SOLUTIONS OF A PIONEER-CLIMAX MODEL

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ABSTRACT. We investigate certain planar dynamical systems that arise in pioneer-climax models. The relative positions of separatrices of stable and unstable manifolds are studied, and it is shown that there are curves of parameter values that give rise to heteroclinic circuits. Existence of periodic solutions is also proven for an open subset of parameter space.

1. Introduction. In this paper we study a system of differential equations that arises by modeling certain pioneer/climax forests as studied by Selgrade and Namkoong [4]. Let \( x \) denote the population density of the pioneer species, and let \( y \) denote the density of the climax species. Define two total density variables as the following linear combinations of the population densities:

\[
\begin{align*}
    z &= ax + y \\
    w &= x + dy.
\end{align*}
\]

The parameters \( a \) and \( d \) are positive and measure the relative intensity of the competition. Note that, for convenience and without loss of generality, we have assumed that the variables have been scaled so that the coefficient of \( y \) in the first sum and the coefficient of \( x \) in the second sum are equal to one. We will analyze how changes in values of the intraspecific coefficients, \( a \) and \( d \), affect the qualitative behavior of the phase plane for the following planar dynamical system that represents a model for competition between \( x \) and \( y \):

\[
\begin{align*}
    x' &= xf(z) \\
    y' &= yg(w),
\end{align*}
\]

where \( x' \) and \( y' \) are derivatives with respect to time, and \( f \) and \( g \) are defined and smooth over the nonnegative reals.
The functions $z \mapsto f(z)$ and $w \mapsto g(w)$ in Equations (2) are the per capita growth rates for the $x$ and $y$ populations, respectively, and are called \textit{fitness functions}. They are assumed to be twice continuously differentiable. Since the $x$ species is the pioneer species, we assume that $f$ is monotone decreasing with $z$, is either linear or concave down, and has exactly one positive zero $\alpha$ as shown in Figure 1(a). Moreover, the climax species $y$ is assumed to have a fitness function $g$ that increases as a function of $w$ up to a maximum and then decreases, is concave down, and has two positive zeros, $\beta < \gamma$, see Figure 1(b).

In other words, we make the following assumptions about the fitness functions:

A1. $f(0) > 0$, $f' < 0$, $f'' \leq 0$ and $f(\alpha) = 0$.

A2. $g(\beta) = g(\gamma) = 0$, $g'(\beta) > 0$, $g'(\gamma) < 0$, $g'' < 0$.

Note that hypotheses A1 and A2 are satisfied in the case that $f$ is linear, and $g$ is quadratic, e.g.,

$$f(z) = K(\alpha - z) \quad \text{and} \quad g(w) = M(\beta - w)(w - \gamma).$$

In fact, solution curves like those that appear in Figures 3–6 below can be obtained using the following fitness functions:

$$f(z) = 1 - z \quad \text{and} \quad g(w) = (1 - w)(w - 3).$$
Systems with linear and quadratic fitness functions have been investigated by Sumner [7]. Systems with more general fitness functions $g$ that satisfy the hypothesis A2 have been investigated by Selgrade and Namkoong [4]–[5], Selgrade and Buchanan [2] and Buchanan [1].

Clearly, the righthand side of system (2) is an autonomous vector field in $x$ and $y$ defined on the positive quadrant $\mathbb{R}^2_+$. The previous studies primarily focused on local behavior of solutions of system (2) near equilibria and, in particular, on the existence of a Hopf bifurcation near one of the interior equilibria. Our study is somewhat more global and geometric in that we investigate behavior of solutions for values of $a$ and $d$ that are not necessarily close to values that lead to a Hopf bifurcation. The paper by Conway and Smoller [3] was helpful.

2. Discussion. System (2) may have up to six equilibria in $\mathbb{R}^2_+$: one is at the origin $O = (0, 0)$, three more of them are on the boundary of $\mathbb{R}^2_+$ at the points $B_1 = (0, \beta/d)$, $B_2 = (0, \gamma/d)$ and $B_3 = (\alpha/a, 0)$, respectively. There may be as many as two more equilibria in the interior. An interior equilibrium occurs when the linear nullcline for $x$, $ax + y = \alpha$, intersects one of the two linear nullclines for $y$, $x + dy = \beta$ or $x + dy = \gamma$, at a point in the interior of $\mathbb{R}^2_+$. The local stability properties of each of these equilibria depend on the values of the parameters $a$ and $d$ and have been discussed by a number of authors, see Selgrade and Namkoong [4], Sumner [6, 7, 8] and, more recently, Buchanan [1]. Buchanan [1] studies nine possible geometric nullcline configurations, illustrated by nine different figures, for the phase plane of system (2) and concludes that there are only two configurations, Figures (7) and (9) in [1], that can have a periodic orbit encircling one of the interior equilibria. In both of these cases it is necessary that $ad < 1$. One of the configurations with a possible periodic orbit has two interior equilibria, Figure 9 in [1], and the other, Figure 7 in [1] and Figure 2 below has just one. In this paper we will restrict ourselves to the latter case, in which system (2) has only one interior equilibrium $E_1$ and the pair $(a, d)$ satisfy $ad < 1$. This is the geometric nullcline configuration in which Selgrade and Namkoong [4] have shown that $E_1$ gives rise to a Hopf bifurcation for certain values of $a$ and $d$. Examples of nullclines for a vector field defined as in equations (2), and satisfying our assumptions, are shown in Figure 2.

Observe that for points above the nullcline $x + dy = \gamma$, the region
FIGURE 2. Nullclines for system (2).

$V$ shown in Figure 2, the vector field is directed down and to the left. Hence all solutions eventually end up on or below this nullcline and thus can be continued for all positive time.

The coordinates for the interior equilibrium $E_1$ are obtained by solving the equations $ax + y = \alpha$, $x + dy = \beta$ for $x$ and $y$ and are

$$x_e = \frac{\beta - d\alpha}{1 - ad} \quad \text{and} \quad y_e = \frac{\alpha - a\beta}{1 - ad}.$$  

The Jacobian matrix for the system (2) at the point $P : (x, y)$ is

$$J(P) = \begin{pmatrix} f(z) + af'(z) & xf'(z) \\ yg'(w) & g(w) + dyg'(w) \end{pmatrix}.$$  

This matrix at the interior equilibrium $E_1$ is

$$J(E_1) = \begin{pmatrix} a((\beta - d\alpha)/(1 - ad))f'(\alpha) & ((\beta - d\alpha)/(1 - ad))f'(\alpha) \\ ((\alpha - a\beta)/(1 - ad))g'(\beta) & d((\alpha - a\beta)/(1 - ad))g'(\beta) \end{pmatrix}.$$  

Local stability of $E_1$ is determined by the sign of trace of the matrix

$$\text{tr} \ J(E_1) = \frac{ad}{1 - ad} \sigma(a, d),$$
where

\[
\sigma(a, d) = \left( \frac{\beta}{d} - \alpha \right) f'(\alpha) + \left( \frac{\alpha}{a} - \beta \right) g'(\beta),
\]

and the discriminant of the characteristic polynomial of \( J(E_1) \),

\[
\text{disc } J(E_1) = \text{tr } J(E_1)^2 + \frac{4ad}{1 - ad} \left( \frac{\beta}{d} - \alpha \right) \left( \frac{\alpha}{a} - \beta \right) f'(\alpha) g'(\beta).
\]

Under the assumptions A1 and A2 the equations (6) and (8) imply that the matrix \( J(E_1) \) has pure imaginary eigenvalues when the pair \((a, d)\) is a point on the hyperbola \( \sigma(a, d) = 0 \), lying within the hyperbolic region \( ad < 1 \). We want to work with a domain of parameter values that properly include these conditions. In the contrary case, when \( ad \geq 1 \), Buchanan [1] has shown that all of the \( \omega \)-limit sets for systems like (2) are single equilibria and consequently in this case there can be no \( \omega \)-limit cycles. We make the following additional assumption.

A3. There is a value \( a_1 \) with \( (\alpha/\gamma) < a_1 \leq (\alpha/\beta) \) and such that for each \( a \) in the open interval \( I = ((\alpha/\gamma), a_1) \) there is a value \( d \) such that \( \alpha < (\beta/d) \) and \( \sigma(a, d) = 0 \).

Observe that, if the pair \((a, d)\) satisfies

\[
\frac{\alpha}{\gamma} < a < \frac{\alpha}{\beta} \quad \text{and} \quad \alpha < \frac{\beta}{d},
\]

then

\[
ad < 1.
\]

In particular, an assumption like A3 is usually assumed in cases in which a Hopf bifurcation exists [4]. Indeed, if assumptions A1–A3 are true, then, according to [4], the equilibrium \( E_1 \) gives rise to a Hopf bifurcation for the system (2) for values of \( a \) and \( d \) satisfying \( \sigma(a, d) = 0 \). Moreover, if \( f \) and \( g \) are linear and quadratic, respectively, then for \((a, d)\) satisfying \( ad < 1 \) and \( \sigma(a, d) = 0 \), the formula, equation (10) in [4], for calculating the stability coefficient, \( \beta_2 \), becomes

\[
8\beta_2 = \frac{dx g''(\beta)}{x_e} - dy_e(1 - ad) \left( \frac{g''(\beta)}{g'(\beta)} \right)^2 < 0.
\]
Thus, if $f$ is linear and $g$ is quadratic, the periodic orbit of the Hopf bifurcation is locally asymptotically stable.

We now investigate the behavior of solutions of equation (2) for values of $a$ and $d$ in an open set about a point $(a_0, d_0)$ satisfying A3.

Since we are assuming that $(\alpha/\gamma) < a < (\alpha/\beta)$ and $ad < 1$, it follows that the eigenvalues of the lower triangular Jacobian matrix of system (2) at the equilibrium $B_2 : (0, (\gamma/d))$ are both negative. Hence, $B_2 : (0, (\gamma/d))$ is locally asymptotically stable for all parameter values that we are considering.

For the equilibrium $B_1 : (0, (\beta/d))$, we observe that $J(B_1)$ is lower triangular and, since $(\beta/d) > \alpha$, the eigenvalue $f(\beta/d)$ is negative. In addition, the eigenvalue $\beta g'(\beta)$ is positive. Thus, $B_1$ is unstable in the $y$ direction, but is stable in the direction of the eigenvector

$$\begin{pmatrix} \beta g'(\beta) - f(\beta/d), -\frac{\beta}{d} g'(\beta) \end{pmatrix}.$$

In the following when we say that a solution curve $\Gamma = (x(t), y(t))$ of system (2) enters an equilibrium $(x_0, y_0)$ as $t \to \infty$ ($t \to -\infty$), we mean that $(x(t), y(t))$ tends to $(x_0, y_0)$ as $t \to \infty$ ($t \to -\infty$) and the vector $(x(t) - x_0, y(t) - y_0)$ has a limiting direction as $t \to \infty$ ($t \to -\infty$).

Next we will analyze the stable manifold $\Gamma_s(B_1)$ which enters $B_1$ with slope

$$m_s = -\frac{1}{d} \frac{1}{1 - f(\beta/d)/(\beta g'(\beta))} \tag{9}$$

as $t \to \infty$. Observe that the tangent to $\Gamma_s(B_1)$ meets the nullcline $x + dy = \beta$ at $B_1$ and lies above the nullcline for $0 < x$.

Of central importance to our results is the line segment

$$\mathcal{L} : \frac{ax}{\alpha} + \frac{dy}{\beta} = 1 \tag{10}$$

drawn from $B_1$ to $B_3$. See Figures 3–4. Observe that $\mathcal{L}$ intersects the vertical line $x = x_\varepsilon$ above the interior equilibrium $E_1$. The closed curve $\mathcal{C}$ consisting of $\mathcal{L}$ and the line segments $\overline{B_1O}$ and $\overline{OB_3}$ encloses a region $\mathcal{R}$ that contains $E_1$ in its interior. Since both the $x$- and $y$-axes
are invariant, no solution curve of the system (2) can leave \( \mathcal{R} \), except possibly by crossing the line segment \( \mathcal{L} \). In particular, suppose that \( \mathcal{L} \) has the property that solution curves of (2) that intersect \( \mathcal{L} \) must move into but cannot move out from \( \mathcal{R} \). If that happens and \( \text{tr} J(E_1) > 0 \), i.e., \( E_1 \) is unstable, then the Poincaré-Bendixon theorem guarantees the existence of a periodic solution contained in \( \mathcal{R} \). In the following we will show that there are values of \( a \) and \( d \) such that the interior of the line segment \( \mathcal{L} \) is transverse to the flow of system (2) and points on orbits that intersect this set move into \( \mathcal{R} \). We will also show that there are other values of \( a \) and \( d \) such that points of the flow move out from \( \mathcal{R} \) through \( \mathcal{L} \).

**Proposition 1.** Suppose assumptions A1–A3 hold and \( a_0 \in \mathcal{I} \). Then, for any \( d \) satisfying \( a_0d < 1 \) and \( \sigma(a_0,d) \leq 0 \), it follows that system (2) has a stable manifold \( \Gamma_s(B_1) \) at \( B_1 \) which enters \( B_1 \) as \( t \to \infty \), with tangent above the nullcline \( x + dy = \beta \) and above or on the line \( \mathcal{L} \). Furthermore, the system has an unstable manifold \( \Gamma_u(B_3) \) which enters \( B_3 \) as \( t \to -\infty \), with tangent line above the nullcline \( ax + y = \alpha \) and below the line \( \mathcal{L} \).

**Proof.** Observe that if the trace of \( J(E_1) \) is nonpositive, i.e.,
\[ \sigma(a_0, d) \leq 0, \] then since \( f'' \leq 0 \) we have

\[ -f(\beta/d) \geq -f'(\alpha) \left( \frac{\beta}{d} - \alpha \right) \geq \left( \frac{\alpha}{a_0} - \beta \right) g'(\beta), \]

from which it follows that, in this case,

\[ m_s = -\frac{1}{d} \left[ \frac{1}{1 - f(\beta/d)/(\beta g'(\beta))} \right] \geq -\frac{a_0 \beta}{d \alpha}. \]

Thus, when the sum of the real parts of the eigenvalues of \( J(E_1) \) are nonpositive the tangent of \( \Gamma_s(B_1) \) enters \( B_1 \) from above or on \( \mathcal{L} \). See Figure 3.

The Jacobian matrix associated with (2) at \( B_3 : (\alpha/a_0, 0) \) is upper triangular with eigenvalues \( \alpha f'(\alpha) \) and \( g(\alpha/a_0) \), respectively. Since \( f'(\alpha) < 0 \), \( B_3 \) is stable in the \( x \)-direction, but since, according to A3, \( \beta < \alpha/a < \gamma \), meaning \( g(\alpha/a_0) > 0 \), \( B_3 \) is unstable in the direction of the eigenvector

\[ \left\langle -\frac{\alpha}{a_0} f'(\alpha), \alpha f'(\alpha) - g(\alpha/a_0) \right\rangle. \]
Thus the system has an unstable manifold $\Gamma_u(B_3)$ emanating from $B_3$ with slope

\begin{equation}
    m_u = -a_0 \left[ 1 - \frac{g(\alpha/a_0)}{\alpha f'(\alpha)} \right].
\end{equation}

The tangent of $\Gamma_u(B_3)$ intersects the nullcline $ax + y = \alpha$ at $B_3$ and lies above it for $x < (\alpha/a)$. If the pair $(a_0, d)$ is chosen so that the sign of the real parts of the eigenvalues of $J(E_1)$ is nonpositive, then since $g(\beta) = 0$ and $g'' < 0$,

$$0 \geq \sigma(a_0, d) > \left( \frac{\beta}{d} - \alpha \right) f'(\alpha) + g(\alpha/a_0).$$

It follows that

\begin{equation}
    m_u > -\frac{a_0 \beta}{d \alpha},
\end{equation}

and, hence, when the sum of the real parts of the eigenvalues of $J(E_1)$ are nonpositive, the tangent to $\Gamma_u(B_3)$ at $B_3$ lies below $\mathcal{L}$. See Figure 3. $\square$

Suppose that $a_0 \in \mathcal{I}$ and $d_0$ satisfies $\sigma(a_0, d_0) = 0$. Then there is an open interval $\mathcal{J}$ such that $d \in \mathcal{J}$ implies $a_0 d < 1$ and the sum of the real parts of the eigenvalues of $J(E_1)$, i.e., $\sigma(a_0, d)$, is negative for $d < d_0$ and positive for $d > d_0$. Let us consider the relationship of the stable manifold $\Gamma_s(B_1)$ and the unstable manifold $\Gamma_u(B_3)$ as $d$ increases with fixed $a_0 \in \mathcal{I}$. Figures 3 and 4 suggest the relationship of these objects for $\sigma(a_0, d) \leq 0$ and $\sigma(a_0, d) \gg 0$, respectively. Now we investigate what happens as $d$ increases so that the factor $((\beta/d) - \alpha)$ in the first term in the expression for $\sigma(a_0, d)$ becomes smaller.

\textbf{Proposition 2.} For each $a_0 \in \mathcal{I}$ there exists $d_0$ such that if $(\beta/d_0) \geq (\beta/d) > \alpha$ then $\Gamma_s(B_1)$ enters $B_1$ as $t \to \infty$ from below $\mathcal{L}$, and $\Gamma_u(B_3)$ enters $B_3$ as $t \to -\infty$ from above the line $\mathcal{L}$.

\textbf{Proof.} Let $a_0 \in \mathcal{I}$ be fixed. Since $f(\alpha) = 0$, we can choose $d$ so that $(\beta/d)$ is near enough to $\alpha$ to imply that

$$-f(\beta/d) < \left( \frac{\alpha}{a_0} - \beta \right) g'(\beta),$$
which implies that

$$m_s = -\frac{1}{d} \left[ \frac{1}{1 - f(\beta/d)/(\beta g'(\beta))} \right] < -\frac{a_0 \beta}{d\alpha}.$$  

Thus, for $(\beta/d)$ greater than but sufficiently close to $\alpha$, we see that $\Gamma_s(B_1)$ enters $B_1$ from below the line $\mathcal{L}$ as $t \to \infty$.

Since

$$1 - \frac{g(\alpha/a_0)}{\alpha f'(\alpha)} > 1$$

we can, by choosing $((\beta/d) - \alpha)$ small but positive, require that

$$1 - \frac{g(\alpha/a_0)}{\alpha f'(\alpha)} > \frac{\beta}{d\alpha},$$

which implies that

$$m_u < -a_0 \frac{\beta}{d\alpha}.$$  

Thus, for $(\beta/d)$ greater than but sufficiently close to $\alpha$ we see that $\Gamma_u(B_1)$ enters $B_3$ from above the line $\mathcal{L}$ as $t \to -\infty$. See Figure 4.  

Next we investigate the flow of the vector field through the line segment $\mathcal{L}$, see equation (10), for various values of $a$ and $d$. If $(x(t), y(t))$ is a point on a solution curve of system (2) that lies on $\mathcal{L}$, then $(x(t), y(t))$ moves into the region $\mathcal{R}$ with increasing $t$ if the following expression is negative at all first quadrant points $(x(t), y(t))$ on $\mathcal{L}$:

$$\left( \frac{a}{\alpha} x + \frac{d}{\beta} y \right)'(t) = \frac{a}{\alpha} x(t)f(ax(t) + y(t)) + \frac{d}{\beta} y(t)g(x(t) + dy(t)).$$

If the expression in (16) is positive at all first quadrant points $(x(t), y(t))$ on $\mathcal{L}$, then $(x(t), y(t))$ moves out and away from $\mathcal{R}$ through $\mathcal{L}$.  

Proposition 3. Suppose assumptions A1–A3 hold and $a_0 \in \mathcal{I}$. Then, for any $d$ satisfying $a_0 d < 1$ and $\sigma(a_0, d) \leq 0$, the points on trajectories of system (2) move into the region $\mathcal{R}$ through $\mathcal{L}$. On the other hand, for each $a_0 \in \mathcal{I}$, there exists $d_0$ such that if $a_0 d < 1$ and $(\beta/d_0) \geq (\beta/d) > \alpha$, then the points on trajectories of system (2) move out from the region $\mathcal{R}$ through $\mathcal{L}$.

Proof. Solving $y(t)$ for $x(t)$ in equation (10) and substituting into the righthand side of (16) becomes

\begin{equation}
\frac{a}{\alpha} \left[ x(t) f \left( \frac{a}{\alpha} \left( \alpha - \frac{\beta}{d} \right) x(t) + \frac{\beta}{d} \right) - \left( x(t) - \frac{\alpha}{a} \right) g \left( \frac{a}{\alpha} \left( \frac{\alpha}{a} - \beta \right) x(t) + \beta \right) \right].
\end{equation}

By expanding $f$ and $g$ in Taylor’s series of order 2 about $\alpha$ and $\beta$, respectively, and then using the fact that the second derivative of $f$ is nonpositive and the second derivative of $g$ is negative, then from (16) and (17) we find that

\begin{equation}
\left( \frac{a}{\alpha} x + \frac{d}{\beta} y \right)'(t) < \left( \frac{a}{\alpha} \right)^2 \left( \frac{\alpha}{a} - x(t) \right) x(t) \sigma(a, d).
\end{equation}
Thus, when the sum of the real parts of the eigenvalues of \( J(E_1) \) are nonpositive, we have \( \sigma(a, d) \leq 0 \), and hence, for these values of \( a \) and \( d \), all trajectories that meet \( \mathcal{L} \) must move directly into \( \mathcal{R} \) through \( \mathcal{L} \) and must remain inside the region \( \mathcal{R} \) for all positive values of \( t \).

Now, for \( a_0 \in \mathcal{I} \), expand \( f \) in (17) in its second order Taylor's expansion about \( \alpha \) and factor; then the expression in square brackets is equal to

\[
\left( \frac{a_0}{\alpha} \right) \left( \frac{\alpha}{a_0} - x(t) \right) \mu(a_0, d, x(t)),
\]

where

\[
\mu(a, d, x) = \left( \frac{\beta}{d} - \alpha \right) f'(\alpha) x + O \left( \left( \frac{\beta}{d} - \alpha \right)^2 \right) + g \left( \frac{a}{\alpha} \left( \frac{\alpha}{a} - \beta \right) x + \beta \right).
\]

Since \( g(\beta) = 0 \) and \( g'' < 0 \) the function \( x \mapsto g((a_0/\alpha)((\alpha/a_0) - \beta)x + \beta) \) vanishes at \( x = 0 \) and is positive (since \( g(\alpha/a_0) > 0 \)) and concave down throughout the interval \( (0, \alpha/a_0) \). The linear expression

\[
\left( \frac{\beta}{d} - \alpha \right) f'(\alpha) x
\]
in (20) is negative but can be made as small in absolute value as desired on the interval \((0, \alpha/a_0]\) by increasing \(d\) so that \(((\beta/d) - \alpha)\) is near zero. For an interval in \(d\) we have \(\mu(a_0, d, x) > 0\), for \(x \in (0, \alpha/a_0]\). Thus, by choice of \(d\), we can guarantee that solutions exit \(\mathcal{R}\) through \(\mathcal{L}\). \(\Box\)

We now show that there are values of \(a\) and \(d\) such that system (2) has periodic orbits, and also values for which the system has a heteroclinic cycle.

**Proposition 4.** Let \(a_0 \in \mathcal{I}\). Then there exists an interval \((d_1, d_2)\) such that, for each \(d_1 \leq d \leq d_2\), the system (2) having these parameter values has at least one periodic orbit that lies in \(\mathcal{R}\). Furthermore, there is at least one point \(d_3\) such that the system (2) with \(a = a_0\), \(d = d_3\), has a heteroclinic cycle consisting of the manifold \(\Gamma_s(B_1) = \Gamma_u(B_3)\) along with the line segments:

\[
\overline{B_1O} \quad \text{and} \quad \overline{OB_3}.
\]

**Proof.** For fixed \(a_0\) in \(\mathcal{I}\) and \(d\) satisfying \(a_0d < 1\), we see from Propositions (1) and (2) that points on the stable manifold \(\Gamma_s(B_1)\) enter \(B_1\) as \(t \to \infty\) from the region IV which is bounded above by the nullcline \(x + dy = \gamma\) and below by the nullclines \(x + dy = \beta\) and \(ax + y = \alpha\). Points on \(\Gamma_s(B_1)\) move in negative time on a curve that moves downward and to the right. So long as the points remain inside region IV they can be continued in negative time until they either exit by way of the nullcline \(x + dy = \gamma\) or tend to the interior equilibrium \(E_1: (x_e, y_e)\) as \(t \to -\infty\). Let \(P\) denote the point of intersection of the vertical line through \(E_1\) and the nullcline \(x + dy = \gamma\). See Figure 7. Define the real valued function \(d \mapsto S(d)\) as follows:

- If \(\Gamma_s(B_1)\) intersects \(x + dy = \gamma\) at a point \(Q\) to the left of the vertical line \(x = x_e\), then define \(S(d)\) to be the \(y\)-coordinate of \(Q\).

- If \(\Gamma_s(B_1)\) does not intersect \(x + dy = \gamma\) to the left of the segment \(\overline{E_1P}\), then it either intersects \(\overline{E_1P}\) for the first time at a point \(Q\) or enters the equilibrium \(E_1\) as \(t \to -\infty\). In the first case define \(S(d)\) to be the \(y\)-coordinate of \(Q\); in the latter, let \(S(d) = y_e\).

Except at the equilibria, the vector field defined by system (2) is
transverse to the lines \( x + dy = \gamma \) and \( x = x_e \). Thus the function \( d \mapsto S(d) \) is continuous on a connected open subset of \( \{ d : a_0 d < 1 \} \).

Similarly, we define a function \( d \mapsto U(d) \) for the unstable manifold \( \Gamma_u(B_3) \). For fixed \( a_0 \) in \( I \) and \( d \) satisfying \( a_0 d < 1 \), we see from Propositions (1) and (2) that points on the unstable manifold \( \Gamma_u(B_3) \) enter \( B_3 \) as \( t \to -\infty \) from the region IV. These points move upward and to the left until they either intersect the vertical segment \( E_1 \overrightarrow{P} \) at a point below \( P \) or enter \( E_1 \) at \( t \to \infty \). In the first case, define \( U(d) \) to be the \( y \)-coordinate of the first point of intersection, and in the latter case define \( U(d) \) to be \( y_e \). As before, the function \( d \mapsto U(d) \) is continuous on an open connected subset of \( \{ d : a_0 d < 1 \} \).

Now by Propositions (1)–(3) we see that if \( \sigma(a_0, d) \leq 0 \), then \( \Gamma_s(B_1) \) starts above \( L \) and remains above that line so long as \( 0 < x < (\alpha/a_0) \). On the other hand, for the same pair \((a_0, d)\), points on the unstable manifold \( \Gamma_u(B_3) \) move in positive time from \( B_3 \) and remain below \( L \) for all positive time. For these values of \( d \) we have \( S(d) > U(d) \). Finally, as \( d \) increases, the situation reverses and there is a sufficiently large \( d_0 \) such that, if \( (\beta/d_0) \geq (\beta/d) > \alpha \), then the stable manifold remains below \( L \) in negative time, and the unstable manifold remains above \( L \) for positive time, or \( S(d) < U(d) \). In particular, for each \( a_0 \in I \), there is some largest interval, say \((d_1, d_2)\), such that if
\(d \in (d_1, d_2)\), then \(\sigma(a_0, d) > 0\) and \(\mathcal{R}\) is invariant in positive time. Thus, for \(d\) in this interval, the Poincaré-Bendixson theorem guarantees the existence of a periodic solution in the region \(\mathcal{R}\). Furthermore, by continuity, there must be a value \(d_3\) such that \(S(d_3) = U(d_3)\). Observe that, since \((x_e, U(d_3))\) must lie below the point \(P\) the point \((x_e, S(d_3))\) is common to \(\Gamma_s(B_1)\) and \(\Gamma_u(B_3)\) which by uniqueness means that the two manifolds coincide. The closed curve \(\mathcal{C}\) defined by this manifold and the segments \(\overline{B_1O}\) and \(\overline{OB_3}\) is a heteroclinic cycle. □

3. Conclusions. For each \(a_0 \in I\) there is an interval of \(d\) values such that \(\sigma(a_0, d) < 0\), i.e., when \(d\) is small, so that for \(d\) in this interval the equilibrium \(E_1\) is locally asymptotically stable. The region \(\mathcal{R}\) is positively invariant but does not necessarily contain a periodic orbit. For these values of \(d\) the pioneer and climax species can stably coexist for solutions with small initial values. As \(d\) gets larger and \(\sigma(a_0, d)\) becomes positive, the equilibrium becomes unstable and, at least for \(d \in (d_1, d_2)\), the region \(\mathcal{R}\) remains positively invariant. Moreover, orbits actually enter into \(\mathcal{R}\) through \(\mathcal{L}\). Hence, for this range the system has at least one period solution \(\Pi\) contained in \(\mathcal{R}\). See Figure 5. In terms of our model, we might say that, as \(d\) gets larger, the effect of the pioneer species becomes less influential on the climax species, the equilibrium loses its stability, and periodic solutions appear. Since for \(d\) in this range the equilibrium is unstable and the region \(\mathcal{R}\) is positively invariant, if the periodic solution is unique then it is asymptotically stable. As \(d\) increases past \(d_2\) there is at least one value \(d_3\) for which the two manifolds coincide. See Figure 6. Numerical experiments with linear-quadratic systems suggest that, for this value of \(d\), the periodic orbit tends to disappear as it merges into the heteroclinic cycle \(\mathcal{C}\).

REFERENCES


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