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CAN MUTUALISM ALTER COMPETITIVE OUTCOME?: A MATHEMATICAL ANALYSIS

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ABSTRACT. A model is described whereby two interacting competitors also interact with a mutualist. After examining equilibria and their stability, the question of "reversal of competitive outcome" due to the mutualism is investigated.

1. Introduction. Even in the general Kolmogorov model of two competitors, it is known (Albrecht et al. [**1**]) that the dynamics are trivial, i.e., all solutions approach an equilibrium. The same is true when two mutualists interact (Freedman et al. [**5**]).

The main purpose of this paper is to consider the situation when two interacting competitor populations each interact with a mutualist as well. We are particularly interested in determining criteria for persistence of all populations in the case when one of the competitors becomes extinct in the absence of its mutualist.

Kirlinger [**9, 10**] has shown for Lotka-Volterra models that the bistable case in two-species competition can be made permanent (uniformly persistent) by two predators, but never by one predator. In this paper we obtain similar results for more general competitive systems regulated by two mutualists.

Original models of mutualism were two dimensional (Dean [**3**], Freedman [**4**], Freedman et al. [**5**]). Three dimensional models where the mutualism arose due to the presence of either a predator or a competitor were first analyzed in Rai et al. [**12**] and expanded upon by Kumar and Freedman [**11**]. Since then other works involving competitor-competitor-mutualist interactions have been published (Freedman and Rai [**6, 7**]).

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This paper, to the best of our knowledge, is the first to incorporate two mutualists, one for each competitor. This will be of particular interest in the case where both competitor-competitor-mutualist subsystems collapse, showing the possibility that in competitive communities, mutualism may be one of the mechanisms leading to coexistence.

The organization of this paper is as follows. In the next section we derive our model. Section 3 deals with the equilibria and their stability. In Section 4 we give persistence criteria for the full model. Section 5 deals with reversal of outcome. We give an example to illustrate our results in Section 6. A brief discussion follows in Section 7.

2. The model. We take as a model of two competitors interacting with mutualists the system of autonomous ordinary differential equations

$$\begin{aligned}\dot{u}_1 &= u_1 h_1(u_1, x_1)\\ \dot{x}_1 &= x_1 g_1(u_1, x_1) - x_1 x_2 q_1(u_1)\\ \dot{u}_2 &= u_2 h_2(u_2, x_2)\\ \dot{x}_2 &= x_2 g_2(u_2, x_2) - x_1 x_2 q_2(u_2),\end{aligned} \tag{2.1}$$

$$u_i(0) \geq 0,\ x_i(0) \geq 0,\ i = 1, 2,$$

where "$\cdot$" $= d/dt$. Here $u_i(t)$ represents the mutualist population of $x_i(t)$ at any time t, $i = 1, 2$, and $x_i(t)$ is the ith competitor. Corresponding to these interpretations, we suppose the following hypotheses hold for our model.

(H0) We assume that h_i, g_i, q_i are sufficiently smooth so that solutions to the initial value problem exist and are unique.

(H1) $h_i(0, x_i) > 0$; $h_{iu_i}(u_i, x_i) < 0$; $h_{ix_i}(u_i, x_i) > 0$; there exists $L_i(x_i)$, $L_i(0) > 0$ such that $h_i(L_i(x_i), x_i) = 0$, $i = 1, 2$.

The above hypotheses impose the following properties on u_i, respectively. The mutualist population is capable of growing on its own, and hence the mutualism of x_i on u_i is facultative. The growth rate, however, is decelerated as its population numbers increase due to environmental limitations. x_i is a mutualist of u_i. There is a carrying capacity of the environment which limits the mutualist populations as a function of the number of x_i.

Note that clearly $dL_i(x_i)/dx_i > 0$.

(H2) $g_i(u_i, 0) > 0$; $g_{ix_i}(u_i, x_i) < 0$; there exists $K_i(u_i)$, $K_i(0) > 0$ such that $g_i(u_i, K_i(u_i)) = 0$ and such that $\lim_{u_i \to \infty} K_i(u_i) = \widetilde{K}_i < \infty$.

These hypotheses are described as follows. Each competitor is capable of growing on its own, but the growth rate decreases as the population increases, limited by its carrying capacity which is a function of the mutualist.

Note that we do not specify the sign of $g_{iu_i}(u_i, x_i)$. If $g_{iu_i} > 0$, then the mutualism is direct. If $g_{iu_i} \leq 0$, then the mutualism is indirect and results only as a consequence of the competition, and in this case $\widetilde{K}_i < K_i(0)$.

(H3) $q_i(u_i) > 0$, $q_{iu_i}(u_i) \leq 0$, $i = 1, 2$.

It may be that the competition effect is reduced by the mutualist. In any case, competition is always increased by a rise in either population.

Note that if $q_{iu_i} = 0$, then $g_{iu_i} > 0$, or else there will be no mutualistic benefits for x_i by u_i.

From the above hypotheses, it is straightforward to show that the system (2.1) is dissipative. In fact, we can describe a region $\mathcal{A}$ which contains the region of attraction.

From $\dot{x}_i = x_i g_i(u_i, x_i) - x_1 x_2 q_i(u_i) \leq x_i g_i(u_i, x_i)$, we see that after a finite amount of time, $0 \leq x_i(t) \leq \widehat{K}_i = \max\{\widetilde{K}_i, K_i(0)\}$. Let $\hat{L}_i = L_i(\widehat{K}_i)$. Then after a finite amount of time, $0 \leq u_i(t) \leq \hat{L}_i$. Hence, $\mathcal{A} = \{(u_1, x_1, u_2, x_2) \mid 0 \leq u_1 \leq \hat{L}_1, 0 \leq x_1 \leq \widehat{K}_1, 0 \leq u_2 \leq \hat{L}_2, 0 \leq x_2 \leq \widehat{K}_2\}$ is such a set.

3. The existence and stability of equilibria. There are a large number of possible equilibria for system (2.1). Some will always exist. Others may or may not exist. We will discuss their existence and possible values in order of complexity. Then we will turn to a discussion of their stability.

First we note that $E_0(0, 0, 0, 0)$ always exists. As well, the following one-dimensional and related two-dimensional equilibria are obvious, $E_1(L_1(0), 0, 0, 0)$, $E_2(0, K_1(0), 0, 0)$, $E_3(0, 0, L_2(0), 0)$, $E_4(0, 0, 0, K_2(0))$, $E_5(L_1(0), 0, L_2(0), 0)$, $E_6(L_1(0), 0, 0, K_2(0))$, $E_7(0, K_1(0), L_2(0), 0)$.

There may or may not be a competitive equilibrium in the absence of mutualism. If it exists, we denote it as $\overline{E}(0, \bar{x}_1, 0, \bar{x}_2)$.

On ecological grounds, there must exist equilibria in the $u_1 - x_1$ and $u_2 - x_2$ planes, for otherwise the dissipativity and two-dimensional dynamics would imply that in the absence of competition and presence of mutualism, one of the populations would become extinct, contradicting the concept of mutualism. Hence we assume that $\widehat{E}_{10}(\hat{u}_1, \hat{x}_1, 0, 0)$ and $\widehat{E}_{02}(0, 0, \hat{u}_2, \hat{x}_2)$ must exist and therefore the associated equilibria $\widehat{E}_{11}(\hat{u}_1, \hat{x}_1, L_2(0), 0)$ and $\widehat{E}_{22}(L_1(0), 0, \hat{u}_2, \hat{x}_2)$ also exist.

There are two other possible equilibria which are in the three dimensional subspaces. Criteria for their existence were given in Freedman and Rai [**7**]. When they exist, we denote them by $\widetilde{E}_1(\tilde{u}_{11}, \tilde{x}_{11}, 0, \tilde{x}_{21})$, $\widetilde{E}_2(0, \tilde{x}_{12}, \tilde{u}_{22}, \tilde{x}_{22})$. Finally, there may be a positive equilibrium denoted $E^*(u_1^*, x_1^*, u_2^*, x_2^*)$. Further on, we give a criterion for such an equilibrium to exist.

In order to discuss the stability of these equilibria, we must compute the variational matrices about the various equilibria. We denote by M the general variational matrix and use corresponding notation for the variational matrices about the corresponding equilibria. For example, $\widetilde{M}_1$ is the variational matrix about $\widetilde{E}_1$, etc.

The general variational matrix M is given by $M = (m_{ij})_{4\times 4}$, where $m_{11} = u_1 h_{1u_1} + h_1$, $m_{12} = u_1 h_{1x_1}$, $m_{13} = 0$, $m_{14} = 0$, $m_{21} = x_1 g_{1u_1} - x_1 x_2 q_{1u_1}$, $m_{22} = x_1 g_{1x_1} + g_1 - x_2 g_1$, $m_{23} = 0$, $m_{24} = -x_1 x_2 q_{1x_2} - x_1 q_1$, $m_{31} = 0$, $m_{32} = 0$, $m_{33} = u_2 h_{2u_2} + h_2$, $m_{34} = u_2 h_{2x_2}$, $m_{41} = 0$, $m_{42} = -x_1 x_2 q_{2x_1} - x_2 q_2$, $m_{43} = x_2 g_{2u_2} - x_1 x_2 q_{2u_2}$, $m_{44} = x_2 g_{2x_2} + g_2 - x_1 q_2$. Hence the variational matrices corresponding to the various equilibria (matching notations, i.e., M_i corresponds to E_i, etc.) have the following nonzero entries.

For M_0, $m_{11} = h_1(0,0)$, $m_{22} = g_1(0,0)$, $m_{33} = h_2(0,0)$, $m_{44} = g_2(0,0)$.

For M_1, $m_{11} = L_1(0) h_{1u_1}(L_1(0), 0)$, $m_{12} = L_1(0) h_{1x_1}(L_1(0), 0)$, $m_{22} = g_1(L_1(0), 0)$, $m_{33} = h_2(0,0)$, $m_{44} = g_2(0,0)$.

For M_2, $m_{11} = h_1(0, K(0))$, $m_{21} = K_1(0) g_{1u_1}(0, K_1(0))$, $m_{22} = K_1(0) g_{1x_1}(0, K_1(0))$, $m_{24} = -K_1(0) q_1(0, K_1(0), 0)$, $m_{33} = h_2(0,0)$, $m_{44} = g_2(0,0) - K_1(0) q_2(0, K_1(0), 0)$.

For M_3, $m_{11} = h_1(0,0)$, $m_{22} = g_1(0,0)$, $m_{33} = L_2(0) h_{2u_2}(L_2(0), 0)$,

$m_{34} = L_2(0)h_{2x_2}(L_2(0), 0)$, $m_{44} = g_2(L_2(0), 0)$.

For M_4, $m_{11} = h_1(0, 0)$, $m_{22} = g_1(0, 0) - K_2(0)q_1(0, 0, K_2(0))$, $m_{33} = h_2(0, K_2(0))$, $m_{42} = -K_2(0)q_2(0, 0, K_2(0))$, $m_{43} = K_2(0)g_{2u_2}(0, K_2(0))$, $m_{44} = K_2(0)g_{2x_2}(0, K_2(0))$.

For M_5, $m_{11} = L_1(0)h_{1u_1}(L_1(0), 0)$, $m_{12} = L_1(0)h_{1x_1}(L_1(0), 0)$, $m_{22} = g_1(L_1(0), 0)$, $m_{33} = L_2(0)h_{2u_2}(L_2(0), 0)$, $m_{34} = L_2(0)h_{2x_2}(L_2(0), 0)$, $m_{44} = g_2(L_2(0), 0)$.

For M_6, $m_{11} = L_1(0)h_{1u_1}(L_1(0), 0)$, $m_{12} = L_1(0)h_{1x_1}(L_1(0), 0)$, $m_{22} = g_1(L_1(0), 0) - K_2(0)q_1(L_1(0), 0, K_2(0))$, $m_{42} = -K_2(0)q_2(0, 0, K_2(0))$, $m_{33} = h_2(0, K_2(0))$, $m_{43} = K_2(0)g_{2u_2}(0, K_2(0))$, $m_{44} = K_2(0)g_{2x_2}(0, K_2(0))$.

For M_7, $m_{11} = h_1(0, K_1(0))$, $m_{21} = K_1(0)g_{1u_1}(0, K_1(0))$, $m_{22} = K_1(0)g_{1x_1}(0, K_1(0))$, $m_{24} = -K_1(0)q_1(0, K_1(0), 0)$, $m_{33} = L_2(0)h_{2u_2} \cdot (L_2(0), 0)$, $m_{34} = L_2(0)h_{2x_2}(L_2(0), 0)$, $m_{44} = g_2(L_2(0), 0) - K_1(0) \cdot q_2(L_2(0), K_1(0), 0)$.

For $\overline{M}$, $m_{11} = h_1(0, \bar{x}_1)$, $m_{21} = \bar{x}_1 g_{1u_1}(0, \bar{x}_1) - \bar{x}_1\bar{x}_2 q_{1u_1}(0)$, $m_{22} = \bar{x}_1 g_{1x_1}(0, \bar{x}_1)$, $m_{24} = -\bar{x}_2 q_2(0) - \bar{x}_1 q_1(0)$, $m_{33} = h_2(0, \bar{x}_2)$, $m_{43} = \bar{x}_2 g_{2u_2}(0, \bar{x}_2) - \bar{x}_1\bar{x}_2 q_{2u_2}(0)$, $m_{44} = \bar{x}_2 g_2(0, \bar{x}_2)$.

For $\widehat{M}_{10}$, $m_{11} = \hat{u}_1 h_{1u_1}(\hat{u}_1, \hat{x}_1)$, $m_{12} = \hat{u}_1 h_{1x_1}(\hat{u}_1, \hat{x}_1)$, $m_{21} = \hat{x}_1 g_{1u_1}(\hat{u}_1, \hat{x}_1)$, $m_{22} = \hat{x}_1 g_{1x_1}(\hat{u}_1, \hat{x}_1)$, $m_{24} = -\hat{x}_1 q_1(\hat{u}_1)$, $m_{33} = h_2(0, 0)$, $m_{44} = g_2(0, 0) - \hat{x}_1 q_2(0)$.

For $\widehat{M}_{02}$, $m_{11} = h_1(0, 0)$, $m_{22} = g_1(0, 0) - \hat{x}_2 q_1(0)$, $m_{33} = \hat{u}_2 h_{2u_2}(\hat{u}_2, \hat{x}_2)$, $m_{34} = \hat{u}_2 h_{2x_2}(\hat{u}_2, \hat{x}_2)$, $m_{42} = -\hat{x}_2 q_2(\hat{u}_2)$, $m_{43} = \hat{x}_2 g_{2u_2}(\hat{u}_2, \hat{x}_2)$, $m_{44} = \hat{x}_2 g_{2x_2}(\hat{u}_2, \hat{x}_2)$.

For $\widehat{M}_{11}$, $m_{11} = \hat{u}_1 h_{1u_1}(\hat{u}_1, \hat{x}_1)$, $m_{12} = \hat{u}_1 h_{1x_1}(\hat{u}_1, \hat{x}_1)$, $m_{21} = \hat{x}_1 g_{1u_1}(\hat{u}_1, \hat{x}_1)$, $m_{22} = \hat{x}_1 g_{1x_1}(\hat{u}_1, \hat{x}_1)$, $m_{24} = -\hat{x}_1 q_1(\hat{u}_1)$, $m_{33} = L_2(0)h_{2u_2}(L_2(0), 0)$, $m_{34} = L_2(0)h_{2x_2}(L_2(0), 0)$, $m_{44} = g_2(L_2(0), 0) - \hat{x}_1 q_2(L_2(0))$.

For $\widehat{M}_{12}$, $m_{11} = L_1(0)h_{1u_1}(L_1(0), 0)$, $m_{12} = L_1(0)h_{1x_1}(L_1(0), 0)$, $m_{22} = g_1(L_1(0), 0) - \hat{x}_2 q_1(L_1(0))$, $m_{33} = \hat{u}_2 h_{2u_2}(\hat{u}_2, \hat{x}_2)$, $m_{34} = \hat{u}_2 h_{2x_2}(\hat{u}_2, \hat{x}_2)$, $m_{42} = -\hat{x}_2 q_2(\hat{u}_2)$, $m_{43} = \hat{x}_2 g_{2u_2}(\hat{u}_2, \hat{x}_2)$, $m_{44} = \hat{x}_2 g_{2x_2}(\hat{u}_2, \hat{x}_2)$.

For $\widetilde{M}_1$, $m_{11} = \tilde{u}_{11}\tilde{h}_{1u_1}$, $m_{12} = \tilde{u}_{11}\tilde{h}_{1x_1}$, $m_{21} = \tilde{x}_{11}\tilde{g}_{1u_1} - \tilde{x}_{11}\tilde{x}_{21}\tilde{q}_{1u_1}$, $m_{22} = \tilde{x}_{11}\tilde{g}_{1x_1} - \tilde{x}_{11}\tilde{x}_{21}\tilde{q}_{1x_1}$, $m_{42} = -\tilde{x}_{21}\tilde{q}_2$, $m_{34} = -\tilde{x}_{11}\tilde{q}_1$, $m_{33} = \tilde{h}_2$, $m_{43} = \tilde{x}_{21}\tilde{g}_{2u_2} - \tilde{x}_{11}\tilde{x}_{21}\tilde{q}_{2u_2}$, $m_{44} = \tilde{x}_{21}\tilde{g}_{2x_2}$, where a function with $\sim$

over it means that the function is evaluated at $\widetilde{E}_1$ and similarly for $\widetilde{M}_2$ at $\widetilde{E}_2$ below.

For $\widetilde{M}_2$, $m_{11} = \tilde{h}_1$, $m_{21} = \tilde{x}_{12}\tilde{g}_{1u_1} - \tilde{x}_{12}\tilde{x}_{22}\tilde{q}_{1u_1}$, $m_{22} = \tilde{x}_{12}\tilde{g}_{1x}$, $m_{24} = -\tilde{x}_{12}\tilde{q}_1$, $m_{33} = \tilde{u}_{22}\tilde{h}_{2u_2}$, $m_{34} = \tilde{u}_{22}\tilde{h}_{2x_2}$, $m_{42} = -\tilde{x}_{22}\tilde{q}_2$, $m_{43} = \tilde{x}_{22}\tilde{g}_{2u_2} - \tilde{x}_{12}\tilde{x}_{22}\tilde{q}_{2u_2}$, $m_{44} = \tilde{x}_{22}\tilde{g}_{2x_2}$.

Of course M^* is just M evaluated at E^*.

From the eigenvalues of the above matrices, we can make the following statements about the local stability of the equilibria.

E_0 is totally unstable (all eigenvalues are positive).

E_1 has the u_1-axis as its stable manifold and $x_1 - u_2 - x_2$ space as its unstable manifold.

E_2 is a saddle point whose stable manifold is the open x_1 axis if $m_{44}^2 = g_2(0,0) - K_1(0)q_2(0, K_1(0), 0) > 0$, and is included in the $x_1 - x_2$ plane if $m_{44}^2 < 0$.

E_3 is a saddle point whose stable manifold is the open u_2 axis.

E_4 is a saddle point whose stable manifold is the open x_2 axis if $m_{22}^4 = g_1(0,0) - K_2(0)q_1(0,0,K_2(0)) > 0$ and is included in the $x_1 - x_2$ plane if $m_{22}^4 < 0$.

E_5 is a saddle point whose stable manifold is the open $u_1 - u_2$ plane.

E_6 is a saddle point whose stable manifold is the open $u_1 - x_2$ plane if $m_{22}^4 > 0$ and is included in $u_1 - x_1 - x_2$ space if $m_{22}^4 < 0$.

E_7 is a saddle point whose stable manifold is the open $x_1 - u_2$ plane if $m_{44}^2 > 0$ and is included in $x_1 - u_2 - x_2$ space if $m_{44}^2 < 0$.

$\overline{E}$ is a saddle point whose stable manifold lies in the $x_1 - x_2$ plane. It is either one-dimensional (the bistable case) or two dimensional (the coexistence cases). This will be discussed to a greater extent in Section 5.

$\widehat{E}_{10}$ is by the nature of the dynamics known to be globally asymptotically stable with respect to solutions in the interior of the $u_1 - x_1$ plane. Let $\hat{m}_{44}^0 = g_2(0,0) - \hat{x}_1 q_2(0, \hat{x}_1, 0)$. Then $\widehat{E}_{10}$ is stable (unstable) locally in the x_2 direction if $\hat{m}_{44}^0 < 0$ (> 0). It is always unstable locally in the u_2 direction.

Similar statements are valid for $\widehat{E}_{02}$ with u_1 and u_2 interchanged, x_1 and x_2 interchanged, and $\hat{m}_{22}^0 = g_1(0,0) - \hat{x}_2 q_1(0,0,\hat{x}_2)$ instead of $\hat{m}_{44}^0$.

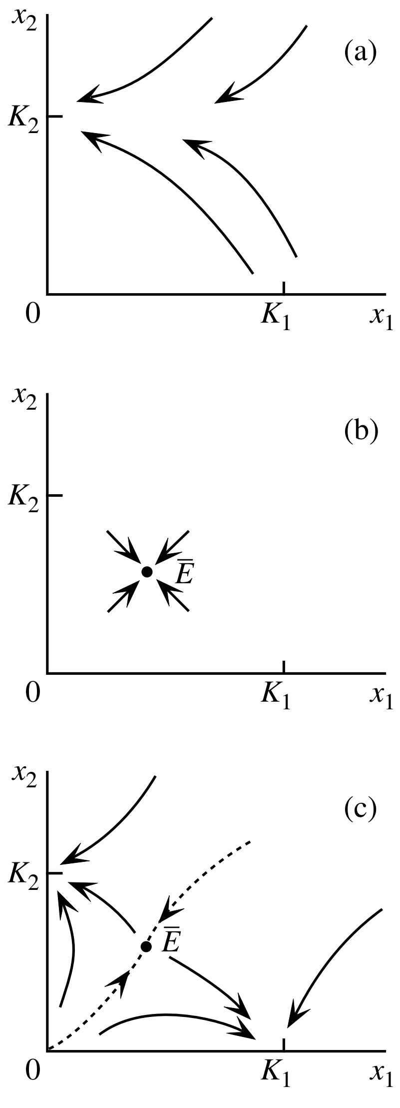

FIGURE 1. (a) $\overline{E}$ does not exist. x_2 always outcompetes x_1. (b) $\overline{E}$ exists. x_1 and x_2 coexist. (c) $\overline{E}$ exists. Either x_1 or x_2 go to extinction, depending on initial conditions, unless they are in $\overline{E}$'s stable manifold.

$\widehat{E}_{11}$ is globally stable for solutions initiating in the positive $u_1 - x_1$ plane and is stable locally in the u_2 direction. Let $\hat{m}_{44}^1 = g_2(L_2(0), 0) - \hat{x}_1 q_2(L_2(0), \hat{x}_1, 0)$. If $\hat{m}_{44}^1 < 0$ (> 0), then $\hat{E}_{11}$ is stable (unstable) locally in the x_2 direction.

$\widehat{E}_{22}$ has analogous properties to $\widehat{E}_{11}$ with u_1 and u_2 interchanged, x_1 and x_2 interchanged, and $\hat{m}_{22}^1 = g_1(L_1(0), 0) - \hat{x}_2 q_1(L_1(0), 0, \hat{x}_2)$ replacing $\hat{m}_{44}^1$.

Not much can be said about $\widetilde{E}_1$ and $\widetilde{E}_2$ without further assumptions, other than $\widetilde{E}_i$ is unstable locally in the u_j direction, $i = 1, 2$, $j \neq i$.

Of course, the stability of E^* is totally unknown at this point.

4. Persistence.

Following Freedman and Waltman [**8**], we say that a system of the form

$$\dot{N}_i(t) = F_i(N(t)), \qquad i = 1, \dots, n \tag{4.1}$$

persists if whenever $N_i(0) > 0$, $i = 1, \dots, n$, then $\liminf_{t\to\infty} N_i(t) > 0$. Further, if there exists $\delta > 0$ independent of $N_i(0)$, such that $\liminf_{t\to\infty} N_i(t) \geq \delta$, then system (4.1) is said to exhibit *uniform persistence.*

In this section we establish criteria for persistence and, as we shall see, uniform persistence for system (2.1), following techniques established in Freedman and Waltman [**8**], it will be sufficient to prove persistence if we can show that all dynamics are trivial on the boundaries of R_+^4, that all equilibria are hyperbolic and acyclic, and that no equilibrium is asymptotically stable. By acyclicity we mean that equilibria which are connected to other equilibria through a chain of saddle connectors are not eventually connected to themselves (see Butler et al. [**2**] for a formal definition).

We first note that all boundary equilibria are acyclic. We then note that E_0 is totally unstable and that $E_1 - E_7$, $\overline{E}$,$\widehat{E}_{10}$, $\widehat{E}_{02}$ are hyperbolic saddle points.

A sufficient condition for $\widehat{E}_{11}$ (respectively, $\widehat{E}_{12}$) to be a hyperbolic saddle point is $\hat{m}_{44}^1 > 0$ (respectively, $\hat{m}_{22}^1 > 0$).

As far as $\widetilde{E}_1$ and $\widetilde{E}_2$ are concerned, we already know that they have unstable manifolds. However, we have no guarantee that they are hyperbolic or that the dynamics in the respective three-dimensional subspaces are trivial. However, conditions (albeit complicated ones) for the interior equlibrium of a competitor-competitor-mutualist system to be globally asymptotically stable were given in Freedman and Rai [**7**].

Hence we will require the following hypotheses.

(H4) $\hat{m}^1_{44} = g_2(L_2(0), 0) - \hat{x}_1 q_2(L_2(0), \hat{x}_1, 0) > 0$, $\hat{m}^1_{22} = g_1(L_1(0), 0) - \hat{x}_2 q_1(L_1(0), 0, \hat{x}_2) > 0$.

(H5) $\widetilde{M_1}$ and $\widetilde{M_2}$ have no eigenvalues with zero real parts.

(H6) $\widetilde{E}_i$, if it exists, is globally asymptotically stable with respect to solutions initiating in the interior of the positive $u_i - x_1 - x_2$ space, $i = 1, 2$.

From the above discussion the following theorem is now valid.

Theorem 4.1. *Let* (H0)–(H6) *hold. Then system* (2.1) *persists.*

From the results in Butler et al. [**2**], the following two corollaries are also valid.

Corollary 4.2. *Let* (H0)–(H6) *hold. Then system* (2.1) *persists uniformly.*

Corollary 4.3. *Let* (H0)–(H6) *hold. Then* E^* *exists.*

Note that by techniques similar to those used in Rai and Freedman [**6, 7**] we could obtain a technique for constructing a Liapunov function to test for global stability of E^*. However, the computations are very messy and the results could not be biologically interpreted. Hence, we choose not to do so in this paper.

Finally, we remark that if (H6) is violated, it still may be possible to prove persistence, provided that in the appropriate subspace all solutions eventually enter a compact set containing $\widetilde{E}_i$ together with a fnite number of periodic and/or almost periodic motions. However, the anaylsis is then extremely complicated and is not given here.

5. Reversal of outcome.

Theorem 4.1 indicates several ways in whch reversal of competitive outcome could occur.

First we consider the two dimensional competitive plane. It is well known (Albrecht et al. [**1**]) that in two dimensional competitive systems the dynamics are always trivial, i.e., all solutions tend to an equlibrium. If there is at most one equilibrium in the $x_1 - x_2$ plane, then the possible competitive outcomes are similar to those of a Lotka-Volterra system as described in Freedman [**4**]. If no positive equilibrium exists, then one species always outcompetes the other, driving it to extinction. If a positive equlibrium exists, then either it is asymptotically stable (both species coexist) or it is a saddle point, (except for singular initial conditions, one of the species will become extinct, depending on initial conditions, i.e., the bistable case occurs as described in Kirlinger [**9, 10**]). Figure 1 shows these three possibilities. In two of them, extinction takes place. However, if the conditions of Theorem 4.1 are satisfied, both competitors persist.

It is of interest to note how the bistable case can be reversed by describing the effect of the mutualists on the isoclines of the competitive subsystem. Figure 2a shows the isocline picture with no mutualism giving bistability (but not persistence). If only one mutualist, say u_1, were involved (as in Freedman and Rai [**7**]) it could effectively move K_1 to the right and α_1 (the solution of $\alpha_1 q_1(0) = g_1(0,0)$) up, resulting in a situation as described in Figure 2b. Now x_2 always goes extinct and there is still no persistence. However, if u_2 also influences the dynamics by moving K_2 up weakly and α_2 (the solution of $\alpha_2 q_2(0) = g_2(0,0)$) strongly to the right so as to put the isoclines as described in Figure 2c, then persistence will occur.

As well, this same argument indicates how the second mutualist could reverse competitive outcome when extinction occurs in either of the three dimensional competitor-competitor-mutualist subsystems. In that case we would suppose that one or both of the $\widetilde{E}_i$ do not occur. Then the competitor without the mutualist will go extinct. The effect of the second mutualist is to aid this second competitor sufficiently so that all populations survive.

6. Example.

In this section we give an example to illustrate our results. The numerical coefficients are for illustrative purposes and do

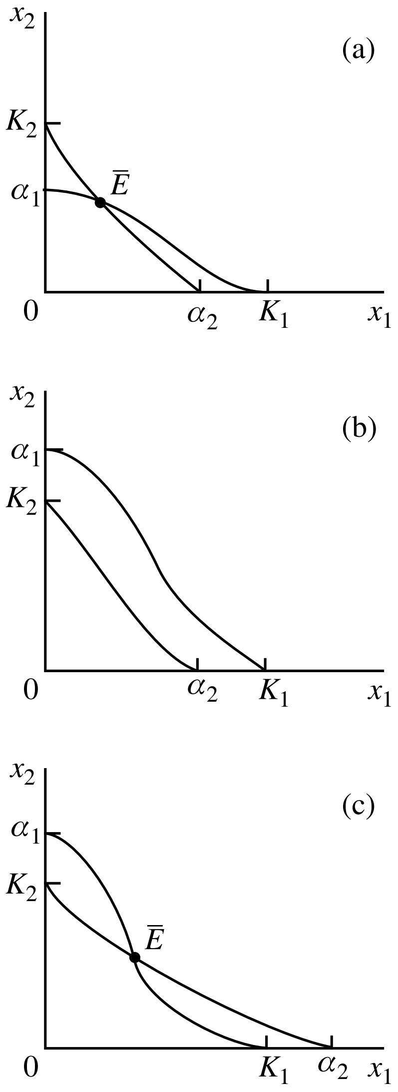

FIGURE 2. (a) $\alpha_1 < K_2$, $\alpha_2 < K_1$. Dynamics are as in Figure 1c. (b) Influence of u_1. $\alpha_1 > K_2$, $\alpha_2 < K_1$. Dynamics are as in Figure 1a. (c) Influence of u_1 and u_2. $\alpha_1 > K_2$, $\alpha_2 > K_1$. Dynamics are as in Figure 1b.

not necessarily represent any real system. Consider the system

$$
\begin{aligned}
\dot{u}_1 &= 400u_1\left(1-\frac{u_1}{1150+4x_1/95}\right)\\
\dot{x}_1 &= 300x_1\left(1-\frac{x_1}{1500}\right)-\frac{14x_1x_2}{9(1+u_1/270)}\\
\dot{u}_2 &= 450u_2\left(1-\frac{u_2}{2394+76x_2/875}\right)\\
\dot{x}_2 &= 250x_2\left(1-\frac{x_2}{1000}\right)-\frac{x_1x_2}{(1+u_2/475)}.
\end{aligned}
\tag{6.1}
$$

Various possible equlibria for the system (6.1) are $E_0(0,0,0,0)$, $E_1(1150,0,0,0)$, $E_2(0,1500,0,0)$, $E_3(0,0,2394,0)$, $E_4(0,0,0,1000)$, $E_5(1150,0,2394,0)$, $E_6(1150,0,0,1000)$, $E_7(0,1500,2394,0)$, $\overline{E}(0,56500/271,0,45000/271)$, $\widehat{E}_{10}(2850/3,1500,0,0)$, $\widehat{E}_{02}(0,0,17366/7,1000)$, $\widehat{E}_{11}(3850/3,1500,2394,0)$, $\widehat{E}_{12}(1150,0,17366/7,1000)$, and $E^*(1200,2375/2,2413,875/4)$.

We obtain that for the system (6.1)

$$
\begin{aligned}
&m^2_{44} = -1250 < 0, \qquad m^4_{22} = -\frac{11300}{9} < 0\\
&\hat{m}^0_{22} = -\frac{11300}{9} < 0, \qquad \hat{m}^0_{44} = -1250 < 0\\
&\hat{m}^1_{22} = 4.2253523 > 0 \quad \text{and} \quad \hat{m}^1_{44} = 1.6556292 > 0.
\end{aligned}
$$

We observe that the conditions (H0)–(H4) are satisfied and the conditions (H5) and (H6) hold vacuously (as $\widetilde{E}_1$ and $\widetilde{E}_2$ do not exist). Hence all the conditions of Theorem 4.1 are satisfied and system (6.1) persists.

Further, the existence of $\overline{E}$, nonexistence of $\widetilde{E}_1$, $\widetilde{E}_2$ and then existence of the interior equilibrium E^* prove the occurrence of the change of the competitive outcome.

7. Discussion.

In this paper we have considered a system of four autonomous ordinary differential equations as a model of four interacting populations, two species competing with each other and two mutualists, one for each competitor. Our main interest was to give criteria for the persistence of all four populations. We have been able to obtain such criteria in terms of the parameters of the system and have illustrated the conclusions with an example. We have shown that in the absence of one of the mutualists the corresponding three-dimensional subspace has no interior equilibrium for our system but if this mutualist is allowed to interact, then we do have an interior equilibrium in the four dimensional space, establishing the fact that the mutualist has altered the competitive outcome, and the four species could persist. Thus, mutualism is a very desirable interaction when we are looking for the co-existence of a multispecies community.

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