A NUTRIENT-PREY-PREDATOR MODEL: STABILITY AND BIFURCATIONS

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Abstract. We model a nutrient-prey-predator system in a chemostat with general functional responses, using the input concentration of nutrient as the bifurcation parameter. We study changes in the existence and the stability of isolated equilibria, as well as changes in the global dynamics, as the nutrient concentration varies. The bifurcations of the system are analytically verified and we identify conditions under which an equilibrium undergoes a Hopf bifurcation and a limit cycle appears. Numerical simulations for specific functional responses illustrate the general results.

1. Introduction. We consider a mathematical model of two-species predator-prey interaction in the chemostat under nutrient limitation. With the exception of one nutrient, all nutrients that the prey species requires are supplied to the growth vessel from the feed vessel in ample supply. The predator species grows exclusively on the prey. With \( N \) the concentration of the limiting nutrient, \( P \) the concentration of prey (say, phytoplankton), and \( Z \) the concentration of predator (say, zooplankton), we consider the following model:

\[
\frac{dN}{dt} = (\mu - N)D - Pf_1(N) \\
\frac{dP}{dt} = \gamma_1Pf_1(N) - D_1P - Zf_2(P) \\
\frac{dZ}{dt} = \gamma_2Zf_2(P) - D_2Z
\]

for initial conditions \( N(0) = N_0 > 0 \), \( P(0) = P_0 \geq 0 \), and \( Z(0) = Z_0 \geq 0 \).

The concentration of the growth-limiting nutrient in the feed vessel is denoted \( \mu \), and will be the bifurcation parameter in our analysis. \( D \) is the input rate from the feed vessel to the growth vessel as well as the washout rate from the growth vessel to the receptacle, so that constant volume is maintained. The parameters \( D_1 = D + \epsilon_1 \) and \( D_2 = D + \epsilon_2 \) are the removal rates of \( P \) and \( Z \), respectively, from the growth vessel, incorporating the washout rate \( D \) and the intrinsic death rates \( \epsilon_i \) of \( P \) and \( Z \). Our analysis does not necessarily require that \( \epsilon_1 \) and \( \epsilon_2 \) are positive; however, \( D_1 \) and \( D_2 \) should be positive. The yield coefficient \( \gamma_1 \) gives the amount

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of prey biomass produced per unit of nutrient consumed, while $\gamma_2$ gives the amount of predator biomass produced per unit of prey biomass consumed.

The function $f_1(N)$ represents the per capita consumption rate of nutrient by the prey populations as a function of the concentration of available nutrient; similarly, the function $f_2(P)$ represents the per capita consumption rate of the prey by the predator as a function of available prey. These functions are assumed to satisfy $f_i(0) = 0$, $i = 1, 2$, $f_i'(|N|) > 0$ for all $N \geq 0$, and $f_2'(P) > 0$ for all $P \geq 0$. We further assume that $f_1(N)$ and $f_2(P)$ are bounded. To avoid the case of washout due to an inadequate resource, we assume that $\lim_{N \to \infty} f_1(N) > D_1/\gamma_1$, and to avoid the case of an inadequate prey, we assume that $\lim_{P \to \infty} f_2(P) > D_2/\gamma_2$. Define $\lambda_P(D_1)$ and $\lambda_Z(D_2)$ to be the unique numbers satisfying

$$f_1(\lambda_P(D_1)) = D_1/\gamma_1 \text{ and } f_2(\lambda_Z(D_2)) = D_2/\gamma_2.$$  

(2)

The number $\lambda_P(D_1)$ is the break-even concentration of nutrient, at which the growth and removal of phytoplankton balance; $\lambda_Z(D_2)$ is similarly interpreted. The number $D$ plays a central role in our investigation, so we assume that $\lambda_P(D)$ and $\lambda_Z(D)$ are also defined. From the perspective of $D$, due to the boundedness assumptions on $f_1$ and $f_2$, $D_1$ and $D_2$ are perturbations of $D$.

**Lemma 1.1.** From a functional point of view, $\lambda_P$ and $\lambda_Z$ are right inverses of $\gamma_1 f_1$ and $\gamma_2 f_2$, respectively. Accordingly, on their respective domains $\lambda_P$ and $\lambda_Z$ are as differentiable as $f_1$ and $f_2$. We note for later use

$$\lambda_P(D_1) = (\gamma_1 \cdot f_1'(\lambda_P(D_1)))^{-1} \quad \text{and} \quad \lambda_Z(D_2) = (\gamma_2 \cdot f_2'(\lambda_P(D_2)))^{-1}. \quad \Box$$  

(3)

Variations on this system have been investigated by many authors over a long period of time. For example, Gard [4] studied a version with a general function representing the rate of nutrient removal and developed a numerical condition for the presence of a cycle. Li and Kuang [9] studied this system with general functional responses and distinct values of $D$, $D_1$, and $D_2$. With the hypothesis that $D=D_1=D_2$, they provide numerical criteria for the stability of a coexistence equilibrium, and prove that a cycle exists when the equilibrium is unstable [9, Theorem 3.2]. When the hypothesis $D=D_1=D_2$ does not hold, they provide numerical evidence that stability of the coexistence equilibrium breaks down and a cycle appears. We note that the input nutrient concentration is fixed in both [4] and [9], whereas we have this as a parameter $\mu$. A similar model was studied in [12] with functional response $f_1(N)$ of Holling type I and $f_2(P)$ of Holling type II, demonstrating the existence of a Hopf bifurcation in response to varying nutrient concentration. These results inspire our work. Our goal is to prove analytically that system (1) undergoes a Hopf bifurcation without restricting a priori either the forms of the uptake functions or the values of the removal rates $D_1$ and $D_2$.

This paper is organized as follows. In Section 2, conditions for the existence of equilibria are obtained for general functional responses $f_1(N)$ and $f_2(P)$. We discuss the stability of predator-free equilibria and begin the discussion of the stability of a coexistence equilibrium which appears as the parameter $\mu$ increases. In Section 3, we study stability of the coexistence equilibrium and prove the existence of a Hopf bifurcation to an orbitally asymptotically stable cycle. This material is quite technical and comprises our main contribution to understanding the system. The analysis depends on Theorem 3.4, a paraphrase of the Hopf bifurcation theorem as developed in [5], stated in a form most useful for us. Accordingly, application of this theorem requires us to develop specific information about the behavior of the
eigenvalues of the linearizations at the coexistence equilibrium as the parameter $\mu$ increases. We first make the assumption $D=D_1=D_2$, which allows us to factor the characteristic polynomial of the linearization at the coexistence equilibrium. We give conditions on the uptake functions that enable us to complete the verification of the hypotheses of the Hopf bifurcation theorem for this case in Theorem 3.7. Under additional conditions on the uptake functions, we can prove that there is a unique value of the bifurcation parameter at which a Hopf bifurcation to an orbitally asymptotically stable cycle occurs. Relaxing the condition $D=D_1=D_2$, we use the inverse function theorem to factor the characteristic polynomials of the linearizations at coexistence equilibria $E_2(\mu,D_1,D_2)$ for $(D_1,D_2)$ near $(D,D)$. By continuity of the factorization, the eigenvalue conditions of the Hopf theorem are fulfilled. In Lemma 3.10 we state a uniform approximation result that implies the transversality and stability conditions of the Hopf theorem are also satisfied. Although the proof of Lemma 3.10 is straightforward, it is technical, so we postpone explanation of the proof to Section 5. In Theorem 3.11 we complete the verification of the hypotheses of Theorem 3.4 for the general case, establishing that the behavior in the case $D=D_1=D_2$ propagates to the general situation. In Section 4 our results are illustrated using simulations arising by choosing rate functions of Holling type II and Holling type III forms.

2. Steady states and their stability. To begin, we establish that the solutions of system (1) are nonnegative and bounded. These are minimum requirements for a reasonable model of the chemostat. We then develop conditions for the existence and stability of equilibria. We conclude the section by proving uniform persistence in the sense of [2] when $\mu$ is sufficiently large and the initial values $P_0$ and $Z_0$ are positive.

Lemma 2.1. All solutions $N(t)$, $P(t)$, and $Z(t)$ of system (1) are nonnegative and bounded.

Proof. The plane $Z = 0$ is invariant for system (1). Therefore, by existence and uniqueness, if $Z_0 > 0$ then $Z(t) > 0$ for all $t \geq 0$. Similarly, since $f_2(0) = 0$, the plane $P = 0$ is invariant, so $P_0 > 0$ implies $P(t) > 0$ for all $t \geq 0$.

Suppose $N_0 > 0$. If there exists a $t > 0$ with $N(t) = 0$, then there is a least such number, say $t_0$. Then $N'(t_0) = \mu D > 0$ since $f_1(0) = 0$. Consequently, there is $t < t_0$ such that $N(t) < 0$, which is a contradiction to the choice of $t_0$.

For the boundedness of solutions, set $U(t) = N(t) + \gamma_1^{-1}P(t) + (\gamma_1\gamma_2)^{-1}Z(t)$. From system (1), it follows that

$$U'(t) = D\mu - DN(t) - \gamma_1^{-1}D_1P(t) - (\gamma_1\gamma_2)^{-1}D_2Z(t) \leq D\mu - \tilde{D}U(t),$$

where $\tilde{D} = \min\{D,D_1,D_2\}$. Then

$$U(t) \leq (D\mu)/\tilde{D} + (U(0) - (D\mu)/\tilde{D})e^{-\tilde{D}t} \begin{cases} U(0), & \text{if } U(0) > (D\mu)/\tilde{D}, \\ (D\mu)/\tilde{D}, & \text{if } U(0) \leq (D\mu)/\tilde{D}. \end{cases}$$

Since $N(t)$, $P(t)$, and $Z(t)$ are nonnegative, the boundedness of $U(t)$ implies the boundedness of $N(t)$, $P(t)$, and $Z(t)$. 

There are at most three biologically relevant equilibria of system (1) depending on the value of $\mu$. The equilibria and the conditions of their existence are summarized in the following theorem.
Theorem 2.2. Let \( \lambda_P(D_1) \) and \( \lambda_Z(D_2) \) be as in (2). The equilibria of the system (1) satisfy the following conditions:
1. The washout equilibrium \( E_0 = (\mu, 0, 0) \) exists for all \( \mu > 0 \).
2. The single-species equilibrium \( E_1(\mu, D_1) = (\lambda_P(D_1), P(\mu, D_1), 0) \) exists for all \( \mu > \lambda_P(D_1) \), where
   \[
   P(\mu, D_1) = (\mu - \lambda_P(D_1)) \frac{D_{\gamma_1}}{D_1}.
   \]
3. The coexistence equilibrium
   \[
   E_2(\mu, D_1, D_2) = (N(\mu, D_1, D_2), \lambda_Z(D_2), Z(\mu, D_1, D_2))
   \]
   exists for all \( \mu > \mu_c(D_1, D_2) \), where
   \[
   \mu_c(D_1, D_2) = \lambda_P(D_1) + \frac{D_1 \lambda_Z(D_2)}{D_{\gamma_1}}
   \]
   and \( N(\mu, D_1, D_2), Z(\mu, D_1, D_2) \) satisfy the simultaneous equations
   \[
   (\mu - N(\mu, D_1, D_2)) D - \lambda_Z(D_2) f_1(N(\mu, D_1, D_2)) = 0,
   \]
   \[
   \gamma_1 \lambda_Z(D_2) f_1(N(\mu, D_1, D_2)) - D_1 \lambda_Z(D_2) - Z(\mu, D_1, D_2) f_2(\lambda_Z(D_2)) = 0.
   \]
   Thus, for \( \mu \leq \lambda_P(D_1) \) only the equilibrium \( E_0 \) exists; for \( \lambda_P(D_1) < \mu \leq \mu_c(D_1, D_2) \), there are two equilibria \( E_0, E_1 \); and, when \( \mu_c(D_1, D_2) < \mu \), there are three equilibria \( E_0, E_1, \) and \( E_2 \).

Proof. From the \( Z \)-equation, either \( Z = 0 \) or \( \gamma_2 f_2(P) - D_2 = 0 \) (so that \( P = \lambda_Z(D_2) \)). If \( Z = 0 \), the \( P \)-equation yields
   \[ 0 = \gamma_1 P f_1(N) - D_1 P, \]
   which implies either \( P = 0 \) or \( \gamma_1 f_1(N) - D_1 = 0 \) (so that \( N = \lambda_P(D_1) \)).
   If \( Z = 0 \) and \( P \neq 0 \), then \( N = \lambda_P(D_1) \) in the \( N \)-equation gives
   \[ 0 = (\mu - \lambda_P(D_1)) D - P \frac{D_1}{\gamma_1} \text{ with solution } P = (\mu - \lambda_P(D_1)) \frac{D_{\gamma_1}}{D_1} := P(\mu, D_1). \]
   Note that \( P(\mu, D_1) > 0 \) for all \( \mu > \lambda_P(D_1) \), and so the single-species equilibrium \( E_1(\mu, D_1) = (\lambda_P(D_1), P(\mu, D_1), 0) \) exists in the positive cone for all \( \mu > \lambda_P(D_1) \).
   This is the proof of the first part of the theorem.
   If \( Z \neq 0 \), then \( P = \lambda_Z(D_2) \) in the \( N \)- and \( P \)-equations, and equations (6) and (7) define \( N \) and \( Z \) as implicit functions of \( \mu, D_1, \) and \( D_2 \).
   We now determine the critical value \( \mu_c(D_1, D_2) \) of \( \mu \) at which \( E_2(\mu, D_1, D_2) \) first appears in the positive cone. Equation (7) implies
   \[
   Z(\mu, D_1, D_2) = \frac{\gamma_2}{D_2} \lambda_Z(D_2) (\gamma_1 f_1(N(\mu, D_1, D_2)) - D_1).
   \]
   Since \( f_1 \) is strictly increasing, \( Z(\mu, D_1, D_2) = 0 \) if and only if \( N(\mu, D_1, D_2) = \lambda_P(D_1) \), and \( Z(\mu, D_1, D_2) > 0 \) for \( N(\mu, D_1, D_2) > \lambda_P(D_1) \). After substituting \( N(\mu, D_1, D_2) = \lambda_P(D_1) \) in (6), we obtain the equation
   \[ 0 = (\mu - \lambda_P(D_1)) D - \lambda_Z(D_2) \frac{D_1}{\gamma_1} \text{ so that } \mu = \lambda_P(D_1) + \frac{D_1 \lambda_Z(D_2)}{D_{\gamma_1}} := \mu_c(D_1, D_2). \]
Thus, $Z(\mu, D_1, D_2)$ is positive when $\mu > \mu_{c_1}(D_1, D_2)$, and the coexistence equilibrium $E_2(\mu, D_1, D_2) = (N(\mu, D_1, D_2), \lambda_2(D_2), Z(\mu, D_1, D_2))$ exists in the positive cone for all $\mu > \mu_{c_1}(D_1, D_2)$. This proves part three of the theorem.

In Theorems 2.3, 2.4, and 2.5 we investigate the stability of the equilibria of system (1) by finding the eigenvalues of the associated Jacobian matrices. The Jacobian matrix of the system (1) takes the form

$$J = \begin{bmatrix} -D - P f'(N) & -f_1(N) & 0 \\ \gamma_1 P f'(N) & \gamma_1 f_1(N) - D_1 - Z f_2'(P) & -f_2(P) \\ 0 & \gamma_2 Z f_2'(P) & \gamma_2 f_2(P) - D_2 \end{bmatrix}. \quad (9)$$

We first summarize the stability of $E_0$ in the following theorem. Here, the breakeven concentration of nutrient given in (2) plays a critical role.

**Theorem 2.3.** The equilibrium point $E_0$ is locally asymptotically stable if $\mu < \lambda_P(D_1)$ and unstable if $\mu > \lambda_P(D_1)$. When $\mu > \lambda_P(D_1)$, $E_0$ is globally asymptotically stable with respect to solutions initiating in $\{(N, P, Z) \in \mathbb{R}^3_+ \mid P = 0\}$. That is, the plane $P = 0$ is $m^+(E_0)$, the stable manifold of $E_0$.

**Proof.** Referring to (9), the Jacobian at $E_0 = (\mu, 0, 0)$ is

$$J(E_0) = \begin{bmatrix} -D & -f_1(\mu) & 0 \\ 0 & \gamma_1 f_1(\mu) - D_1 & 0 \\ 0 & 0 & -D_2 \end{bmatrix},$$

so that the eigenvalues of $J(E_0)$ are $x_1 = -D$, $x_2 = \gamma_1 f_1(\mu) - D_1$, and $x_3 = -D_2$. The stability of $E_0$ now follows from (2) and the fact that $f_1$ is strictly increasing: $x_2 < 0$ when $\mu < \lambda_P(D_1)$ and $x_2 > 0$ when $\mu > \lambda_P(D_1)$. To see that $m^+(E_0) = \{(N, P, Z) \in \mathbb{R}^3_+ \mid P = 0\}$ when $\mu > \lambda_P(D_1)$, consider the Lyapunov function

$$L(N, Z) = \frac{(\mu - N)^2}{2} + \frac{Z^2}{2}.$$ 

Clearly, $L(\mu, 0) = 0$ and $L(N, Z) > 0$ if $(N, Z) \neq (\mu, 0)$. The time derivative of $L(N, Z)$ at a point $(N, 0, Z)$ on a trajectory of system (1) is

$$L'(N, Z) = -D(\mu - N)^2 - D_2 Z^2 < 0$$

for $(N, Z) \neq (\mu, 0)$. Thus $E_0$ is globally asymptotically stable in the plane $P=0$. □

For $\mu = \lambda_P(D_1)$, $P(\lambda_P(D_1), D_1) = 0$, so that $E_0$ and $E_1$ coalesce (see equation (4)). When $\mu > \lambda_P(D_1)$, $E_1(\mu, D_1) = (\lambda_P(D_1), P(\mu, D_1), 0)$ enters the positive cone. We summarize the stability of $E_1(\mu, D_1)$ in the following theorem. Note that the critical value of $\mu$ given in (5) now plays a central role.

**Theorem 2.4.** The equilibrium point $E_1(\mu, D_1)$ is locally stable if $\lambda_P(D_1) < \mu < \mu_{c_1}(D_1, D_2)$ and unstable if $\mu > \mu_{c_1}(D_1, D_2)$. When $\mu > \mu_{c_1}(D_1, D_2)$, $E_1(\mu, D_1)$ is globally asymptotically stable with respect to solutions initiating in $\{(N, P, Z) \in \mathbb{R}^3_+ \mid Z = 0\}$. That is, the plane $Z = 0$ is $m^+(E_1(\mu, D_1))$, the stable manifold of $E_1(\mu, D_1)$.

**Proof.** Referring to (9), the Jacobian matrix at $E_1(\mu, D_1)$ is

$$J(E_1(\mu, D_1)) = \begin{bmatrix} -D - P(\mu, D_1) f'_1(\lambda_P(D_1)) & -f_1(\lambda_P(D_1)) & 0 \\ \gamma_1 P(\mu, D_1) f'_1(\lambda_P(D_1)) & 0 & -f_2(\lambda_P(D_1)) \\ 0 & 0 & \gamma_2 f_2(\lambda_P(D_1)) - D_2 \end{bmatrix}.$$
The determinant of the upper lefthand 2-by-2 submatrix is positive and its trace is negative, so its eigenvalues have negative real parts. The third eigenvalue is
\[ x_3 = \gamma_2 f_2(P(\mu, D_1)) - D_2. \]
If \( \mu < \mu_{c_1}(D_1, D_2) \), so that \( P(\mu, D_1) < \lambda_2(D_2) \), then \( x_3 < 0 \), and \( E_1(\mu, D_1) \) is locally stable. Similarly, if \( \mu > \mu_{c_1}(D_1, D_2) \), so that \( P(\mu, D_1) > \lambda_2(D_2) \), then \( x_3 > 0 \) and \( E_1(\mu, D_1) \) is unstable with one dimension of instability.

To see that \( m^+(E_1) = \{(N, P, Z) \in \mathbb{R}^3 \mid Z = 0\} \) when \( \mu > \mu_{c_1} \), consider the Lyapunov function introduced by Hsu in [6]

\[
L(N, P) = \int_{\lambda P(D_1)}^N \frac{f_1(n) - f_1(\lambda P(D_1))}{f_1(n)} \, dn + \frac{1}{\gamma_1} \left( P - P(\mu, D_1) - P(\mu, D_1) \ln(P/P(\mu, D_1)) \right) \]

Notice that \( L(\lambda P(D_1), P(\mu, D_1)) = 0 \), and that

\[
\frac{\partial L}{\partial N} = \frac{f_1(N) - f_1(\lambda P(D_1))}{f_1(N)} = 0 \quad \text{and} \quad \frac{\partial L}{\partial P} = \frac{1}{\gamma_1} (1 - P(\mu, D_1)/P) = 0
\]

precisely when \((N, P) = (\lambda P(D_1), P(\mu, D_1))\). Moreover,

\[
\frac{\partial^2 L}{\partial N^2}(\lambda P(D_1), P(\mu, D_1)) = \frac{f_1(\lambda P(D_1))}{f_1(\lambda P(D_1))} > 0
\]

and

\[
\frac{\partial^2 L}{\partial P^2}(\lambda P(D_1), P(\mu, D_1)) = \frac{1}{\gamma_1 P(\mu, D_1)} > 0.
\]

Therefore, \((\lambda P(D_1), P(\mu, D_1))\) is the only critical point of \(L(P, N)\) and it is a local minimum, so that \(L(N, P) > 0\) for all \((N, P) \neq (\lambda P(D_1), P(\mu, D_1))\).

Now we compute the time derivative of \(L(N, P)\) at a point \((N, P, 0)\) along a trajectory of system (1). Noting from (2) and (4) that

\[
f_1(\lambda P(D_1)) = \frac{D_1}{\gamma_1} \quad \text{and} \quad P(\mu, D_1) = \frac{(\mu - \lambda P(D_1)) D}{f_1(\lambda P(D_1))},
\]

we have

\[
L'(N, P) = \frac{f_1(N) - f_1(\lambda P(D_1))}{f_1(N)} ((\mu - N) D - P f_1(N))
\]

\[
+ \frac{1}{\gamma_1} \left( 1 - \frac{P(\mu, D_1)}{P} \right) (\gamma_1 f_1(N) - D_1) P
\]

\[
= (f_1(N) - f_1(\lambda P(D_1))) \left( \frac{(\mu - N) D}{f_1(N)} - \frac{(\mu - \lambda P(D_1)) D}{f_1(\lambda P(D_1))} \right)
\]

\[
= (f_1(N) - f_1(\lambda P(D_1))) \left( \frac{(\mu - N)}{\mu - \lambda P(D_1)} - \frac{f_1(N)}{f_1(\lambda P(D_1))} \right) \frac{(\mu - \lambda P(D_1)) D}{f_1(N)}.
\]

If \( N < \lambda P(D_1) \), then \( f_1(N) - f_1(\lambda P(D_1)) < 0 \), so that \( f_1(N)/f_1(\lambda P(D_1)) < 1 \). Also, \( \mu - N > \mu - \lambda P(D_1) \), so that

\[
\frac{\mu - N}{\mu - \lambda P(D_1)} > 1 > \frac{f_1(N)}{f_1(\lambda P(D_1))}, \quad \text{and} \quad \frac{\mu - N}{\mu - \lambda P(D_1)} - \frac{f_1(N)}{f_1(\lambda P(D_1))} > 0.
\]

Thus, \( L'(N, P) < 0 \) when \( N < \lambda P(D_1) \).
If \( N > \lambda_P(D_1) \), then \( f_1(N) - f_1(\lambda_P(D_1)) > 0 \), so that \( f_1(N)/f_1(\lambda_P(D_1)) > 1 \). When \( \mu > N > \lambda_P(D_1) \), we have \( \mu - N < \mu - \lambda_P(D_1) \), so that
\[
\frac{\mu - N}{\mu - \lambda_P(D_1)} < 1 < \frac{f_1(N)}{f_1(\lambda_P(D_1))},
\]
while for \( N \geq \mu \), then \( \frac{\mu - N}{\mu - \lambda_P(D_1)} \leq 0 \). In either case,
\[
\frac{\mu - N}{\mu - \lambda_P(D_1)} - \frac{f_1(N)}{f_1(\lambda_P(D_1))} < 0,
\]
and so \( L'(N, P) < 0 \) when \( N > \lambda_P(D_1) \).

Finally, \( L'(N, P) = 0 \) if and only if \( N = \lambda_P(D_1) \). By LaSalle’s extension theorem [8], any trajectory of system (1) in the plane \( Z = 0 \) for which \( P_0 > 0 \) approaches the largest invariant set in the line \( N = \lambda_P(D_1) \), and this is simply \( \{E_1(\mu, D_1)\} \). Therefore, \( E_1(\mu, D_1) \) is globally asymptotically stable in the plane \( Z = 0 \).

When \( \mu = \mu_{c_1}(D_1, D_2) \), observe that \( E_1(\mu, D_1) \) and \( E_2(\mu, D_1, D_2) \) coalesce. With \( \mu = \mu_{c_1}(D_1, D_2) \), we have \( P(\mu_{c_1}(D_1, D_2), D_1) = \lambda_Z(D_2) \) (see (5) and (4)). Also \( N(\mu, D_1, D_2) = \lambda_P(D_1) \), so that \( Z(\mu, D_1, D_2) = 0 \) (see the discussion around (8)). Thus,
\[
E_2(\mu_{c_1}(D_1, D_2), D_1, D_2) = (\lambda_P(D_1), \lambda_Z(D_2), 0) = E_1(\mu_{c_1}(D_1, D_2), D_1).
\]

Said another way, as \( \mu \) increases through \( \mu_{c_1}(D_1, D_2) \), \( E_2(\mu, D_1, D_2) \) enters the positive cone by passing through \( E_1(\mu, D_1) \).

With \( f_2(\lambda_Z(D_2)) = D_2/\gamma_2 \), refer to (9) to see that the Jacobian matrix at \( E_2(\mu, D_1, D_2) \) takes the form
\[
J(E_2(\mu, D_1, D_2)) = \begin{bmatrix}
-D - \lambda_Z(D_2)f_1'(N(\mu, D_1, D_2)) & -f_1(N(\mu, D_1, D_2)) & 0 \\
\gamma_1 \lambda_Z(D_2)f_1'(N(\mu, D_1, D_2)) & \left(\gamma_1 f_1(N(\mu, D_1, D_2)) - D_1\right) - Z(\mu, D_1, D_2)f_2'(\lambda_Z(D_2)) & -D_2/\gamma_2 \\
0 & \gamma_2 Z(\mu, D_1, D_2)f_2'(\lambda_Z(D_2)) & 0
\end{bmatrix}.
\]

(10)

The eigenvalues of \( J(E_2(\mu, D_1, D_2)) \) satisfy
\[
x^3 + a_1x^2 + a_2x + a_3 = 0,
\]
where
\[
a_1(\mu, D_1, D_2) = Z(\mu, D_1, D_2)f_2'(\lambda_Z(D_2)) + \lambda_Z(D_2)f_1'(N(\mu, D_1, D_2)) - \gamma_1 f_1(N(\mu, D_1, D_2)) + D_1 + D,
\]
\[
a_2(\mu, D_1, D_2) = \lambda_Z(D_2)Z(\mu, D_1, D_2)f_2'(\lambda_Z(D_2)) + Z(\mu, D_1, D_2)f_2'(\lambda_Z(D_2)) + D_Z(\mu, D_1, D_2)f_2'(\lambda_Z(D_2)) + D_1 \lambda_Z(D_2)f_1'(N(\mu, D_1, D_2)) - D_1 \gamma_1 f_1(N(\mu, D_1, D_2)) + DD_1,
\]
(11)

(12)
Assume that Theorem 2.6.

The concept of uniform persistence introduced in [2].

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Proof. Since \( a_3 \) is positive, this follows from the Routh-Hurwitz criterion.

We conclude this section with a significant strengthening of Lemma 2.1. We use the concept of uniform persistence introduced in [2].

Theorem 2.6. Assume that \( \mu > \mu_{c_1}(D_1, D_2) \). Then system (1) is uniformly persistent with respect to all solutions satisfying \( P_0 > 0 \) and \( Z_0 > 0 \).

Proof. Recall from Lemma 2.1 that all solutions of system (1) for which \( P_0 > 0 \) and \( Z_0 > 0 \) are positive and bounded. We first show that \( \lim \inf_{t \to \infty} N(t) > 0 \).

If \( \lim \inf_{t \to \infty} N(t) = 0 \) and \( \lim \sup_{t \to \infty} N(t) = 0 \), then \( \lim_{t \to \infty} N(t) = 0 \). But this is impossible, for then it follows from the \( N \)-equation that \( N'(t) \to \mu D > 0 \) as \( t \to \infty \) and this, in turn, contradicts the fact that \( N(t) \) is bounded.

Now, suppose \( \lim \inf_{t \to \infty} N(t) = 0 \) while \( \lim \sup_{t \to \infty} N(t) > 0 \). Then there exists a sequence \( \{\tau_n\}_{n=1}^\infty \) of local minima of \( N(t) \) satisfying \( \tau_n \to \infty \) as \( n \to \infty \). Thus,

1. \( N'(\tau_n) = 0 \), since \( \tau_n \) is a local minimum, and
2. \( N(\tau_n) \to 0 \) as \( n \to \infty \), since \( \lim \inf_{t \to \infty} N(t) = 0 \).

From the \( N \)-equation we have

\[
N'(\tau_n) = \mu D - \left( N(\tau_n) D + P(\tau_n) f_1(N(\tau_n)) \right),
\]

so that

\[
0 = \left| N'(\tau_n) \right| \geq \left| \mu D \right| - \left| N(\tau_n) D + P(\tau_n) f_1(N(\tau_n)) \right|
\]

Rearranging and using the facts that \( N(\tau_n) \to 0 \) as \( n \to \infty \), \( f_1 \) is continuous and \( f_1(0) = 0 \), we get

\[
0 = \lim_{\tau_n \to \infty} \left| N(\tau_n) D + P(\tau_n) f_1(N(\tau_n)) \right| \geq \mu D > 0,
\]

a contradiction. Hence, \( \lim \inf_{t \to \infty} N(t) > 0 \).

Choose \( X(0) = (N_0, P_0, Z_0) \in \mathbb{R}_+^3 \). Then \( \omega(X(0)) \) is a nonempty, compact invariant set with respect to system (1). We claim \( E_0 = (\mu, 0, 0) \) and \( E_1(\mu, D_1) = (\lambda_p(D_1), P(\mu, D_1), 0) \) are not in \( \omega(X(0)) \). Suppose \( E_0 = (\mu, 0, 0) \in \omega(X(0)) \). Since \( \mu > \mu_{c_1}(D_1, D_2) \), \( E_0 \) is an unstable hyperbolic equilibrium point. By Theorem 2.3, \( E_0 \) is globally asymptotically stable with respect to solutions initiating in the plane \( P = 0 \). Since \( X(0) \notin m^+(E_0), \{E_0\} \neq \omega(X(0)) \). By the Butler-McGehee lemma (see lemma A1, [3]), there exists \( Q \in \{m^+(E_0) \cap \omega(X(0)) \}, \) so that \( \partial \Omega(Q) \subset \omega(X(0)) \). For such an initial condition, the governing system is \( N'(t) = D(\mu - N(t)) \), and \( Z'(t) = -D_2 Z(t) \). But then \( \Omega(Q) \) becomes unbounded as \( t \to -\infty \). This is a contradiction to the compactness of \( \omega(X(0)) \), and so \( E_0 \notin \omega(X(0)) \).

Suppose \( E_1(\mu, D_1) = (\lambda_p(D_1), P(\mu, D_1), 0) \) is in \( \omega(X(0)) \). Since \( \mu > \mu_{c_1}(D_1, D_2) \), \( E_1(\mu, D_1) \) is an unstable hyperbolic equilibrium point. By Theorem 2.4 \( E_1(\mu, D_1) \) is globally asymptotically stable with respect to solutions initiating in the plane.
Z = 0. Since X(0) \not\in m^+(E_1(\mu, D_1)), \{E_1(\mu, D_1)\} \neq \omega(X(0)). By the Butler-McGehee lemma, there exists \( \tilde{Q} \in (m^+(E_1(\mu, D_1)) \backslash \{E_1(\mu, D_1)\}) \cap \omega(X(0)) \), so that cl \( \mathcal{O} (\tilde{Q}) \subset \omega(X(0)) \). If \( \tilde{Q} \in m^-(E_0) \), then \( E_0 \in \text{cl} \mathcal{O} (\tilde{Q}) \subset \omega(X(0)) \), a contradiction. Thus \( \tilde{Q} \not\in m^-(E_0) \), and this implies \( \mathcal{O} (\tilde{Q}) \) is unbounded as \( t \to -\infty \), contradicting the compactness of \( \omega(X(0)) \). Therefore, \( E_1(\mu, D_1) \not\in \omega(X(0)) \).

Suppose the system (1) is not persistent. Then there exists \( \tilde{Q} \in \omega(X(0)) \) such that \( \tilde{Q} \not\in m^+(E_0) \) or \( \tilde{Q} \not\in m^+(E_1(\mu, D_1)) \). Then cl \( \mathcal{O} (\tilde{Q}) \subset \omega(X(0)) \), which implies either \( E_0 \in \omega(X(0)) \) or \( E_1(\mu, D_1) \in \omega(X(0)) \), neither of which can be true. Thus, \( \liminf_{t \to \infty} P(t) > 0 \) and \( \liminf_{t \to \infty} Z(t) > 0 \), and it follows from the main result of [2] that system (1) is uniformly persistent.

\[ \square \]

3. Stability of the coexistence equilibrium. In this section we study the coexistence equilibrium point

\[ E_2(\mu, D_1, D_2) = (N(\mu, D_1, D_2), \lambda_Z(D_2), Z(\mu, D_1, D_2)) \]

as \( \mu \) varies, first when \( D_1 = D_2 \) and then after relaxing this assumption. In particular, we study the eigenvalues of the Jacobians at the coexistence equilibria as \( \mu \) increases. To prepare for the study of the evolution of the equilibrium \( E_2(\mu, D_1, D_2) \), we observe the following consequence of the implicit function theorem [7, p.122].

**Lemma 3.1.** For \( D_1 > 0, D_2 > 0, \) and \( \mu > \mu_{c_1}(D_1, D_2) \) there is a local parameterization of the locus of coexistence equilibria

\[ E_2(\mu, D_1, D_2) = (N(\mu, D_1, D_2), \lambda_Z(D_2), Z(\mu, D_1, D_2)) \]

defined on an interval containing \( \mu \) and a disc around \((D_1, D_2)\) that is smooth to the smaller of the degree of smoothness of \( f_1(N) \) and the degree of smoothness of \( f_2(P) \).

**Proof.** Set \( P = \lambda_Z(D_2) \) in the \( N \)- and \( P \)-equations of system (1). Let

\[ G_1(N, Z, \mu, D_1, D_2) = D(\mu - N) - f_1(N)\lambda_Z(D_2) \]

and

\[ G_2(N, Z, \mu, D_1, D_2) = \gamma_1 f_1(N)\lambda_Z(D_2) - D_1\lambda_Z(D_2) - (D_2/\gamma_2)Z, \]

where we use \( f_2(\lambda_Z(D_2)) = D_2/\gamma_2 \) from (2). Define \( G : \mathbb{R}^5 \to \mathbb{R}^2 \) by

\[ G(N, Z, \mu, D_1, D_2) = (G_1(N, Z, \mu, D_1, D_2), G_2(N, Z, \mu, D_1, D_2)). \]

Then we want to parametrize the set \( G^{-1}(0, 0) \).

The derivative of \( G \) is represented by the matrix

\[ DG = \begin{bmatrix} \frac{\partial G_1}{\partial N} & \frac{\partial G_1}{\partial Z} & \frac{\partial G_1}{\partial \mu} & \frac{\partial G_1}{\partial D_1} & \frac{\partial G_1}{\partial D_2} \\ \frac{\partial G_2}{\partial N} & \frac{\partial G_2}{\partial Z} & \frac{\partial G_2}{\partial \mu} & \frac{\partial G_2}{\partial D_1} & \frac{\partial G_2}{\partial D_2} \end{bmatrix}. \]

Observe that, for fixed \( \mu_0 > \mu_{c_1}(D_1, D_2) \), the first two columns of \( DG \) at the point

\[ (N(\mu_0, D_1, D_2), Z(\mu_0, D_1, D_2), \mu_0, D_1, D_2) \]

evaluate to

\[ \begin{bmatrix} -D - f_1'(N(\mu_0, D_1, D_2))\lambda_Z(D_2) & 0 \\ \gamma_1 f_1'(N(\mu_0, D_1, D_2))\lambda_Z(D_2) & -D_2/\gamma_2 \end{bmatrix}. \]

Since \( f_1'(N) > 0 \), the first two columns are linearly independent and so the implicit function theorem applies. There exists a ball \( B_1 \) around \((\mu_0, D_1, D_2)\) and a ball \( B_2 \)
around \((N(\mu_0, D_1, D_2), Z(\mu_0, D_1, D_2))\) such that for each \((\mu, D_1, D_2)\) in \(B_1\) there is a unique point \((N(\mu, D_1, D_2), Z(\mu, D_1, D_2))\) in \(B_2\) such that
\[
G(N(\mu, D_1, D_2), Z(\mu, D_1, D_2), \mu) = 0.
\]
Moreover, the functions \(N(\mu, D_1, D_2)\) and \(Z(\mu, D_1, D_2)\) have the same degree of differentiability as does \(G\), which is the minimum of the degrees of differentiability of \(f_1(N)\) and \(f_2(P)\). To explain how the differentiability of \(f_2\) enters, note that the computation of \(\partial N/\partial D_2\) and \(\partial Z/\partial D_2\) via \(\partial G/\partial D_2\) involves \(\lambda_Z(D_2) = (\gamma_2 \cdot f'_2(\lambda_P(D_2)))^{-1}\) by (3). This all gives us a smooth parameterization of the equilibrium locus, as desired.

\[\square\]

**Remark 3.2.** From the point of view of calculus, each of the independent variables \(\mu, D_1, D_2\) is on an equal footing with the others. However, viewed through the lens of the structure of system (1), we can describe the variable \(\mu\) as a control parameter and the variables \(D_1\) and \(D_2\) as experimental parameters fixed at some earlier time. This distinction informs our analysis where we first consider the model when \(D=D_1=D_2\) as \(\mu\) varies, and subsequently vary \(D_1\) and \(D_2\) in a neighborhood of \(D\).

**Theorem 3.3.** Fix \(D_1\) and \(D_2\) and suppose \(\mu > \mu_{c_1}(D_1, D_2)\), so that the coexistence equilibrium point \(E_2(\mu, D_1, D_2) = (N(\mu, D_1, D_2), \lambda_Z(D_2), Z(\mu, D_1, D_2))\) exists. Then

1. the \(\mu\)-derivatives \(N'(\mu, D_1, D_2)\) and \(Z'(\mu, D_1, D_2)\) are positive.
2. \(\lim_{\mu \to \infty} N(\mu, D_1, D_2) = \infty\) and \(Z(\mu, D_1, D_2)\) is bounded.

**Proof.** Since \(D_1\) and \(D_2\) are fixed throughout this proof, we drop these symbols and write simply \(N(\mu)\) and \(Z(\mu)\). To show \(N'(\mu) > 0\), recall equation (6) from Theorem 2.2:
\[
0 = (\mu - N(\mu))D - \lambda_Z(D_2) \cdot f_1(N(\mu)).
\]
Differentiating (6) with respect to \(\mu\) and rearranging, we get
\[
N'(\mu) \cdot \left(D + \lambda_Z(D_2)f'_1(N(\mu))\right) = D.
\]
Since \(f'_1(N)\) is positive, it follows that \(N'(\mu)\) is positive.

To show \(Z'(\mu) > 0\), set \(f_2(\lambda_Z(D_2)) = D_2/\gamma_2\) in equation (7), obtaining
\[
0 = \gamma_1 \lambda_Z(D_2)f_1(N(\mu)) - D_1 \lambda_Z(D_2) - Z(\mu) \cdot (D_2/\gamma_2).
\]
Differentiating with respect to \(\mu\) and rearranging, we get
\[
Z'(\mu) = (\gamma_1 \gamma_2/D_2) \cdot \lambda_Z(D_2) \cdot f'_1(N(\mu)) \cdot N'(\mu).
\]
Since \(N'(\mu)\) and \(f'_1(N)\) are positive, it follows that \(Z'(\mu)\) is positive. This proves part one.

To prove part two, note that equation (6) implies
\[
N(\mu) = \mu - (\lambda_Z(D_2)/D) \cdot f_1(N(\mu)).
\]
Since \(f_1(N)\) is bounded, \(\lim_{\mu \to \infty} N(\mu) = \infty\). From (7) we have
\[
Z(\mu) = (\gamma_2/D_2) \cdot (\gamma_1 \lambda_Z(D_2)f_1(N(\mu)) - D_1 \lambda_Z(D_2)).
\]
Since \(f_1(N)\) is bounded, \(Z(\mu)\) is bounded. \[\square\]
Before we turn to a study of the stability properties of the coexistence equilibrium, we include a partial paraphrase of the $C^L$ Hopf bifurcation theorem as stated in [5, p.16]. Since our goal is to make an application of this result to the coexistence equilibrium $E_2$, and because the verification of the hypotheses is lengthy, we refer to our paraphrase to keep track of progress.

**Theorem 3.4.** Consider a system $dX/dt = F(X,\mu)$ with $X \in \mathbb{R}^n$ and $\mu$ a real parameter. If,

1. for $\mu$ in an open interval containing $\mu_c$ (characterized in 3 below), $F(0,\mu) = 0$ and $0 \in \mathbb{R}^n$ is an isolated equilibrium point of $dX/dt=F(X,\mu)$;
2. all partial derivatives of the components $F^\ell$ of the vector $F$ of orders $\leq L+2$, ($L \geq 2$) exist and are continuous in $X$ and $\mu$ in a neighborhood of $(0,\mu_c)$ in $\mathbb{R}^n \times \mathbb{R}$;
3. the Jacobian $J(0,\mu)=DXF(0,\mu)$ has paired complex eigenvalues $\alpha(\mu)\pm i\omega(\mu)$, where $\alpha(\mu_c) = 0$ and $\alpha'(\mu_c) \neq 0$;
4. the remaining $n-2$ eigenvalues of $J(0,\mu_c)$ have strictly negative real parts,

then the system $dX/dt = F(X,\mu)$ has a family of periodic solutions.

Moreover, if $\alpha'(\mu_c) > 0$, then the family of periodic solutions arises for $\mu > \mu_c$ and for $\mu$ sufficiently close to $\mu_c$ these periodic solutions are orbitally asymptotically stable.

**Remark 3.5.** For the purposes of the proof in [5] the authors assume the critical value of the bifurcation parameter is $\mu_c = 0$ and that the isolated critical point is at the origin. A straightforward linear adjustment of the bifurcation variable moves the critical value of the bifurcation parameter to 0, but a more serious issue with hypothesis 1 is that, for us, the coordinates of the equilibrium $E_2(N(\mu,D_1,D_2),\lambda_Z(D_2),Z(\mu,D_1,D_2))$ in system (1) are changing with the parameter $\mu$. Figure 1 shows an example. In [5, p.14] a linear change of variables is recommended to translate the equilibrium smoothly varying with the bifurcation parameter back to the origin. The reader interested in the details of this adjustment is referred to the preprint [1], where we use the inverse function theorem to overcome this difficulty. After the change of variables, hypothesis 1 is satisfied and the Jacobian at the origin is simply a conjugate of the Jacobian at $E_2(N(\mu,D_1,D_2),\lambda_Z(D_2),Z(\mu,D_1,D_2))$.

![Figure 1. A curve of coexistence equilibria](image-url)
Hypothesis 2 is fulfilled by imposing more differentiability conditions on the functions \( f_1(N) \) and \( f_2(P) \) at an appropriate point in the exposition. Verification of hypotheses 3 and 4 in the statement of Theorem 3.4 is the most involved part of our process and occupies the rest of this section.

Hypotheses 3 and 4 concern the eigenvalues of the Jacobian \( J(E_2) \), but the characteristic polynomial of \( J(E_2) \) given in Equation (10) is not immediately amenable to factorization, a standard approach to eigenvalue study. Motivated by the choice of the auxiliary variable \( U(t) \) defined in Lemma 2.1, we conjugate the Jacobian \( J(E_2) \) in (10) by

\[
W = \begin{bmatrix}
1 & \gamma_1^{-1}(\gamma_1\gamma_2)^{-1} \\
0 & 1 \\
0 & 0
\end{bmatrix}
\]

to obtain a more convenient form, as follows.

Using \( f_2(\lambda_Z(D_2)) = D_2/\gamma_2 \) and writing \( D_1 = D + \epsilon_1, D_2 = D + \epsilon_2 \), conjugation by \( W \) yields the matrix

\[
WJ(E_2)W^{-1} = \begin{bmatrix}
-D & -\gamma_1^{-1}\epsilon_1 & -\gamma_1\gamma_2^{-1}\epsilon_2 \\
\gamma_1\lambda_Z(D_2)f_1'(N(\mu, D_1, D_2)) & A & B \\
0 & C & 0
\end{bmatrix}, \tag{14}
\]

where

\[
A = \gamma_1 f_1(N(\mu, D_1, D_2)) - \lambda_Z(D_2)f_1'(N(\mu, D_1, D_2)) - D_1 - Z(\mu, D_1, D_2)f_2'(\lambda_Z(D_2)),
\]

\[
B = -\left(\lambda_Z(D_2)/\gamma_2\right)f_1'(N(\mu, D_1, D_2)) - f_2(\lambda_Z(D_2))
\]

\[
= -\left(\lambda_Z(D_2)f_1'(N(\mu, D_1, D_2)) + D_2\right)/\gamma_2 < 0,
\]

\[
C = \gamma_2 Z(\mu, D_1, D_2)f_2'(\lambda_Z(D_2)) > 0.
\]

First we make the assumption that \( D = D_1 = D_2 \), so that \( \epsilon_1 = \epsilon_2 = 0 \); that is, we assume the death rates of \( P \) and \( Z \) are negligible with respect to washout rate \( D \). The results of [9] suggest this is a useful initial assumption. Since we regard \( D \) as fixed for the discussion, we will abbreviate \( N(\mu, D, D) \) by \( N(\mu) \) and \( Z(\mu, D, D) \) by \( Z(\mu) \). Similarly, we will abbreviate \( E_2(\mu, D, D) \) by \( E_2(\mu) \).

From (14) we can explicitly compute the characteristic polynomial and eigenvalues of \( J(E_2(\mu)) \), since conjugation does not change them. The characteristic polynomial of \( J(E_2(\mu)) \) is, therefore,

\[
p(x) = (-D - x)(-BC - Ax + x^2), \tag{15}
\]

where

\[
A = \gamma_1 f_1(N(\mu)) - \lambda_Z(D)f_1'(N(\mu)) - D - Z(\mu)f_2'(\lambda_Z(D)), \tag{16}
\]

\[
B = -\left(\lambda_Z f_1'(N(\mu)) + D\right)/\gamma_2, \tag{17}
\]

and

\[
C = \gamma_2 Z(\mu)f_2'(\lambda_Z(D)). \tag{18}
\]

The next result amplifies Theorem 2.5 in the case \( D = D_1 = D_2 \).

**Theorem 3.6.** Assume \( D = D_1 = D_2 \) and that \( \mu > \mu_{c_1}(D, D) \), so the coexistence equilibrium \( E_2(\mu) = (N(\mu), \lambda_Z(D), Z(\mu)) \) exists. Then
1. $E_2(\mu)$ is locally asymptotically stable if

$$Z(\mu)\left(\frac{D}{\gamma_2\lambda_Z(D)} - f_2'(\lambda_Z(D))\right) < \lambda_Z(D)f_1'(N(\mu)).$$

2. $E_2(\mu)$ is unstable if

$$Z(\mu)\left(\frac{D}{\gamma_2\lambda_Z(D)} - f_2'(\lambda_Z(D))\right) > \lambda_Z(D)f_1'(N(\mu)).$$

Proof. With $f_2(\lambda_Z(D)) = D/\gamma_2$ in (7) we have

$$\gamma_1f_1(N(\mu)) - D = (DZ(\mu))/(\gamma_2\lambda_Z(D)).$$

Then, from (16)

$$A = \gamma_1f_1(N(\mu)) - D - Z(\mu)f_2'(\lambda_Z(D)) - \lambda_Z(D)f_1'(N(\mu))$$

$$= Z(\mu)\left(\frac{D}{\gamma_2\lambda_Z(D)} - f_2'(\lambda_Z(D))\right) - \lambda_Z(D)f_1'(N(\mu)).$$

The result now follows from the Routh-Hurwitz criterion, since $-BC > 0$ is easily verified from (17) and (18).

In [9, Theorem 3.2] it is shown that, under the assumption $D=D_1=D_2$, cycles exist for certain values of the parameters. To prove this, Li and Kuang observe that there is a limiting plane for solutions of the system, given by

$$N + \gamma_1^{-1}P + (\gamma_1\gamma_2)^{-1}Z = \mu$$

in terms of our variables. Using their form of (20), they eliminate explicit consideration of the nutrient equation and reduce the number of variables to two. The Poincaré-Bendixon theorem is then applied to the resulting two-dimensional limit system, providing a cycle for the $(N, P, Z)$-system in the plane (20). Now we amplify their result by proving cycles arise from Hopf bifurcations.

From the factorization of the characteristic polynomial of $J(E_2(\mu))$ given in (15) it is immediate that the Jacobian at $E_2(\mu)$ has one negative eigenvalue. Thus, hypothesis 4 of Theorem 3.4 for $E_2(\mu)$ is satisfied in the case $D=D_1=D_2$. Now we verify hypothesis 3 for this situation.

**Theorem 3.7.** Assume $D=D_1=D_2$ and let $\mu > \mu_{c_2}(D, D)$, so that the coexistence equilibrium $E_2(\mu) = (N(\mu), \lambda_Z, Z(\mu))$ exists.

1. If $f_1'(N)$ is continuous and $D/(\gamma_2\lambda_Z(D)) > f_2'(\lambda_Z(D))$, then there exists a value $\mu_{c_2} > \mu_{c_2}(D, D)$ for which $A(\mu_{c_2}) = 0$. Consequently, when $\mu = \mu_{c_2}$, the Jacobian has a conjugate pair of imaginary eigenvalues.

2. If, in addition, $f_1$ is twice differentiable with respect to $N$ and $f_1^{(2)}(N(\mu_{c_2})) < 0$, then $A'(\mu_{c_2}) > 0$. Combining this with part 1, we have that hypothesis 3 of Theorem 3.4 is satisfied for $E_2(\mu)$.

3. If, in addition, $f_1$ and $f_2$ are four times continuously differentiable, then all parts of Theorem 3.4 are satisfied. Moreover, the last sentence in the statement also applies, and we conclude there is a Hopf bifurcation at $\mu_{c_2}$ to an orbitally asymptotically stable cycle.

4. If, in addition to the hypotheses in parts 1, 2, and 3, $f_1^{(2)}(N) < 0$ for all $N$, then there is a unique Hopf bifurcation at $\mu_{c_2}$ to a stable cycle.
Remark 3.8. Concerning part 1 of the theorem, if we assume $f_2^{(2)}(P) < 0$, i.e.,
that $f_2$ is is concave down, then the slope of the secant that passes through the
points $(0, 0)$ and $(\lambda_2(D), (D/\gamma_2))$ is greater than the slope of the tangent line to
the graph of $f_2$ at $\lambda_2(D)$; that is, $D/(\gamma_2\lambda_2(D)) > f_2'(\lambda_2(D))$. This will be the
case, for example, when $f_2(P)$ is Holling Type II. However, the one-point condition
$D/(\gamma_2\lambda_2(D)) - f_2'(\lambda_2(D)) > 0$ may hold even if $f_2$ is not concave down. We will
give such an example in Section 4.

Concerning part 2 of the theorem, our argument for the existence of a parameter
value $\mu_{c_2}$ such that $A(\mu_{c_2}) = 0$ is based on the intermediate value theorem, so we
cannot a priori exclude the possibility that there is more than one parameter value
meeting this condition. If $f_1^{(2)} \leq 0$ at a zero of $A(\mu)$, then the sign of $A'$ is positive
at that zero. On the other hand, if $f_1^{(2)} > 0$ at some zero of $A(\mu)$, the sign of $A'$
at that zero cannot be determined. Consequently, it may be possible that more than
one Hopf bifurcation occurs and that some may result in bifurcations to unstable
cycles.

Concerning part 4, the assumption that $f_1^{(2)}(N) < 0$ for all $N$ is fulfilled if $f_1$ is a
function of Holling type II and the possibility of a multiplicity of zeroes of $A(\mu)$ is
eliminated. As such, the assumption is natural in some respects, although one can
conceive of examples not fulfilling the assumption.

Proof. Consider the expression
\[ A(\mu) = Z(\mu) \left( \frac{D}{\gamma_2\lambda_2(D)} - f_2'(\lambda_2(D)) \right) - \lambda_2(D)f_1'(N(\mu)) \]
given in (19). Since $f_1'(N)$ is a continuous function, $A$ is a continuous function of
$\mu$ by Lemma 3.1. To prove that $A(\mu)$ has a zero value for some $\mu > \mu_{c_1}(D, D)$, it
is enough to prove that $A(\mu)$ passes from negative to positive. For $\mu = \mu_{c_1}(D, D)$,
$Z(\mu_{c_1}(D, D)) = 0$, so
\[ A(\mu_{c_1}(D, D)) = -\lambda_2(D)f_1'(N(\mu_{c_1}(D, D))) < 0. \]

Now we find a value of $\mu > \mu_{c_1}(D, D)$ at which $A(\mu)$ is positive. By Theorem 3.3,
$Z(\mu)$ is increasing and bounded for $\mu > \mu_{c_1}(D, D)$. Let $Z_{\infty} = \sup_{\mu > \mu_{c_1}(D, D)} Z(\mu)$.
Then there exists an $M_1$ such that for $\mu > M_1$, $Z(\mu) > Z_{\infty}/2$. Since $f_1$ is bounded
and increasing, $\lim_{N \to +\infty} f_1'(N) = 0$. Then, for any $\epsilon > 0$, there exists an $N_\epsilon > 0$
such that $0 < f_1'(N) < \epsilon$ for all $N > N_\epsilon$. With $\epsilon = (Z_{\infty}/2\lambda_2(D)) \cdot \left( \frac{D}{\gamma_2\lambda_2(D)} - f_2'(\lambda_2(D)) \right)$, this implies that there exists an $N^*$ such that, if $N > N^*$,
then
\[ 0 < f_1'(N) < (Z_{\infty}/2\lambda_2(D)) \cdot \left( \frac{D}{\gamma_2\lambda_2(D)} - f_2'(\lambda_2(D)) \right). \]

In addition, $N(\mu)$ is increasing without bound by Theorem 3.3, so there is an $M_2 > \mu_{c_1}(D, D)$ such that, if $\mu > M_2$, then $N(\mu) > N^*$. Choose $\mu^* > \max\{M_1, M_2\}$. Then
\[ A(\mu^*) = Z(\mu^*) \cdot \left( \frac{D}{\gamma_2\lambda_2(D)} - f_2'(\lambda_2(D)) \right) - \lambda_2(D)f_1'(N(\mu^*)) \]
\[ > (Z_{\infty}/2) \cdot \left( \frac{D}{\gamma_2\lambda_2(D)} - f_2'(\lambda_2(D)) \right) \]
\[ - \lambda_2(D) \cdot (Z_{\infty}/2\lambda_2(D)) \cdot \left( \frac{D}{\gamma_2\lambda_2(D)} - f_2'(\lambda_2(D)) \right) = 0. \]
Since \( A(\mu_{c_1}(D,D)) < 0 \) and \( A(\mu^*) > 0 \), there is a number \( \mu_{c_2} > \mu_{c_1}(D,D) \) such that \( A(\mu_{c_2}) = 0 \). Note that when \( \mu = \mu_{c_2} \) the discriminant of the quadratic factor of the characteristic polynomial in (15) is

\[
A(\mu_{c_2})^2 + 4B(\mu_{c_2}) \cdot C(\mu_{c_2}) = -4(\lambda_Z(D) f_1'(N(\mu_{c_2}))+D) \cdot (f_2'(\lambda Z(D))Z(\mu_{c_2})) < 0,
\]

so its roots are indeed purely imaginary. This proves part one.

For part two, by continuity of the discriminant as a function of \( \mu \), there is a neighborhood of \( \mu_{c_2} \) on which the discriminant is negative. Continuing, differentiate \( A(\mu) \) with respect to \( \mu \) to obtain

\[
A'(\mu) = Z'(\mu) \left( D/(\gamma_2 \lambda Z(D)) - f_2'(\lambda Z(D)) \right) - \lambda Z(D)f_1'(N(\mu)) \cdot N'(\mu). \quad (22)
\]

By Theorem 3.3, \( N'(\mu) \) and \( Z'(\mu) \) are positive. By the hypotheses of the present theorem, \( D/(\gamma_2 \lambda Z(D)) - f_2'(\lambda Z(D)) > 0 \) and \( f_1'(N(\mu_{c_2})) < 0 \). Thus, \( A'(\mu_{c_2}) > 0 \). Combining parts one and two means that hypothesis 3 of Theorem 3.4 holds at \( \mu_{c_2} \) for the case \( D=D_1=D_2 \). This completes the proof of part 2.

With \( f_1 \) and \( f_2 \) four times continuously differentiable, all parts of Theorem 3.4 are satisfied. In particular, the last sentence of Theorem 3.4 also applies, and we conclude that at \( \mu_{c_2} \) there is a Hopf bifurcation to an orbitally asymptotically stable cycle.

For part four, if \( f_1'(N) < 0 \) for all \( N \), then \( A'(\mu) > 0 \) for \( \mu > \mu_{c_2}(D,D) \). \( \square \)

Let us now discuss weakening the condition \( D=D_1=D_2 \). Intuitively, for \( (D_1, D_2) \) sufficiently close to \( (D, D) \) the eigenvalues of \( J(E_2(\mu, D_1, D_2)) \) should exhibit behavior similar to those of \( J(E_2(\mu, D, D)) \). It is a well-known consequence of the inverse function theorem that, for a degree \( n \) polynomial with \( n \) distinct real roots, the roots and, hence, the linear factors, are smooth functions of the coefficients. In our situation we may specialize this fact in the form of the following lemma.

**Lemma 3.9.** Let \( P_1(x)^- = \{ (\alpha - x) \mid \alpha < 0 \} \) be the space of polynomials of degree 1 in \( x \), with leading coefficient \(-1\) and negative constant term, let \( P_2(x)^- = \{ \beta - \gamma x + x^2 \mid \gamma^2 - 4\beta < 0 \} \) be the space of monic quadratic polynomials in \( x \) with real coefficients and having a complex conjugate pair of roots, and let \( P_3(x)^- = \{ p_0 + p_1 x + p_2 x^2 - x^3 \} \) be the space of cubic polynomials in \( x \) with leading coefficient \(-1\) and real coefficients.

Then the multiplication map \( M : P_1^- \times P_2^- \rightarrow P_3^- \) is a diffeomorphism. \( \square \)

To explain how Lemma 3.9 comes into play, consider the map \( \chi : M_{3,3}(\mathbb{R}) \rightarrow P_3^- \) which takes as input a real-valued 3 by 3 matrix \( R \) and produces its characteristic polynomial \( \chi(R) = \det(R - xI) \). The map \( \chi \) has a coordinate expression by taking the coefficients in degrees 0, 1, and 2. These coefficients are polynomials in the matrix entries, so \( \chi \) is smooth. Now look at

\[
M_{3,3}(\mathbb{R}) \xrightarrow{\chi} P_3^- \leftarrow P_1^- \times P_2^-.
\]

Suppose we are in the situation of Theorem 3.7, where it is easy to factor the characteristic polynomial of \( J(E_2(\mu, D, D)) \), and we have seen the Jacobian has a negative real eigenvalue and a complex conjugate pair of eigenvalues as \( \mu \) varies near a potential bifurcation value \( \mu_{c_2} \). The observed factorization of the characteristic polynomial of \( J(E_2(\mu, D, D)) \) explicitly inverts the polynomial multiplication \( M \) at particular points, and Lemma 3.9 implies the characteristic polynomial of
$J(E_2(\mu, D_1, D_2))$ has a similar factorization smoothly depending on the entries of $J(E_2(\mu, D_1, D_2))$, for $(D_1, D_2)$ sufficiently close $(D, D)$.

More precisely, we have proved in Theorem 3.7 that there is an interval of parameters $\mu$ in which the characteristic polynomials

$$p(x) = (-D - x)(-BC - Ax + x^2)$$

of $J(E_2(\mu, D, D))$ have a complex conjugate pair of roots in addition to the eigenvalue $-D<0$, so they are in the image of the multiplication map $M: P_1^-(x) \times P_2^-(x) \to P_0^-(x)$. For $(D_1, D_2)$ close to $(D, D)$ the entries in $J(E_2(\mu, D_1, D_2))$ are close to the entries in $J(E_2(\mu, D, D))$, so the characteristic polynomial of $J(E_2(\mu, D_1, D_2))$ is close to the characteristic polynomial of $J(E_2(\mu, D, D))$. To see this explicitly, refer to the formulas (11), (12), and (13); to account for the normalization of the characteristic polynomial to leading coefficient $-1$, multiply each expression by $-1$.

Therefore, in view of Lemma 3.9, the characteristic polynomial of $J(E_2(\mu, D_1, D_2))$ has a decomposition of the same form as that of the characteristic polynomial of $J(E_2(\mu, D, D))$. Written formally, the decomposition is

$$M^{-1}(\chi(J(E_2(\mu, D_1, D_2)))) = (\alpha(D_1, D_2)(\mu) - x, \beta(D_1, D_2)(\mu) - \gamma(D_1, D_2)(\mu)) x + x^2).$$

We remind the reader that we think of $\mu$ as a control parameter, adjustable by the experimenter, and $D_1$ and $D_2$ as experimental parameters, set at the beginning of an experiment. To bring out this distinction, we have written the components of the formal factorization of the characteristic polynomial of $J(E_2(\mu, D_1, D_2))$ as $\alpha(D_1, D_2)(\mu)$, $\beta(D_1, D_2)(\mu)$, and $\gamma(D_1, D_2)(\mu)$.

The map $M$ is infinitely differentiable, so the local inverse $M^{-1}$ is also. In particular, for a fixed value $\mu$, the coefficients of the decomposition are smooth functions of $(D_1, D_2)$ defined in a neighborhood of $(D, D)$.

The first consequence is that, by definition of $P_1^-$, the characteristic polynomial of $J(E_2(\mu, D_1, D_2))$ has a linear factor $\alpha(D_1, D_2)(\mu) - x$ with $\alpha(D_1, D_2)(\mu) < 0$. This shows that hypothesis 4 of Theorem 3.4 can be satisfied.

We are primarily interested in the behavior of the eigenvalues of the Jacobian $J(E_2(\mu, D_1, D_2))$ in the neighborhood of a value of $\mu$ where the Jacobian $J(E_2(\mu, D, D))$ has a purely imaginary pair of eigenvalues. Let $\mu_{c_2}$ meet this condition, as provided by part 1 of Theorem 3.7. The discriminant of the quadratic factor of the characteristic polynomial of $J(E_2(\mu, D_1, D_2))$ is

$$\gamma(D_1, D_2)(\mu)^2 - 4\beta(D_1, D_2)(\mu).$$

At $\mu_{c_2}$ and for $(D_1, D_2)$ sufficiently close to $(D, D)$, this is close to the expression

$$\left(\gamma(D_1, D_2)(\mu_{c_2})\right)^2 - 4\beta(D_1, D_2)(\mu_{c_2}) = A(\mu_{c_2})^2 + 4 B(\mu_{c_2}) C(\mu_{c_2}),$$

which is negative, because it’s the discriminant of the quadratic factor of the characteristic polynomial of $J(E_2(\mu, D, D))$ given in (21). Therefore, at $\mu_{c_2}$, the discriminant $(\gamma(D_1, D_2)(\mu))^2 - 4\beta(D_1, D_2)(\mu)$ is also negative. By continuity of the discriminant as a function of $\mu$, there is an interval $[\mu_{c_2} - \delta_0, \mu_{c_2} + \delta_0]$ through which it is negative. Therefore, the characteristic polynomial of $J(E_2(\mu, D_1, D_2))$ has a complex conjugate pair of roots on this interval, satisfying part of hypothesis 3 of Theorem 3.4.
However, preservation of the transversality condition is more challenging and requires the uniform approximation of $\gamma'(D_1, D_2)$ by $\gamma'(D, D)$ when $(D_1, D_2)$ is sufficiently close to $(D, D)$. This is the content of Lemma 3.10, the proof of which is relegated to Section 5 so as not to disturb the flow of the exposition.

**Lemma 3.10.** Assume $f_1$ is three times continuously differentiable and $f_2$ is two times continuously differentiable. Then there exists a $\mu$-interval $[\mu-\delta, \mu+\delta]$ on which the $\mu$-derivative $\gamma'(D_1, D_2)(\mu)$ is uniformly approximated by $\gamma'(D, D)(\mu) = A'(\mu)$. In fact, there exists a constant $C$ such that

$$|\gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu)| \leq C \cdot \text{dist}((D_1, D_2), (D, D))$$

for any $\mu \in [\mu_c - \delta, \mu_c + \delta]$.

**Theorem 3.11.** Let $\mu > \mu_c(D_1, D_2)$, so that the equilibrium point $E_2(\mu, D_1, D_2)$ exists in the interior of the positive octant. Assume $f_1$ and $f_2$ are three-times and two-times continuously differentiable, respectively.

1. If $D/\gamma(\lambda_2\lambda_2(D)) > f_2'(\lambda_2(D))$, so that $\mu_c$ of part 1 of Theorem 3.7 exists, and if $f_2''(\lambda_2(D)) < 0$ as in part 2 of Theorem 3.7, then there is $\mu_c(D_1, D_2)$ in a neighborhood $[\mu_c - \delta_0, \mu_c + \delta_0]$ of $\mu_c$ for which

$$\gamma(D_1, D_2)(\mu_c(D_1, D_2)) = 0,$$

assuming $(D_1, D_2)$ is sufficiently close to $(D, D)$. Consequently, the Jacobian $J(E_2(\mu, D_1, D_2))$ has a conjugate pair of imaginary eigenvalues when $\mu = \mu_c(D_1, D_2)$.

2. Moreover, there is an interval around $\mu_c$ containing $\mu_c(D_1, D_2)$ on which $\gamma'(D_1, D_2)(\mu)$ is positive. Consequently, $\mu_c(D_1, D_2)$ is the unique point of the interval at which the Jacobian $J(E_2(\mu, D_1, D_2))$ has a conjugate pair of imaginary eigenvalues, and the transversality condition $\gamma'(D_1, D_2)(\mu_c(D_1, D_2)) > 0$ holds.

3. If, in addition, $f_1$ and $f_2$ are four times continuously differentiable, then all parts of Theorem 3.4 are satisfied, and there is a Hopf bifurcation at $\mu_c(D_1, D_2)$ to an orbitally asymptotically stable cycle.

4. If, in addition to the hypotheses in parts 1, 2, and 3, $f_2''(N) < 0$ for all $N$, then there is a unique Hopf bifurcation at $\mu_c(D_1, D_2)$ to an orbitally asymptotically stable cycle.

**Remark 3.12.** Wolkowicz [11] considers a model in which the uptake function of the predator is Lotka-Volterra, i.e., $f_2(P) = mP$. There it is shown that no Hopf bifurcation can occur, regardless of the functional response of the prey. Since $f_2(P)$ so defined cannot satisfy the condition $D/\gamma(\lambda_2\lambda_2(D)) > f_2'(\lambda_2(D))$, the result is consistent with our own.

**Proof of Theorem 3.11.** From the discussion preceding Lemma 3.10, we have an interval $[\mu_c - \delta_0, \mu_c + \delta_0]$ on which the discriminant $\gamma(D_1, D_2)(\mu)^2 - 4\beta(D_1, D_2)(\mu) = 0$, where $\beta(D_1, D_2)(\mu)$ is negative. Under the assumptions that $f_1''(\lambda_2(D))$ is continuous and $f_2''(\lambda_2(D)) < 0$, $A'(\mu)$ as calculated in (22) is continuous and $A'(\mu_c) > 0$. So there is a $\delta_1 > 0$ such that $A'(\mu) > A'(\mu_c)/2$ on the interval $[\mu_c - \delta_1, \mu_c + \delta_1]$. Choose $\delta = \min\{\delta_0, \delta_1\}$. Put $\eta_1 = -A(\mu_c-\delta)/2 > 0$.

By continuity of $\gamma$ as a function of $(D_1, D_2)$, there is a $\rho_1 > 0$ such that $\text{dist}((D_1, D_2), (D, D)) < \rho_1$ implies

$$|\gamma(D_1, D_2)(\mu_c-\delta) - \gamma(D, D)(\mu_c-\delta)| < \eta_1.$$
Remembering that \( \gamma(D, D)(\mu) = A(\mu) \), we have
\[
|\gamma(D_1, D_2)(\mu_{c_2} - \delta) - A(\mu_{c_2} - \delta)| < \eta_1,
\]
\[
\gamma(D_1, D_2)(\mu_{c_2} - \delta) - A(\mu_{c_2} - \delta) < -A(\mu_{c_2} - \delta)/2,
\]
\[
\gamma(D_1, D_2)(\mu_{c_2} - \delta) < A(\mu_{c_2} - \delta)/2 < 0.
\]
Similarly, if we put \( \eta_2 = A(\mu_{c_2} + \delta)/2 > 0 \), then there is a number \( \rho_2 > 0 \) such that dist\((D_1, D_2), (D, D)\)\( < \rho_2 \) implies
\[
|\gamma(D_1, D_2)(\mu_{c_2} + \delta) - \gamma(D, D)(\mu_{c_2} + \delta)| < \eta_2,
\]
\[
|\gamma(D_1, D_2)(\mu_{c_2} + \delta) - A(\mu_{c_2} + \delta)| < \eta_2,
\]
\[
-A(\mu_{c_2} + \delta)/2 < \gamma(D_1, D_2)(\mu_{c_2} + \delta) - A(\mu_{c_2} + \delta)
\]
\[
0 < A(\mu_{c_2} + \delta)/2 < \gamma(D_1, D_2)(\mu_{c_2} + \delta).
\]
Since \( \gamma(D_1, D_2)(\mu) \) is a continuous function of \( \mu \), we find \( \gamma(D_1, D_2)(\mu) \) has a zero in the interval \( [\mu_{c_2} - \delta, \mu_{c_2} + \delta] \), provided dist\((D_1, D_2), (D, D)\)\( < \min\{\rho_1, \rho_2\} \).

Thus, the characteristic polynomial of \( J(E_2(\mu, D_1, D_2)) \) has a complex conjugate pair of roots and at least one pair of purely imaginary roots on the interval \( [\mu_{c_2} - \delta, \mu_{c_2} + \delta] \) for \( (D_1, D_2) \) sufficiently close to \( (D, D) \), proving part one.

By choice of \( \delta \), \( \gamma'(D, D)(\mu) = A'(\mu) > A'(\mu_{c_2})/2 > 0 \) on this interval. To see that the transversality condition holds, let \( \eta_3 = A'(\mu_{c_2})/2 > 0 \). By Lemma 3.10, if \( (D_1, D_2) \) is sufficiently close to \( (D, D) \), on the interval \( [\mu_{c_2} - \delta, \mu_{c_2} + \delta] \) we have
\[
|\gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu)| \leq \eta_3,
\]
\[
-A'(\mu_{c_2})/2 < \gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu),
\]
\[
\gamma'(D, D)(\mu) - A'(\mu_{c_2})/2 < \gamma'(D_1, D_2)(\mu),
\]
\[
0 < \gamma'(D_1, D_2)(\mu),
\]
since \( \gamma'(D, D)(\mu) = A'(\mu) > A'(\mu_{c_2})/2 \) on the interval \( [\mu_{c_2} - \delta, \mu_{c_2} + \delta] \), in particular, at the point where \( \gamma(D_1, D_2)(\mu) \) has a zero. This completes the proof of part 2 of the theorem.

Provided that \( (D_1, D_2) \) is sufficiently close to \( (D, D) \), parts 3 and 4 of the theorem hold by the same reasoning as for the corresponding parts of Theorem 3.7.

4. Simulations and examples. We present some simulations illustrating concretely our results. First we consider system (1) and take \( f_1 \) and \( f_2 \) to be Holling type II. We choose notations as follows.
\[
f_1(N) = m_1 N/(\alpha_1 + N) \quad \text{and} \quad f_2(P) = m_2 P/(\alpha_2 + P).
\]
With these choices explicit formulas can be given for many quantities studied in earlier sections. For example, we obtain formulas for the numbers \( \lambda_P(D_1) \) and \( \lambda_Z(D_2) \) defined in Equation (2). For \( \lambda_P(D_1) \) we have
\[
\gamma_1 \cdot (m_1 N/(\alpha_1 + N)) = D_1 \text{ with solution } N = D_1 \alpha_1/(\gamma_1 m_1 - D_1) := \lambda_P(D_1);
\]
for \( \lambda_Z(D_2) \) we have
\[
\gamma_2(2 m_2 P/(\alpha_2 + P)) = D_2 \text{ with solution } P = D_2 \alpha_2/(\gamma_2 m_2 - D_2) := \lambda_Z(D_2).
\]
For rate functions of this type, Equation (6) determining \( N(\mu, D_1, D_2) \) reduces to a quadratic equation. In principle, one obtains explicit solutions for \( N(\mu, D_1, D_2) \) and the nonnegative solution is easily identified. Then Equation (7) for \( Z(\mu, D_1, D_2) \) is linear and easily solved for \( Z(\mu, D_1, D_2) \).
With these remarks we can turn to an illustration of Theorems 3.7 and 3.11 in a case using Holling type II rate functions. With these rate functions, the concavity of the function $f_2$ guarantees that the condition $D/(\gamma_2 \lambda_2(D)) > f_2'(\lambda_2(D))$ is satisfied. First, we set $D=D_1=D_2=1.0$ and the remaining parameters to the following values.

$$
m_1 = 1 \quad \alpha_1 = 0.2 \quad \gamma_1 = 2
$$

$$
m_2 = 2 \quad \alpha_2 = 0.5 \quad \gamma_2 = 1.5
$$

With all quantities involved explicitly computed, the formula given in Equation (19) for the real part of the complex conjugate pair of eigenvalues of the linearization of the system at the coexistence equilibrium can be made explicit, though messy, and is easily plotted by a computer algebra system. This is the solid curve in Figure 2, which shows that a Hopf bifurcation occurs in the vicinity of $\mu = 0.6$. Figure 3 exhibits solutions of the system for $\mu$ slightly smaller and slightly larger than the bifurcation value $\mu_{c_2}(D, D) \approx 0.6$.

Next, keep $D=1$ and set $D_1=1.2$ and $D_2=1.3$. The proof of Theorem 3.11 says that the graph of the function defined by taking the real part of the complex conjugate pair of eigenvalues associated with the coexistence equilibrium is an increasing
function whose graph lies in a neighborhood of the curve we discussed in the preceding paragraph. We do not have an explicit formula for this function with the new values for \( D_1 \) and \( D_2 \), but we can estimate its values by numerically computing the eigenvalues of the linearization along a sequence of \( \mu \)-values. Figure 2 also shows a sequence of points derived from eigenvalue approximations when \( D_1 = 1.2 \) and \( D_2 = 1.3 \). Interpolating a curve through the plotted points, we see a Hopf bifurcation occurs in the vicinity of \( \mu = 0.9 \). Figure 4 shows trajectories of this system for values of \( \mu \) slightly smaller and slightly larger than the bifurcation value.

To provide an additional illustration of the result of Theorem 3.11, we consider a version of system (1) incorporating rate functions with the property that the graphs have inflection points. Consider

\[
f_1(N) = \frac{m_1 N^2}{(\alpha_1 + N^2)} \quad \text{and} \quad f_2(P) = \frac{m_2 P^2}{(\alpha_2 + P^2)}.
\]

with the parameter values

\[
m_1 = 1.7, \quad \alpha_1 = 0.8, \quad m_2 = 1.6, \quad \alpha_2 = 0.9.
\]

Further, set

\[
\gamma_1 = 0.8, \quad \gamma_2 = 0.9, \quad D = 1, \quad D_1 = 1.2, \quad D_2 = 1.1.
\]

Then the condition \( D/(\gamma_2 \lambda_2(D)) > f_2'(\lambda_2(D)) \) of Theorem 3.11 is satisfied, but this is not a consequence of the concavity of the graph of \( f_2 \).

Determining \( \lambda_P(D_1) \) and \( \lambda_Z(D_2) \) in this example requires solving quadratic equations, so obtaining exact values is quite easy. Consequently, one can compute explicitly from (5) the value \( \mu_c (D_1, D_2) \) beyond which the coexistence equilibrium exists. Locating a coexistence equilibrium \( E_2(\mu, D_1, D_2) \) requires solving a cubic equation for \( N(\mu, D_1, D_2) \), for which it is more appropriate to use numerical methods. We choose a sequence of \( \mu \) values starting beyond \( \mu_c (D_1, D_2) \), approximate the coexistence equilibria and their Jacobian matrices \( J(E_2(\mu, D_1, D_2)) \), and numerically compute the real part of the complex pair of eigenvalues of the Jacobian for each \( \mu \) value. Plotting the real part against \( \mu \) produces Figure 5, which exhibits the expected change of sign and shows that a Hopf bifurcation occurs in the vicinity of \( \mu = 7.25 \); trajectories for parameters slightly smaller and slightly larger than the bifurcation value are shown in Figure 6.

The conservative nature of system (1) for the case \( D = D_1 = D_2 \) implies that the orbitally asymptotically stable limit cycle lies in the limiting plane given by Equation (20). In the general case, there is no expectation that the limit cycle lies in a plane. That the cycles in Figures 4 and 6 are not planar is hard to see in the...
Figure 5. Real part using rate functions (23)

Figure 6. Before and after Hopf bifurcation: $D=1$, $D_1=1.2$, and $D_2=1.1$ and using rate functions (23)

presented figures, because the scales of the axes are not uniform. However, calculations of estimates for the torsion of the cycles in these figures yield non-zero values, so the cycles are not planar curves, by a basic result of differential geometry.

5. **Preservation of the transversality condition.** For Theorem 3.11, we need Lemma 3.10, which states that, when $(D_1, D_2)$ is close to $(D, D)$, $\gamma'(D_1, D_2)(\mu)$ is uniformly approximated by $\gamma'(D, D)(\mu) = A'\mu$ on an interval $[\mu_{c_2} - \delta_0, \mu_{c_2} + \delta_0]$, where $\mu_{c_2}$ is a point where $A(\mu_{c_2})=0$ and $A'(\mu_{c_2}) > 0$. This fact ensures that the transversality condition is preserved as $(D, D)$ is varied slightly. Expanding, uniform approximation of $\gamma'(D_1, D_2)(\mu)$ by $\gamma'(D, D)(\mu)$ implies that, for the coexistence equilibrium $E_2(\mu, D_1, D_2)$, there is a $\mu$-interval in $I$ for which the eigenvalues of the linearizations exhibit the same change in qualitative behavior as described for $E_2(\mu, D, D)$, as shown in Theorem 3.11.

Backtracking farther, we recapitulate Theorem 3.7, where the working assumptions are that a value $D$ is fixed, a coexistence equilibrium $E_2(\mu, D, D)$ exists, and that there is a range of parameters $\mu$ for which the linearizations at the coexistence equilibrium have a complex conjugate pair of eigenvalues. Moreover, at the parameter value $\mu_{c_2}$, the linearization of the system has a purely imaginary pair of eigenvalues. For any $\mu$ slightly smaller than $\mu_{c_2}$, the pair of complex eigenvalues has a negative real part and for any $\mu$ slightly larger than $\mu_{c_2}$ the pair of complex eigenvalues has a positive real part. By Lemma 3.1 there is an interval $I$ containing $\mu_{c_2}$ and a disc $\Delta$ centered at $(D, D)$ such that the functions $N(\mu, D_1, D_2)$
and $Z(\mu, D_1, D_2)$ defined on $I \times \Delta$ smoothly parametrize the locus of coexistence equilibria near $E_2(\mu, D, D)$.

**Proposition 5.1** (Lemma 3.10). Assume $f_1$ is three times continuously differentiable and $f_2$ is two times continuously differentiable. Then there exists a $\mu$-interval $[\mu-\delta, \mu+\delta]$ on which the $\mu$-derivative $\gamma'(D_1, D_2)(\mu)$ is uniformly approximated by $\gamma'(D, D)(\mu)$. In fact, there exists a constant $C$ such that

$$|\gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu)| \leq C \cdot \text{dist}((D_1, D_2), (D, D))$$

for any $\mu \in [\mu_c - \delta, \mu_c + \delta]$.

The proposition follows from a sequence of lemmas and estimates, given below. In the course of proving these results, we find it necessary to impose the differentiability conditions on $f_1$ and $f_2$. An essential ingredient in the process is to obtain bounds on magnitudes of the differences

$$p_0(\mu, D_1, D_2) - p_0(\mu, D, D), \quad p_1(\mu, D_1, D_2) - p_1(\mu, D, D), \quad p_2(\mu, D_1, D_2) - p_2(\mu, D, D),$$

in terms of $\text{dist}((D_1, D_2), (D, D))$, and where the $p_i(\mu, D_1, D_2) = -a_{3-i}(\mu, D_1, D_2)$, $0 \leq i \leq 2$ are given by the formulas (11), (12), and (13). The bounds are obtained in Propositions 5.6, 5.7, and 5.8.

We now explain the role played by these bounds. By the chain rule, we compute $\gamma'(D_1, D_2)(\mu)$ as the inner product of a row vector $\nabla \gamma$ with a column vector $(p'_0, p'_1, p'_2)$:

$$\gamma'(D_1, D_2)(\mu) = \langle \nabla \gamma(p_0, p_1, p_2), (p'_0, p'_1, p'_2) \rangle(\mu, D_1, D_2).$$

**Remark 5.2.** In order to avoid extremely long expressions in the following analysis, we use abbreviations such as

$$[D(M^{-1})](\mu, D_1, D_2) := D(M^{-1})(p_0(\mu, D_1, D_2), p_1(\mu, D_1, D_2), p_2(\mu, D_1, D_2)).$$

We can write

$$[\nabla \gamma(p_0, p_1, p_2)](\mu, D_1, D_2) = \pi_3 \circ [D(M^{-1})(p_0, p_1, p_2)](\mu, D_1, D_2)$$

$$= \langle 0, 0, 1 \rangle \cdot \begin{bmatrix} \nabla \alpha(p_0, p_1, p_2) \\ \nabla \beta(p_0, p_1, p_2) \\ \nabla \gamma(p_0, p_1, p_2) \end{bmatrix}(\mu, D_1, D_2),$$

where the projection $\pi_3$ to the third coordinate $\gamma$ in $P_1(x)^{-} \times P_2(x)^{-}$ is represented by $\langle 0, 0, 1 \rangle$. The gradients $\nabla \alpha$, $\nabla \beta$, and $\nabla \gamma$ are evaluated at

$$p_0(\mu, D_1, D_2) = -a_3(\mu, D_1, D_2),$$

$$p_1(\mu, D_1, D_2) = -a_2(\mu, D_1, D_2),$$

and

$$p_2(\mu, D_1, D_2) = -a_1(\mu, D_1, D_2),$$

where explicit expressions for $a_i(\mu, D_1, D_2)$ are given in (11), (12), and (13). The derivatives $p'_0$, $p'_1$, and $p'_2$ are evaluated at $(\mu, D_1, D_2)$. 


Applying the convention of (24), we have

\[ \gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu) = [\pi_3 \circ D(M^{-1})(p_0, p_1, p_2) \cdot (p'_0, p'_1, p'_2)](\mu, D_1, D_2) \]

\[ - [\pi_3 \circ D(M^{-1})(p_0, p_1, p_2) \cdot (p'_0, p'_1, p'_2)](\mu, D, D). \]

Before we go farther, we compress taking the derivative \(D(M^{-1})\) at \((p_0, p_1, p_2)\) and evaluating on the vector \((p'_0, p'_1, p'_2)\), writing

\[ D(M^{-1}) \cdot (p'_0, p'_1, p'_2) := D(M^{-1})(p_0, p_1, p_2) \cdot (p'_0, p'_1, p'_2). \]

Then the previous equation becomes

\[ \gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu) = [\pi_3 \circ D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D_1, D_2) - [\pi_3 \circ D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D). \]

We can estimate using operator norms computed in terms of the Euclidean metrics.

\[ |\gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu)| = |[\pi_3 \circ D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D_1, D_2) - [\pi_3 \circ D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D)| \]

\[ \leq \|\pi_3\| \|[D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D_1, D_2) - [D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D)\| \]

\[ \leq \|[D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D_1, D_2) - [D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D)\|. \quad (25) \]

since the norm of a projection is 1. Now we use the triangle inequality to bound the last expression.

\[ \|[D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D_1, D_2) - [D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D)\| \]

\[ \leq \|[D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D_1, D_2) \]

\[ - [D(M^{-1})](\mu, D_1, D_2) \cdot [D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D)\| \]

\[ + \|[D(M^{-1})](\mu, D_1, D_2) \cdot [D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D) \]

\[ - [D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D)\]. \quad (26) \]

Explicit expansion of the first summand in (26) is given in the proof of Lemma 5.4, where we will see the role of the bounds on

\[ p'_0(\mu, D_1, D_2) - p'_0(\mu, D, D), \quad p'_1(\mu, D_1, D_2) - p'_1(\mu, D, D), \quad p'_2(\mu, D_1, D_2) - p'_2(\mu, D, D). \]

Similarly, explicit expansion of the second summand in (26) is given in the proof of Lemma 5.3, where we will see the role of the bounds on

\[ p_0(\mu, D_1, D_2) - p_0(\mu, D, D), \quad p_1(\mu, D_1, D_2) - p_1(\mu, D, D), \quad p_2(\mu, D_1, D_2) - p_2(\mu, D, D). \]

Now we bound the two summands on the right side of the inequality in (26). The argument for the second summand is more complicated than that for the first, so we give a detailed explanation.

**Lemma 5.3.** There is a constant \( C_4 \) such that the second summand in the expansion (26) satisfies

\[ \|[D(M^{-1})](\mu, D_1, D_2) \cdot [(p'_0, p'_1, p'_2)](\mu, D, D) - [D(M^{-1}) \cdot (p'_0, p'_1, p'_2)](\mu, D, D)\| \]

\[ \leq C_4 \cdot \text{dist}((D_1, D_2), (D, D)). \]
Proof. To handle the second summand in (26), we have the bound
\[ \| [D(M^{-1})](\mu, D_1, D_2) - [D(M^{-1})](\mu, D, D) \| \]
\[ \leq \| [D(M^{-1})](\mu, D_1, D_2) - [D(M^{-1})](D, D, \mu) \| \cdot \| [\{p_0, p_1', p_2']](\mu, D, D) \|. \] (27)
To the first factor in the bounding term, apply the mean value theorem \[7, p.103, Corollary 1\] for vector-valued functions of several variables, obtaining
\[ \| [D(M^{-1})](\mu, D_1, D_2) - [D(M^{-1})](D, D, \mu) \| \]
\[ \leq \| [D(D^{-1})](q_0, q_1, q_2) \| \cdot \| [\{p_0, p_1, p_2\}](\mu, D_1, D_2) - [\{p_0, p_1, p_2\}](\mu, D, D) \|. \]
The derivative of the map \( P_3(x) \rightarrow M_{3, 3}(\mathbb{R}) \), \((p_0, p_1, p_2) \rightarrow D(M^{-1})(p_0, p_1, p_2)\) is continuous, because \( M^{-1} \) is \( C^\infty \). The evaluation point \((q_0, q_1, q_2)\) is on the line segment connecting \([\{p_0, p_1, p_2\}](\mu, D_1, D_2)\) and \([\{p_0, p_1, p_2\}](\mu, D, D)\). Again the possibilities range over a compact set, so the norm of the second derivative satisfies
\[ \| [D(D^{-1})](q_0, q_1, q_2) \| \leq C_{D^2(M^{-1})}, \] (28)
for a constant \( C_{D^2(M^{-1})} \) independent of \((D_1, D_2, \mu)\). We compute
\[ \|p(\mu, D_1, D_2) - p(\mu, D, D)\|^2 = \]
\[ |p_0(\mu, D_1, D_2) - p_0(\mu, D, D)|^2 + |p_1(\mu, D_1, D_2) - p_1(\mu, D, D)|^2 + |p_2(\mu, D_1, D_2) - p_2(\mu, D, D)|^2 \]
\[ \leq (C_0)^2 + (C_1)^2 + (C_2)^2 \cdot \text{dist}((D_1, D_2), (D, D))^2, \] (29)
by combining (30), (31), and (32). Assembling (28) and (29),
\[ \| [D(M^{-1})](\mu, D_1, D_2) - [D(M^{-1})](D, D, \mu) \|
\[ \leq C_{D^2(M^{-1})} \cdot \sqrt{(C_0)^2 + (C_1)^2 + (C_2)^2} \cdot \text{dist}((D_1, D_2), (D, D)). \]
This takes care of the first factor on the righthand side of (27).

For the remaining factor in the bounding term in (27), the norm of the tangent vector satisfies
\[ \| [\{p_0, p_1', p_2\}](\mu, D, D) \| \leq C_T, \]
for some constant \( C_T \), independent of \( \mu \). Now that we have taken care of both factors on the righthand side of (27) the second summand in (26) is bounded by a constant times \( \text{dist}((D_1, D_2), (D, D)) \), as claimed. \( \square \)

Lemma 5.4. There is a constant \( C_3 \) such that the first summand in the expansion (26) satisfies
\[ \| [D(M^{-1})](\mu, D_1, D_2) - [D(M^{-1})](\mu, D_1, D_2) \cdot [\{p_0, p_1', p_2\}](\mu, D, D) \|
\[ \leq C_3 \cdot \text{dist}((D_1, D_2), (D, D)). \]

Proof. The proof is similar to the proof of Lemma 5.3 but slightly simpler, because the mean value theorem is not needed. For details, see [1]. \( \square \)

We can now prove the uniform convergence result.
Proof of Proposition 5.1. Combining the inequalities (25) and (26), we have

\[ |\gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu)| \]
\[ \leq \| [D(M^{-1}) \cdot (\mu, D_1, D_2)] - [D(M^{-1})] (\mu, D_1, D_2) \cdot |(p_0', p_1', p_2')| (\mu, D, D) \]
\[ + \| [D(M^{-1})] (\mu, D_1, D_2) \cdot |(p_0', p_1', p_2')| (\mu, D, D) - [D(M^{-1})] (\mu, D, D)|. \]

Using the observations detailed in Lemma 5.4 and Lemma 5.3,

\[ |\gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu)| \leq (C_3 + C_4) \cdot \text{dist}(\mu, (D_1, D_2), (D, D)). \]

Thus, there is a constant $C$ such that

\[ |\gamma'(D_1, D_2)(\mu) - \gamma'(D, D)(\mu)| \leq C \cdot \text{dist}(\mu, (D_1, D_2), (D, D)) \]

for any $\mu \in [\mu_2 - \delta_0, \mu_2 + \delta_0]$. \(\square\)

We have already used a technique of obtaining bounds by splitting quantities. As we will continue to exploit the technique in the following results, we formulate the Lemma 5.5 for reference, leaving the elementary proof to the reader.

Lemma 5.5. Let $Q_1(\mu, D_1, D_2)$ and $Q_2(\mu, D_1, D_2)$ be quantities defined on a domain $I \times \Delta$ satisfying the following conditions.

1. There is a constant $c_1$ such that

\[ |Q_1(\mu, D_1, D_2) - Q_1(\mu, D, D)| \leq c_1 \cdot \text{dist}(\mu, (D_1, D_2), (D, D)). \]

2. There is a constant $c_2$ such that

\[ |Q_2(\mu, D_1, D_2) - Q_2(\mu, D, D)| \leq c_2 \cdot \text{dist}(\mu, (D_1, D_2), (D, D)). \]

3. There are constants $c_3$ and $c_4$ such that $|Q_1(\mu, D_1, D_2)| \leq c_3$ for $(\mu, D_1, D_2) \in I \times \Delta$ and for $\text{dist}(\mu, (D_1, D_2), (D, D))$ sufficiently small, and $|Q_2(\mu, D, D)| \leq c_4$ for $\mu \in I$.

Then there is a constant $c_5$ such that, for $\text{dist}(\mu, (D_1, D_2), (D, D))$ sufficiently small,

\[ |Q_1(\mu, D_1, D_2) \cdot Q_2(\mu, D_1, D_2) - Q_1(\mu, D, D) \cdot Q_2(\mu, D, D)| \leq c_5 \cdot \text{dist}(\mu, (D_1, D_2), (D, D)). \] \(\square\)

As has been seen, the proof of 5.1 depends on the following three propositions.

Proposition 5.6. There are constants $C_0$ and $C_0'$ such that

\[ |p_0(\mu, D_1, D_2) - p_0(\mu, D, D)| \leq C_0 \cdot \text{dist}(\mu, (D_1, D_2), (D, D)). \]

Proposition 5.7. There are constants $C_1$ and $C_1'$ such that

\[ |p_1(\mu, D_1, D_2) - p_1(\mu, D, D)| \leq C_1 \cdot \text{dist}(\mu, (D_1, D_2), (D, D)). \]

Proposition 5.8. There are constants $C_2$ and $C_2'$ such that

\[ |p_2(\mu, D_1, D_2) - p_2(\mu, D, D)| \leq C_2 \cdot \text{dist}(\mu, (D_1, D_2), (D, D)). \]
The proofs of Propositions 5.6, 5.7, and 5.8 depend in turn on a number of elementary bounds and estimates, given below in Lemma 5.9 and Propositions 5.10, 5.11, and 5.12. We give the quick proofs of Lemma 5.9 and Propositions 5.10 and 5.11, because they are quite short, postponing the discussion of the many parts of 5.12 to the end of the section. After we state these results, we prove Proposition 5.11, and 5.12. We give the quick proofs of Lemma 5.9 and Propositions 5.10 and 5.11, and leaving the proofs of Propositions 5.6, 5.7, and 5.8 to the reader.

**Lemma 5.9.** Given $D$, there is an interval $J$ containing $\lambda_Z(D)$ such that
\[
f'_2(P) > f'_2(\lambda_Z(D))/2 > 0
\]
for all $P \in J$. Thus, for all $P \in J$, $f'_2(P)$ is bounded away from zero, and, for all $D_2$ in the preimage $\lambda_Z^{-1}(J)$, $f'_2(\lambda_Z(D_2))$ is bounded away from zero.

**Proof.** By assumption on $f_2$, $f'_2(\lambda_Z(D)) > 0$. By continuity of $f'_2$, there is an interval $J$ containing $\lambda_Z(D)$ such that, for all $P \in J$,
\[
-f'_2(\lambda_Z(D))/2 < f'_2(P) - f'_2(\lambda_Z(D)) < f'_2(\lambda_Z(D))/2.
\]

**Proposition 5.10.** Each of the quantities
\[
f_1(N(\mu, D, D)), \quad f'_1(N(\mu, D, D)), \quad Z(\mu, D, D),
\]
\[
f''_1(N(\mu, D, D)), \quad N'(\mu, D, D), \quad \text{and } Z'(\mu, D, D)
\]
is bounded by some constant on the interval $I$.

**Proof.** Each of the listed functions is continuous on the closed interval $I$, so each one is bounded.

**Proposition 5.11.** Each of the quantities
\[
\lambda_Z(D_2), \quad f_1(N(\mu, D_1, D_2)), \quad f'_1(N(\mu, D_1, D_2)), \quad Z(\mu, D_1, D_2),
\]
\[
f'_2(\lambda_Z(D_2)), \quad f''_1(N(\mu, D_1, D_2)), \quad N'(\mu, D_1, D_2) \quad \text{and } Z'(\mu, D_1, D_2)
\]
is bounded by some constant on the domain $I \times \Delta$.

**Proof.** Each of the listed functions is continuous on the compact set $I \times \Delta$, so each one is bounded.

The proof of the next result depends on many more details of system (1) and consequences drawn from them. We present the details for items selected to be typical, referring the interested reader to the preprint [1] for details on other items.

**Proposition 5.12.** Suppose $N(\mu, D_1, D_2)$ and $Z(\mu, D_1, D_2)$ are defined on a domain $I \times \Delta \subset I \times \mathbb{R} \times \lambda_Z^{-1}(J)$, where $J$ is as in Lemma 5.9. Then these differences are bounded by constants times $\text{dist}((D_1, D_2), (D, D))$ for $\mu \in I$ and $(D_1, D_2) \in \Delta$.

1. $\lambda_Z(D) - \lambda_Z(D_2)$.
2. $f_1(N(\mu, D_1, D_2)) - f_1(N(\mu, D, D))$.
3. $f'_1(N(\mu, D_1, D_2)) - f'_1(N(\mu, D, D))$.
4. $Z(\mu, D_1, D_2) - Z(\mu, D, D)$.
5. $f'_2(\lambda_Z(D_2)) - f'_2(\lambda_Z(D))$.
6. $f''_1(2)(N(\mu, D_1, D_2)) - f''_1(2)(N(\mu, D, D))$.
7. $N'(\mu, D_1, D_2) - N'(\mu, D, D)$.
8. $Z'(\mu, D_1, D_2) - Z'(\mu, D, D)$.

Moreover,

7. $N'(\mu, D_1, D_2) - N'(\mu, D, D)$.
8. $Z'(\mu, D_1, D_2) - Z'(\mu, D, D)$.
Proof of Proposition 5.6. After some reorganization, we have from (13)

\[ p_0(\mu, D_1, D_2) - p_0(D, D, \mu) = -a_3(\mu, D_1, D_2) + a_3(D, D, \mu) \]

\[ = -D_2 f_2'(\lambda Z(D_2)) Z(\mu, D_1, D_2) \left( D + \lambda Z(D_2) f_1'(N(\mu, D_1, D_2)) \right) \]

\[ + D f_2'(\lambda Z(D)) Z(\mu, D, D) \left( D + \lambda Z(D) f_1'(N(\mu, D, D)) \right) \]

\[ = \left( D f_2'(\lambda Z(D)) Z(\mu, D, D) - D_2 f_2'(\lambda Z(D_2)) Z(\mu, D_1, D_2) \right) D \]

\[ + \left[ D f_2'(\lambda Z(D)) Z(\mu, D, D) \lambda Z(D) f_1'(N(\mu, D, D)) \right. \]

\[ \left. - D_2 f_2'(\lambda Z(D_2)) Z(\mu, D_1, D_2) \lambda Z(D_2) f_1'(N(\mu, D_1, D_2)) \right] \].

(33)

To bound \(|p_0(\mu, D_1, D_2) - p_0(D, D, \mu)|\), we bound the absolute values of summands in (33) as follows. First, note \(|D-D_2| \leq \text{dist}((D_1, D_2), (D, D))\), so we bound

\[ |D f_2'(\lambda Z(D)) Z(\mu, D, D) - D_2 f_2'(\lambda Z(D_2)) Z(\mu, D_1, D_2)| \]

by using Lemma 5.5 and Propositions 5.10 and 5.11 to combine the noted bound with bounds 4 and 5 from 5.12; bound

\[ |D f_2'(\lambda Z(D)) Z(\mu, D, D) \lambda Z(D) f_1'(N(\mu, D, D)) - D_2 f_2'(\lambda Z(D_2)) Z(\mu, D_1, D_2) \lambda Z(D_2) f_1'(N(\mu, D_1, D_2))| \]

by combining bounds 1, 3, 4 and 5 with \(|D-D_2| \leq \text{dist}((D_1, D_2), (D, D))\) using Lemma 5.5.

Moving on to part 2, we compute from (33)

\[ p_0'(\mu, D_1, D_2) - p_0'(D, D, \mu) \]

\[ = \left( D f_2'(\lambda Z(D)) Z'(\mu, D, D) - D_2 f_2'(\lambda Z(D_2)) Z'(\mu, D_1, D_2) \right) D \]

\[ + \left[ D f_2'(\lambda Z(D)) Z'(\mu, D, D) \lambda Z(D) f_1'(N(\mu, D, D)) - D_2 f_2'(\lambda Z(D_2)) Z'(\mu, D_1, D_2) \lambda Z(D_2) f_1'(N(\mu, D_1, D_2)) \right] \]

\[ + \left[ D f_2'(\lambda Z(D)) Z(\mu, D, D) \lambda Z(D) f_1'(N(\mu, D, D)) N'(\mu, D, D) - D_2 f_2'(\lambda Z(D_2)) Z(\mu, D_1, D_2) \lambda Z(D_2) f_1'(N(\mu, D_1, D_2)) N'(\mu, D_1, D_2) \right] \].

For \(|p_0'(\mu, D_1, D_2) - p_0'(D, D, \mu)|\), we bound from the first line of the expansion

\[ |D f_2'(\lambda Z(D)) Z'(\mu, D, D) - D_2 f_2'(\lambda Z(D_2)) Z'(\mu, D_1, D_2)| \]

by combining \(|D-D_2| \leq \text{dist}((D_1, D_2), (D, D))\) with bounds 5 and 8 from 5.12; bound from the second and third lines

\[ |D f_2'(\lambda Z(D)) Z'(\mu, D, D) \lambda Z(D) f_1'(N(\mu, D, D)) - D_2 f_2'(\lambda Z(D_2)) Z'(\mu, D_1, D_2) \lambda Z(D_2) f_1'(N(\mu, D_1, D_2))| \]

by combining \(|D-D_2| \leq \text{dist}((D_1, D_2), (D, D))\) with the bounds 1, 3, 5, and 8; bound from the fourth and fifth lines

\[ |D f_2'(\lambda Z(D)) Z(\mu, D, D) \lambda Z(D) f_1'(N(\mu, D, D)) N'(\mu, D, D) - D_2 f_2'(\lambda Z(D_2)) Z(\mu, D_1, D_2) \lambda Z(D_2) f_1'(N(\mu, D_1, D_2)) N'(\mu, D_1, D_2)| \]
Proof of bound 1. By definition and the mean value theorem applied to $D_P$ other hand, because other quantities such as $N$, $P$, and $Z$ depend implicitly on $D$, $D_1$, and $D_2$, the details of the analyses are somewhat lengthy.

Proof of bound 2. Fix $\mu$ in the interval $I$. We may use the mean-value theorem [7, p.103, Corollary 1] for functions of variables $(D_1, D_2)$, obtaining

$$|f_1(N(\mu, D_1, D_2)) - f_1(N(\mu, D, D))| \leq \|\nabla(f_1 \circ N)(\tilde{D}_1, \tilde{D}_2)||\cdot \text{dist}((D_1, D_2), (D, D)),$$

where $(\tilde{D}_1, \tilde{D}_2)$ is a point on the line segment connecting $(D_1, D_2)$ and $(D, D)$.

Therefore, we have to bound the magnitude of the gradient $\|\nabla(f_1 \circ N)(\tilde{D}_1, \tilde{D}_2)||$ in a disc surrounding $(D, D)$ by a constant.

To bound the gradient, we need information on the components, namely, the partial derivatives

$$\partial(f_1 \circ N)/\partial D_1 = f'_1(N) \cdot (\partial N/\partial D_1) \quad \text{and} \quad \partial(f_1 \circ N)/\partial D_2 = f'_1(N) \cdot (\partial N/\partial D_2).$$

We return to the defining equation

$$0 = G_1(N, Z, \mu, D_1, D_2) = D(\mu - N) - f_1(N)\lambda_Z(D_2).$$

Differentiating with respect to $D_1$, we get

$$0 = \partial G_1/\partial D_1 = \partial G_1/\partial N \cdot (\partial N/\partial D_1)$$

$$= (-D - f'_1(N) \cdot \lambda_Z(D_2)) \cdot (\partial N/\partial D_1).$$

Then

$$\frac{\partial N}{\partial D_1}(\mu, D_1, D_2) = 0,$$

since $D + f'_1(N(\mu, D_1, D_2)) \cdot \lambda_Z(D_2) > 0$.

Differentiating with respect to $D_2$

$$0 = \partial G_1/\partial D_2 = \partial(D(\mu - N))/\partial D_2 - \partial(f_1(N)\lambda_Z(D_2))/\partial D_2$$

$$= -D \cdot (\partial N/\partial D_2) - (f'_1(N) \cdot (\partial N/\partial D_2) \cdot \lambda_Z(D_2) + f_1(N)\lambda'_Z(D_2)),$$

so

$$\frac{\partial N}{\partial D_2}(\mu, D_1, D_2) = -\frac{f_1(N(\mu, D_1, D_2))\lambda'_Z(D_2)}{D + f'_1(N(\mu, D_1, D_2)) \cdot \lambda_Z(D_2)}. $$
Now we obtain a bound on the gradient via

\[
\left| \frac{\partial N}{\partial D_2} (\mu, D_1, D_2) \right| = \frac{f_1(N(\mu, D_1, D_2)) \lambda_2(D_2)}{D + f'_1(N(\mu, D_1, D_2)) \cdot \lambda_2(D_2)} < \frac{f_1(N(\mu, D_1, D_2)) \lambda_2(D_2)}{D},
\]

since \( f'_1(N(\mu, D_1, D_2)) \cdot \lambda_2(D_2) > 0 \),

\[
= \frac{f_1(\mu, D_1, D_2)}{D \cdot \gamma_2 \cdot f'_2(\lambda_2(D_2))},
\]

because the relation \( f_2(\lambda_2(D_2)) = D_2/\gamma_2 \) implies \( \lambda_2'(D_2) = 1/(\gamma_2 \cdot f'_2(\lambda_2(D_2))) \).

Finally, \( f'_2(\lambda_2(D_2)) > f'_2(\lambda_2(D)) \) by choice of \( \Delta \) and Lemma 5.9, and \( f_1(N) \) is bounded by hypothesis, so that \( f_1(N(\mu, D_1, D_2)) < B \). Thus,

\[
\left| \frac{\partial N}{\partial D_2} (\mu, D_1, D_2) \right| < \frac{2 \cdot f_1(N(\mu, D_1, D_2))}{D \cdot \gamma_2 \cdot f'_2(\lambda_2(D))} < \frac{2 \cdot B}{D \cdot \gamma_2 \cdot f'_2(\lambda_2(D))}, \tag{34}
\]

and \( |\partial N/\partial D_2(\mu, D_1, D_2)| \) is bounded by a constant in the disc \( \Delta \).

We also observe that \( f'_1(N(\mu, D_1, D_2)) \) is bounded by a constant depending only on \( I \times \Delta \), because of the convexity of the closed disc \( \Delta \) centered at \((D, D)\) from which we choose \((D_1, D_2)\).

Combining all this information, \( \|\nabla(f_1 \circ N)(\hat{D}_1, \hat{D}_2)\| \) is bounded by a constant depending on \( I \times \Delta \). Therefore, \( |f_1(N(\mu, D_1, D_2)) - f_1(N(\mu, D, D))| \) is bounded by a constant times \( \text{dist}((D_1, D_2), (D, D)) \).

**Proofs of bounds 3 and 4.** The ingredients are the same as in the proof of bound 2, but the manipulations differ somewhat.

**Proof of bound 5.** This is very similar to the proof of bound 1.

**Proof of bound 6.** At this point the continuity of \( f_1^{(3)} \) is needed; the remaining details are parallel to the proofs of bounds 2 and 3.

**Proof of bound 7.** For this proof, return to the defining relation for \( N(\mu, D_1, D_2) \), namely,

\[
0 = G_1(N, Z, \mu, D_1, D_2) = D(\mu - N) - f_1(N) \lambda_2(D_2),
\]

and differentiate with respect to \( \mu \), obtaining

\[
0 = D + \left( -D - f'_1(N(\mu, D_1, D_2)) \cdot \lambda_2(D_2) \right) \cdot N'(\mu, D_1, D_2),
\]

so

\[
N'(\mu, D_1, D_2) = \frac{D}{D + f'_1(N(\mu, D_1, D_2)) \cdot \lambda_2(D_2)},
\]
Consequently,

\[
\|N'(\mu, D_1, D_2) - N'(\mu, D, D)\| = \left| \frac{D}{D + f_1'(N(\mu, D_1, D_2)) \cdot \lambda Z(D_2)} - \frac{D}{D + f_1'(N(\mu, D, D)) \cdot \lambda Z(D)} \right| \\
= \left| \frac{D}{D + f_1'(N(\mu, D, D)) \cdot \lambda Z(D) - D f_1'(N(\mu, D_1, D_2)) \cdot \lambda Z(D_2)} \cdot \lambda Z(D) \right| \\
\leq \frac{\|f_1'(N(\mu, D, D)) \cdot \lambda Z(D) - f_1'(N(\mu, D_1, D_2)) \cdot \lambda Z(D_2)\|}{D}. \tag{35}
\]

Applying Lemma 5.5 and (35) with bounds 1 and 3 as input, we see that the quantity \( |N'(\mu, D_1, D_2) - N'(\mu, D, D)| \) is bounded by dist\((D_1, D_2), (D, D)\) times a constant.

\[\square\]

Proof of bound 8. This is similar to the proof of bound 7. \[\square\]

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