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Analysis of Dynamics in a Complex Food Chain with Ratio-Dependent Functional Response

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Abstract In this paper, we study a new model obtained as an extension of a three-species food chain model with ratio-dependent functional response. We provide non-persistence and permanence results and investigate the stability of all possible equilibria in relation to the ecological parameters. Results are obtained for the trivial and prey-only equilibria where the singularity of the model prevents linearization, and the remaining semi-trivial equilibria are studied using linearization. We provide a detailed analysis of conditions for existence, uniqueness, and multiplicity of coexistence equilibria, as well as permanent effect for all species. The complexity of the dynamics in this model is theoretically discussed and graphically demonstrated through various examples and numerical simulations.

Keywords Coexistence and Permanence, local and global stability, asymptotic behavior, population dynamics, ratio-dependent food chain, numerical simulations.

MSC(2010) 34A34, 34C11, 34D20.

1. Introduction

The ratio-dependent predator-prey interaction with Michaelis-Menten-Holling functional response [1,7,9,13] has been used for more than 20 years in various models of population dynamics. These models are based on the biological evidence that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. The three-species food chain (with prey, predator and super-predator) under different functional responses has also been studied in both the ordinary and partial differential equation models. See for example, [2–6,8,10–12,14,17]. Particularly, Hsu et al. [8] studied the asymptotic behavior of the solution of the following simple food chain model with ratio-dependence:

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{c_1 xy}{x+y}, \\ \dfrac{dy}{dt} = \dfrac{m_1 xy}{x+y} - d_2 y - \dfrac{c_2 yz}{y+z}, \\ \dfrac{dz}{dt} = \dfrac{m_2 yz}{y+z} - d_3 z, \\ x(0) > 0,\ y(0) > 0,\ z(0) > 0. \end{cases} \tag{1.1}$$

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In this article, we study an extension of the simple food chain model 1.1 to a more general and complex case: this model has a prey (x) with logistic growth, a predator (y) that consumes the prey with ratio-dependent functional response, and a super-predator (z) that has the ability to consume both the predator and the prey with ratio-dependent functional response:

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{c_1 xy}{x+y} - \dfrac{c_2 xz}{x+z}, \\ \dfrac{dy}{dt} = \dfrac{m_1 xy}{x+y} - d_2 y - \dfrac{c_3 yz}{y+z}, \\ \dfrac{dz}{dt} = \dfrac{m_2 xz}{x+z} + \dfrac{m_3 yz}{y+z} - d_3 z, \\ x(0) > 0,\ y(0) > 0,\ z(0) > 0. \end{cases} \tag{1.2}$$

In the above model, the prey species is scaled to have 1 as its intrinsic growth rate and carrying capacity, c_i are the capturing rates, m_i are the predator growth rates (with $c_i > m_i$), and d_i are the death rates. The ratio-dependent models produce richer and more complicated dynamics, partially because of the mathematical difficulty at the singular point $(0,0,0)$. The purpose of this paper is to analyze and demonstrate the complexity of population dynamics for the three ecological species in the food chain model (1.2). In the beginning of Section 2, we will show that the population function $(x(t), y(t), z(t))$ remains positive as long as the initial population $(x(0), y(0), z(0))$ is positive. We also give some preliminary results on the ultimate upper bounds of the predator and prey populations, as well as a non-persistence result for larger rates c_1, c_2. These results further lead to conditions in Section 3 on the stability of the trivial equilibrium $(0,0,0)$ and semi-trivial equilibrium $(1,0,0)$, which cannot be obtained by linearization method through the Jacobian matrix. In Section 3 we also give necessary conditions for the existence of the equilibria with presence of at least two species and the stability analysis of those semi-trivial equilibria, along with sets of ecological parameters satisfying stability conditions and numerical simulations for the population solutions. In Section 4 we explore the condition of permanence (existence of a positive global attractor) in the extended model (1.2) and study the dynamics in relation to the component-wise positive equilibrium, which indicates the coexistence steady state of all three biological species. Because of the complexity of interactions in model (1.2), it is quite difficult to express and analyze the coexistence equilibrium in terms of all the ecological parameters. We give detailed discussions on the conditions for existence, uniqueness, and multiplicity of this equilibrium, upper and lower bounds for the population sizes, and stability criteria. Several numerical examples are also given to demonstrate unique or multiple coexistence equilibria, and to graphically display the dynamics and pattern of the populations in the ecological system by utilizing the conditions obtained.

2. Ultimate Bounds and Extinction Scenarios

In this section we focus on finding the upper-bound functions for the prey, predator and super-predator populations $x(t)$, $y(t)$ and $z(t)$. These bounds will provide us with crucial information on extinction, co-existence, and exponential convergence of the species.

2.1. Exponential bounds and extinction scenarios

In this section we study the ultimate bounds for the populations in model (1.2). The first theorem concerns the exponential bounds of the predator and super-predator, which leads to conditions for extinction of these populations.

Theorem 2.1. *The population function* $(x(t), y(t), z(t))$ *for solution of model* (1.2) *satisfies*

$$\begin{cases} x(t) > 0 \text{ for } x(0) > 0 \text{ and } \limsup_{t\to\infty} x(t) \le 1, \\ y(0)e^{-(d_2+c_3)t} \le y(t) \le y(0)e^{(m_1-d_2)t}, \\ z(0)e^{-d_3 t} \le z(t) \le z(0)e^{(m_2+m_3-d_3)t}. \end{cases} \tag{2.1}$$

If $m_1 < d_2$*, then the predator population* $y(t)$ *converges to* 0 *exponentially as* $t \to \infty$*. If* $m_2+m_3 < d_3$*, then the super-predator population* $z(t)$ *converges to* 0 *exponentially as* $t \to \infty$*.*

Proof. Recall that the original equation for the prey population is

$$\frac{dx}{dt} = x\,(1-x) - \frac{c_1xy}{x+y} - \frac{c_2xz}{x+z}.$$

The non-negativity of the density functions allows us to obtain the inequality:

$$x(1-c_1-c_2-x) \le \frac{dx}{dt} \le x\,(1-x) \quad \text{in } (0,\infty).$$

We can see from the comparison argument that

$$\limsup_{t\to\infty} x(t) \le 1,$$

and

$$x(t) \ge \frac{(1-c_1-c_2)x(0)}{x(0)+[1-c_1-c_2-x(0)]e^{-(1-c_1-c_2)t}}, \qquad \text{if } c_1+c_2<1,$$
$$x(t) \ge \frac{(c_1+c_2-1)x(0)}{[c_1+c_2-1+x(0)]e^{(c_1+c_2-1)t}-x(0)}, \qquad \text{if } c_1+c_2>1.$$

Also, from the second and third equation in model (1.2), we have

$$(-d_2-c_3)y \le \frac{dy}{dt} \le (m_1-d_2)y,$$

and

$$-d_3z \le \frac{dz}{dt} \le (m_2+m_3-d_3)z.$$

The comparison argument also implies that $y(t)$ and $z(t)$ satisfy the inequalities in (2.1) and remain positive at any finite time. The upper bound $y(0)e^{(m_1-d_2)t}$ for $y(t)$ converges to 0 as $t\to\infty$ when $m_1<d_2$, and the upper bound $z(0)e^{(m_2+m_3-d_3)t}$ for $z(t)$ converges to 0 as $t\to\infty$ when $m_2+m_3<d_3$. □

We observe from the above proof that if $c_1+c_2<1$, then the prey species is persistent with

$$\liminf_{t\to\infty} x(t) \ge 1-c_1-c_2.$$

The following theorem indicates that model (1.2) is not persistent for larger c_1+c_2.

Theorem 2.2. *If $c_1 + c_2 > 1 + \max\{c_3 + d_2, d_3\}$, then there exist positive solutions $(x(t), y(t), z(t))$ of model (1.2) with*

$$\lim_{t\to\infty}(x(t), y(t), z(t)) = (0, 0, 0).$$

Proof. Let $d = \max\{c_3 + d_2, d_3\}$. Assume that $0 < \frac{x(0)}{y(0)}, \frac{x(0)}{z(0)} < \alpha$, where $\alpha > 0$ with $\frac{c_1+c_2}{1+\alpha} > 1 + d$. Let $F(t) = \max\left\{\frac{x(t)}{y(t)}, \frac{x(t)}{z(t)}\right\}$. We claim that for all $t > 0$, $F(t) < \alpha$ and $\lim_{t\to\infty} x(t) = 0$.

By contradiction, assume that $F(T) = \alpha$ and $F(t) < \alpha$ for $0 < t < T$. By standard comparison argument, we then have $\frac{dx}{dt} \le -dx$ for $0 \le t \le T$ and $x(t) \le x(0)e^{-dt}$ for $0 \le t \le T$. From Theorem 2.1, we also know that $y(t) \ge y(0)e^{-(c_3+d_2)t}$ and $z(t) \ge z(0)e^{-d_3 t}$. It follows that $F(t) < \alpha$ on the interval $0 \le t \le T$, contradicting the assumption that $F(T) = \alpha$. It follows that $\frac{dx}{dt} \le -dx$ for $0 < t < \infty$, and we have $\lim_{t\to\infty} x(t) = 0$. Arguing in a similar fashion, we obtain $\lim_{t\to\infty} y(t) = 0$ and $\lim_{t\to\infty} z(t) = 0$ as well. □

2.2. Ultimate upper bounds for the populations

In order to investigate the global boundedness and permanence effect (in Section 4) of the populations in the food-chain model when $m_1 > d_2$ and $m_2 + m_3 > d_3$, we follow the approach of Pao in [15], defining a pair of upper-lower solutions $(\tilde{x}, \tilde{y}, \tilde{z})$ and $(\hat{x}, \hat{y}, \hat{z})$ for system (1.2) satisfying the following differential inequalities:

$$\begin{aligned}
\frac{d\tilde{x}}{dt} &\ge \tilde{x}(1-\tilde{x}) - \frac{c_1\tilde{x}\hat{y}}{\tilde{x}+\hat{y}} - \frac{c_2\tilde{x}\hat{z}}{\tilde{x}+\hat{z}},\\
\frac{d\tilde{y}}{dt} &\ge \frac{m_1\tilde{x}\tilde{y}}{\tilde{x}+\tilde{y}} - d_2\tilde{y} - \frac{c_3\tilde{y}\hat{z}}{\tilde{y}+\hat{z}},\\
\frac{d\tilde{z}}{dt} &\ge \frac{m_2\tilde{x}\tilde{z}}{\tilde{x}+\tilde{z}} + \frac{m_3\tilde{y}\tilde{z}}{\tilde{y}+\tilde{z}} - d_3\tilde{z},\\
\frac{d\hat{x}}{dt} &\le \hat{x}(1-\hat{x}) - \frac{c_1\hat{x}\tilde{y}}{\hat{x}+\tilde{y}} - \frac{c_2\hat{x}\tilde{z}}{\hat{x}+\tilde{z}},\\
\frac{d\hat{y}}{dt} &\le \frac{m_1\hat{x}\hat{y}}{\hat{x}+\hat{y}} - d_2\hat{y} - \frac{c_3\hat{y}\tilde{z}}{\hat{y}+\tilde{z}},\\
\frac{d\hat{z}}{dt} &\le \frac{m_2\hat{x}\hat{z}}{\hat{x}+\hat{z}} + \frac{m_3\hat{y}\hat{z}}{\hat{y}+\hat{z}} - d_3\hat{z},
\end{aligned} \tag{2.2}$$

and with $(\tilde{x}(t), \tilde{y}(t), \tilde{z}(t)) \ge (\hat{x}(t), \hat{y}(t), \hat{z}(t))$ for all $t \ge 0$. It is well-known by comparison arguments in differential equation systems (see [15]) that if there exists a pair of upper-lower solutions, then the solution of model (1.2) satisfies

$$(\tilde{x}(t), \tilde{y}(t), \tilde{z}(t)) \ge (x(t), y(t), z(t)) \ge (\hat{x}(t), \hat{y}(t), \hat{z}(t))$$

for all $t > 0$ as long as

$$(\tilde{x}(0), \tilde{y}(0), \tilde{z}(0)) \ge (x(0), y(0), z(0)) \ge (\hat{x}(0), \hat{y}(0), \hat{z}(0)).$$

The three inequalities in (2.2) for lower solutions can be easily satisfied by setting

$$(\hat{x}(t), \hat{y}(t), \hat{z}(t)) = (0, 0, 0),$$

which gives the nonnegativity of the populations. For ultimate upper bounds of the populations, it suffices to suitably construct upper solutions $(\tilde{x}(t), \tilde{y}(t), \tilde{z}(t))$ with $(\tilde{x}(0), \tilde{y}(0), \tilde{z}(0)) = (x(0), y(0), z(0))$.

Theorem 2.3. *Assume that* $m_1 > d_2$ *and* $m_2 + m_3 > d_3$.
If $(x(0), y(0), z(0)) > (0,0,0)$, *then the population function* $(x(t), y(t), z(t))$ *as solution of model (1.2) remains nonnegative and satisfies*

$$\begin{cases} \limsup_{t\to\infty} x(t) \le 1, \\ \limsup_{t\to\infty} y(t) \le \dfrac{m_1 - d_2}{d_2}, \\ \limsup_{t\to\infty} z(t) \le \dfrac{B + \sqrt{B^2 + 4d_2d_3(m_1-d_2)(m_2+m_3-d_3)}}{2d_2d_3}, \\ \text{where } B = m_1(m_3 - d_3) + d_2(m_2 - m_3). \end{cases} \tag{2.3}$$

Proof. By setting $(\hat{x}(t), \hat{y}(t), \hat{z}(t)) = (0,0,0)$, we can find an upper solution $\tilde{x}$ for $x(t)$ in model (1.2) that satisfies

$$\frac{d\tilde{x}}{dt} = \tilde{x}(1 - \tilde{x}),\ \ \tilde{x}(0) = x(0). \tag{2.4}$$

It is known through a simple stability analysis of the Logistic equation that

$$\limsup_{t\to\infty} x(t) \le \lim_{t\to\infty} \tilde{x}(t) = 1. \tag{2.5}$$

For any $\epsilon > 0$, there exists a $T_\epsilon > 0$ such that

$$\frac{dy}{dt} \le \frac{m_1 y}{1+y} - d_2 y + \epsilon \ \ \text{in } (T_\epsilon, \infty).$$

From the arbitrariness of ϵ, we can find an upper solution $\tilde{y}$ for $y(t)$ in (T_ϵ, ∞),

$$\frac{d\tilde{y}}{dt} = \frac{m_1\tilde{y}}{1+\tilde{y}} - d_2\tilde{y},\ \ \tilde{y}(T_\epsilon) = y(T_\epsilon). \tag{2.6}$$

Seeing that for $m_1 > d_2$ the positive equilibrium $\dfrac{m_1 - d_2}{d_2}$ for (2.6) is globally asymptotically stable, we can also conclude that

$$\limsup_{t\to\infty} y(t) \le \lim_{t\to\infty} \tilde{y}(t) = \frac{m_1 - d_2}{d_2}. \tag{2.7}$$

Finally, by the ultimate upper bounds for $x(t)$ and $y(t)$ given in (2.5) and (2.7), we see that for any $\epsilon > 0$, there exists a $T_\epsilon^* > 0$ such that

$$\frac{dz}{dt} \le \frac{m_2 z}{1+z} + \frac{m_3(m_1-d_2)z}{(m_1-d_2)+d_2 z} - d_3 z + \epsilon \ \ \text{in } (T_\epsilon^*, \infty).$$

Again from the arbitrariness of ϵ, we can find an upper solution $\tilde{z}$ for $z(t)$ in (T_ϵ^*, ∞),

$$\frac{d\tilde{z}}{dt} = \frac{m_2\tilde{z}}{1+\tilde{z}} + \frac{m_3(m_1-d_2)\tilde{z}}{(m_1-d_2)+d_2\tilde{z}} - d_3\tilde{z},\ \ \tilde{z}(T_\epsilon^*) = z(T_\epsilon^*). \tag{2.8}$$

When $m_1 > d_2$ and $m_2 + m_3 > d_3$, the nonlinear equation (2.8) has only one positive equilibrium $\dfrac{B + \sqrt{B^2 + 4d_2d_3(m_1 - d_2)(m_2 + m_3 - d_3)}}{2d_2d_3}$ (with B given in (2.3)) which is globally asymptotically stable. This implies that

$$\limsup_{t\to\infty} z(t) \le \lim_{t\to\infty} \tilde{z}(t) = \frac{B + \sqrt{B^2 + 4d_2d_3(m_1 - d_2)(m_2 + m_3 - d_3)}}{2d_2d_3}. \tag{2.9}$$

□

3. Stability Analysis for Trivial and Semi-Trivial Equilibria

In this section, we study the stability of all the trivial and semi-trivial equilibria of model (1.2). Those equilibria are:

1. $E_1 = (0, 0, 0)$
2. $E_2 = (1, 0, 0)$
3. $E_3 = \left(\dfrac{m_1 - c_1(m_1 - d_2)}{m_1}, \dfrac{(m_1 - d_2)[m_1 - c_1(m_1 - d_2)]}{m_1 d_2}, 0\right)$,
   where we must have $m_1 > d_2$ and $\frac{m_1}{m_1 - d_2} > c_1$ to ensure that this equilibrium is non-negative
4. $E_4 = \left(\dfrac{m_2 - c_2(m_2 - d_3)}{m_2}, 0, \dfrac{(m_2 - d_3)[m_2 - c_2(m_2 - d_3)]}{m_2 d_3}\right)$,
   where we must have $m_2 > d_3$ and $\frac{m_2}{m_2 - d_3} > c_2$ to ensure that this equilibrium is non-negative

3.1. Stability of the trivial equilibrium E_1

Since model (1.2) has a singularity at $(0, 0, 0)$, we cannot obtain stability results for the trivial equilibrium by linearization through the Jacobian matrix. Note, however, that when $c_1 + c_2 < 1$, refinement of the comparison argument in the proof of Theorem 2.1, yields that

$$\liminf_{t\to\infty} x(t) \ge 1 - c_1 - c_2 > 0.$$

Hence we have the following instability result.

Theorem 3.1. *The trivial equilibrium $E_1 = (0, 0, 0)$ for model (1.2) is unstable when $c_1 + c_2 < 1$.*

If $c_1 + c_2 > 1 + \max\{c_3 + d_2, d_3\}$, then by Theorem 2.2 we have that

$$\lim_{t\to\infty} (x(t), y(t), z(t)) = (0, 0, 0).$$

When the initial population $x(0)$ is relatively smaller than $y(0)$ and $z(0)$. However, the restrictions on the ratio of initial population sizes required in the proof of Theorem 2.2 do not allow us to obtain even local asymptotic stability for the trivial equilibrium.

3.2. Stability of the prey-only equilibrium E_2

We are able to obtain conditions for global asymptotic stability of the prey-only equilibrium $E_2 = (1, 0, 0)$, though we still cannot use a linearization approach.

Theorem 3.2. *The second equilibrium $E_2 = (1, 0, 0)$ for model (1.2) is:*

1. *unstable if $c_1 + c_2 > 1 + \max\{c_3 + d_2, d_3\}$*
2. *globally asymptotically stable if $c_1 + c_2 < 1$, $m_1 < d_2$, and $m_2 + m_3 < d_3$.*

Proof. If $c_1 + c_2 > 1 + \max\{c_3 + d_2, d_3\}$, then by Theorem 2.2 we know that there exist solutions of model (1.2) with $(x(0), y(0), z(0))$ arbitrarily close to $(0, 0, 0)$ such that

$$\lim_{t\to\infty} (x(t), y(t), z(t)) = (0, 0, 0).$$

If $c_1 + c_2 < 1$, $m_1 < d_2$, and $m_2 + m_3 < d_3$, then from Theorem 2.1, we know that

$$\lim_{t\to\infty} y(t) = \lim_{t\to\infty} z(t) = 0,$$

and from the proof of Theorem 3.1 we know that

$$\liminf_{t\to\infty} x(t) \geq 1 - c_1 - c_2 > 0.$$

Thus for each $\epsilon > 0$, there exists $T_\epsilon > 0$ such that

$$x\left[(1 - x) - \frac{c_1 + c_2}{1 - c_1 - c_2}\epsilon\right] \leq \frac{dx}{dt} \leq x(1 - x)$$

for $t \geq T_\epsilon$. By comparison argument we then have that

$$1 - \left(\frac{c_1 + c_2}{1 - c_1 - c_2}\right)\epsilon \leq x(t) \leq 1$$

for $t \geq T_\epsilon$. Since $\epsilon > 0$ is arbitrary, we obtain that $\lim_{t\to\infty} x(t) = 1$. □

Example 3.1. We illustrate the asymptotic stability of the equilibrium E_2 through numerical simulations of model (1.2), with parameters:

$$\{c_1 = .41, c_2 = .49, c_3 = .15, d_2 = .25, d_3 = .4, m_1 = .3, m_2 = .25, m_3 = .23\}.$$

These ecological parameters satisfy the conditions of part 2 of Theorem 3.2, so the prey-only equilibrium $(1, 0, 0)$ is asymptotically stable.

With initial populations $x(0) = .2$, $y(0) = .3$, $z(0) = .4$, the numerical simulation of model (1.2) depicted in Figure 1 shows the convergence of the solution to this equilibrium.

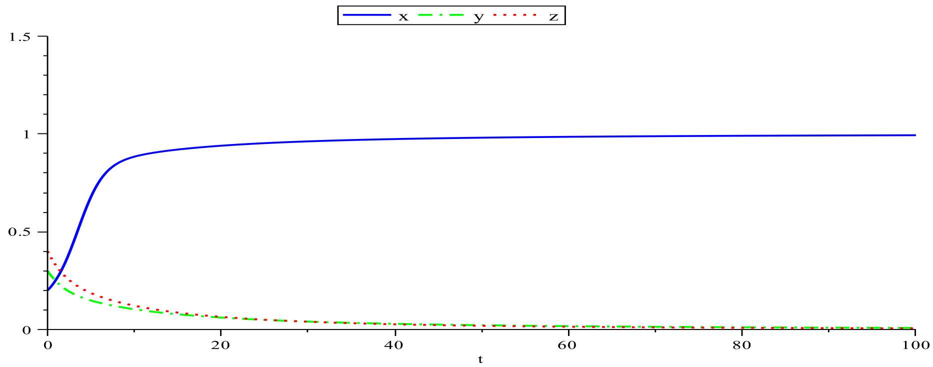

Figure 1. Asymptotically stable prey-only equilibrium

3.3. Stability of the absence-of-super-predator equilibrium E_3

The Jacobian matrix $J(x, y, z)$ for the food chain model (1.2) is:

$$\begin{bmatrix} 1-2x-\dfrac{c_1y^2}{(x+y)^2}-\dfrac{c_2z^2}{(x+z)^2} & -\dfrac{c_1x^2}{(x+y)^2} & -\dfrac{c_2x^2}{(x+z)^2} \\ \dfrac{m_1y^2}{(x+y)^2} & \dfrac{m_1x^2}{(x+y)^2}-\dfrac{c_3z^2}{(y+z)^2}-d_2 & -\dfrac{c_3y^2}{(y+z)^2} \\ \dfrac{m_2z^2}{(x+z)^2} & \dfrac{m_3z^2}{(y+z)^2} & \dfrac{m_2x^2}{(x+z)^2}+\dfrac{m_3y^2}{(y+z)^2}-d_3 \end{bmatrix}. \tag{3.1}$$

Theorem 3.3. *If* $\frac{m_1}{c_1} > m_1 - d_2 > 0$*, then model (1.2) has its third equilibrium*

$$E_3 = \left(\frac{m_1 - c_1(m_1 - d_2)}{m_1}, \frac{(m_1 - d_2)[m_1 - c_1(m_1 - d_2)}{m_1 d_2}, 0 \right).$$

This equilibrium E_3 *with absence of super-predator is:*

1. *unstable if* $m_2 + m_3 > d_3$
2. *asymptotically stable if* $m_2 + m_3 < d_3$.

Proof. The Jacobian matrix for the equilibrium E_3 is:

$$\begin{bmatrix} \frac{m_1^2c_1-m_1^2-c_1d_2^2}{m_1^2} & -\frac{c_1d_2^2}{m_1^2} & -c_2 \\ \frac{(d_2-m_1)^2}{m_1} & \frac{(d_2-m_1)d_2}{m_1} & -c_3 \\ 0 & 0 & m_2+m_3-d_3 \end{bmatrix}. \tag{3.2}$$

The eigenvalues of the Jacobian in (3.2) are: $\lambda_1 = m_2 + m_3 - d_3$, λ_2 and λ_3 are the roots of the quadratic equation

$$m_1^2\lambda^2 + [(m_1^2(1-c_1) + m_1d_2(m_1-d_2) + c_1d_2^2]\lambda + d_2(m_1-d_2)[m_1(1-c_1) + c_1d_2].$$

Observe that the coefficient of λ and the constant term are both positive. This implies either λ_2 and λ_3 are both real and negative, or are both complex with negative real parts.

We see that when $m_2 + m_3 > d_3$, we have $\lambda_1 > 0$, which indicates that E_3 is unstable. On the other hand, when $m_2 + m_3 < d_3$, we have $\lambda_1 < 0$ and conclude that E_3 is asymptotically stable. □

Example 3.2. We illustrate the asymptotic stability of the equilibrium E_3 through numerical simulations of model (1.2) with parameters:

$$\{c_1 = 0.41, c_2 = 0.49, c_3 = 0.153, d_2 = 0.25, d_3 = 0.5,$$
$$m_1 = 0.3, m_2 = 0.25, m_3 = 0.23\}.$$

These ecological parameters satisfy the conditions for asymptotic stability given in Theorem 2.4, so the equilibrium with absence of super-predator $(0.932, 0.185, 0)$ is asymptotically stable.

With initial populations $x(0) = .2$, $y(0) = .3$, $z(0) = .4$, the numerical simulation of model (1.2) demonstrated in Figure 2 shows the convergence of the solution to this equilibrium.

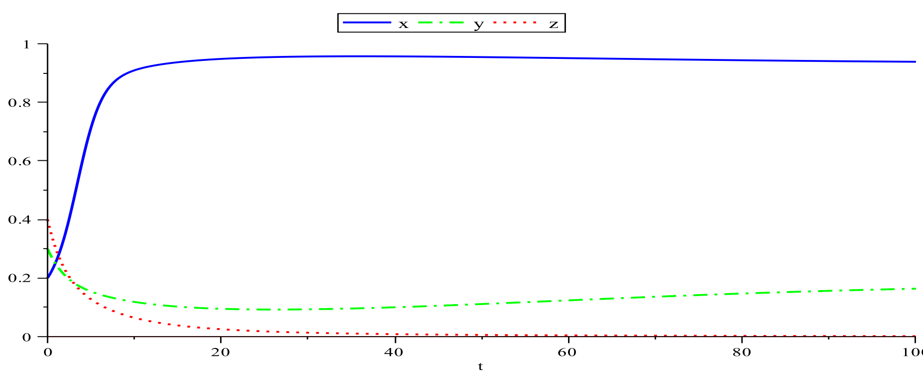

Figure 2. Asymptotically stable absence-of-super-predator equilibrium

3.4. Stability of the absence-of-predator equilibrium E_4

Theorem 3.4. *If $\frac{m_2}{c_2} > m_2 - d_3 > 0$, then model (1.2) has its fourth equilibrium*

$$E_4 = \left(\frac{m_2 - c_2(m_2 - d_3)}{m_2}, 0, \frac{(m_2 - d_3)[m_2 - c_2(m_2 - d_3)]}{m_2 d_3} \right).$$

This equilibrium E_4 with absence of predator is:

1. *unstable if $m_1 > d_2 + c_3$*
2. *asymptotically stable if $m_1 < d_2 + c_3$.*

Proof. The Jacobian matrix for E_4 is:

$$\begin{bmatrix} \frac{m_2^2 c_2 - m_2^2 - c_2 d_3^2}{m_2^2} & -c_1 & -\frac{c_2 d_3^2}{m_2^2} \\ 0 & m_1 - c_3 - d_2 & 0 \\ \frac{(d_3 - m_2)^2}{m_2} & m_3 & \frac{(d_2 - m_2) d_3}{m_2} \end{bmatrix}. \tag{3.3}$$

The eigenvalues of the Jacobian in (3.3) are: $\lambda_1 = m_1 - c_3 - d_2$, λ_2 and λ_3 are the roots of the quadratic equation

$$m_2^2\lambda^2 + [(m_2^2(1-c_2) + m_2 d_3(m_2 - d_3) + c_2 d_3^2]\lambda + d_3(m_2 - d_3)[m_2(1-c_2) + c_2 d_3].$$

The coefficient of λ and the constant term are both positive, so λ_2 and λ_3 are both negative, or both have negative real parts. When $m_1 > c_3 + d_2$, we have $\lambda_1 > 0$ which indicates that E_4 is unstable. On the other hand, when $m_1 < c_3 + d_2$, we have $\lambda_1 < 0$ and conclude that E_4 is asymptotically stable. □

Example 3.3. We illustrate the asymptotic stability of the equilibrium E_4 through numerical simulations of model (1.2) with parameters:

$$\{c_1 = 0.41, c_2 = 0.49, c_3 = 0.153, d_2 = 0.25, d_3 = 0.15,$$
$$m_1 = 0.30, m_2 = 0.25, m_3 = 0.23\}.$$

These ecological parameters satisfy the conditions for asymptotic stability given in Theorem 3.4, so the equilibrium with absence of predator $(0.804, 0, 0.536)$ is asymptotically stable.

With initial populations $x(0) = 0.2$, $y(0) = 0.3$, $z(0) = 0.4$, the numerical simulation of model (1.2) demonstrated in Figure 3 shows the convergence of the solution to this equilibrium.

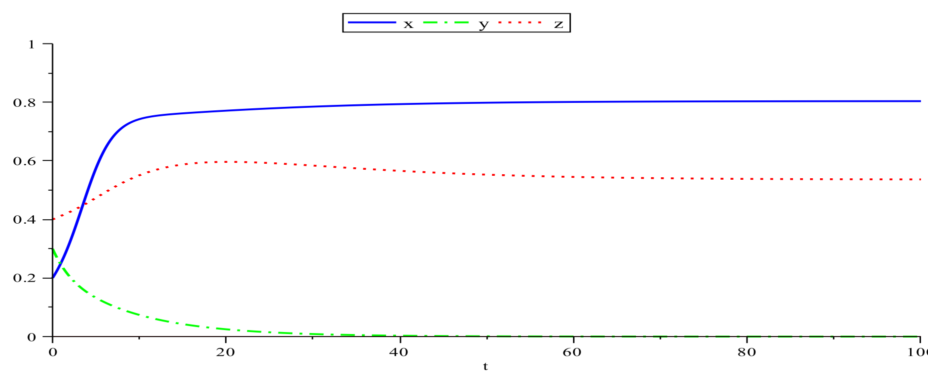

Figure 3. Asymptotically stable absence-of-predator equilibrium

4. Permanence and Coexistence Equilibria

It is seen in the previous section that when $m_2 + m_3 > d_3$ and $m_1 > d_2 + c_3$, the semi-trivial equilibria E_3 and E_4 are both unstable. We first show that in this case, the food chain model (1.2) is permanent with all populations ultimately bounded away from 0 provided that $c_1 + c_2 < 1$. Therefore, the conditions in the following proposition also imply the instability of all trivial and semi-trivial equilibria discussed in Section 3.

Proposition 4.1. *Assume that $m_1 > d_2 + c_3$, $m_2 + m_3 > d_3$, and $c_1 + c_2 < 1$. If $(x(0), y(0), z(0)) > (0, 0, 0)$, then the population function $(x(t), y(t), z(t))$ as solution* *of model (1.2) satisfies*

$$\begin{cases} \liminf_{t\to\infty} x(t) \geq 1 - c_1 - c_2, \\ \liminf_{t\to\infty} y(t) \geq \dfrac{m_1 - d_2 - c_3}{d_2 + c_3}(1 - c_1 - c_2), \\ \liminf_{t\to\infty} z(t) \geq \dfrac{b + \sqrt{b^2 + 4d_3(d_2 + c_3)(m_1 - d_2 - c_3)(m_2 + m_3 - d_3)}}{2d_3(d_2 + c_3)}(1 - c_1 - c_2), \\ \text{where } b = m_1(m_3 - d_3) + (d_2 + c_3)(m_2 - m_3). \end{cases} \tag{4.1}$$

Proof. The upper and lower solutions for model (1.2) serve as upper and lower bounds of the populations $(x(t), y(t), z(t))$ in respective time intervals. From the nonnegativity of the populations, we see that a lower solution for $x(t)$ can be obtained by the Logistic equation

$$\frac{d\hat{x}}{dt} \geq \hat{x}(1 - c_1 - c_2 - \hat{x}) \text{ in } (0, \infty),\ \hat{x}(0) = x(0). \tag{4.2}$$

By the assumption that $c_1 + c_2 < 1$, we have

$$\liminf_{t\to\infty} x(t) \geq \lim_{t\to\infty} \hat{x}(t) = 1 - c_1 - c_2 > 0. \tag{4.3}$$

Also using the nonnegativity of $z(t)$, for any $\epsilon > 0$ there exists a $T_\epsilon > 0$ such that

$$\frac{dy}{dt} \geq \frac{m_1(1 - c_1 - c_2)y}{1 - c_1 - c_2 + y} - (d_2 + c_3)y + \epsilon \text{ in } (T_\epsilon, \infty).$$

From the arbitrariness of ϵ, we can find an lower solution $\hat{y}$ for $y(t)$ in (T_ϵ, ∞),

$$\frac{d\hat{y}}{dt} = \frac{m_1(1 - c_1 - c_2)y}{1 - c_1 - c_2 + y} - (d_2 + c_3)y,\ \tilde{y}(T_\epsilon) = y(T_\epsilon). \tag{4.4}$$

Seeing that the nontrivial equilibrium $\dfrac{m_1 - d_2 - c_3}{d_2 + c_3}(1 - c_1 - c_2) > 0$ when $m_1 > d_2 + c_3$ for (4.4) is globally asymptotically stable, we can also conclude that

$$\liminf_{t\to\infty} y(t) \geq \lim_{t\to\infty} \hat{y}(t) = \frac{m_1 - d_2 - c_3}{d_2 + c_3}(1 - c_1 - c_2) > 0. \tag{4.5}$$

Finally, by the ultimate lower bounds for $x(t)$ and $y(t)$ obtained in (4.3) and (4.5), we see that for any $\epsilon > 0$, there exists a $T_\epsilon^* > 0$ such that

$$\frac{dz}{dt} \geq \frac{m_2 z}{1 - c_1 - c_2 + z} + \frac{m_3(m_1 - d_2 - c_3)(1 - c_1 - c_2)z}{(m_1 - d_2 - c_3)(1 - c_1 - c_2) + (d_2 + c_3)z} - d_3 z + \epsilon \text{ in } (T_\epsilon^*, \infty).$$

Again from the arbitrariness of ϵ, we can find an upper solution $\hat{z}$ for $z(t)$ in (T_ϵ^*, ∞).

$$\begin{aligned} &\frac{d\hat{z}}{dt} = \frac{m_2\hat{z}}{1 - c_1 - c_2 + \hat{z}} + \frac{m_3(m_1 - d_2 - c_3)(1 - c_1 - c_2)\hat{z}}{(m_1 - d_2 - c_3)(1 - c_1 - c_2) + (d_2 + c_3)\hat{z}} - d_3\hat{z}, \\ &\hat{z}(T_\epsilon^*) = z(T_\epsilon^*). \end{aligned} \tag{4.6}$$

When $m_1 > d_2 - c_3$ and $m_2 + m_3 > d_3$, the nonlinear equation (4.6) has only one positive equilibrium (with $b = m_1(m_3 - d_3) + (d_2 + c_3)(m_2 - m_3)$)

$$\frac{b + \sqrt{b^2 + 4d_3(d_2 + c_3)(m_1 - d_2 - c_3)(m_2 + m_3 - d_3)}}{2d_3(d_2 + c_3)}(1 - c_1 - c_2),$$

which is globally asymptotically stable. This implies that

$$\begin{aligned}\liminf_{t\to\infty} z(t) &\geq \lim_{t\to\infty} \hat{z}(t) \\ &= \frac{b + \sqrt{b^2 + 4d_3(d_2 + c_3)(m_1 - d_2 - c_3)(m_2 + m_3 - d_3)}}{2d_3(d_2 + c_3)}(1 - c_1 - c_2) \\ &> 0. \end{aligned} \tag{4.7}$$

□

When the conditions in Proposition 4.1 hold, the obtained ultimate lower bounds and the ultimate upper bounds given in Theorem 2.3 form a positive global attractor for the food-chain model (1.2) so that the ecological system is permanent. Define

$$\begin{cases} \underline{X}^{(0)} = 1 - c_1 - c_2, \\ \overline{X}^{(0)} = 1, \\ \underline{Y}^{(0)} = \dfrac{m_1 - d_2 - c_3}{d_2 + c_3}(1 - c_1 - c_2), \\ \overline{Y}^{(0)} = \dfrac{m_1 - d_2}{d_2}, \\ \underline{Z}^{(0)} = \dfrac{b + \sqrt{b^2 + 4d_3(d_2 + c_3)(m_1 - d_2 - c_3)(m_2 + m_3 - d_3)}}{2d_3(d_2 + c_3)}(1 - c_1 - c_2), \\ \overline{Z}^{(0)} = \dfrac{B + \sqrt{B^2 + 4d_2d_3(m_1 - d_2)(m_2 + m_3 - d_3)}}{2d_2d_3}, \\ b = m_1(m_3 - d_3) + (d_2 + c_3)(m_2 - m_3), \ B = m_1(m_3 - d_3) + d_2(m_2 - m_3). \end{cases} \tag{4.8}$$

It is already proven that

$$\begin{aligned}(\underline{X}^{(0)}, \underline{Y}^{(0)}, \underline{Z}^{(0)}) &\leq \liminf_{t\to\infty}(x(t), y(t), z(t)) \\ &\leq \limsup_{t\to\infty}(x(t), y(t), z(t)) \leq (\overline{X}^{(0)}, \overline{Y}^{(0)}, \overline{Z}^{(0)}). \end{aligned} \tag{4.9}$$

For any $\epsilon > 0$ there exists a $T_\epsilon > 0$ such that in (T_ϵ, ∞),

$$\begin{cases} \dfrac{dx}{dt} \leq x(1 - x) - \dfrac{c_1\underline{Y}^{(0)}x}{x + \underline{Y}^{(0)}} - \dfrac{c_2\underline{Z}^{(0)}x}{x + \underline{Z}^{(0)}} + \epsilon, \\ \dfrac{dx}{dt} \geq x(1 - x) - \dfrac{c_1\overline{Y}^{(0)}x}{x + \overline{Y}^{(0)}} - \dfrac{c_2\overline{Z}^{(0)}x}{x + \overline{Z}^{(0)}} - \epsilon, \\ \dfrac{dy}{dt} \leq \dfrac{m_1\overline{X}^{(0)}y}{\overline{X}^{(0)} + y} - d_2y - \dfrac{c_3y\underline{Z}^{(0)}}{y + \underline{Z}^{(0)}} + \epsilon, \\ \dfrac{dy}{dt} \geq \dfrac{m_1\underline{X}^{(0)}y}{\underline{X}^{(0)} + y} - d_2y - \dfrac{c_3y\overline{Z}^{(0)}}{y + \overline{Z}^{(0)}} - \epsilon, \\ \dfrac{dz}{dt} \leq \dfrac{m_2\overline{X}^{(0)}z}{\overline{X}^{(0)} + z} + \dfrac{m_3\overline{Y}^{(0)}z}{\overline{Y}^{(0)} + z} - d_3z + \epsilon, \\ \dfrac{dz}{dt} \geq \dfrac{m_2\underline{X}^{(0)}z}{\underline{X}^{(0)} + z} + \dfrac{m_3\underline{Y}^{(0)}z}{\underline{Y}^{(0)} + z} - d_3z - \epsilon. \end{cases} \tag{4.10}$$

One can uniquely solve for the new values of ultimate bounds $(\underline{X}^{(1)}, \underline{Y}^{(1)}, \underline{Z}^{(1)})$ and $(\overline{X}^{(1)}, \overline{Y}^{(1)}, \overline{Z}^{(1)})$ from the following system:

$$\begin{cases} 1-\overline{X}^{(1)}-\dfrac{c_1\underline{Y}^{(0)}}{\overline{X}^{(1)}+\underline{Y}^{(0)}}-\dfrac{c_2\underline{Z}^{(0)}}{\overline{X}^{(1)}+\underline{Z}^{(0)}}=0, \\ 1-\underline{X}^{(1)}-\dfrac{c_1\overline{Y}^{(0)}}{\underline{X}^{(1)}+\overline{Y}^{(0)}}-\dfrac{c_2\overline{Z}^{(0)}}{\underline{X}^{(1)}+\overline{Z}^{(0)}}=0, \\ \dfrac{m_1\overline{X}^{(0)}}{\overline{X}^{(0)}+\overline{Y}^{(1)}}-d_2-\dfrac{c_3\underline{Z}^{(0)}}{\overline{Y}^{(1)}+\underline{Z}^{(0)}}=0, \\ \dfrac{m_1\underline{X}^{(0)}}{\underline{X}^{(0)}+\underline{Y}^{(1)}}-d_2-\dfrac{c_3\overline{Z}^{(0)}}{\underline{Y}^{(1)}+\overline{Z}^{(0)}}=0, \\ \dfrac{m_2\overline{X}^{(0)}}{\overline{X}^{(0)}+\overline{Z}^{(1)}}+\dfrac{m_3\overline{Y}^{(0)}}{\overline{Y}^{(0)}+\overline{Z}^{(1)}}-d_3=0, \\ \dfrac{m_2\underline{X}^{(0)}}{\underline{X}^{(0)}+\underline{Z}^{(1)}}+\dfrac{m_3\underline{Y}^{(0)}}{\underline{Y}^{(0)}+\underline{Z}^{(1)}}-d_3=0. \end{cases} \tag{4.11}$$

By the arbitrariness of ϵ and the stability analysis of each single equation related to the inequalities in (4.10), we see that each of the unique positive steady-state value solved in (4.11) is globally asymptotically stable in the respective differential equation. The comparison argument implies that

$$\begin{aligned}(\underline{X}^{(0)}, \underline{Y}^{(0)}, \underline{Z}^{(0)}) &\le (\underline{X}^{(1)}, \underline{Y}^{(1)}, \underline{Z}^{(1)}) \\ &\le \liminf_{t\to\infty}(x(t), y(t), z(t)) \le \limsup_{t\to\infty}(x(t), y(t), z(t)) \\ &\le (\overline{X}^{(1)}, \overline{Y}^{(1)}, \overline{Z}^{(1)}) \le (\overline{X}^{(0)}, \overline{Y}^{(0)}, \overline{Z}^{(0)}).\end{aligned} \tag{4.12}$$

Through induction, it can be shown that two monotone sequences $(\underline{X}^{(n)}, \underline{Y}^{(n)}, \underline{Z}^{(n)})$ and $(\overline{X}^{(n)}, \overline{Y}^{(n)}, \overline{Z}^{(n)})$ will be generated such that

$$\begin{cases} 1-\overline{X}^{(n+1)}-\dfrac{c_1\underline{Y}^{(n)}}{\overline{X}^{(n+1)}+\underline{Y}^{(n)}}-\dfrac{c_2\underline{Z}^{(n)}}{\overline{X}^{(n+1)}+\underline{Z}^{(n)}}=0, \\ 1-\underline{X}^{(n+1)}-\dfrac{c_1\overline{Y}^{(n)}}{\underline{X}^{(n+1)}+\overline{Y}^{(n)}}-\dfrac{c_2\overline{Z}^{(n)}}{\underline{X}^{(n+1)}+\overline{Z}^{(n)}}=0, \\ \dfrac{m_1\overline{X}^{(n)}}{\overline{X}^{(n)}+\overline{Y}^{(n+1)}}-d_2-\dfrac{c_3\underline{Z}^{(n)}}{\overline{Y}^{(n+1)}+\underline{Z}^{(n)}}=0, \\ \dfrac{m_1\underline{X}^{(n)}}{\underline{X}^{(n)}+\underline{Y}^{(n+1)}}-d_2-\dfrac{c_3\overline{Z}^{(n)}}{\underline{Y}^{(n+1)}+\overline{Z}^{(n)}}=0, \\ \dfrac{m_2\overline{X}^{(n)}}{\overline{X}^{(n)}+\overline{Z}^{(n+1)}}+\dfrac{m_3\overline{Y}^{(n)}}{\overline{Y}^{(n)}+\overline{Z}^{(n+1)}}-d_3=0, \\ \dfrac{m_2\underline{X}^{(n)}}{\underline{X}^{(n)}+\underline{Z}^{(n+1)}}+\dfrac{m_3\underline{Y}^{(n)}}{\underline{Y}^{(n)}+\underline{Z}^{(n+1)}}-d_3=0. \end{cases} \tag{4.13}$$

Moreover, they are ultimate upper and lower bounds for $(x(t), y(t), z(t))$ in model (1.2).

$$\begin{aligned}(\underline{X}^{(n)}, \underline{Y}^{(n)}, \underline{Z}^{(n)}) &\leq (\underline{X}^{(n+1)}, \underline{Y}^{(n+1)}, \underline{Z}^{(n+1)}) \\ &\leq \liminf_{t\to\infty}(x(t), y(t), z(t)) \leq \limsup_{t\to\infty}(x(t), y(t), z(t)) \\ &\leq (\overline{X}^{(n+1)}, \overline{Y}^{(n+1)}, \overline{Z}^{(n+1)}) \leq (\overline{X}^{(n)}, \overline{Y}^{(n)}, \overline{Z}^{(n)}). \end{aligned} \tag{4.14}$$

Since the non-decreasing sequence $(\underline{X}^{(n)}, \underline{Y}^{(n)}, \underline{Z}^{(n)})$ and non-increasing sequence $(\overline{X}^{(n)}, \overline{Y}^{(n)}, \overline{Z}^{(n)})$ are both bounded by $(\underline{X}^{(0)}, \underline{Y}^{(0)}, \underline{Z}^{(0)})$ and $(\overline{X}^{(0)}, \overline{Y}^{(0)}, \overline{Z}^{(0)})$, $(\underline{X}^{(n)}, \underline{Y}^{(n)}, \underline{Z}^{(n)})$ converges to $(\underline{X}, \underline{Y}, \underline{Z})$ and $(\overline{X}^{(n)}, \overline{Y}^{(n)}, \overline{Z}^{(n)})$ converges to $(\overline{X}, \overline{Y}, \overline{Z})$. By letting $n \to \infty$ in (4.13) and (4.14) we can conclude that

$$\begin{cases} 1 - \overline{X} - \dfrac{c_1\underline{Y}}{\overline{X} + \underline{Y}} - \dfrac{c_2\underline{Z}}{\overline{X} + \underline{Z}} = 0, \\ 1 - \underline{X} - \dfrac{c_1\overline{Y}}{\underline{X} + \overline{Y}} - \dfrac{c_2\overline{Z}}{\underline{X} + \overline{Z}} = 0, \\ \dfrac{m_1\overline{X}}{\overline{X} + \overline{Y}} - d_2 - \dfrac{c_3\underline{Z}}{\overline{Y} + \underline{Z}} = 0, \\ \dfrac{m_1\underline{X}}{\underline{X} + \underline{Y}} - d_2 - \dfrac{c_3\overline{Z}}{\underline{Y} + \overline{Z}} = 0, \\ \dfrac{m_2\overline{X}}{\overline{X} + \overline{Z}} + \dfrac{m_3\overline{Y}}{\overline{Y} + \overline{Z}} - d_3 = 0, \\ \dfrac{m_2\underline{X}}{\underline{X} + \underline{Z}} + \dfrac{m_3\underline{Y}}{\underline{Y} + \underline{Z}} - d_3 = 0, \end{cases} \tag{4.15}$$

and

$$\begin{aligned}(\underline{X}, \underline{Y}, \underline{Z}) &\leq \liminf_{t\to\infty}(x(t), y(t), z(t)) \\ &\leq \limsup_{t\to\infty}(x(t), y(t), z(t)) \leq (\overline{X}, \overline{Y}, \overline{Z}). \end{aligned} \tag{4.16}$$

From the existence-comparison theory in [15], there exists a component-wise positive equilibrium bounded by $(\underline{X}, \underline{Y}, \underline{Z})$ and $(\overline{X}, \overline{Y}, \overline{Z})$. Thus, we have the following theorem on permanence and coexistence.

Theorem 4.1. *Assume that* $m_1 > d_2 + c_3$, $m_2 + m_3 > d_3$, *and* $c_1 + c_2 < 1$, *and let* $(\underline{X}, \underline{Y}, \underline{Z})$ *and* $(\overline{X}, \overline{Y}, \overline{Z})$ *be the respective limits of the monotone sequences* $(\underline{X}^{(n)}, \underline{Y}^{(n)}, \underline{Z}^{(n)})$ *and* $(\overline{X}^{(n)}, \overline{Y}^{(n)}, \overline{Z}^{(n)})$ *generated in (4.13). The food-chain model (1.2) is permanent, with a positive global attractor* $[\underline{X}, \overline{X}] \times [\underline{Y}, \overline{Y}] \times [\underline{Z}, \overline{Z}]$ *which contains a coexistence equilibrium* (X, Y, Z). *If* $(\underline{X}, \underline{Y}, \underline{Z}) = (\overline{X}, \overline{Y}, \overline{Z})$, *then the coexistence equilibrium* (X, Y, Z) *is unique and globally asymptotically stable.*

Next, we investigate on a sufficient condition for $(\underline{X}, \underline{Y}, \underline{Z}) = (\overline{X}, \overline{Y}, \overline{Z})$, which ensures the uniqueness and global stability of the coexistence equilibrium (X, Y, Z).

Theorem 4.2. *Assume that* $m_1 > d_2 + c_3$, $m_2 + m_3 > d_3$, *and* $c_1 + c_2 < 1$, *and let the monotone sequences* $(\underline{X}^{(n)}, \underline{Y}^{(n)}, \underline{Z}^{(n)})$ *and* $(\overline{X}^{(n)}, \overline{Y}^{(n)}, \overline{Z}^{(n)})$ *be generated in (4.13). If, for some* n,

$$m_2\left(\frac{\underline{X}^{(n)}}{\underline{X}^{(n)} + \overline{Z}^{(n)}}\right)^2 + m_3\left(\frac{\underline{Y}^{(n)}}{\underline{Y}^{(n)} + \overline{Z}^{(n)}}\right)^2 > d_3, \tag{4.17}$$

then the food chain model (1.2) has a unique coexistence state (X, Y, Z). *When* $(x(0), y(0), z(0)) > (0, 0, 0)$, *the population function* $(x(t), y(t), z(t))$ *in model (1.2) satisfies*

$$\lim_{t\to\infty}(x(t), y(t), z(t)) = (X, Y, Z). \tag{4.18}$$

Proof. Denote $f_3(x, y, z) = \dfrac{m_2xz}{x+z} + \dfrac{m_3yz}{y+z} - d_3z$, from (4.15) we see that

$$f_3(\overline{X}, \overline{Y}, \overline{Z}) - f_3(\underline{X}, \underline{Y}, \underline{Z}) = 0,$$

which is equivalent to

$$\left[f_3(\overline{X}, \overline{Y}, \overline{Z}) - f_3(\underline{X}, \underline{Y}, \overline{Z})\right] + \left[f_3(\underline{X}, \underline{Y}, \overline{Z}) - f_3(\underline{X}, \underline{Y}, \underline{Z})\right] = 0.$$

Since

$$\frac{\partial f_3}{\partial x} = \frac{m_2z^2}{(x+z)^2} > 0 \text{ and } \frac{\partial f_3}{\partial y} = \frac{m_3z^2}{(y+z)^2} > 0,$$

we see that $f_3(\overline{X}, \overline{Y}, \overline{Z}) - f_3(\underline{X}, \underline{Y}, \overline{Z}) \geq 0$. On the other hand, by Mean Value Theorem,

$$f_3(\underline{X}, \underline{Y}, \overline{Z}) - f_3(\underline{X}, \underline{Y}, \underline{Z}) = \frac{\partial f_3}{\partial z}(\underline{X}, \underline{Y}, \eta)(\overline{Z} - \underline{Z}),$$

where $\underline{Z} \leq \eta \leq \overline{Z}$. This implies that $\overline{Z} - \underline{Z} = 0$ if $\dfrac{\partial f_3}{\partial z}(\underline{X}, \underline{Y}, \eta) > 0$ for all $\eta \in [\underline{Z}, \overline{Z}]$. From

$$\frac{\partial f_3}{\partial z} = m_2\left(\frac{x}{x+z}\right)^2 + m_3\left(\frac{y}{y+z}\right)^2 - d_3,$$

and by the monotonicity of the sequences, we can see that for any n,

$$\begin{aligned}
\frac{\partial f_3}{\partial z}(\underline{X}, \underline{Y}, \eta) &= m_2\left(\frac{\underline{X}}{\underline{X}+\eta}\right)^2 + m_3\left(\frac{\underline{Y}}{\underline{Y}+\eta}\right)^2 - d_3 \\
&\geq m_2\left(\frac{\underline{X}}{\underline{X}+\overline{Z}}\right)^2 + m_3\left(\frac{\underline{Y}}{\underline{Y}+\overline{Z}}\right)^2 - d_3 \\
&\geq m_2\left(\frac{\underline{X}^{(n)}}{\underline{X}^{(n)}+\overline{Z}^{(n)}}\right)^2 + m_3\left(\frac{\underline{Y}^{(n)}}{\underline{Y}^{(n)}+\overline{Z}^{(n)}}\right)^2 - d_3.
\end{aligned}$$

We conclude that $\overline{Z} = \underline{Z}$ if (4.17) holds. In this case, we also have $f_3(\overline{X}, \overline{Y}, \overline{Z}) - f_3(\underline{X}, \underline{Y}, \overline{Z}) = 0$ which shows that

$$m_2\frac{\overline{Z}(\overline{X} - \underline{X})}{(\underline{X} + \overline{Z})(\overline{Y} + \overline{Z})} + m_3\frac{\overline{Z}(\overline{Y} - \underline{Y})}{(\underline{Y} + \overline{Z})(\overline{Y} + \overline{Z})} = 0.$$

Hence $\overline{X} = \underline{X}$ and $\overline{Y} = \underline{Y}$. □

The above theorem actually states that the model (1.2) has a unique and globally stable coexistence state as long as there is a positive global attractor with the ultimate upper bound of super-predator and the ultimate lower bounds of its two preys satisfy the inequality (4.17).

We observe that coexistence equilibria for model (1.2) need not be stable. Consider the following example.

Example 4.1. For the ecological parameters

$$\{c_1 = .63475, c_2 = .35952, c_3 = .74812, d_2 = 0.00614, d_3 = .39057,$$
$$m_1 = .63264, m_2 = .35202, m_3 = .30768\},$$

the coexistence equilibrium $(0.98098, 0.00803, 0.03936)$ is unstable. With initial populations $x(0) = 0.9$, $y(0) = 0.1$, and $z(0) = 0.1$, the numerical simulation of model (1.2) is shown in Figure 4.

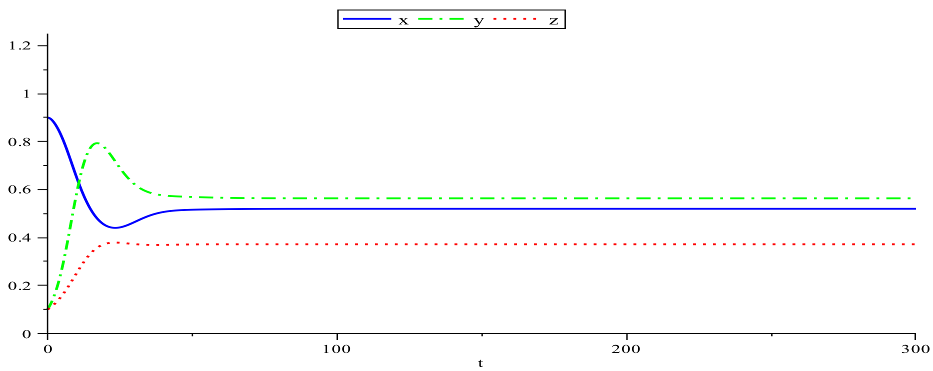

Figure 4. Unstable coexistence equilibrium

Furthermore, stable coexistence equilibria for model (1.2) need not satisfy the conditions of Theorem 4.1. Consider the following example.

Example 4.2. For the ecological parameters

$$\{c_1 = .46204, c_2 = .72978, c_3 = .33700, d_2 = 0.06052, d_3 = .48726,$$
$$m_1 = .38693, m_2 = .51853, m_3 = .13052\},$$

the coexistence equilibrium $(0.45435, 1.27220, 0.17772)$ is locally asymptotically stable. With initial populations $x(0) = 0.4$, $y(0) = 0.9$, and $z(0) = 0.2$, the numerical simulation of model (1.2) depicted in Figure 5 shows the convergence of the solution to the stable coexistence equilibrium.

Multiple coexistence equilibria can happen for model (1.2). We now provide sufficient conditions for their presence. Consider $f(x) = A_3x^3 + A_2x^2 + A_1x + A_0$ where

$$\begin{aligned}
A_3 &= -c_3m_3d_3 - d_2m_3d_3 + c_3d_3^2,\\
A_2 &= -m_1m_3d_3 + c_3m_2m_3 - d_2m_3^2 - c_3m_3^2 + d_2m_3m_2 + c_3d_3^2\\
&\quad + m_1m_3^2 - d_2m_3d_3 - 2c_3m_2d_3,\\
A_1 &= -c_3m_2m_3 + 3c_3m_3d_3 - 2d_2m_3^2 + m_1m_3m_2 + d_2m_3d_3\\
&\quad - 2m_1m_3d_3 - 2c_3m_3^2 + 2m_1m_3^2 - c_3d_3^2 + c_3m_2^2,\\
A_0 &= -m_1m_3d_3 - d_2m_3m_2 + d_2m_3d_3 + m_1m_3^2 - d_2m_3^2 - c_3m_2^2 - c_3m_3^2 - c_3d_3^2\\
&\quad + m_1m_3m_2 + 2c_3m_2d_3 + 2c_3m_3d_3 - 2c_3m_2m_3.
\end{aligned}$$

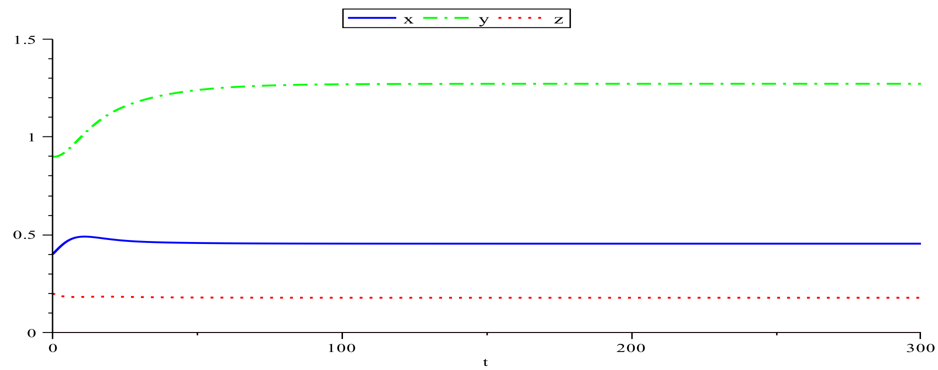

Figure 5. Asymptotically stable coexistence equilibrium

Construct the following Sturm sequence for $f(x)$:

$$f_1(x) = 3A_3x^2 + 2A_2x + A_1,$$
$$f_2(x) = -\frac{1}{9A_3}\left[2(3A_3A_1 - A_2^2)x + 9A_3A_0 - A_2A_1\right],$$
$$f_3(x) = -\frac{9A_3}{4(3A_3A_1 - A_2^2)^2}\left(4A_3A_1^3 - A_1^2A_2^2 - 18A_3A_2A_1A_0 + 4A_2^3A_0 + 27A_3^2A_0^2\right).$$

We write $\text{sgn}([f(c), f_1(c), f_2(c), f_3(c)])$ for $[\text{sgn}(f(c)), \text{sgn}(f_1(c)), \text{sgn}(f_2(c)), \text{sgn}(f_3(c))]$, where $\text{sgn}(x) = \frac{|x|}{x}$ for $x \neq 0$.

Theorem 4.3. *Assume that* $m_3 < d_3 < m_2$, $m_2 + 2m_3 < 2d_3$, *and* $c_1 + \frac{1}{2}c_2 < 1$. *Let* $\zeta_1 = \frac{m_2 - d_3}{d_3}$ *and* $\zeta_2 = \frac{m_2 + m_3 - d_3}{d_3 - m_3}$. *If*

$$\text{sgn}([f(\zeta_1), f_1(\zeta_1), f_2(\zeta_1), f_3(\zeta_1)]) = [-1, 1, -1, 1]$$

and

$$\text{sgn}([f(\zeta_2), f_1(\zeta_2), f_2(\zeta_2), f_3(\zeta_2)]) = [-1, 1, 1, 1],$$

then model (1.2) has multiple coexistence equilibria.

Proof. Since the difference of the number of sign changes in the Sturm sequences is $3 - 1 = 2$, we deduce from Sturm's Theorem (see [16]) that f has two roots in the interval (ζ_1, ζ_2). Let b be such a root and define

$$r = \frac{b(-m_2 + d_3(1 + b))}{-m_2 + (d_3 - m_3)(1 + b)},$$

noting that $\zeta_1 < b < \zeta_2$ ensures that r is positive. Take the following values of X, Y, and Z:

$$X = \frac{(1 + b)(1 + r) - c_1r(1 + b) - c_2b(1 + r)}{(1 + r)(1 + b)},$$
$$Y = rX,$$
$$Z = bX.$$

The conditions $m_2 + 2m_3 < 2d_3$ and $c_1 + \frac{1}{2}c_2 < 1$ guarantee that X is positive, and the positivity of Y and Z follows. A simple calculation verifies that (X, Y, Z) is an equilibrium of model (1.2) for each of the roots of f in (ζ_1, ζ_2). □

To find examples of multiple coexistence equilibria, we simply determine ecological parameters so that the conditions of Theorem 4.3 are satisfied.

Example 4.3. For the ecological parameters

$$\{c_1 = 0.46884, c_2 = 0.86707, c_3 = 0.36937, d_2 = 0.00079, d_3 = 0.48665,$$
$$m_1 = 0.33295, m_2 = 0.76392, m_3 = 0.10396\},$$

the coexistence equilibrium $(0.28151, 0.60185, 0.24004)$ is locally asymptotically stable and the coexistence equilibrium $(0.53141, 0.17418, 0.36465)$ is unstable. With initial populations $x(0) = 0.3$, $y(0) = 0.7$, and $z(0) = 0.1$, the numerical simulation of model (1.2) demonstrated in Figure 6 shows the convergence of the solution to the stable coexistence equilibrium.

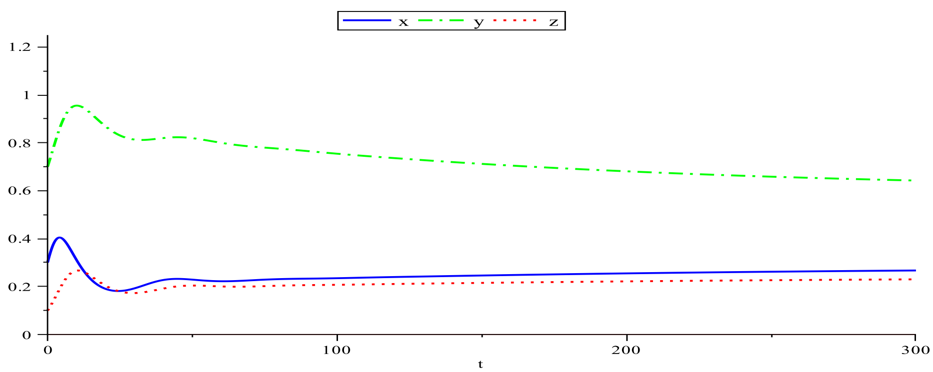

Figure 6. Multiple coexistence, stable equilibrium

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