{21} < \alpha_{23}r_1(1 - 1/K_1)$ and $(r_1 - \alpha_{12}) < (1/\alpha_{23})r_2(1 - 1/K_2)$. Under the assumption $K_1 > 1$, $K_2 > 1$, the only possible case is $r_1 < \alpha_{12}$ and $r_2 < \alpha_{21}$. That is the case $N_1 \Leftrightarrow N_2$, since $N_1^* + N_2^* - 1 < 0$ if and only if $r_1 r_2(1 - 1/K_2)(1 - 1/K_2) < (r_1 - \alpha_{12})(r_2 - \alpha_{21})$. By linear stability analysis about (E_{12}), it follows that (E_{12}) is a saddle point with a 2-dimensional stable manifold through it.

Proof of Theorem 4.5. From the reversed inequalities of (6.2), (6.3), we have $r_2 - \alpha_{21} > \alpha_{23}r_1(1 - 1/K_1) > 0$, $(r_1 - \alpha_{12}) > (1/\alpha_{23})r_2(1 - 1/K_2) > 0$. By previous computation, we have $0 < N_{1c} < 1$, and $P_c > 0$. Hence (E_c) exists. If $\lim_{t \to \infty} P(t) = 0$, from Theorem 4.3, case 1, we have a contradiction. If $\lim_{t \to \infty} N_2(t) = 0$, then $\lim_{t \to \infty} P(t) = C > 0$ or $\lim_{t \to \infty} P(t)$ doesn't exist.

Case 1. If $\lim_{t \to \infty} P(t) = C > 0$, by Coppel's theorem, then $\lim_{t \to \infty} N_1(t) = 1$ and $C = r_1(1 - 1/K_1)$. Then the identity

$$\frac{\dot{N}_2(t)}{N_2(t)} = r_2\left(1 - \frac{N_2}{K_2}\right) - \alpha_{21}N_1 - \alpha_{23}P$$

and the instability of (E_{1P}) imply that $N_2(t)$ becomes unbounded as t gets large. This is a contradiction.

Case 2. If $\lim_{t \to \infty} P(t)$ doesn't exist, then there exist $\varepsilon > 0$ and a sequence $\{t_n\}$ such that $\dot{P}(t_n) = 0$, $P(t_n) > \varepsilon$. Choose a subsequence $\{t_{n_i}\}$ of $\{t_n\}$ such that $\lim_{n_i \to \infty} P(t_{n_i}) = P_\omega \geq \varepsilon$. Since $\dot{P}(t_{n_i}) = 0$, then $\lim_{n_i \to \infty} N_1(t_{n_i})$ $= 1$. Hence $(1, 0, P_\omega) \in \Omega$ and $(1, 0, r_1(1 - 1/K_1)) \in \Omega$. Compare the asymptotic autonomous system and its limiting equations, i.e.,

$$\dot{N}_1 = N_1 \left[r_1 \left(1 - \frac{N_1}{K_1} \right) - P \right] - \alpha_{12} N_1 N_2(t),$$

$$\dot{P} = P[N_1 - 1] + PN_2(t)$$

and

$$\dot{N}_1 = N_1 \left[r_1 \left(1 - \frac{N_1}{K_1} \right) - P \right],$$

$$\dot{P} = P[N_1 - 1].$$

Then

$$\lim_{t \to \infty} N_1(t) = 1, \qquad \lim_{n \to \infty} N_2(t) = 0, \qquad \lim_{t \to \infty} P_3(t) = r_1 \left(1 - \frac{1}{K_1} \right).$$

Again we have a contradiction. If $\lim_{t \to \infty} N_1(t) = 0$, since (E_{23}) is unstable, the same arguments as above yields a contradiction. Hence (2.1) is persistent.

The author wishes to acknowledge with thanks the comments of the referee.

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