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The stable and unstable manifolds in a two-predator one-prey chemostat model with parasitic fungi

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Abstract

We consider a chemostat model that describes the competition between a small and a large group of phytoplankton for the same nutrient, where parasitic fungi infects the large phytoplankton. This model describes a food web, which is part of an aquatic ecosystem studied by Takeshi Miki, Gaku Takimoto and Maiko Kagami. We determine the stable and unstable manifolds of each given saddle point. In particular, we obtain the necessary parametric condition for a class of solutions to satisfy a limiting property, particularly those that converge to the saddle point in forward time. This condition, together with the global dynamics of a food-chain subsystem, establishes the intersection of the stable manifold with the nonnegative octant.

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1 Introduction

In an ecosystem that involves *exploitative competition*, different species vie for dominance by only consuming a single nutrient resource. We observe this in many aquatic ecosystems that can be simulated with a device called the *chemostat* [18]. There are a number of ecological factors that can influence competition. Specifically, we may introduce a *specialist* [24], that is, a species from a higher trophic level which affects one competitor.

Our study focuses on an ecosystem comprising two exploitative competitors and a single specialist. In particular, we analyze a mathematical model based on an ecological study by

Miki, Takimoto and Kagami [9, 14]. Their study considers two groups of phytoplankton competing for a single nutrient. The specialist is parasitic fungi, whose ecological role is the subject of an ongoing area of research [8, 14, 19].

We focus on describing two sets corresponding to a given saddle point, namely the *stable and unstable manifolds*. These sets provide useful information on the global dynamics [10]. For instance, we may find a homoclinic or heteroclinic orbit in the intersection of a stable manifold and an unstable manifold. A cycle of heteroclinic orbits can influence the behavior of nearby orbits, as demonstrated in the May-Leonard population model [13].

This paper is organized as follows. We introduce the model in Section 2 together with the equilibrium points. We identify the saddle points through local stability analysis in Section 3. To obtain the stable manifolds, we establish preliminary results in Sections 4 and 5. In Section 4, we obtain the necessary initial condition for a class of solutions to satisfy a limiting property. This class includes solutions that converge to an equilibrium point. Section 5 deals with the limiting behavior of the food-chain subsystem, obtained by assuming the absence of the small phytoplankton. We establish the main results in Section 6 and conclude this paper in Section 7.

We make use of the following notations. First, we define the *nonnegative octant*

$$\mathbb{R}^4_+ := \{(N, P_1, P_2, F) : N \geq 0,\ P_1 \geq 0,\ P_2 \geq 0 \text{ and } F \geq 0\}.$$

Given an equilibrium point $E \in \mathbb{R}^4_+$, let $W^S(E)$ and $W^U(E)$ denote the intersection of $\mathbb{R}^4_+$ with the stable and unstable manifolds of E, respectively. Finally, we denote the transpose of a matrix A by A^T and identify each point $(N, P_1, P_2, F) \in \mathbb{R}^4$ with the column vector $\begin{bmatrix} N & P_1 & P_2 & F \end{bmatrix}^T$, in order to describe the subspace that is tangent to $W^U(E)$ at E.

2 The model

Consider an aquatic ecosystem, where two groups of phytoplankton are exploitative competitors for a single inorganic self-limiting nutrient (N). The first group (P_1) consists of small phytoplankton, while the second group (P_2) comprises large phytoplankton. Furthermore, parasitic fungi (F) impedes the growth of P_2 through infection. We study a mathematical model given by the following system:

$$\begin{cases} N' = q\left[N^{(0)} - N\right] - (a_1 P_1 + a_2 P_2)N, & N(0) \geq 0, \\ P_1' = P_1(a_1 N - q), & P_1(0) \geq 0, \\ P_2' = P_2(a_2 N - q) - \beta P_2 F, & P_2(0) \geq 0, \\ F' = F(f_F \beta P_2 - q), & F(0) \geq 0, \end{cases} \tag{1}$$

where the prime symbol ($'$) denotes the ordinary derivative with respect to time t.

System (1) is a chemostat model, where $N^{(0)}$ is the *constant nutrient input* and q is the *washout rate* [18]. We may consider washout as natural decay. It is assumed in (1) that external factors, such as an omnivore that feeds on both P_1 and F (see [14]), do not affect the ecosystem. Hence, all species naturally decay at the same rate q. The *phosphorus affinity* a_K of P_K to the nutrient measures its competitive strength, while β and f_F denote the *infectivity* and the *growth efficiency* of the fungi respectively [14].

Let us assume that the parameters are positive and fix all but $N^{(0)}$. We also denote

$$\lambda_1 = \frac{q}{a_1}, \qquad \lambda_2 = \frac{q}{a_2}.$$

The parameter λ_K is called the *break-even concentration* for P_K. The values of $N^{(0)}$ and the break-even concentrations typically determine whether a competitor survives or not [18]. We also follow an assumption in [14] that

$$a_1 > a_2 \iff \lambda_1 < \lambda_2 \tag{2}$$

which ecologically means that the small phytoplankton P_1 is stronger than the large phytoplankton P_2. Observe that the vector field associated with System (1) is continuously differentiable on the Euclidean space. Thus, according to standard results in dynamical systems, each point $x_0 \in \mathbb{R}^4_+$ corresponds to a unique solution $\varphi(t)$ of System (1), such that $\varphi(0) = x_0$ and $\varphi(t) \in \mathbb{R}^4_+$ for all $t \geq 0$.

2.1 Equilibrium points

For biological significance, we require the equilibrium points of (1) to lie in the nonnegative octant $\mathbb{R}^4_+$. Let

$$\overline{P_2} = \frac{q}{f_F\beta}, \qquad \overline{N} = \frac{\lambda_2 N^{(0)}}{\lambda_2 + \overline{P_2}}, \qquad \overline{F} = \frac{q\left[N^{(0)} - (\lambda_2 + \overline{P_2})\right]}{\beta(\lambda_2 + \overline{P_2})}.$$

Then System (1) admits the following equilibrium points on the boundary of $\mathbb{R}^4_+$:

$$\begin{aligned} E_0 &= (N^{(0)}, 0, 0, 0), \\ E_1 &= (\lambda_1, N^{(0)} - \lambda_1, 0, 0), \\ E_2 &= (\lambda_2, 0, N^{(0)} - \lambda_2, 0), \\ E_3 &= (\overline{N}, 0, \overline{P_2}, \overline{F}). \end{aligned}$$

The equilibrium point E_0 always exists because we are assuming that $N^{(0)} > 0$. Since λ_1, λ_2, $\overline{N}$ and $\overline{P_2}$ are always positive, we obtain the following results:

1. For $K = 1, 2$, the equilibrium point E_K exists if and only if $N^{(0)} > \lambda_K$.
2. A necessary and sufficient condition for E_3 to exist is the inequality $N^{(0)} > \lambda_2 + \overline{P_2}$, from which

$$\overline{N} = \left[\frac{N^{(0)}}{\lambda_2 + \overline{P_2}}\right]\lambda_2 > \lambda_2 > \lambda_1. \tag{3}$$

The trivial equilibrium point $(0, 0, 0, 0)$ does not exist, otherwise we get $0 = qN^{(0)}$ from the first equation of (1). This contradicts our assumption that the parameters are positive.

Suppose that System (1) admits an equilibrium point $E^* = (N^*, P_1^*, P_2^*, F^*)$ in the interior of $\mathbb{R}^4_+$ (also called the *positive octant*). Then $N^* > 0$ and $F^* > 0$. Moreover, the equations for P_1' and P_2' in System (1) yield the following:

$$a_1 N^* - q = 0, \qquad (a_2 N^* - q) - \beta F^* = 0.$$

Thus, we have

$$N^* = \frac{q}{a_1} = \lambda_1, \qquad F^* = \frac{a_2 N^* - q}{\beta} = \frac{a_2}{\beta}(\lambda_1 - \lambda_2).$$

Our parametric assumption (2) implies $F^* < 0$, which is a contradiction. Therefore, E^* does not exist. The following theorem is a summary regarding the equilibrium points of (1).

Theorem 1. *System* (1) *admits up to four equilibrium points in the nonnegative octant. We present each equilibrium point E_K below, together with the necessary and sufficient condition for $E_K \in \mathbb{R}^4_+$:*

$$\begin{aligned} E_0 &= (N^{(0)}, 0, 0, 0), && N^{(0)} > 0, \\ E_1 &= (\lambda_1, N^{(0)} - \lambda_1, 0, 0), && N^{(0)} > \lambda_1, \\ E_2 &= (\lambda_2, 0, N^{(0)} - \lambda_2, 0), && N^{(0)} > \lambda_2, \\ E_3 &= (\overline{N}, 0, \overline{P_2}, \overline{F}), && N^{(0)} > \lambda_2 + \overline{P_2}. \end{aligned}$$

Furthermore, System (1) *admits neither the trivial equilibrium point nor a positive equilibrium point.*

3 Local stability

To establish the local stability of the equilibrium points, we consider the community matrix associated with the vector field of (1),

$$J(N, P_1, P_2, F) = \begin{bmatrix} -(a_1P_1 + a_2P_2 + q) & -a_1N & -a_2N & 0 \\ a_1P_1 & a_1N - q & 0 & 0 \\ a_2P_2 & 0 & a_2N - q - \beta F & -\beta P_2 \\ 0 & 0 & f_F\beta F & f_F\beta P_2 - q \end{bmatrix}. \tag{4}$$

Evaluating (4) at E_0 yields the matrix

$$J(E_0) = \begin{bmatrix} -q & -a_1N^{(0)} & -a_2N^{(0)} & 0 \\ 0 & a_1N^{(0)} - q & 0 & 0 \\ 0 & 0 & a_2N^{(0)} - q & 0 \\ 0 & 0 & 0 & -q \end{bmatrix}. \tag{5}$$

The distinct eigenvalues of $J(E_0)$ are real numbers given by $-q$ and

$$\sigma_0^{(K)} := a_KN^{(0)} - q = a_K\left[N^{(0)} - \lambda_K\right], \qquad K = 1, 2. \tag{6}$$

The sign of each distinct eigenvalue is given in Table 1.

Parametric condition	Sign of $-q$	Sign of $\sigma_0^{(1)}$	Sign of $\sigma_0^{(2)}$
$N^{(0)} < \lambda_1$	Negative	Negative	Negative
$N^{(0)} = \lambda_1$	Negative	Zero	Negative
$\lambda_1 < N^{(0)} < \lambda_2$	Negative	Positive	Negative
$N^{(0)} = \lambda_2$	Negative	Positive	Zero
$N^{(0)} > \lambda_2$	Negative	Positive	Positive

Table 1: The signs of each distinct eigenvalue of $J(E_0)$ under different parametric conditions.

To determine the local stability of E_0, we count the (real) eigenvalues of $J(E_0)$ that have the same sign. We count the eigenvalue $-q$ twice, because it appears two times in the diagonal of $J(E_0)$. Thus, we obtain the following result.

Theorem 2. *Consider the equilibrium point $E_0 = (N^{(0)}, 0, 0, 0)$ of System* (1)*. Then the following statements hold:*

1. *If $N^{(0)} = \lambda_1$ or $N^{(0)} = \lambda_2$, then E_0 is nonhyperbolic.*
2. *If $N^{(0)} < \lambda_1$, then E_0 is asymptotically stable.*
3. *If $\lambda_1 < N^{(0)} < \lambda_2$, then E_0 is a saddle point with a one-dimensional unstable manifold.*
4. *If $N^{(0)} > \lambda_2$, then E_0 is a saddle point with a two-dimensional unstable manifold.*

We now determine the local stability of E_1.

Theorem 3. *If $N^{(0)} > \lambda_1$, then the equilibrium point $E_1 = (\lambda_1, N^{(0)} - \lambda_1, 0, 0)$ of (1) is asymptotically stable.*

Proof: Recalling that $\lambda_1 = q/a_1$, we evaluate (4) at E_1 to obtain the following matrix:

$$J(E_1) = \begin{bmatrix} -a_1 N^{(0)} & -q & -a_2\lambda_1 & 0 \\ a_1\left[N^{(0)} - \lambda_1\right] & 0 & 0 & 0 \\ 0 & 0 & -a_2(\lambda_2 - \lambda_1) & 0 \\ 0 & 0 & 0 & -q \end{bmatrix}.$$

The distinct eigenvalues of $J(E_1)$ are $-q < 0$, $-a_2(\lambda_2 - \lambda_1) < 0$ and $-a_1\left[N^{(0)} - \lambda_1\right] < 0$. Thus, E_1 is asymptotically stable.
Let us now consider the community matrix of (1) evaluated at E_2. We compute this matrix to be

$$J(E_2) = \begin{bmatrix} -a_2 N^{(0)} & -a_1\lambda_2 & -q & 0 \\ 0 & a_1(\lambda_2 - \lambda_1) & 0 & 0 \\ a_2\left[N^{(0)} - \lambda_2\right] & 0 & 0 & -\beta\left[N^{(0)} - \lambda_2\right] \\ 0 & 0 & 0 & f_F\beta\left[N^{(0)} - (\lambda_2 + \overline{P_2})\right] \end{bmatrix} \tag{7}$$

since $a_1\lambda_1 = a_2\lambda_2 = f_F\beta\overline{P_2} = q$. The distinct eigenvalues of $J(E_2)$ are given by $-q$, $-a_2\left[N^{(0)} - \lambda_2\right]$ and the following:

$$\sigma_2^{(1)} := a_1(\lambda_2 - \lambda_1), \qquad \sigma_2^{(2)} := f_F\beta\left[N^{(0)} - (\lambda_2 + \overline{P_2})\right]. \tag{8}$$

The signs of each eigenvalue of $J(E_2)$ is given in Table 2. Following the same arguments as in Theorem 2, we count the eigenvalues of $J(E_2)$ whose real parts have the same sign, and obtain the following result.

Theorem 4. *Consider the equilibrium point $E_2 = (\lambda_2, 0, N^{(0)} - \lambda_2, 0)$ of System (1) where $N^{(0)} > \lambda_2$. Then the following statements are valid:*

1. *If $N^{(0)} < \lambda_2 + \overline{P_2}$, then E_2 is a saddle point with a one-dimensional unstable manifold.*
2. *If $N^{(0)} = \lambda_2 + \overline{P_2}$, then E_2 is nonhyperbolic.*
3. *If $N^{(0)} > \lambda_2 + \overline{P_2}$, then E_2 is a saddle point with a two-dimensional unstable manifold.*

Turning to the stability of E_3, note that the nonzero components of E_3 satisfy the equation $f_F\beta\overline{P_2} = q = a_2\overline{N} - \beta\overline{F}$. Thus, evaluating (4) at E_3 yields the community matrix

$$J(E_3) = \begin{bmatrix} -(a_2\overline{P_2} + q) & -a_1\overline{N} & -a_2\overline{N} & 0 \\ 0 & a_1\overline{N} - q & 0 & 0 \\ a_2\overline{P_2} & 0 & 0 & -\beta\overline{P_2} \\ 0 & 0 & f_F\beta\overline{F} & 0 \end{bmatrix}, \tag{9}$$

Parametric condition	Sign of $-q$	Sign of $-a_2\left[N^{(0)}-\lambda_2\right]$	Sign of $\sigma_2^{(1)}$	Sign of $\sigma_2^{(2)}$
$\lambda_2 < N^{(0)} < \lambda_2 + \overline{P_2}$	Negative	Negative	Positive	Negative
$N^{(0)} = \lambda_2 + \overline{P_2}$	Negative	Negative	Positive	Zero
$N^{(0)} > \lambda_2 + \overline{P_2}$	Negative	Negative	Positive	Positive

Table 2: The signs of each eigenvalue of $J(E_2)$ under different parametric conditions.

where one of its eigenvalues is given by

$$\sigma := a_1\overline{N} - q = a_1(\overline{N} - \lambda_1). \tag{10}$$

Note that if E_3 exists, equivalently $N^{(0)} > \lambda_2 + \overline{P_2}$, then $\sigma > 0$ by inequality (3). Moreover, the following theorem states that E_3 must be a saddle point.

Theorem 5. *Assume that $N^{(0)} > \lambda_2 + \overline{P_2}$. Then E_3 is a saddle point with a one-dimensional unstable manifold.*

Proof: Keeping in mind the positive eigenvalue σ of $J(E_3)$, let us consider a matrix

$$M = \begin{bmatrix} -(a_2\overline{P_2}+q) & -a_2\overline{N} & 0 \\ a_2\overline{P_2} & 0 & -\beta\overline{P_2} \\ 0 & f_F\beta\overline{F} & 0 \end{bmatrix}$$

obtained by removing the row and column of $J(E_3)$ containing σ. According to matrix theory (see e.g. [5]), if each eigenvalue of M has a negative real part, then the remaining three eigenvalues of $J(E_3)$ have negative real parts. Hence, to show that E_3 is a saddle point with a one-dimensional unstable manifold, we only need to claim that each eigenvalue of M has a negative real part.

The characteristic polynomial of M is given by

$$p(x) = x^3 + b_1x^2 + b_2x + b_3$$

where

$$\begin{aligned} b_1 &= a_2\overline{P_2} + q, \\ b_2 &= a_2^2\overline{N}\,\overline{P_2} + \beta^2 f_F\overline{F}\,\overline{P_2}, \\ b_3 &= \beta^2 f_F\overline{F}\,\overline{P_2}(a_2\overline{P_2}+q) = (b_2 - a_2^2\overline{N}\,\overline{P_2})b_1. \end{aligned}$$

Since each coefficient of $p(x)$ is positive and $b_1b_2 - b_3 = b_1a_2^2\overline{N}\,\overline{P_2} > 0$, the polynomial $p(x)$ satisfies the Routh-Hurwitz conditions (see [15]). Therefore, each eigenvalue of M has a negative real part, as claimed.

From now on, we focus on the saddle points of System (1), given by the following remark, and determine their stable and unstable manifolds.

Remark 6. *According to Theorems 2–5, the only possible saddle points of (1) are E_0, E_2 and E_3. We must require $N^{(0)} > \lambda_1$ for (1) to admit saddle points, otherwise we have $N^{(0)} \leq \lambda_1$ and the only equilibrium point that exists (E_0) is either nonhyperbolic or asymptotically stable.*

4 Necessary initial conditions

We seek necessary initial conditions for a given solution $\varphi(t)$ with some limits as assumptions, specifically when $\lim_{t\to\infty}\varphi(t)$ is equal to one of the possible saddle points E_0 (under the assumption that $N^{(0)} > \lambda_1$), E_2 or E_3, from which the initial point $\varphi(0)$ must lie in the corresponding stable manifold (we recall from Theorem 3 that E_1 is asymptotically stable, hence is not a saddle point, when it exists).

Proposition 7. *Consider a solution* $(N(t), P_1(t), P_2(t), F(t))$ *of* (1) *such that*

$$\lim_{t\to\infty} N(t) > \lambda_1 \text{ and } \lim_{t\to\infty} P_1(t) = 0. \tag{11}$$

Then $P_1(0) = 0$.

Proof: Seeking a contradiction, we assume that $P_1(0) > 0$. Then by the differential inequality $P_1' \geq -qP_1$, we have $P_1(t) \geq P_1(0)\exp(-qt) > 0$ for all $t \geq 0$. Now, the given solution satisfies

$$\frac{P_1'(t)}{P_1(t)} = a_1 N(t) - q = a_1 [N(t) - \lambda_1] \text{ for all } t \geq 0. \tag{12}$$

Passing the limit infimum to (12) as $t \to \infty$, we get

$$\liminf_{t\to\infty} \frac{P_1'(t)}{P_1(t)} = a_1 \left[\lim_{t\to\infty} N(t) - \lambda_1\right]. \tag{13}$$

Denote the right-hand side of (13) by ρ, which is positive by our assumption of $\lim_{t\to\infty} N(t)$ in (11). Then for an arbitrarily small ε with $0 < \varepsilon < \rho$, inequality (13) implies that there exists $T > 0$ such that

$$\frac{P_1'(t)}{P_1(t)} > \rho - \varepsilon \text{ for all } t \geq T.$$

This yields

$$P_1(t) \geq P_1(T) \exp[(\rho - \varepsilon)t] \text{ for all } t \geq T. \tag{14}$$

Passing the limit infimum to (14) as $t \to \infty$, we get

$$\liminf_{t\to\infty} P_1(t) \geq \liminf_{t\to\infty} P_1(T)\exp[(\rho-\varepsilon)t] = \infty.$$

This contradicts (11) because $\liminf_{t\to\infty} P_1(t) = \lim_{t\to\infty} P_1(t) = 0$. Therefore, we must have $P_1(0) = 0$.

Proposition 8. *Consider a solution* $(N(t), P_1(t), P_2(t), F(t))$ *of* (1) *such that*

$$\lim_{t\to\infty}\left[N(t) - \frac{\beta}{a_2}F(t)\right] > \lambda_2 \text{ and } \lim_{t\to\infty} P_2(t) = 0.$$

Then $P_2(0) = 0$.

Proof: By way of contradiction, we suppose that the given solution satisfies $P_2(0) > 0$. Then the differential inequality

$$\frac{d}{dt}\left(P_2 + \frac{F}{f_F}\right) \geq -\left(P_2 + \frac{F}{f_F}\right) q$$

yields

$$P_2(t) + \frac{F(t)}{f_F} \geq \left[P_2(0) + \frac{F(0)}{f_F}\right] \exp(-qt) > 0 \text{ for all } t \geq 0.$$

Moreover, $P_2(t) > 0$ for all $t \geq 0$ and

$$\liminf_{t\to\infty} \frac{P_2'(t)}{P_2(t)} = a_2 \left\{ \lim_{t\to\infty} \left[N(t) - \frac{\beta}{a_2}F(t)\right] - \lambda_2 \right\} > 0.$$

But this yields $\lim_{t\to\infty} P_2(t) = \infty$ contrary to our assumption. Therefore, $P_2(0) = 0$.

Proposition 9. *Consider a solution* $(N(t), P_1(t), P_2(t), F(t))$ *of* (1) *such that*

$$\lim_{t\to\infty} P_2(t) > \overline{P_2} \text{ and } \lim_{t\to\infty} F(t) = 0.$$

Then $F(0) = 0$.

Proof: We seek a contradiction by supposing that $F(0) > 0$. Then the differential inequality $F' \geq -qF$ implies that $F(t) > 0$ for all $t \geq 0$. Moreover,

$$\liminf_{t\to\infty} \frac{F'(t)}{F(t)} = f_F \beta \left[\lim_{t\to\infty} P_2(t) - \overline{P_2}\right] > 0.$$

However, this yields $\lim_{t\to\infty} F(t) = \infty$, which contradicts our hypothesis. Therefore, we have $F(0) = 0$.

5 Dynamics in the $P_1 = 0$ plane

Turning to the dynamics of (1) in the $P_1 = 0$ coordinate plane, let us introduce the following subsets of $\mathbb{R}^4_+$:

$$\begin{cases} H_1 = \{(N, P_1, P_2, F) \in \mathbb{R}^4_+ : P_1 = 0\}, \\ H_2 = \{(N, P_1, P_2, F) \in \mathbb{R}^4_+ : P_1 = 0,\ P_2 = 0\}, \\ H_3 = \{(N, P_1, P_2, F) \in \mathbb{R}^4_+ : P_1 = 0,\ P_2 > 0\}, \\ H_4 = \{(N, P_1, P_2, F) \in \mathbb{R}^4_+ : P_1 = 0,\ P_2 > 0,\ F = 0\}, \\ H_5 = \{(N, P_1, P_2, F) \in \mathbb{R}^4_+ : P_1 = 0,\ P_2 > 0,\ F > 0\}. \end{cases} \tag{15}$$

Note that we may express H_1 and H_3 as the following disjoint unions:

$$H_1 = H_2 \cup H_4 \cup H_5, \qquad H_3 = H_4 \cup H_5.$$

In the next three propositions, we determine the limiting behavior of (1) restricted to the set $H_1 = H_2 \cup H_4 \cup H_5$.

Proposition 10. *Consider a solution* $\varphi(t) = (N(t), P_1(t), P_2(t), F(t))$ *with* $\varphi(0) \in H_2$. *Then* $\lim_{t\to\infty} \varphi(t) = E_0$.

Proof: The given solution satisfies $P_1(0) = P_2(0) = 0$, from which $P_1(t) = P_2(t) = 0$ for all $t \geq 0$. By taking $P_1 = P_2 = 0$ in (1), we see that the solution also satisfies a decoupled system:

$$\begin{cases} N' = q\left[N^{(0)} - N\right], & N(0) \geq 0, \\ F' = -qF, & F(0) \geq 0. \end{cases}$$

Hence, $\lim_{t\to\infty} N(t) = N^{(0)}$ and $\lim_{t\to\infty} F(t) = 0$. This proves that $\lim_{t\to\infty} \varphi(t) = E_0$.

Proposition 11. *Assuming that $N^{(0)} \neq \lambda_2$, the following statements hold for a solution $\varphi(t) = (N(t), P_1(t), P_2(t), F(t))$ with $\varphi(0) \in H_4$:*

1. *If $N^{(0)} < \lambda_2$, then $\lim_{t\to\infty} \varphi(t) = E_0$.*
2. *If $N^{(0)} > \lambda_2$, then $\lim_{t\to\infty} \varphi(t) = E_2$.*

Proof: The given solution satisfies $P_1(0) = 0$, $P_2(0) > 0$ and $F(0) = 0$, so that we have $P_1(t) = F(t) = 0$ for all $t \geq 0$. Taking $P_1 = F = 0$ in (1), we see that the solution also satisfies

$$\begin{cases} N' = q\left[N^{(0)} - N\right] - a_2 N P_2, & N(0) \geq 0, \\ P_2' = P_2(a_2 N - q), & P_2(0) > 0. \end{cases}$$

We deduce the following by phase plane analysis:

$$\lim_{t\to\infty}(N(t), P_2(t)) = \begin{cases} (N^{(0)}, 0) & \text{if } N^{(0)} < \lambda_2, \\ (\lambda_2, N^{(0)} - \lambda_2) & \text{if } N^{(0)} > \lambda_2. \end{cases}$$

Consequently, statements (1) and (2) hold.
For the next proposition, we consider the following system, obtained by taking $P_1 = 0$ in (1):

$$\begin{cases} N' = q\left[N^{(0)} - N\right] - a_2 N P_2, & N(0) \geq 0, \\ P_2' = P_2(a_2 N - q) - \beta P_2 F, & P_2(0) \geq 0, \\ F' = F(f_F \beta P_2 - q), & F(0) \geq 0. \end{cases} \tag{16}$$

System (16) is a food chain chemostat model, where fungi infects its host, and the host feeds on the nutrient without its competitor. Food chain models like (16) have been studied extensively in the literature, particularly on local and global stability (a small sample of papers include [1, 3, 7, 12]).

Proposition 12. *Assuming that $N^{(0)} \neq \lambda_2$ and $N^{(0)} \neq \lambda_2 + \overline{P_2}$, the following statements hold for a solution $\varphi(t) = (N(t), P_1(t), P_2(t), F(t))$ with $\varphi(0) \in H_5$:*

1. *If $N^{(0)} < \lambda_2$, then $\lim_{t\to\infty} \varphi(t) = E_0$.*
2. *If $\lambda_2 < N^{(0)} < \lambda_2 + \overline{P_2}$, then $\lim_{t\to\infty} \varphi(t) = E_2$.*
3. *If $N^{(0)} > \lambda_2 + \overline{P_2}$, then $\lim_{t\to\infty} \varphi(t) = E_3$.*

Proof: The given solution satisfies $P_1(0) = 0$ and System (16), where both $P_2(0)$ and $F(0)$ are positive. We appeal to the results of Butler and Wolkowicz [1], and Li and Kuang [12], on the global dynamics of (16), and obtain

$$\lim_{t\to\infty}(N(t), P_2(t), F(t)) = \begin{cases} (N^{(0)}, 0, 0) & \text{if } N^{(0)} < \lambda_2, \\ (\lambda_2, N^{(0)} - \lambda_2, 0) & \text{if } \lambda_2 < N^{(0)} < \lambda_2 + \overline{P_2}, \\ (\overline{N}, \overline{P_2}, \overline{F}) & \text{if } N^{(0)} > \lambda_2 + \overline{P_2}. \end{cases}$$

With $P_1(t) = 0$ for all $t \geq 0$, we obtain statements (1), (2) and (3).

6 The stable and unstable manifolds of a saddle point

We are now ready to establish the main results of this paper. Recall from Remark 6 that E_0, E_2 and E_3 are the only possible saddle points of System (1). Given a saddle point E_K ($K = 0, 2, 3$), we use the results of Sections 4 and 5 to determine $W^S(E_K)$, which is one of the sets in (15). On the other hand, we invoke the stable manifold theorem to determine the subspace of $\mathbb{R}^4$ tangent to $W^U(E_K)$ at E_K.

6.1 The equilibrium point E_0

First, we consider the equilibrium point $E_0 = (N^{(0)}, 0, 0, 0)$. According to Theorem 2, E_0 is a saddle point if and only if either $\lambda_1 < N^{(0)} < \lambda_2$ or $N^{(0)} > \lambda_2 > \lambda_1$. To establish our results on $W^S(E_0)$ and $W^U(E_0)$, let us recall the eigenvalues $\sigma_0^{(K)}$ ($K = 1, 2$) of $J(E_0)$, given by equation (6). Note that $\sigma_0^{(K)}$ is a simple eigenvalue, since $a_1 \neq a_2$ by (2). Moreover, $\sigma_0^{(K)}$ corresponds to a unique eigenvector $v_0^{(K)}$ of $J(E_0)$ (up to a scalar multiple). We choose

$$v_0^{(1)} = \begin{bmatrix} -1 & 1 & 0 & 0 \end{bmatrix}^T, \qquad v_0^{(2)} = \begin{bmatrix} -1 & 0 & 1 & 0 \end{bmatrix}^T,$$

by noting that $J(E_0)$ is an upper-triangular matrix.

Theorem 13. *Suppose that $\lambda_1 < N^{(0)} < \lambda_2$. Then $W^U(E_0)$ is tangent to*

$$\mathcal{L}_0 = \{(r, -r, 0, 0) \in \mathbb{R}^4 : r \in \mathbb{R}\}$$

at E_0, and $W^S(E_0) = H_1$.

Proof: Note that $\mathcal{L}_0$ is a subspace of $\mathbb{R}^4$ generated by $v_0^{(1)}$. Under the hypothesis, the community matrix $J(E_0)$ has exactly one eigenvalue $\sigma_0^{(1)}$ with positive real part (see Table 1). Hence by the stable manifold theorem, $W^U(E_0)$ is tangent to the subspace $\mathcal{L}_0$ at E_0.

To show that $W^S(E_0) = H_1$, we note that $H_1 = H_2 \cup H_4 \cup H_5$ and establish that $\varphi(0) \in W^S(E_0)$ if and only if $\varphi(0) \in H_1$, for a given solution $\varphi(t) = (N(t), P_1(t), P_2(t), F(t))$ of (1).

1. If $\varphi(0) \in W^S(E_0)$, then

$$\lim_{t\to\infty} N(t) = N^{(0)} > \lambda_1 \text{ and } \lim_{t\to\infty} P_1(t) = 0.$$

   Hence, $P_1(0) = 0$ and $\varphi(0) \in H_1$ by Proposition 7.

2. Conversely, we suppose that $\varphi(0) \in H_1$. Then $\varphi(0)$ lies in exactly one of the sets H_2, H_4 and H_5. Under our hypothesis and Propositions 10, 11 and 12, we have

$$\lim_{t\to\infty} \varphi(t) = E_0,$$

   and $\varphi(0) \in W^S(E_0)$.

Therefore, $W^S(E_0) = H_1$.

Theorem 14. *Suppose that $N^{(0)} > \lambda_2 > \lambda_1$. Then $W^U(E_0)$ is tangent to*

$$\mathcal{P}_0 = \{(-r - s, r, s, 0) \in \mathbb{R}^4 : r, s \in \mathbb{R}\}$$

at E_0 and $W^S(E_0) = H_2$.

Proof: Note that $\mathcal{P}_0$ is a subspace of $\mathbb{R}^4$ generated by the eigenvectors $v_0^{(1)}$ and $v_0^{(2)}$. By our hypothesis, the eigenvalues of $J(E_0)$ with positive real part are given by $\sigma_0^{(1)}$ and $\sigma_0^{(2)}$. Moreover, it follows from the stable manifold theorem that $W^U(E_0)$ is tangent to $\mathcal{P}_0$ at E_0.

Let us consider a solution $\varphi(t) = (N(t), P_1(t), P_2(t), F(t))$ of (1) and show that the initial point $\varphi(0) \in W^S(E_0)$ if and only if $\varphi(0) \in H_2$.

1. Suppose that $\varphi(0) \in W^S(E_0)$. Then the hypotheses of Proposition 7 holds, with

$$\lim_{t\to\infty} N(t) = N^{(0)} > \lambda_2 > \lambda_1 \text{ and } \lim_{t\to\infty} P_1(t) = 0.$$

   The hypotheses of Proposition 8 also hold, with

$$\lim_{t\to\infty} \left[N(t) - \frac{\beta}{a_2} F(t)\right] = N^{(0)} > \lambda_2 \text{ and } \lim_{t\to\infty} P_2(t) = 0.$$

   Thus, $P_1(0) = P_2(0) = 0$ and $\varphi(0) \in H_2$.

2. Conversely, $\varphi(0) \in H_2$ implies $\lim_{t\to\infty} \varphi(t) = E_0$ and $\varphi(0) \in W^S(E_0)$ by Proposition 10 under our hypothesis. Therefore, $\varphi(0) \in W^S(E_0)$ if and only if $\varphi(0) \in H_2$.

This establishes $W^S(E_0) = H_2$.

6.2 The equilibrium point E_2

Turning our attention to $E_2 = (\lambda_2, 0, N^{(0)} - \lambda_2, 0)$, there are exactly two cases in Theorem 4 where E_2 becomes a saddle point: $\lambda_2 < N^{(0)} < \lambda_2 + \overline{P_2}$ and $N^{(0)} > \lambda_2 + \overline{P_2} > \lambda_2$. Meanwhile, let us recall the eigenvalues $\sigma_2^{(K)}$ $(K = 1, 2)$ of $J(E_2)$, given in equation (8). We can establish that

$$v_2^{(1)} = -\xi_1 \begin{bmatrix} \dfrac{-\sigma_2^{(1)}}{\xi_1} & 1 & \dfrac{\sigma_2^{(1)} - \xi_1}{\xi_1} & 0 \end{bmatrix}^T, \qquad \text{where } \xi_1 = a_2 \left[N^{(0)} - \lambda_2\right] + \sigma_2^{(1)},$$

and

$$v_2^{(2)} = \begin{bmatrix} \dfrac{q}{f_F \xi_2} & 0 & -\left(\dfrac{\xi_2 + q}{f_F \xi_2}\right) & 1 \end{bmatrix}^T, \qquad \text{where } \xi_2 = a_2 \left[N^{(0)} - \lambda_2\right] + \sigma_2^{(2)},$$

are eigenvectors corresponding to $\sigma_2^{(1)}$ and $\sigma_2^{(2)}$ respectively.

Theorem 15. *Assume $\lambda_2 < N^{(0)} < \lambda_2 + \overline{P_2}$. Then $W^U(E_2)$ is tangent to*

$$\mathcal{L}_2 = \left\{ \left(r\sigma_2^{(1)}, -r\xi_1, \left[\xi_1 - \sigma_2^{(1)}\right] r, 0\right) \in \mathbb{R}^4 : r \in \mathbb{R} \right\}$$

at E_2, and $W^S(E_2) = H_3$.

Proof: By the hypothesis, $J(E_2)$ has exactly one eigenvalue $\sigma_2^{(1)}$ with positive real part (see Table 2). Note that $\mathcal{L}_2$ is generated by the eigenvector $v_2^{(1)}$, so that $W^U(E_2)$ is tangent to $\mathcal{L}_2$ at E_2 by the stable manifold theorem.

Now, considering a solution $\varphi(t) = (N(t), P_1(t), P_2(t), F(t))$ of (1), we claim that $\varphi(0) \in W^S(E_2)$ if and only if $\varphi(0) \in H_3$.

1. If $\varphi(0) \in W^S(E_2)$, then

$$\lim_{t\to\infty} N(t) = \lambda_2 > \lambda_1 \text{ and } \lim_{t\to\infty} P_1(t) = 0,$$

so that $P_1(0) = 0$ by Proposition 7. Meanwhile, the equation for P_2 in (1) yields the following property:

$$P_2(0) = 0 \text{ implies } P_2(t) = 0 \text{ for all } t \geq 0 \text{ and } \lim_{t\to\infty} P_2(t) = 0.$$

Since $\lim_{t\to\infty} P_2(t) = N^{(0)} - \lambda_2 > 0$, we must have $P_2(0) > 0$. Thus, $\varphi(0) \in H_3$.

2. Conversely, if $\varphi(0) \in H_3$, then either $\varphi(0) \in H_4$ or $\varphi(0) \in H_5$. Appealing to Propositions 11 and 12 with our hypothesis, it follows that $\lim_{t\to\infty} \varphi(t) = E_2$ and $\varphi(0) \in W^S(E_2)$.

Therefore, the claim holds and we have $W^S(E_2) = H_3$.

Theorem 16. *Assume $N^{(0)} > \lambda_2 + \overline{P_2} > \lambda_2$. Let $\mathcal{P}_2$ denote the plane in $\mathbb{R}^4$ where each point (N, P_1, P_2, F) satisfies the following equations:*

$$N = \left(\frac{q}{f_F \xi_2}\right) F - \left[\frac{\sigma_2^{(1)}}{\xi_1}\right] P_1, \qquad P_2 = \left[\frac{\sigma_2^{(1)} - \xi_1}{\xi_1}\right] P_1 - \left(\frac{\xi_2 + q}{f_F \xi_2}\right) F. \tag{17}$$

Then $W^U(E_2)$ is tangent to $\mathcal{P}_2$ at E_2, and $W^S(E_2) = H_4$.

Proof: The hypothesis implies that $J(E_2)$ has exactly two eigenvalues with positive real part, namely $\sigma_2^{(K)}$ for $K = 1, 2$. Thus, by the stable manifold theorem, $W^U(E_2)$ is tangent to $\mathcal{P}$ at E_2, where $\mathcal{P}$ denotes the subspace of $\mathbb{R}^4$ generated by $v_2^{(1)}$ and $v_2^{(2)}$. We claim that $\mathcal{P} = \mathcal{P}_2$. Now, each point $p = (N, P_1, P_2, F)$ in $\mathcal{P}$ takes the form

$$p = r_1 v_2^{(1)} + r_2 v_2^{(2)}, \; r_1, r_2 \in \mathbb{R}. \tag{18}$$

Expressing (18) as the following system of equations,

$$N = r_1 \sigma_2^{(1)} + \frac{q r_2}{f_F \xi_2}, \quad P_1 = -r_1 \xi_1, \quad P_2 = \left[\xi_1 - \sigma_2^{(1)}\right] r_1 - \left(\frac{\xi_2 + q}{f_F \xi_2}\right) r_2, \quad F = r_2,$$

we obtain (17). Therefore, $\mathcal{P} = \mathcal{P}_2$ as claimed and $W^U(E_2)$ is tangent to $\mathcal{P}_2$ at E_2.

To show that $W^S(E_2) = H_4$, we prove that $\varphi(0) \in W^S(E_2)$ if and only if $\varphi(0) \in H_4$ for a given solution $\varphi(t) = (N(t), P_1(t), P_2(t), F(t))$ of (1).

1. If $\varphi(0) \in W^S(E_2)$, then $P_1(0) = 0$ and $P_2(0) > 0$, as shown in the proof of Theorem 15. Furthermore, the hypothesis of Proposition 9 holds with

$$\lim_{t\to\infty} P_2(t) = N^{(0)} - \lambda_2 > \overline{P_2} \text{ and } \lim_{t\to\infty} F(t) = 0,$$

from which $F(0) = 0$. Thus, we obtain $\varphi(0) \in H_4$.

2. Conversely, suppose that $\varphi(0) \in H_4$. Since our hypothesis satisfies the inequality $N^{(0)} > \lambda_2$, we have $\varphi(0) \in W^S(E_2)$ by Proposition 11.

Therefore, $W^S(E_2) = H_4$.

6.3 The equilibrium point E_3

Finally, we consider the equilibrium point $E_3 = (\overline{N}, 0, \overline{P_2}, \overline{F})$. By Theorem 5, E_3 exists as a saddle point if $N^{(0)} > \lambda_2 + \overline{P_2}$. In this case, $J(E_3)$ admits exactly one eigenvalue $\sigma > 0$ with positive real part, defined in (10).

Theorem 17. *Assume that $N^{(0)} > \lambda_2 + \overline{P_2}$. Then there exists $\eta_1 > 0$ and $\eta_2 > 0$ such that*

$$\ell = \left\{ \left(r\eta_1, -r\eta_2, \frac{r\sigma}{f_F \beta \overline{F}}, r \right) \mathbb{R}^4 : r \in \mathbb{R} \right\}$$

is tangent to $W^U(E_3)$ at E_3. Furthermore, $W^S(E_3) = H_5$.

Proof: After solving an algebraic system, we find that there exists $\eta_1 > 0$ and $\eta_2 > 0$, such that

$$v := \begin{bmatrix} \eta_1 & -\eta_2 & \dfrac{\sigma}{f_F \beta \overline{F}} & 1 \end{bmatrix}^T$$

is an eigenvector of $J(E_3)$ corresponding to σ. Note that v generates the line ℓ. Thus, ℓ is tangent to $W^U(E_3)$ at E_3 by the stable manifold theorem.

We show that $W^S(E_3) = H_5$, by letting $\varphi(t) = (N(t), P_1(t), P_2(t), F(t))$ be a given solution of (1), and arguing as follows.

1. If $\varphi(0) \in W^S(E_3)$, then

$$\lim_{t\to\infty} N(t) = \overline{N} = \left(\frac{N^{(0)}}{\lambda_2 + \overline{P_2}} \right) \lambda_2 > \lambda_2 > \lambda_1 \text{ and } \lim_{t\to\infty} P_1(t) = 0,$$

   and $P_1(0) = 0$ by Proposition 7. Furthermore, both of the limits $\lim_{t\to\infty} P_2(t) = \overline{P_2}$ and $\lim_{t\to\infty} F(t) = \overline{F}$ are positive. Following the same arguments in the proof of Theorem 15 we have $P_2(0) > 0$ and $F(0) > 0$. Hence, we obtain $\varphi(0) \in H_5$.

2. Conversely, $\varphi(0) \in H_5$ implies $\varphi(0) \in W^S(E_3)$, by Proposition 12 and our hypothesis.

Therefore, $\varphi(0) \in W^S(E_3)$ if and only if $\varphi(0) \in H_5$. Consequently, we have shown that $W^S(E_3) = H_5$.

7 Conclusion

We have considered the local dynamics and the stable and unstable manifolds of a chemostat model (1), where a small and a large group of phytoplankton compete for the same nutrient and fungi infects the large phytoplankton. This paper focuses on local stability and the description of the stable and unstable manifolds of a given saddle point.

We summarize the local stability for System (1) in Table 3. This verifies an observation made in [24] that System (1) admits a unique asymptotically stable equilibrium point in $\mathbb{R}^4_+$: E_0 (for $N^{(0)} < \lambda_1$) and E_1 (for $N^{(0)} > \lambda_1$). Moreover, it follows from the main result of [24] that

$$\lim_{t\to\infty} (N(t), P_1(t), P_2(t), F(t)) = \begin{cases} E_0, & \text{if } N^{(0)} < \lambda_1, \\ E_1, & \text{if } N^{(0)} > \lambda_1, \end{cases} \tag{19}$$

Parametric condition	E_0	E_1	E_2	E_3
$N^{(0)} < \lambda_1$	(A)			
$N^{(0)} = \lambda_1$	(N)			
$\lambda_1 < N^{(0)} < \lambda_2$	(S1)	(A)		
$N^{(0)} = \lambda_2$	(N)	(A)		
$\lambda_2 < N^{(0)} < \lambda_2 + \overline{P_2}$	(S2)	(A)	(S1)	
$N^{(0)} = \lambda_2 + \overline{P_2}$	(S2)	(A)	(N)	
$N^{(0)} > \lambda_2 + \overline{P_2}$	(S2)	(A)	(S2)	(S1)

Table 3: Local stability of each equilibrium point of (1) under different parametric conditions: (A) asymptotically stable; (S1) saddle point with a one-dimensional unstable manifold; (S2) saddle point with a two-dimensional unstable manifold; (N) nonhyperbolic. Blank entries indicate where an equilibrium point does not exist.

and particularly $\lim_{t\to\infty} P_2(t) = \lim_{t\to\infty} F(t) = 0$, for every solution of (1) where $N(0)$, $P_1(0)$, $P_2(0)$ and $F(0)$ are all positive.

Let us explain why the lack of the trivial and positive equilibrium points in Theorem 1 makes ecological sense. Due to the positive constant supply of the nutrient (i.e. $qN^{(0)} > 0$), it follows from System (1) that the nutrient grows when initially unavailable (i.e. $N'(0) > 0$ whenever $N(0) = 0$). Thus, *the nutrient becomes available, and at least one species becomes present*. This does not agree with the trivial equilibrium point. The lack of a positive equilibrium point indicates *competitive exclusion*, where only one competitor survives [18]. This is supported by equation (19), where P_2 dies out for all but one value of $N^{(0)}$. This makes sense, because P_2 suffers from being weaker than P_1 and being infected by fungi.

From our main results, we succeeded in establishing the following stable manifolds:

$$W^S(E_0) = \begin{cases} H_1 & \text{if } \lambda_1 < N^{(0)} < \lambda_2, \\ H_2 & \text{if } N^{(0)} > \lambda_2, \end{cases}$$

$$W^S(E_2) = \begin{cases} H_3 & \text{if } \lambda_2 < N^{(0)} < \lambda_2 + \overline{P_2}, \\ H_4 & \text{if } N^{(0)} > \lambda_2 + \overline{P_2}. \end{cases}$$

For $N^{(0)} > \lambda_2 + \overline{P_2}$, we also showed that $W^S(E_3) = H_5$. On the other hand, we were able to determine the subspace tangent to an unstable manifold at its corresponding saddle point.

We are currently determining the local and global dynamics of the model in paper [14], which extends System (1) by introducing zooplankton as predator for both P_1 and F. That is, the model in [14] considers (1) as one of its four-dimensional subsystems. Our main results may be used to establish the *uniform persistence* of the system (see [21]).

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A Theoretical background

For reference, we recall enough theoretical background on the local stability of ordinary differential equations. The definitions and results in this section can be found in standard texts, [4, 6, 11, 15, 16, 23] to name a few. Consider the system

$$x' = G(x), \qquad x = (x_1, \ldots, x_n), \tag{20}$$

where $G = (G_1, \ldots, G_n)$ is continuously differentiable on $\mathbb{R}^n$. Furthermore, we assume that each point x_0 corresponds to a unique solution $x(t)$ of (20) defined for all $t \in \mathbb{R}$, such that $x(0) = x_0$. We call x^* an *equilibrium point* of (20) if $G(x^*) = 0$.

Definition 18. *We call the equilibrium point x^* of* (20)*:*

1. Stable *if, given an arbitrary $\varepsilon > 0$, there exists $\delta > 0$ such that every solution $x(t)$ of* (1) *with $|x^* - x(0)| < \delta$ satisfies $|x^* - x(t)| < \varepsilon$; and,*
2. Asymptotically stable *if x^* is stable, and δ can be chosen such that every solution $x(t)$ of* (1) *with $|x^* - x(0)| < \delta$ satisfies* $\lim_{t\to\infty} x(t) = x^*$.

If x^* is not stable, then we say that x^* is unstable.

We can determine how solutions of (20) behave near an equilibrium point x^* by looking at the linear system

$$x' = (x - x^*)G'(x^*), \tag{21}$$

called the *linearization of* (20) *at* x^*. The derivative G' is computed as the Jacobian matrix

$$\begin{bmatrix} \dfrac{\partial G_1}{\partial x_1} & \cdots & \dfrac{\partial G_1}{\partial x_n} \\ \vdots & \ddots & \vdots \\ \dfrac{\partial G_n}{\partial x_1} & \cdots & \dfrac{\partial G_n}{\partial x_n} \end{bmatrix},$$

which is also called a *community matrix* in mathematical biology [15]. Given the eigenvalues of $G'(x^*)$, we can classify the equilibrium point x^* according to the following definition.

Definition 19. *We call x^** hyperbolic *if the eigenvalues of $G'(x^*)$ have nonzero real part, and* nonhyperbolic *otherwise. In the case where x^* is hyperbolic, we also call x^*:*

1. *A* sink *if all eigenvalues of $G'(x^*)$ have negative real part;*
2. *A* source *if all eigenvalues of $G'(x^*)$ have positive real part; and,*
3. *A* saddle point *otherwise.*

According to the *Hartman-Grobman Theorem*, the dynamics of (20) near a hyperbolic equilibrium point x^* and the dynamics of (21) near the origin are qualitatively the same.

Theorem 20. *Suppose x^* is a sink, that is, the eigenvalues of $G'(x^*)$ have negative real part. Then x^* is asymptotically stable.*

Given a hyperbolic equilibrium point x^* of (20), let m and $n-m$ be the number of eigenvalues of $G'(x^*)$ (counting multiplicity) with negative and positive real parts respectively. Then (20) admits two sets called the *stable manifold* $W^S(x^*)$ and the *unstable manifold* $W^U(x^*)$. Given an initial point x_0 with the corresponding solution $x(t)$ of (1), we have the following:

$$x_0 \in W^S(x^*) \iff \lim_{t\to+\infty} x(t) = x^*;$$
$$x_0 \in W^U(x^*) \iff \lim_{t\to-\infty} x(t) = x^*.$$

The eigenvalues of $G'(x^*)$ determine the following properties of $W^S(x^*)$ and $W^U(x^*)$, as part of the *stable and unstable manifold theorem.*

Theorem 21. *If x^* is a hyperbolic equilibrium point of (20), then $W^S(x^*)$ and $W^U(x^*)$ have dimensions m and $n-m$ respectively. Furthermore, $W^U(x^*)$ is tangent at x^* to the $(n-m)$-dimensional subspace spanned by the generalized eigenvectors of $G'(x^*)$ corresponding to the eigenvalues with positive real part.*

To establish our results in Section 4, we need the following theorem.

Theorem 22. *[6] Let $y:[0,\infty)\to\mathbb{R}$ and $z:[0,\infty)\to\mathbb{R}$ be differentiable functions, such that $y(t)$ is the unique solution of $y'=f(y)$ with $y(0)=y_0$, and*

$$z'(t) \geq f(z(t)), \qquad z(0) \geq y_0,$$

for all $t\geq 0$. Then $z(t)\geq y(t)$ for all $t\geq 0$.

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