Global Dynamics of Three Species Omnivory Models with Lotka-Volterra Interaction

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Abstract

In this work, we consider the community of three species food web model with Lotka-Volterra type predator-prey interaction. In the absence of other species, each species follows the traditional logistical growth model and the top predator is an omnivore which is defined as feeding on the other two species. It can be seen as a model with one basal resource and two generalist predators, and pairwise interactions of all species are predator-prey type. It is well known that the omnivory module blends the attributes of several well-studied community modules, such as food chains (food chain models), exploitative competition (two predators-one prey models), and apparent competition (one predator-two preys models). With a mild biological restriction, we completely classify all parameters. All local dynamics and most parts of global dynamics are established corresponding to the classification. Moreover, the whole is uniformly persistent when coexistence appears. Finally, we conclude by discussing the strategy of inferior species to survive and the mechanism of uniform persistence for the three species ecosystem.

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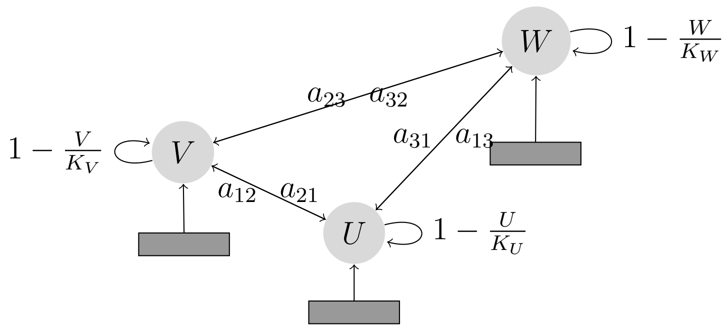

Figure 1: The diagram of Three species intraguild predator models is illustrated and each species has its own nutrient resource.

1 Introduction

In this work, we consider the following three species food web model

$$\begin{cases} \dfrac{dU}{dt} = r_U U(1 - \dfrac{U}{K_U}) - a_{12}UV - a_{13}UW, \\ \dfrac{dV}{dt} = r_V V(1 - \dfrac{V}{K_V}) + a_{21}UV - a_{23}VW, \\ \dfrac{dW}{dt} = r_W W(1 - \dfrac{W}{K_W}) + a_{31}UW + a_{32}VW, \end{cases} \tag{1.1}$$

where all parameters are nonnegative real constants. In the absence of other species, each species follows the traditional logistic population growth with birth rates, r_U, r_V, r_W, and environmental carrying capacities, K_U, K_V, K_W, for the species U, V, W, respectively. And the nonlinear interactions between species are Lotka-Volterra type with omnivory which means the top predator (intraguid-predator) W are feeding on two resources, intraguild-prey V and prey U [6]. Biologically, we assume that all coefficients of interactions a_{ij} are non-negative and a_{ij} is the rate of consumption for $i < j$ or measures the contribution of the victim (resource or prey) to the growth of the consumer for $i > j$ [10].

System (1.1) can be regarded as a food-chain model, a two predators-one prey model or a one prey-two predators model when $a_{13} = a_{31} = 0$, $a_{23} = a_{32} = 0$ or $a_{12} = a_{21} = 0$, respectively. Please refer Figure 1. It is well known that system (1.1) blends the attributes of several well-studied community modules, such as food chains, exploitative competition (two predators-one prey) and apparent competition (one predator-two preys) [6]. The most important feature of system (1.1) is involved omnivory which are believed that this property is crucial to to the stability of food web structure and its global dynamics.

Re-examine previous known three species food web model with omnivory [6, 12, 13, 8, 7], for the intermediate predator (intraguild prey) there is only one nutrient resource from the basal prey. However, in system (1.1) each species has its own nutrient resource governed by the logistic growth terms. Moreover, they affect each other weakly by the nonlinear terms. So system (1.1) can be seen as a type of three species food web system with *diversity of food resources* and *weakly effects* to each others. We think that these features appear in some situations. Our main purpose of this work is to answer what is the best strategy for each species to survive and what is the condition of uniform persistence for the whole system.

The rest of the paper is organized as follows. In Section 2, we first show the boundedness of solutions of (1.1). Then local stability of all boundary equilibria are investigated by the linear method. Moreover, global behaviors of the the methods of Lyapunov and Bultler-McGehee Lemma. Next, with assumption **(A)** we classify all parameters to investigate the existence of positive equilibria and its global dynamics analytically. In the final section, numerical simulations are presented, and some discussions and remarks are given.

2 Existence and Stability of Boundary Equilibria

In this section, we first rescale the model and show the boundedness and positivity of solution of (1.1). Secondly, all boundary equilibria are found and their local stabilities are established by linear method. Then some global dynamics are investigated by differential inequalities coupling with LaSalle's invariant principle and McGehee Lemma. Finally, we summarize a table which could completely classify all dynamics by the parameters.

To simplify the arguments, we apply the following scaling transformation to (1.1),

$$\begin{cases} x = U/K_U, \quad y = a_{12}V/r_U, \quad z = a_{13}W/r_U, \\ r_x = r_U, \quad r_y = r_V, \quad r_z = r_W, \\ a = \dfrac{a_{21}K_U}{r_V}, \; b = \dfrac{r_U}{a_{12}K_V}, \; c = \dfrac{a_{23}r_U}{a_{13}r_V}, \\ d = \dfrac{a_{31}K_U}{r_W}, \; e = \dfrac{a_{32}r_U}{a_{12}r_W}, \; \text{and } f = \dfrac{r_U}{a_{13}K_W}. \end{cases} \tag{2.1}$$

then we obtain a simplified ODE model,

$$\frac{dx}{dt} = r_x x(1 - x - y - z), \tag{2.2a}$$

$$\frac{dy}{dt} = r_y y(1 + ax - by - cz), \tag{2.2b}$$

$$\frac{dz}{dt} = r_z z(1 + dx + ey - fz). \tag{2.2c}$$

Lemma 2.1. *Solutions of* (2.2) *with nonnegative (positive) initial conditions are nonnegative (positive). Moreover, all solutions of* (2.2) *are bounded.*

Proof. By Theorem 3 in [9], we know that solutions of (2.2) is bounded. It is also easy to see that x-axis, y-axis, z-axis, xy-plane, xz-plane, and yz-plane are invariant subspaces of (2.2). Hence, one can easily show that solutions with nonnegative (positive) initial conditions are nonnegative (positive) by the uniqueness of solutions. □

Throughout this work, we always assume that

(A) $r_U > a_{12}K_V$ or $b > 1$.

Assumption **(A)** is actually a biological restriction which means that species U can sustain the negative effect with maximal amount of species V. Since it is easy to see that if assumption **(A)** does not hold then species U will die out eventually in the two-dimensional subsystem without species W. So this hypothesis can keep interest and complexity of system (2.2).

2.1 Existence of Boundary Equilibria and its Local Stability

In this subsection, we will find all corresponding conditions to establish the existence of boundary equilibria and their local stabilities.

By direct computations, we have the Jacobian matrix of system (2.2) is given by

$$J(x, y, z) = \begin{pmatrix} r_x(1 - 2x - y - z) & -r_x x & -r_x x \\ ar_y y & r_y(1 + ax - 2by - cz) & -cr_y y \\ dr_z z & er_z z & r_z(1 + dx + ey - 2fz) \end{pmatrix}.$$

All boundary equilibria can be easily found and their Jacobian matrix are considered as follows.

(a) $E_0 = (0,0,0)$. It is clear that

$$J(E_0) = \begin{pmatrix} r_x & 0 & 0 \\ 0 & r_y & 0 \\ 0 & 0 & r_z \end{pmatrix}.$$

All eigenvalues of $J(E_0)$ are positive and hence E_0 is expansive.
(b) $E_x = (1,0,0)$. By direct computations, we have that

$$J(E_x) = \begin{pmatrix} -r_x & -r_x & -r_x \\ 0 & r_y(1+a) & 0 \\ 0 & 0 & r_z(1+d) \end{pmatrix}.$$

The matrix $J(E_x)$ has two positive eigenvalues and one negative eigenvalue. Clearly, E_x is a saddle with one-dimensional stable manifold, the interior of the x-axis and two-dimensional unstable manifold with one tangent vector on the x-y plane and another one on the x-z plane.

(c) $E_y = (0, \frac{1}{b}, 0)$. Direct computations imply that

$$J(E_y) = \begin{pmatrix} r_x(1-\frac{1}{b}) & 0 & 0 \\ \frac{ar_y}{b} & -r_y & \frac{-cr_y}{b} \\ 0 & 0 & r_z(1+\frac{e}{b}) \end{pmatrix}.$$

Since $b > 1$, the matrix $J(E_y)$ has two positive eigenvalues and one negative eigenvalue. It follows that E_y is a saddle with one-dimensional stable manifold, the interior of the y-axis and two-dimensional unstable manifold with one tangent vector on the x-y plane and another one on the y-z plane.

(d) $E_z = (0, 0, \frac{1}{f})$. It is easy to check that

$$J(E_z) = \begin{pmatrix} r_x(1-\frac{1}{f}) & 0 & 0 \\ 0 & r_y(1-\frac{c}{f}) & 0 \\ \frac{dr_z}{f} & \frac{er_z}{f} & -r_z \end{pmatrix}.$$

By the ordering of 1, c, and f, we state local stability of E_z and omit the proof.

(i) If $f < 1$ and $f < c$, then $J(E_z)$ has three negative eigenvalues and it follows that E_z is stable;

(ii) if $f > 1$ and $f < c$, then it is saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the x coordinate and two-dimensional stable manifold, the interior of the y-z plane;

(iii) if $f < 1$ and $f > c$, then it is saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the y coordinate and two-dimensional stable manifold, the interior of the x-z plane;

(iv) if $f > 1$ and $f > c$, E_z is a saddle with one-dimensional stable manifold the interior of the z-axis and two-dimensional unstable manifold with one tangent vector on the x-z plane and another one on the y-z plane.

(e) $E_{xy} = (\frac{b-1}{a+b}, \frac{a+1}{a+b}, 0)$. Let $\rho = \frac{b-1}{a+b}$, then $1 - \rho = \frac{a+1}{a+b}$. One can easily verify that $J(E_{xy})$ is of the following form

$$\begin{pmatrix} -r_x\rho & -r_x\rho & -r_x\rho \\ ar_y(1-\rho) & r_y[1 + a\rho - 2b(1-\rho)] & -cr_y(1-\rho) \\ 0 & 0 & r_z[1 + d\rho + e(1-\rho)] \end{pmatrix}. \tag{2.3}$$

Since $b > 1$, the equilibrium E_{xy} exists. It is clear that $J(E_{xy})$ has at least one positive eigenvalue $r_z[1 + d\rho + e(1-\rho)]$. Consider another two eigenvalues, λ_2 and λ_3, of (2.3). They are actually the eigenvalues of the up-left 2×2 submatrix of (2.3). By direct computations, we obtain

$$\lambda_2\lambda_3 = r_x r_y \rho(1 + a) > 0,$$

$$\lambda_2 + \lambda_3 = -r_x\rho - r_y b(1-\rho) < 0.$$

Hence it is saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the z coordinate and two-dimensional stable manifold, the interior of the x-y plane.

(f) $E_{xz} = (\frac{f-1}{d+f}, 0, \frac{d+1}{d+f})$. Let $\sigma = \frac{f-1}{d+f}$, then $1 - \sigma = \frac{d+1}{d+f}$. One can easily verify that $J(E_{xz})$ is of the following form

$$\begin{pmatrix} -r_x\sigma & -r_x\sigma & -r_x\sigma \\ 0 & r_y[1 + a\sigma - c(1-\sigma)] & 0 \\ dr_z(1-\sigma) & er_z(1-\sigma) & -fr_z(1-\sigma) \end{pmatrix}. \tag{2.4}$$

The equilibrium E_{xz} can exist only if $f > 1$. Clearly, $J(E_{xz})$ has one eigenvalue $\lambda_1 = r_y[1 + a\sigma - c(1-\sigma)] = r_y(\frac{af - cd - a - c + d + f}{d+f})$. Consider another two eigenvalues, λ_2 and λ_3, of (2.4). They are actually the eigenvalues of the 2×2 submatrix of (2.4) by removing the second column and the second row. By direct computations, we have

$$\lambda_2\lambda_3 = r_x r_z \sigma(d + 1) > 0,$$
$$\lambda_2 + \lambda_3 = -r_x\sigma - r_z f(1-\sigma) < 0.$$

So $J(E_{xz})$ has at least two negative eigenvalues. Hence, if

$$af - cd - a - c + d + f < 0, \tag{2.5}$$

then $J(E_{xz})$ has three negative eigenvalues and it follows that E_{xz} is stable; and if

$$af - cd - a - c + d + f > 0, \tag{2.6}$$

then $J(E_{xz})$ has one positive eigenvalue and two negative eigenvalues. Similarly, E_{xz} is saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the y coordinate and two-dimensional stable manifold, the interior of the x-z plane.

(g) $E_{yz} = (0, \frac{f-c}{bf+ce}, \frac{b+e}{bf+ce})$. One can easily verify that $J(E_{yz})$ is of the following form

$$\begin{pmatrix} (\frac{bf+ce-b+c-e-f}{bf+ce})r_x & 0 & 0 \\ ar_y(\frac{f-c}{bf+ce}) & -r_y b(\frac{f-c}{bf+ce}) & -cr_y(\frac{f-c}{bf+ce}) \\ dr_z(\frac{b+e}{bf+ce}) & er_z(\frac{b+e}{bf+ce}) & -fr_z(\frac{b+e}{bf+ce}) \end{pmatrix}. \tag{2.7}$$

Similarly the equilibrium E_{yz} can exist only if $f > c$. Clearly, $J(E_{yz})$ has one eigenvalue

$$\lambda_1 = (\frac{bf + ce - b + c - e - f}{bf + ce})r_x. \tag{2.8}$$

Consider another two eigenvalues, λ_2 and λ_3, of (2.7). They are actually the eigenvalues of the low-right 2×2 submatrix of (2.7). By direct computations, we obtain

$$\lambda_2\lambda_3 = r_y r_z (bf + ce)(\frac{f-c}{bf+ce})(\frac{b+e}{bf+ce}) > 0,$$

$$\lambda_2 + \lambda_3 = -r_y b(\frac{f-c}{bf+ce}) - r_z f(\frac{b+e}{bf+ce}) < 0.$$

Then we have $\lambda_2 < 0$ and $\lambda_3 < 0$. Similarly, we find the following condition of stability for E_{yz}. If

$$bf + ce - b + c - e - f < 0, \tag{2.9}$$

then E_{yz} is stable; and if

$$bf + ce - b + c - e - f > 0, \tag{2.10}$$

then E_{yz} is saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the x coordinate and two-dimensional stable manifold, the interior of the y-z plane. Here we summarize all local stability results for boundary equilibria in the following proposition.

Proposition 2.2. *For system* (2.2)*, the following statements are true.*

(i) *The trivial equilibrium E_0 is expansive.*

(ii) *The semi-trivial equilibrium E_x always exists and is a saddle with one-dimensional stable manifold, the interior of the x-axis and two-dimensional unstable manifold with one tangent vector on the x-y plane and another one on the x-z plane.*

(iii) *The semi-trivial equilibrium E_y always exists and is a saddle with one-dimensional stable manifold, the interior of the y-axis and two-dimensional unstable manifold with one tangent vector on the x-y plane and another one on the y-z plane.*

(iv) *The semi-trivial equilibrium E_z always exists. And*

  (a) *if $f < 1$ and $f < c$ then it is stable;*

  (b) *if $f > 1$ and $f < c$, then it is saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the x coordinate and two-dimensional stable manifold, the interior of the y-z plane;*

  (c) *if $f < 1$ and $f > c$, then it is saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the y coordinate and two-dimensional stable manifold, the interior of the x-z plane;*

  (d) *if $f > 1$ and $f > c$, it is a saddle with one-dimensional stable manifold the interior of the z-axis and two-dimensional unstable manifold with one tangent vector on the x-z plane and another one on the y-z plane.*

(v) *The boundary equilibrium E_{xy} always exists. Moreover, it is a saddle point with one-dimensional unstable manifold with tangent vectors which are non-zero in the z coordinate and two-dimensional stable manifold, the interior of the x-y plane.*

(vi) *The boundary equilibrium E_{xz} exists if $f > 1$ and it is stable if* (2.5) *holds. If* (2.6) *holds, then E_{xz} is a saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the y coordinate and two-dimensional stable manifold, the interior of the x-z plane.*

(vii) *The boundary equilibrium E_{yz} exists if $f > c$ and it is stable if* (2.9) *holds. Otherwise, if* (2.10) *holds, then E_{yz} is a saddle with one-dimensional unstable manifold with tangent vectors which are non-zero in the x coordinate and two-dimensional stable manifold, the interior of the y-z plane.*

2.2 Global Dynamics of Boundary Equilibria

In this subsection, we investigate some global dynamics of boundary equilibria. By the foregoing subsection, we have the following conclusions: E_0, E_x, E_y and E_{xy} are unstable. So we will consider the other boundary equilibria, E_z, E_{xz} and E_{yz}. For reader's convenience, in Table 1 we present all local and global dynamics which will be investigated in Section 2 and Section 3.

First, we classify all parameters into two main categories, $c < 1$ and $c > 1$. Biologically, the parameter $c = a_{23}r_U/(a_{13}r_V) < 1$ can be rewritten as the form

$$\frac{r_U}{a_{13}} < \frac{r_V}{a_{23}}, \tag{2.11}$$

which means that the species x is inferior to the species y in apparent competition [4]. By Proposition 2.2, we may further classify all parameters by the ordering of f, c and 1. Hence generically we consider the following six sub-cases:
(B)-1 $f < c < 1$,
(B)-2 $c < f < 1$,
(B)-3 $c < 1 < f$,
and
(C)-1 $f < 1 < c$,
(C)-2 $1 < f < c$,
(C)-3 $1 < c < f$.

By the result (iv) of Proposition 2.2, E_z is stable if $f < \min\{1, c\}$. Actually, we can further show that it is globally asymptotically stable. This also clarify the global dynamics of cases **(B)-1** and **(C)-1**. It is clear that E_z is unstable for all other cases. Please refer "E_z" column of Table 1.

Proposition 2.3. *If $f < \min\{1, c\}$ which is equivalent to cases of* **(B)-1** *and* **(C)-1**, *then*

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

and E_z is globally asymptotically stable.

Proof. By (2.2c), we have

$$\frac{dz}{dt} = r_z z(1 - fz) + r_z dxz + r_z eyz \geq r_z z(1 - fz).$$

Let $\overline{z}(t)$ be the solution of the differential equation

$$\frac{d\overline{z}}{dt} = r_z\overline{z}(1 - \frac{\overline{z}}{1/f})$$

with the same initial condition of $z(t)$. Then we have the following facts:

$$z(t) \geq \overline{z}(t) \text{ for all } t > 0 \text{ and } \lim_{t\to\infty} \overline{z}(t) = \frac{1}{f}.$$

So for any $\varepsilon > 0$, we can find a $T > 0$ such that $z(t) \geq \frac{1}{f} - \varepsilon$ whenever $t > T$. Take $\varepsilon = \frac{1}{2}(\frac{1}{f} - 1) > 0$. By (2.2a), we have

$$\begin{aligned}\frac{1}{r_x x}\frac{dx}{dt} = (1-x) - y - z \leq 1 - z& \\ \leq 1 - \frac{1}{f} + \varepsilon& \\ = (1-\frac{1}{f}) + \frac{1}{2}(\frac{1}{f} - 1) < 0&\end{aligned}$$

for all $t > T$. Then $x(t)$ converges to 0 as t tends to infinity. Finally, we consider the differential equation (2.2b):

$$\frac{dy}{dt} = r_y y(1 - by) + r_y axy - r_y cyz.$$

Take $\varepsilon = \frac{1}{2}(\frac{1}{f} - \frac{1}{c}) > 0$, then we can find a $T > 0$ such that $x(t) < \frac{1}{4a}(\frac{c}{f} - 1)$ and $z(t) > \frac{1}{f} - \varepsilon$ for $t \geq T$. Then

$$\begin{aligned}\frac{1}{r_y y}\frac{dy}{dt} &= (1 - by) + ax - cz \\ &\leq 1 + ax - cz \\ &\leq 1 + ax - \frac{c}{f} + c\varepsilon \\ &= 1 + ax - \frac{c}{f} + \frac{1}{2}(\frac{c}{f} - 1) \\ &= \frac{1}{2}(1 - \frac{c}{f}) + ax < \frac{1}{4}(1 - \frac{c}{f}) < 0\end{aligned}$$

for all $t > T$. So $y(t)$ converges to 0 as t tends to infinity. Hence we can conclude that E_z is globally asymptotically stable in the positive sector. □

Biologically, the conditions

$$f = \frac{r_U}{a_{13}K_W} < 1 \quad \text{and} \quad f = \frac{r_U}{a_{13}K_W} < c = \frac{a_{23}r_U}{a_{13}r_V}$$

can be rewritten as the form

$$r_U < a_{13}K_W \quad \text{and} \quad r_V < a_{23}K_W,$$

which imply that species x and y *cannot* sustain the negative effect with maximal amount of species z, then species x and y will become extinct eventually.

Next, we investigate global dynamics of equilibrium E_{xz}. The equilibrium E_{xz} can exist only if $f = r_U/(a_{13}K_W) > 1$. This can be seen that the species x can stand the exploitation of maximal amount of the species z. So this clarifies the cases of **(B)-1**, **(B)-2**, and **(C)-1**. Furthermore, by the foregoing discussion, the Jacobian matrix $J(E_{xz})$ has two negative eigenvalues and one eigenvalue,

$$\lambda = r_y(\frac{af - cd - a - c + d + f}{d + f}).$$

The following lemma says that equilibrium E_{xz} is always saddle in the case of **(B)-3**.

Lemma 2.4. *In the case of* **(B)-3**, *the inequality* $af - cd - a - c + d + f > 0$ *is always true, that is,* (2.6) *holds.*

The quantity $af-cd-a-c+d+f = a(f-1)+(f-c)+d(1-c) > 0$, since $c < 1 < f$.

However, it follows that E_{xz} is stable if (2.5) holds. Consequently, we have the following global result which clarify partial global dynamics of cases **(C)-2** and **(C)-3**. The complete dynamics of E_{xz} can be found in the column E_{xz} of Table 1.

Proposition 2.5. *For cases* **(C)-2** *and* **(C)-3**, *assume that*

$$af - cd + d + f < 0, \tag{2.12}$$

then E_{xz} is globally asymptotically stable.

Proof. Assumption (2.12) is equivalent to $(1 + a)/d < (c - 1)/f$. Hence we can take a positive number k such that $(1 + a)/d < k < (c - 1)/f$. Then consider

$$\begin{aligned}\frac{\dot{y}}{r_y y} - \frac{\dot{x}}{r_x x} - k\frac{\dot{z}}{r_z z} &\leq -k + (1 + a - kd)x + (1 - c + kf)z \\ &\leq -k < 0.\end{aligned}$$

Therefore we have $\lim_{t\to\infty} y(t) = 0$. Asymptotically, system (2.2) will approach the following two-dimensional subsystem,

$$\begin{cases} \dfrac{dx}{dt} = r_x x(1 - x - z), \\ \dfrac{dz}{dt} = r_z z(1 + dx - fz). \end{cases} \tag{2.13}$$

If we can show equilibrium E_{xz} is GAS in the x-z plane, then we conclude that E_{xz} is GAS in the positive octant of $\mathbb{R}^3$.
Let $E_{xz} = (\bar{x}, \bar{z})$ be the positive equilibrium, that is ,

$$1 = \bar{x} + \bar{z}, \text{ and } 1 = -d\bar{x} + f\bar{z}.$$

Consider the Lyapunov function

$$L(x(t), z(t)) = \frac{1}{r_x} \int_{x(0)}^{x(t)} \frac{\eta - \bar{x}}{\eta} \, d\eta + \frac{1}{r_z d} \int_{z(0)}^{z(t)} \frac{\eta - \bar{z}}{\eta} \, d\eta$$

and by computation we obtain

$$\frac{d}{dt} L(x(t), z(t)) = -(x - \bar{x})^2 - \frac{f}{d}(z - \bar{z})^2 \leq 0.$$

Then by LaSalle Invariant Principle, we can get that E_{xz} is GAS in x-z plane. This completes the proof. □

Remark 2.6. *It is clear that* (2.12) *is a sufficient condition of* (2.5)*.*

For equilibrium $E_{yz} = (0, \frac{f-c}{bf+ce}, \frac{b+e}{bf+ce})$, it can exist only if $f > c$. So in cases of **(B)-1**, **(C)-1** and **(C)-2**, E_{yz} does not exist. It is easy to see that the inequality $f > c$ is equivalent to

$$r_V > a_{23} K_W.$$

Similarly, this inequality suggests that the species y can sustain the exploitation of maximal amount of the species z. If the equilibrium E_{yz} exists, then its Jacobian matrix $J(E_{yz})$ has two negative eigenvalues and one eigenvalue,

$$\lambda = r_x \left(\frac{bf + ce - b + c - e - f}{bf + ce} \right).$$

The following lemma says that equilibrium E_{yz} is always saddle in the case of **(C)-3**.

Lemma 2.7. *In the case of* **(C)-3***, the inequality* $bf + ce - b + c - e - f > 0$ *is always true, that is,* (2.10) *holds.*

If $bf+ce-b+c-e-f \leq 0$ then $c \leq \frac{e+(b+f-bf)}{e+1}$ which implies $b+f-bf > 1$ because of $c > 1$. But $b+f-bf > 1$ implies that $b < 1$ which contradicts to assumption **(A)**.

In the case of **(B)-2**, we always have

$$bf + ce - b + c - e - f = b(f - 1) + e(c - 1) + (c - f) < 0,$$

and this implies E_{yz} is stable. Moreover, we can prove the following global behavior.

Proposition 2.8. *In the case of* **(B)-2**, *we can obtain*

$$\lim_{t\to\infty} x(t) = 0$$

and equilibrium E_{yz} is globally asymptotically stable.

Proof. Consider

$$\frac{\dot{x}}{r_x x} - \frac{1}{f}\frac{\dot{z}}{r_z z} \leq 1 - \frac{1}{f} < 0.$$

So we have $\lim_{t\to\infty} x(t) = 0$. The following arguments are similar, so we omit them.

□

In the case of **(B)-3**, if inequality (2.9) hold, then the equilibrium E_{yz} is stable. Moreover, we have the following global result which clarifies partial dynamics of **(B)-3**.

Proposition 2.9. *For case of* **(B)-3**, *assume that*

$$bf + ce - b - e < 0, \tag{2.14}$$

then E_{yz} is globally asymptotically stable.

Proof. Assumption (2.14) is equivalent to $c/b + f/e < 1/b + 1/e$. Hence we can take a positive number k such that $c/b + f/e < k < 1/b + 1/e$. Then consider

$$k\frac{\dot{x}}{r_x x} - \frac{1}{b}\frac{\dot{y}}{r_y y} - \frac{1}{e}\frac{\dot{z}}{r_z z} \leq (k - \frac{1}{b} - \frac{1}{e}) - (k - \frac{c}{e} - \frac{f}{e}) < 0.$$

Therefore we have $\lim_{t\to\infty} x(t) = 0$. The remaining arguments are similar, so we omit them. □

Remark 2.10. *It is clear that* (2.14) *is a sufficient condition of* (2.9).

Finally, we summarise all results in Table 1.

3 Existence of Positive Equilibrium and Uniform Persistence

In this section, we first find the necessary and sufficient conditions to guarantee the existence of positive equilibrium $E_* = (x_*, y_*, z_*)$. Then the condition of local stability of E_* is presented by the Routh-Hurwitz Criterion. Although we cannot

Table 1: Existence and dynamics of equilibria by the classifications. The notations "U" means unstable, "$\nexists$" means non-existence of equilibrium, "$\exists$" means existence of equilibrium, and "GAS" means globally asymptotically stable.

$b > 1$	E_0, E_x, E_y, E_{xy}	E_z	E_{xz}	E_{yz}	E_*
(B)-1 : $f < c < 1$	U	GAS	$\nexists$	$\nexists$	$\nexists$
(B)-2 : $c < f < 1$	U	U	$\nexists$	GAS	$\nexists$
(B)-3 : $c < 1 < f$					
$bf + ce - b + c - e - f < 0$	U	U	U	GAS*	$\nexists$
$bf + ce - b + c - e - f > 0$	U	U	U	U	$\exists$
(C)-1 : $f < 1 < c$	U	GAS	$\nexists$	$\nexists$	$\nexists$
(C)-2 : $1 < f < c$					
$af - cd - a - c + d + f > 0$	U	U	U	$\nexists$	$\exists$
$af - cd - a - c + d + f < 0$	U	U	GAS$^\diamond$	$\nexists$	$\nexists$
(C)-3 : $1 < c < f$					
$af - cd - a - c + d + f > 0$	U	U	U	U	$\exists$
$af - cd - a - c + d + f < 0$	U	U	GAS$^\diamond$	U	$\nexists$

* With assumption $bf + ce - b - e < 0$

$^\diamond$ With assumption $af - cd + d + f < 0$

show the globally asymptotically stability of E_* analytically, we can verify the system (2.2) is uniformly persistent when E_* exists.

In cases of **(B)-1**, **(B)-2** and **(C)-1**, the global dynamics of (2.2) is classified in Section 2. So it is easy to see that E_* does not exist in this three cases (Please refer Table 1). Therefore, we investigate the other cases in this section. To find positive equilibrium $E_* = (x_*, y_*, z_*)$ is equivalent to find the solution (x_*, y_*, z_*) of the linear system ,

$$\begin{cases} x + y + z = 1, \\ ax - by - cz = -1, \\ dx + ey - fz = -1, \end{cases} \tag{3.1}$$

with $0 < x_*, y_*, z_* < 1$. Here are the necessary and sufficient conditions for the existence of the positive equilibrium E_*.

Proposition 3.1. *Let assumption* **(A)** *hold. The coexistence equilibrium E_* exists if and only if* (2.6) *and* (2.10) *hold.*

Proof. Assume that the positive equilibrium $E_* = (x_*, y_*, z_*)$ exists, that is, there are three positive real numbers, x_*, y_* and z_*, less than 1 and satisfying (3.1). By straightforward computation of system (3.1), we get the explicit formulations of solution (x_*, y_*, z_*),

$$x_* = (bf + ce - b + c - e - f)/(ae + af + bd + bf - cd + ce), \tag{3.2a}$$
$$y_* = (af - cd - a - c + d + f)/(ae + af + bd + bf - cd + ce), \tag{3.2b}$$
$$z_* = (ae + bd + a + b - d + e)/(ae + af + bd + bf - cd + ce). \tag{3.2c}$$

Since $z_* > 0$ and $ae + bd + a + b - d + e = ae + d(b-1) + a + b + e > 0$, we have $ae + af + bd + bf - cd + ce > 0$ by (3.2c). Therefore we also have $bf + ce - b + c - e - f > 0$ and $af - cd - a - c + d + f > 0$, that is, (2.6) and (2.10) hold. We complete the proof of this implication.
For the other implication, we assume that (2.6) and (2.10) hold, that is, $bf + ce - b + c - e - f > 0$ and $af - cd - a - c + d + f > 0$. Then by adding these two inequalities, we obtain

$$af + bf + ce - cd > a + b - d + e. \tag{3.3}$$

Consider the determinant of the linear system (3.1),

$$\begin{vmatrix} 1 & 1 & 1 \\ a & -b & -c \\ d & e & -f \end{vmatrix} = af + bf + ce - cd + bd + ae > a + b - d + e + bd + ae > 0$$

by assumption **(A)**. So the solution of system (3.1) exists, and has the form

$$x_* = (bf + ce - b + c - e - f)/(ae + af + bd + bf - cd + ce),$$
$$y_* = (af - cd - a - c + d + f)/(ae + af + bd + bf - cd + ce),$$
$$z_* = (ae + bd + a + b - d + e)/(ae + af + bd + bf - cd + ce).$$

Finally, it can clearly be seen that $0 < x_*, y_*, z_* < 1$. This show the existence of E_*. We complete the proof. □

Remark 3.2.

(i) *In case of* **(B)-3** *with inequality* (2.10)*, by Lemma 2.4 the inequality* (2.6) *is true. Hence E_* exists.*

(ii) *In case of* **(C)-2** *with inequality* (2.6)*, if* (2.10) *does not hold, that is,* $bf + ce - f + c - b - e \le 0$ *then* $b(f-1) \le e(1-c) + f - c < 0$ *which contradicts to* **(C)-2***,* $1 < f < c$*. Hence E_* exists.*

(iii) *In case of* **(C)-3** *with inequality* (2.6)*, by Lemma 2.7 the inequality* (2.10) *is true. Hence E_* exists. We summarize the existence results of E_* in the column "E_*" of Table 1.*

(iv) *The local stability of E_* can be verified by Routh-Hurwitz criterion. The computations are tedious, so we put it in the Appendix. By observing the form, it suggests that E_* is stable whenever it exists. But we cannot prove that. Some numerical simulations are discussed in the last section.*

Finally, we can obtain the following uniform persistence of solutions for system (2.2).

Proposition 3.3. *Let assumptions* **(A)** *hold. If the positive equilibrium E_* exists, then system* (2.2) *is uniformly persistent.*

Proof. To show this proposition, we need to consider the following three cases,

(i) **(B)-3** and (2.10),

(ii) **(C)-2** and (2.6),

(iii) **(C)-3** and (2.6).

Please refer Table 1. The method is similar, so we only investigate case (i). It is easy to check that system (2.2) is persistent by the results of [3]. Our strategy is to use the main results in [1, 2] to verify the uniform persistence of (2.2). It is sufficient to show that the boundary of the first octant for the solution of (2.2) is isolated and acyclic.
Under assumptions **(A)**, **(B)-3** and (2.10), the isolated invariant sets of solutions on the boundary are $\{E_0,\ E_x,\ E_y,\ E_z,\ E_{xy},\ E_{xz},\ E_{yz}\}$. All possible chain from E_0 to other semi-trivial equilibria can been found for six cases :

1. $E_0 \to E_x \to E_{xy}$;
2. $E_0 \to E_x \to E_{xz}$;
3. $E_0 \to E_y \to E_{xy}$;
4. $E_0 \to E_y \to E_{yz}$;
5. $E_0 \to E_z \to E_{xz}$;
6. $E_0 \to E_z \to E_{yz}$.

We only consider the first case, and the other cases are similar. If $E_0 \to E_x \to E_{xy}$ happens, then it is clear that E_{xy} can not be chained to E_0 or E_x by Proposition 2.2 (v). Thus, the set of equilibria,

$$\{E_0, E_x, E_y, E_z, E_{xy}, E_{xz}, E_{yz}\},$$

on the boundary is acyclic and the system (2.2) is uniformly persistent. □

4 Discussions

In this work, we consider the community of three species food web model with Lotka-Volterra type predator-prey interaction. Each species has its own nutrient resource governed by the traditional logistical growth. And they affect each other by the interplay of competition and predation. In particular, the top predator is an omnivore which is defined as feeding on the other two species. With a mild biological restriction **(A)** we have classified all parameters and investigated their corresponding dynamics which are summerized in Table 1.

First, in case **(B)-1** and case **(C)-1**, we showed that species U and V die out and W survives. Since the inequalities $f < 1$ and $f < c$ represent that species U and V cannot stand the exploitation by species W in the following equivalent forms,

$$r_U < a_{13}K_W \quad \text{and} \quad r_V < a_{23}K_W,$$

respectively. Hence E_z is globally asymptotically stable.

In Section 2, we have classified all parameters into two main categories, $c < 1$ and $c > 1$. Biologically, the parameter $c = a_{23}r_U/(a_{13}r_V)$ can be rewritten as the form

$$\frac{r_U}{a_{13}}/(\frac{r_V}{a_{23}}),$$

where the ratio r_U/a_{13} means the birth-rate of U overs consuming rate a_{13} by predator W and the ratio r_V/a_{23} means the birth-rate of V overs consuming rate a_{23} by predator W. Hence assumption $c < 1 (c > 1)$ can be interpreted that species U is inferior (superior) to species V under the apparent competition [4]. So in the category **(B)**, any equilibrium involved species U is unstable or does not exist except for the case of **(B)-3** with (2.10). Similarly, in the category **(C)**, any equilibrium involved species V is unstable or does not exist except for the cases **(C)-2** and **(C)-3)** with (2.6). This three exceptions are exactly cases where E_* exists and the system uniformly persists. We will discuss in more detail later.

Next, in case **(B)-2**, we showed that species U dies out, and V, W survives, since V can sustain the exploitation by W, because of $f > c$ $(r_V > a_{23}K_W)$. In addition, species U lost the apparent competition. Hence we have the globally asymptotical stability of E_{yz}.

Let us discuss the most interesting and complex cases, **(B)-3**, **(C)-2** and **(C)-3**. In the case of **(B)-3**, that is $c < 1 < f$, inequalities $f > c$ and $f > 1$ imply that species U and species V can sustain the exploitation of maximal amount of species W, respectively. But $c < 1$ means that species U is inferior to species V in apparent competition. How does species U survive? The inequality (2.6) can be rewritten as the form,

$$0 < bf + ce - b + c - e - f = b(f - 1) + e(c - 1) + (c - f).$$

In right hand side, the only positive term is $b(f - 1)$. So the only possibility to make (2.6) true if $b = r_U/(a_{12}K_V)$ is large enough. Either species U take r-strategy or the amount of species V is small. So in the case of **(B)-3** with (2.6), species U can survive and E_* exists.

For the case of **(C)-2**, that is $1 < f < c$, inequalities $f > 1$ and $f < c$ represent that species U can sustain the exploitation of maximal amount of species z, but species y cannot. Moreover, the inequality $c > 1$ means species V lost the apparent competition. Similarly, how does species V survive? The inequality (2.10) can be rewritten as the form,

$$0 < af - cd - a - c + d + f = a(f - 1) + d(1 - c) + (f - c). \tag{4.1}$$

In right hand side, the only positive term is $a(f - 1)$. The only possibility to make (2.10) true if $a = a_{21}K_U/r_V$ is large enough. The possible strategy for species V to survive is to improve the efficiency of consuming species U. Hence in the case of **(C)-2** with (2.10), species V can survive and E_* exists.

For the case of **(C)-3**, that is $1 < c < f$, species U and species V can stand the exploitation of maximal amount of species W, but species V lost the apparent competition. Similarly, in the right hand side of (4.1), there are two positive terms, $a(f - 1)$ and $(f - c)$. There are possible strategies for species V. One is to improve the efficiency of consuming species U, and another one is r-strategy.

Finally, we try to answer the questions which we propose, *what is the best strategy for each species to survive and what is the condition of uniform persistence for the whole system*. For species U, to survive in any cases discussed above is r-strategy. And for species V the best strategy is to improve the efficiency of consuming rate.

Appendix

In this appendix, we investigate the local stability of the coexistence equilibrium E_*. The Jacobian matrix evaluated at $E_* = (x_*, y_*, z_*)$ is

$$J(x_*, y_*, z_*) = \begin{pmatrix} -r_x x_* & -r_x x_* & -r_x x_* \\ a r_y y_* & -b r_y y_* & -c r_y y_* \\ d r_z z_* & e r_z z_* & -f r_z z_* \end{pmatrix}.$$

By direct computations, the characteristic polynomial of $J(x_*, y_*, z_*)$ is

$$P(\lambda) = \lambda^3 + (b r_y y_* + f r_z z_* + r_x x_*)\lambda^2 + (b f r_y r_z y_* z_* + c e r_y r_z y_* z_* + a r_x r_y x_* y_* + b r_x r_y x_* y_* + d r_x r_z x_* z_* + f r_x r_z x_* z_*)\lambda + r_x r_y r_z x_* y_* z_* (ae + af + bd + bf - cd + ce).$$

Using the Routh-Hurwitz Criterion, we obtain that all roots have negative real part if and only if the following three conditions hold:

1. $b r_y y_* + f r_z z_* + r_x x_* > 0$,
2. $r_x r_y r_z x_* y_* z_* (ae + af + bd + bf - cd + ce) > 0$,
3. $b^2 f r_y^2 r_z y_*^2 z_* + b c e r_y^2 r_z y_*^2 z_* + b f^2 r_y r_z^2 y_* z_*^2 + c e f r_y r_z^2 y_* z_*^2 + a b r_x r_y^2 x_* y_*^2 + b^2 r_x r_y^2 x_* y_*^2 + d f r_x r_z^2 x_* z_*^2 + f^2 r_x r_z^2 x_* z_*^2 + a r_x^2 r_y x_*^2 y_* + b r_x^2 r_y x_*^2 y_* + d r_x^2 r_z * x_*^2 z_* + f r_x^2 r_z x_*^2 z_* + (2bf + cd - ae) r_x r_y r_z x_* y_* z_* > 0$.

It is clear that condition 1 and 2 of the Routh-Hurwitz Criterion are always true, if the coexistence equilibrium E_* exists. The Condition 3 are also verified numerically by the following algorithm and we find that the condition 3 is also true for all the discrete value of parameters with $b = 1.1$ to 10.0 and others from 0.1 to 10.0 with step-size 0.1. So we conjecture that E_* is stable whenever it exists.

Algorithm 1: Evaluate condition 3 of the Routh-Hurwitz Criterion

```
for b = 1.1, ··· , 10 (stepsize 0.1) do
    for a, c, d, e, f, r_x, r_y, r_z = 0.1, ··· , 10 (stepsize 0.1) do
        if (2.6) and (2.10) hold then
            Evaluate condition 3 of the Routh-Hurwitz Criterion
        end
    end
end
```

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