A REFUGE-MEDIATED APPARENT COMPETITION MODEL

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Dedicated to Professor Herb Freedman on the occasion of his 70th birthday

ABSTRACT. We analyze a competition model of two plant species for a single-limited resource while the competition is apparent: an indirect interaction where the invading plants provide a refuge for a shared consumer, subsequently increasing the consumer pressure on the resident plant species. When there is no refuge effect, the resident species is a superior species. As the refuge effect increases, the coexistence state appears as a saddle point with a two-dimensional stable manifold while the two extinction equilibria are locally stable. Thus the refuge-mediated apparent competition creates an Allee effect for both the invading and the resident species. A Lyapunov function is found to show the global stability of the equilibrium in which only the resident species survives.

1. INTRODUCTION AND THE MODEL

In this paper we study a mathematical model of a refuge-mediated apparent competition of two plant species for a single limited resource [9]. In the model we assume that the two plant species not only share the same resource but also share the same consumer (their predator). Without predation, the resident species is the superior species while the invading species is the inferior. However, when the two plant species share the same consumer the competition may become a refuge-mediated apparent competition: an indirect interaction where invading species provides a refuge for the shared consumer, subsequently increasing consumer pressure on the resident species. Refuge-mediated apparent competition is common in plant communities. For example, the consumer foraging is assumed to be altered by the presence of a refuge; consumers have differential effects on the plants that are sufficiently large to outweigh direct competitive asymmetries between residents and invaders. In fact refuge-mediated competition occurs not only in terrestrial system but also in aquatic system. Readers who are interested in this subject may consult [9] for the biological references.

The model takes the form:

$$
\begin{aligned}
S' &= g(S) - f_1(S)\frac{x_1}{\gamma_1} - f_2(S)\frac{x_2}{\gamma_2}, \\
x_1' &= (f_1(S) - d_1 - \delta\Phi(x_2))\, x_1, \\
x_2' &= (f_2(S) - d_2)\, x_2.
\end{aligned}
\tag{1}
$$

Here $S(t)$ is the concentration of the abiotic resource; $x_1(t)$ and $x_2(t)$ are the population densities of the resident species and the invading species, respectively. The two species compete for the same limited resource S. The function $g(S)$ is the resource recruitment. A standard recruitment function is the chemostat expression for an abiotic nutrient, $g(S) = (S^{(0)} - S)D$, where D is the washout rate and $S^{(0)}$ is the input external resource (e.g. nitrogen mineralization in soil, or nutrient input loading in aquatic system [9]). The parameters γ_i's, $i = 1, 2$, are the "yield" constants reflecting the conversion of resource to plant species; d_1, d_2 are the death rates for resident species and invading species, respectively. The proportional constant $\delta > 0$ is the per-capita rate of mortality of each consumer imposed upon the resident species. The function $f_i(S)$, the growth rate of the ith species, satisfies

$$(2) \qquad f_i(0) = 0, \ f_i'(S) > 0, \ i = 1, 2.$$

The typical examples for $f_i(S)$ are

$$f_i(S) = m_i S, \ i = 1, 2,$$

and

$$(3) \qquad f_i(S) = \frac{m_i S}{a_i + S}, \ i = 1, 2. \ \text{(Holling-Type II)}$$

We assume that the consumers are attracted to the refuge availability of the environment. The number of consumers is an increasing function of the refuge availability. Also, the amount of refuge availability is an increasing function of the population density of the invading species since the invading species are providing the refuge to the consumers. Thus we conclude that the number of consumers, C, is an increasing function of the density of the invading species, i.e. $C = \Phi(x_2)$. We assume

$$(4) \qquad \Phi(0) = 0, \ \Phi'(x) > 0.$$

The break-even concentration λ_i of the ith species for the resource S satisfies $f_i(\lambda_i) = d_i$. If $f_i(S)$ is of Holling-Type II, then

$$(5) \qquad \lambda_i = \frac{a_i d_i}{m_i - d_i}, \ i = 1, 2.$$

If $\delta = 0$, Hsu [4], Li [8], Wolkowicz and Lu [11] showed that under various conditions on the monotone functional responses the solution of the system satisfying $\lim_{t \to \infty} (S(t), x_1(t), x_2(t)) = (\lambda_1, x_1^*, 0)$, $x_1^* > 0$; i.e., the species with the lowest break-even concentration, x_1, wins the competition [10]. When the competition is not refuge-mediated, i.e. $\delta = 0$, we assume the resident species x_1 is the superior competitor; thus our basic hypothesis is

$$(6) \qquad 0 < \lambda_1 < \lambda_2 < S^{(0)}.$$

By rescaling $x_1 \to x_1/\gamma_1$, $x_2 \to x_2/\gamma_2$, $\Phi(x_2) \to \Phi(x_2/\gamma_2)$, and letting $g(S) = (S^{(0)} - S)D$, system (1) can be reduced to:

$$(7) \qquad \begin{aligned} S' &= (S^{(0)} - S)D - f_1(S)x_1 - f_2(S)x_2, \\ x_1' &= (f_1(S) - d_1 - \delta\Phi(x_2)) \, x_1, \\ x_2' &= (f_2(S) - d_2) \, x_2. \end{aligned}$$

System (7) has at most four equilibria: the extinction equilibrium $E_0 = (S^{(0)}, 0, 0)$; the one-species equilibria $E_1 = (\lambda_1, x_1^*, 0) = (\lambda_1, (S^{(0)} - \lambda_1)D/d_1, 0)$ and $E_2 = (\lambda_2, 0, x_2^*) = (\lambda_2, 0, (S^{(0)} - \lambda_2)D/d_2)$; and the coexistence equilibrium $E_c = (\lambda_2, \hat{x}_1^*, \hat{x}_2^*)$.

In Section 2, we present the equilibria and their local stability conditions. In Section 3, we provide a Lyapunov function for the global stability of E_1, the equilibrium with only the resident species (x_1) existing. Discussion and possible future research are presented in Section 4.

2. The equilibria and their local stability

Define a critical rate for δ as δ^*:

(8)
$$\delta^* = \frac{f_1(\lambda_2) - d_1}{\Phi(x_2^*)}.$$

Then the rate δ needs to be sufficiently large for $E_2 = (\lambda_2, 0, x_2^*)$ to be stable as it is stated in the following lemma.

LEMMA 1. E_0 is unstable; E_1 is stable; and E_2 is stable if $\delta > \delta^*$.

Proof. The eigenvalues of the Jacobian matrix at E_0 are $-D < 0$, $f_1(S^{(0)}) - d_1 > 0$, and $f_2(S^{(0)}) - d_2 > 0$. Therefore, E_0 is always unstable.

On the other hand, the Jacobian matrix at $E_1 = (\lambda_1, x_1^*, 0)$ is

$$J(E_1) = \begin{pmatrix} -D - f_1'(\lambda_1)x_1^* & -f_1(\lambda_1) & -f_2(\lambda_1) \\ f_1'(\lambda_1)x_1^* & 0 & -\delta\Phi'(0)x_1^* \\ 0 & 0 & f_2(\lambda_1) - d_2 \end{pmatrix}.$$

Eigenvalues of $J(E_1)$ are

$$f_2(\lambda_1) - d_2 = f_2(\lambda_1) - f_2(\lambda_2) < 0$$

and the other two eigenvalues satisfying the characteristic equation

$$\mu^2 + A_1\mu + B_1 = 0,$$

where

$$A_1 = D + f_1'(\lambda_1)x_1^* > 0, \ \ B_1 = f_1(\lambda_1)f_1'(\lambda_1)x_1^* > 0,$$

since $f_1' > 0$. Since both $A_1 > 0$ and $B_1 > 0$, the two eigenvalues have negative real parts. Therefore, E_1 is locally asymptotically stable, always.

The Jacobian matrix at $E_2 = (\lambda_2, 0, x_2^*)$ is

$$J(E_2) = \begin{pmatrix} -D - f_2'(\lambda_2)x_2^* & -f_1(\lambda_2) & -f_2(\lambda_2) \\ 0 & f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*) & 0 \\ f_2'(\lambda_2)x_2^* & 0 & 0 \end{pmatrix}.$$

Eigenvalues of $J(E_2)$ are

$$f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*)$$

and two others satisfying the characteristic equation

$$\mu^2 + A_2\mu + B_2 = 0,$$

where

$$A_2 = D + f_2'(\lambda_2)x_2^* > 0, \ \ B_2 = f_2(\lambda_2)f_2'(\lambda_2)x_2^* > 0.$$

Since both $A_2 > 0$ and $B_2 > 0$, the two eigenvalues have negative real parts. Therefore, E_2 is locally asymptotically stable if the first eigenvalue is negative, $f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*) < 0$, which is equivalent to $\delta > \delta^*$. $\square$

The coexistence equilibrium $E_c = (\lambda_2, \hat{x}_1^*, \hat{x}_2^*)$ may not exist. It depends on the stability of E_2, as seen in the following lemma.

LEMMA 2. *If E_2 is locally asymptotically stable then E_c exists if and only if $x_2^* > \hat{x}_2^*$. If E_2 is unstable then E_c does not exist.*

Proof. The species 2 equilibrium $E_2 = (\lambda_2, 0, x_2^*)$ satisfies $(S^{(0)} - \lambda_2)D - f_2(\lambda_2)x_2^* = 0$ and $f_2(\lambda_2) = d_2$. The coexistence equilibrium $E_c = (\lambda_2, \hat{x}_1^*, \hat{x}_2^*)$ satisfies the three equations:

$$(S^{(0)} - \lambda_2)D - f_1(\lambda_2)\hat{x}_1^* - f_2(\lambda_2)\hat{x}_2^* = 0,$$
$$f_1(\lambda_2) - d_1 - \delta\Phi(\hat{x}_2^*) = 0,$$
$$f_2(\lambda_2) - d_2 = 0.$$

E_c exists if and only if the first two equations are true. That is,

$$\hat{x}_2^* = \Phi^{-1}\left(f_1(\lambda_2) - d_1\right) > 0$$

and

$$(S^{(0)} - \lambda_2)D > f_2(\lambda_2)\hat{x}_2^* = d_2\hat{x}_2^*.$$

Assume that E_2 is locally stable. Then x_2^* satisfies $f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*) < 0$ and $(S^{(0)} - \lambda_2)D = d_2 x_2^*$. So we have the two inequalities relating x_2^* and $\hat{x}_2^*$:

$$f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*) < 0 = f_1(\lambda_2) - d_1 - \delta\Phi(\hat{x}_2^*)$$
$$\Leftrightarrow \Phi(x_2^*) > \Phi(\hat{x}_2^*)$$
$$\Leftrightarrow x_2^* > \hat{x}_2^*$$

since $\Phi(x)$ is an increasing function, and

$$d_2 x_2^* = (S^{(0)} - \lambda_2)D > d_2\hat{x}_2^* \Leftrightarrow x_2^* > \hat{x}_2^*.$$

On the other hand, if E_2 is unstable, then x_2^* satisfies $f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*) > 0$, which implies $x_2^* < \hat{x}_2^*$. That is, E_c does not exist. □

THEOREM 1. *If E_c exists then E_1 and E_2 are locally stable and E_c is a saddle point with a 2-dimensional stable manifold.*

Proof. The Jacobian matrix evaluated at $E_c = (\lambda_2, \hat{x}_1^*, \hat{x}_2^*)$ is

$$J(E_c) = \begin{pmatrix} -D - f_1'(\lambda_2)\hat{x}_1^* - f_2'(\lambda_2)\hat{x}_2^* & -f_1(\lambda_2) & -f_2(\lambda_2) \\ f_1'(\lambda_2)\hat{x}_1^* & 0 & -\delta\Phi'(\hat{x}_2^*)\hat{x}_1^* \\ f_2'(\lambda_2)\hat{x}_2^* & 0 & 0 \end{pmatrix}.$$

The characteristic equation is $\mu^3 + A\mu^2 + B\mu + C = 0$, where

(9)
$$A = D + f_1'(\lambda_2)\hat{x}_1^* + f_2'(\lambda_2)\hat{x}_2^*,$$
$$B = f_1'(\lambda_2)f_1(\lambda_2)\hat{x}_1^* + f_2'(\lambda_2)f_2(\lambda_2)\hat{x}_2^*,$$
$$C = -\delta\Phi'(\hat{x}_2^*)\hat{x}_1^*\hat{x}_2^* f_1(\lambda_2)f_2'(\lambda_2).$$

Routh-Hurwitz criterion states that the equilibrium E_c is stable if $A > 0$, $B > 0$, $C > 0$, and $AB - C > 0$. The only criterion that is not satisfied is $C > 0$. This indicates that the characteristic equation has one positive root and two negative roots or two roots with negative real parts. Therefore, if E_c exists, E_c is a saddle point with a two-dimensional stable manifold and a one-dimensional unstable manifold. □

	Existence	Stability
E_0	always	unstable
E_1	always	stable
E_2	always	stable if $\delta > \delta^*$
		unstable if $\delta < \delta^*$
E_c	$f_1(\lambda_2) - d_1 - \delta\Phi(\hat{x}_2^*) > 0$	saddle

TABLE 1. The local stability condition results. δ^* is defined in (8).

All of the local stability results are summarized in Table 1. If E_2 is locally unstable, then E_c does not exist, but E_1 is locally stable. In this case, we suspect that E_1 is globally stable. In next section, we show under certain conditions that E_1 is globally stable by constructing a Lyapunov function.

3. GLOBAL STABILITY OF $E_1 = (\lambda_1, x_1^*, 0)$

In this section, we restrict our attention to the important case where $f_i(S)$ is of Holling type II. In the following lemma we state that system (7) is "well-defined" as one intuits from the biological problem. The proof of Lemma 3 is standard and we omit it.

LEMMA 3. *The solution $(S(t),\ x_1(t),\ x_2(t))$ of system (7) is positive and bounded for $t \geq 0$.*

The following theorem states that if E_1 is locally stable, then under certain conditions, E_1 is also globally stable.

THEOREM 2. *Assume $0 < \lambda_1 < \lambda_2 < S^{(0)}$ and in addition to the assumption (4), $\Phi(x)$ satisfies*

$$(10) \qquad f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*) > 0,$$

and

$$(H1) \qquad \Phi(x) \leq \frac{\Phi(x_2^*)}{x_2^*}x, \text{ for } x \geq 0.$$

(See Fig. 1.) Then if E_1 is locally stable then E_1 is globally stable. That is,

$$\lim_{t\to\infty}(S(t), x_1(t), x_2(t)) = (\lambda_1, x_1^*, 0).$$

Proof. Define a Lyapunov function $V(S, x_1, x_2)$ as follows:

$$V(S, x_1, x_2) = \int_{\lambda_1}^{S} Q(\xi)d\xi + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi}d\xi + c_2 x_2,$$

on the set $\Omega = \{(S, x_1, x_2) : S \in (0, S^{(0)}), x_i \in (0, \infty), i = 1, 2\}$, where $Q(\xi)$ and the positive constant c_2 are to be determined. It is obvious that $V(\lambda_1, x_1^*, 0) = 0$.
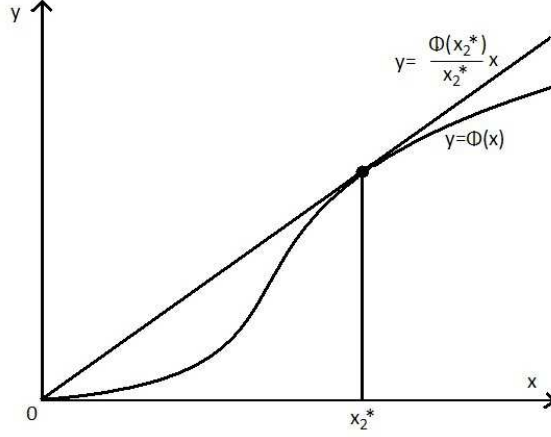
FIGURE 1. $\Phi(x)$ satisfies hypothesis (H1): $\Phi(x) \leq \frac{\Phi(x_2^*)}{x_2^*}x$.

Taking the time derivative of V along the trajectory of (7), we obtain

$$
\begin{aligned}
\dot{V} &= Q(S)\left[(S^{(0)} - S)D - f_1(S)x_1 - f_2(S)x_2\right] + (x_1 - x_1^*)\left(f_1(S) - d_1 - \delta\Phi(x_2)\right) \\
&\quad + c_2(f_2(S) - d_2)x_2 \\
&= \left[Q(S)(S^{(0)} - S)D - x_1^*\left(f_1(S) - d_1\right)\right] \\
&\quad + x_1\left[-f_1(S)Q(S) + (f_1(S) - d_1 - \delta\Phi(x_2))\right] \\
&\quad + x_2\left[-f_2(S)Q(S) + c_2(f_2(S) - d_2) + \frac{\delta\Phi(x_2)}{x_2}x_1^*\right] \\
&= F(S) + x_1 F_1(S, x_2) + x_2 F_2(S, x_2).
\end{aligned}
$$

We would like to find $Q(S)$, and c_2 such that $\dot{V} < 0$ for all $S \in (0, S^{(0)})$.

Let $F(S) = 0$, so we have

$$
Q(S) = \frac{x_1^*\left(f_1(S) - d_1\right)}{(S^{(0)} - S)D}.
$$

Then $Q(\xi) \geq 0$, for all $\xi \in (\lambda_1, S^{(0)})$; the first integral in V is nonnegative. The second integral of V is obviously nonnegative. Also, the term $c_2 x_2 > 0$. Therefore, we have $V(S, x_1, x_2) > 0$ for all $(S, x_1, x_2) \in \Omega - \{(\lambda_1, x_1^*, 0)\}$.

Next, we need to find conditions such that $\dot{V} < 0$.

$$
\begin{aligned}
F_1(S, x_2) &= -f_1(S)Q(S) + (f_1(S) - d_1 - \delta\Phi(x_2)) \\
&= (f_1(S) - d_1)\left(1 - \frac{f_1(S)x_1^*}{(S^{(0)} - S)D}\right) - \delta\Phi(x_2) \\
&= -\frac{(m_1 - d_1)(S - \lambda_1)^2(a_1 S^{(0)} + \lambda_1 S)}{(a_1 + S)^2 \lambda_1(S^{(0)} - S)} - \delta\Phi(x_2) < 0
\end{aligned}
$$

for all $S \in (0, S^{(0)})$.

From (4) we have

$$F_2(S, x_2) = -f_2(S)Q(S) + c_2(f_2(S) - d_2) + \delta\frac{\Phi(x_2)}{x_2}x_1^*$$

$$= -\frac{x_1^*}{x_2^*} \cdot \frac{S^{(0)} - \lambda_2}{S^{(0)} - S} \cdot \frac{f_2(S)}{f_2(\lambda_2)} \cdot (f_1(S) - d_1) + c_2(f_2(S) - d_2) + \delta\frac{x_1^*}{x_2^*}\Phi(x_2^*)$$

$$+ \delta x_1^* \left(\frac{\Phi(x_2)}{x_2} - \frac{\Phi(x_2^*)}{x_2^*} \right)$$

$$= \widetilde{F}_2(S) + \delta x_1^* \left(\frac{\Phi(x_2)}{x_2} - \frac{\Phi(x_2^*)}{x_2^*} \right)$$

$$\leq \widetilde{F}_2(S) := (f_2(S) - d_2)\left(c_2 - W(S)\frac{x_1^*}{x_2^*} \right),$$

since the assumption (H1) of $\Phi(x)$ in the theorem implies $\frac{\Phi(x_2)}{x_2} - \frac{\Phi(x_2^*)}{x_2^*} \leq 0$. $W(S)$ is a rational function of S:

(11)
$$W(S) = \frac{S^{(0)} - \lambda_2}{S^{(0)} - S} \cdot \frac{f_2(S)}{f_2(\lambda_2)} \cdot \frac{f_1(S) - d_1}{f_2(S) - d_2} - \frac{\delta\Phi(x_2^*)}{f_2(S) - d_2}$$

$$= K_1 \cdot \frac{S(S - \lambda_1)}{(S^{(0)} - S)(S + a_1)(S - \lambda_2)} - K_2 \cdot \frac{S + a_2}{S - \lambda_2},$$

and

(12)
$$K_1 = \frac{(S^{(0)} - \lambda_2)(m_1 - d_1)(a_2 + \lambda_2)}{\lambda_2(m_2 - d_2)} > 0, \quad K_2 = \frac{\delta\Phi(x_2^*)}{m_2 - d_2} > 0.$$

$\widetilde{F}_2(S) \leq 0$ if and only if

$$(f_2(S) - d_2)\left(W(S)\frac{x_1^*}{x_2^*} - c_2 \right) \geq 0$$

which is equivalent to

(13)
$$c_2 \begin{cases} \leq \frac{x_1^*}{x_2^*}W(S), & S \in (\lambda_2, S^{(0)}), \\ \geq \frac{x_1^*}{x_2^*}W(S), & S \in (0, \lambda_2). \end{cases}$$

It is easy to see that $\widetilde{F}_2(S)$ is less than zero at λ_2 from the second equality in $F_2(S, x_2)$:

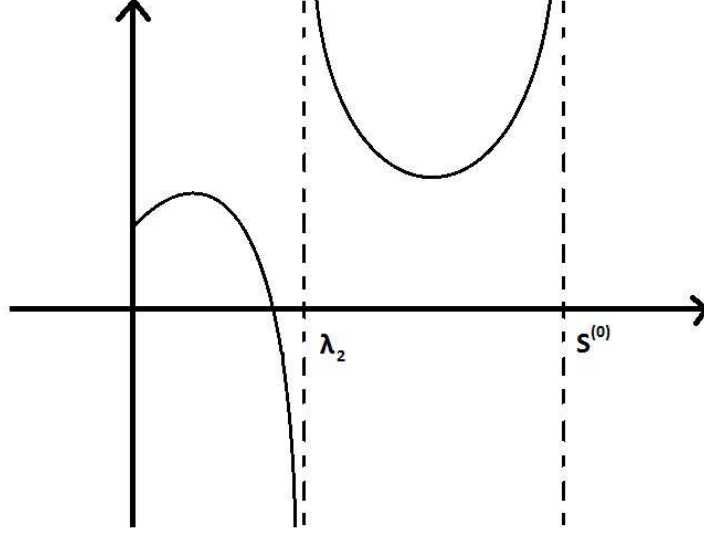$$F_2(\lambda_2, x_2) = -\frac{x_1^*}{x_2^*}(f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*)) < 0$$

since the inequality (10) holds.

Then we have from (10)

$$\lim_{S \to \lambda_2^-} W(S) = \lim_{S \to \lambda_2^-} \frac{f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*)}{f_2(S) - d_2} = -\infty,$$

$$\lim_{S \to \lambda_2^+} W(S) = \lim_{S \to \lambda_2^+} \frac{f_1(\lambda_2) - d_1 - \delta\Phi(x_2^*)}{f_2(S) - d_2} = \infty,$$

and

$$\lim_{S \to S^{(0)-}} W(S) = \infty.$$

FIGURE 2. The general shape of $W(S)$.

$S = \lambda_2$ and $S = S^{(0)}$ are two vertical asymptotes for the rational function $W(S)$. Also,

$$W(\lambda_1) = \frac{\delta\Phi(x_2^*)}{d_2 - f_2(\lambda_1)} > 0, \; W(0) = \frac{\delta\Phi(x_2^*)}{d_2} > 0,$$

and

$$W(0) < W(\lambda_1).$$

Therefore, the general shape of the curve sketch of $W(S)$ on $(0, S^{(0)})$ can be seen in Fig. 2; $W(S)$ has a relative maximum in $(0, \lambda_2)$ and a relative minimum in $(\lambda_2, S^{(0)})$.

Claim:

$$(14) \qquad \max_{S \in (0,\lambda_2)} W(S) \leq \min_{S \in (\lambda_2, S^{(0)})} W(S).$$

To prove (14), we apply the arguments in Chiu and Hsu [2]. If (14) does not hold, then there exists $\beta > 0$ such that

$$\max_{S \in (0,\lambda_2)} W(S) > \beta > \min_{S \in (\lambda_2, S^{(0)})} W(S)$$

and $W(S) - \beta = 0$ has four real solutions. See Figure 3. The statement that $W(S) - \beta = 0$ has four real roots is equivalent to the statement that $G(S) = 0$ has four real roots, where

$$G(S) = K_1 S(S - \lambda_1) - K_2(S^{(0)} - S)(S + a_1)(S + a_2) - \beta(S^{(0)} - S)(S + a_1)(S - \lambda_2),$$

K_1 and K_2 are two positive constants in (12). $G(S)$ is a polynomial in S of degree 3 and therefore it has at most three real roots, a contradiction to the assumption.
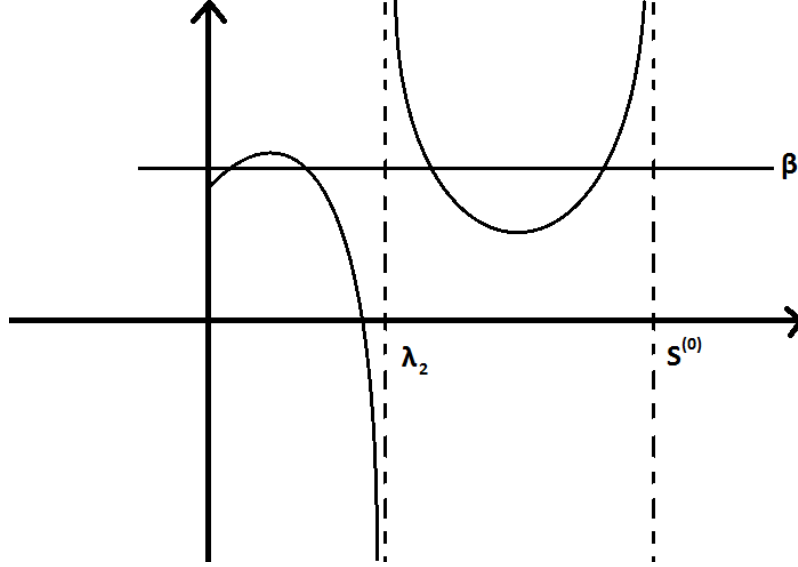
FIGURE 3

This proves that there exists a positive constant c_2 that satisfies (13) and

$$\max_{S \in (0, \lambda_2)} W(S) \leq c_2 \frac{x_2^*}{x_1^*} \leq \min_{S \in (\lambda_2, S^{(0)})} W(S).$$

such that $\widetilde{F}_2(S) \leq 0$.

From Lemma 3 and LaSalle's invariance principle, the ω-limit set of the trajectory $(S(t), x_1(t), x_2(t))$ of system (7) lies in the maximal invariant set M of $\{\dot{V} = 0\}$. It is easy to show that $M = \{(\lambda_1, x_1^*, 0)\}$. Hence we complete the proof of the theorem.   □

Different types of $\Phi(x)$ would also guarantee the global stability of E_1. In the following theorem, we choose $\Phi(x)$ satisfying $\Phi''(x) < 0$ as seen in Fig. 4.

THEOREM 3. *Assume* $0 < \lambda_1 < \lambda_2 < S^{(0)}$ *and in addition to the assumption* (4), $\Phi(x)$ *satisfies*

$$f_1(\lambda_2) - d_1 - \delta \Phi'(0) x_2^* > 0,$$

and

$$\text{(H2)} \qquad \Phi''(x) < 0 \text{ for } x \geq 0.$$

(See Fig. 4.) Then if E_1 *is locally stable,* E_1 *is globally stable. That is,*

$$\lim_{t \to \infty} (S(t), x_1(t), x_2(t)) = (\lambda_1, x_1^*, 0).$$

Proof. The proof is identical to that of Theorem 2 except for the function $F_2(S, x_2)$. We can express $\Phi(x_2)$ as its Taylor expansion $\Phi(x_2) = \Phi(0) + \Phi'(0)x_2 + \frac{1}{2!}\Phi''(\zeta)x_2^2$
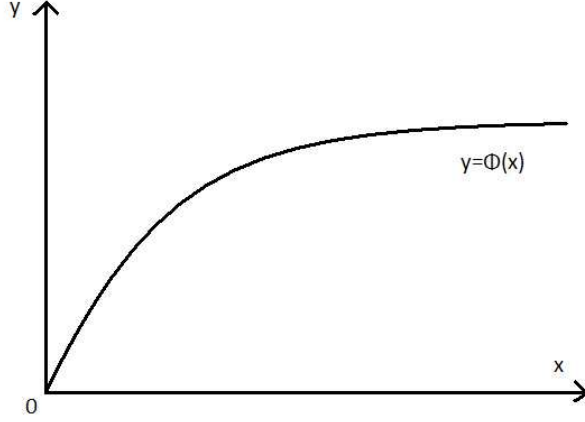
FIGURE 4. $\Phi(x)$ satisfies hypothesis (H2): $\Phi''(x) < 0$.

for some $\zeta \in (0, x_2)$. Then we have

$$F_2(S, x_2) = -\frac{x_1^*}{x_2^*} \cdot \frac{S^{(0)} - \lambda_2}{S^{(0)} - S} \cdot \frac{f_2(S)}{f_2(\lambda_2)} \cdot (f_1(S) - d_1) + c_2(f_2(S) - d_2)$$

$$+ \delta \left(\Phi'(0) + \frac{1}{2}\Phi''(\zeta)x_2 \right) x_1^*$$

$$= \widetilde{F}_2(S) + \frac{\delta}{2}\Phi''(\zeta)x_2 x_1^*$$

$$\leq \widetilde{F}_2(S) := (f_2(S) - d_2)\left(c_2 - W(S)\frac{x_1^*}{x_2^*} \right),$$

where

$$
\begin{aligned}
W(S) &= \frac{S^{(0)} - \lambda_2}{S^{(0)} - S} \cdot \frac{f_2(S)}{f_2(\lambda_2)} \cdot \frac{f_1(S) - d_1}{f_2(S) - d_2} - \frac{\delta\Phi'(0)x_2^*}{f_2(S) - d_2} \\
&= K_1 \cdot \frac{S(S - \lambda_1)}{(S^{(0)} - S)(S + a_1)(S - \lambda_2)} - K_2 \cdot \frac{S + a_2}{S - \lambda_2},
\end{aligned}
$$
(15)

and

(16) $\qquad K_1 = \frac{(S^{(0)} - \lambda_2)(m_1 - d_1)(a_2 + \lambda_2)}{\lambda_2(m_2 - d_2)} > 0, \ K_2 = \frac{\delta\Phi'(0)x_2^*}{m_2 - d_2} > 0.$

$\square$

Corollary 1. *Assume* $0 < \lambda_1 < \lambda_2 < S^{(0)}$ *and* $\Phi(x_2) = \alpha x_2,$ $\alpha > 0$. *If* E_c *does not exist then* E_1 *is globally stable. That is,*

$$\lim_{t \to \infty} (S(t), x_1(t), x_2(t)) = (\lambda_1, x_1^*, 0).$$

4. DISCUSSION

We analyze the general mathematical model proposed in [9] for the refuge-mediated apparent competition of two plant species which share a resource and a common predator (consumer). Without predation, it is assumed that the resident

species is a superior species while invading species is inferior. With the presence of consumer it is assume that the invading species provides a refuge for the consumer, subsequently increasing the consumer pressure on the resident species. Thus the competition is a refuge-mediated apparent competition. In our model equation (1) the consumer pressure on the resident species is propositional to the population of consumer C which is assumed to be an increasing function of the population density of invading species, $\Phi(x)$ satisfying (4). The proportional constant δ is the per-capita rate of mortality of each consumer imposed upon the resident species.

Our analysis shows that if δ is small then the resident species is still the superior species. When δ is greater than the critical rate δ^*, $\delta^* = \frac{f_1(\lambda_2)-d_1}{\Phi(x_2^*)}$, then we have bi-stability : both of the extinction states E_1 and E_2 are locally stable and the outcome of competition depends on the initial populations. Thus as the consumer pressure on the resident species is sufficiently large, Allee effect for both of the resident and the invading species emerges. In particular if the two species are nearly identical with close break-even concentrations $\lambda_1 \approx \lambda_2$. Then from Theorem 1, Allee effect emerges for both species. Thus, refuge-mediated apparent competition may be the most important in the systems where competitors are thought to exhibit neutral, or nearly neutral, dynamics, e.g. as has been suggested for tropical forest trees [6, 9].

In Theorems 2 and 3 we give sufficient conditions for the global stability of E_1 provided the functional responses are of Holling Type II which fits the growth of of plant species. We construct a Lyapunov function of the type in [11] instead of that in [4].

If we consider the dynamics of the consumer having no other food supply other than the resident species, then the results in [1] showed that the resident and the invading species may coexist, possibly in stable cycle.

In the future we shall investigate the case of two complementary resources, nutrient and light for the refuge-mediated apparent competition.

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