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Dynamics of a three-species food chain model with adaptive traits ☆

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ABSTRACT

A three-species food chain model is proposed with dynamically variable adaptive traits in the intermediate consumer. We prove that its solutions are non-negative and bounded, and we analyze the existence and stability of its equilibria. By applying Li and Muldowney's [Li MY, Muldowney J. On Bendixson's criterion. J Differ Equ 1993;106:27–39] high-dimensional Bendixson criterion, we show that the positive equilibrium is globally stable under specific conditions. We support our analytical findings with numerical simulations.

1. Introduction

Ecologists and mathematicians have often used food chains to describe the feeding relationships between species within ecosystems (see [1–5,21,22,24]). The simplest and most classical food chain model is the two-dimensional predator-prey Lotka–Volterra model, which was first introduced by the famous Italian mathematician Vito Volterra [1]. Recently there has been considerable interest in predator-prey models, especially for systems of three-species (see [3,6,7,21–23]). Among them is the resource-prey-predator model with a self-limiting term in the resource:

$$\begin{aligned}
\frac{dx}{dt} &= x\left[r\left(1-\frac{x}{K}\right)-ay\right],\\
\frac{dy}{dt} &= y(c_1ax-bz-d_1),\\
\frac{dz}{dt} &= z(c_2by-d_2),
\end{aligned} \tag{1.1}$$

where $x(t), y(t)$ and $z(t)$ represent, respectively, the resource population, the prey population, and the predator population as functions of time. The positive parameters $r, K, a, b, c_1, c_2, d_1$ and d_2 are interpreted as follows:

- r represents the intrinsic rate of natural increase of the resource in the absence of consumers;
- K represents its carrying capacity;
- a represents the consumption rate of the prey on the resource;
- b represents the predation rate of the predator on the prey;
- c_1 represents the conversion efficiency of consumed resource into new prey;
- c_2 represents the conversion efficiency of consumed prey into new predators;
- d_1 represents the natural death rate of the prey;
- d_2 represents the natural death rate of the predator.

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Model (1.1) is based on the traditional assumption that all species interact with each other simply via changes in population density. Such interactions are called density-mediated interactions. Mathematicians have already given a comprehensive analysis of its local and global properties, including the existence, local stability and global stability of its critical points, and the boundedness of the system (see [8,24]). But in recent years, biologists have showed theoretically and empirically that in natural systems preys often display anti-predator responses, i.e., they alter their foraging behavior on resources to reduce predation risk (for example, seeking refuge or becoming vigilant at the expense of feeding). Altered foraging can result in an increased risk of starvation, and hence in a reduction in prey density (see [9,16,17] and the references therein). These indirect effects of changes in species traits are called trait-mediated indirect effects. Trait-mediated indirect effects have been shown to profoundly alter the dynamics of all trophic levels in food webs (see [18]).

2. The model establishment

Based on the biological information we provided in the introduction, we assume that the two consumption rates a and b are adaptive traits in model (1.1). These two traits are positively related to each other, such that prey increases resource consumption (greater a) at the expense of a higher predation risk by carnivores (greater b), which implies that herbivores can be caught more easily by carnivores when they are actively searching for and consuming food. Here we assume that $b = \beta a^2 (\beta > 0)$, where the constant β measures the predation risk incurred by an individual prey per unit foraging time per unit density of the predator. This simple relationship arises from the fact that the two predation rates are proportional to the amount of time that herbivores spend foraging, which implies that the herbivore can only be caught by its predator when it is actively searching for food. Therefore we only need to model the dynamics of a since the dynamics of b can be known through a due to the assumption $b = \beta a^2$. Applying Abrams' [19] method and differentiating the fitness of species y with respect to the trait a, we obtain the following dynamical equation for trait a:

$$\frac{da}{dt} = \xi(c_1 x - 2\beta a z), \tag{2.1}$$

where the parameter ξ scales the rate at which the adaptive trait changes. Incorporating Eq. (2.1) into model (1.1), we obtain model (2.2), which describes a food chain with a non-instantaneous dynamic trait. Dynamic traits are common in the eco-evolutionary dynamics of community and ecosystems [20].

$$\begin{aligned}
\frac{dx}{dt} &= x\left[r\left(1 - \frac{x}{K}\right) - ay\right], \\
\frac{dy}{dt} &= y(c_1 a x - \beta a^2 z - d_1), \\
\frac{dz}{dt} &= z(c_2 \beta a^2 y - d_2), \\
\frac{da}{dt} &= \xi(c_1 x - 2\beta a z).
\end{aligned} \tag{2.2}$$

The rest of our paper is organized as follows. In Section 3, we analyze the equilibria and their stability using a linear analysis; we also study the non-negativity and boundedness of model (2.2) with a non-instantaneous dynamic trait. In Section 4, we study the global stability of model (2.2) using the high-dimensional Bendixson criterion.

3. Basic analysis results

Model (2.2) always has a positive equilibrium. The positive a-axis of (2.2) is an invariant singular line (each point $E_0(0, 0, 0, \hat{a})$ on the positive a- axis is an equilibrium of model (2.2)). A variational matrix analysis at the boundary equilibrium E_0 shows that E_0, is a saddle, and hence is always unstable. Thus, the singular line of model (2.2) is a repellor, and model (2.2) is a uniformly persistent system.

Lemma 3.1. *All solutions $(x(t), y(t), z(t), a(t))$ of model (2.2) with initial value $(x_0, y_0, z_0, a_0) \in R_+^{4,0}$ are non-negative.*

The non-negativity of $x(t), y(t)$ and $z(t)$ can be verified by the equations

$$\begin{aligned}
x(t) &= x_0 \exp\left\{\int_0^t \left[r\left(1 - \frac{x(s)}{K}\right) - a(s)y(s)\right] ds\right\}, \\
y(t) &= y_0 \exp\left\{\int_0^t [c_1 a(s)x(s) - \beta a^2(s)z(s) - d_1] ds\right\}, \\
z(t) &= z_0 \exp\left\{\int_0^t [c_2 \beta a^2(t)y(t) - d_2] ds\right\},
\end{aligned} \tag{3.1}$$

with $x_0, y_0, z_0 \geqslant 0$. The non-negativity of $a(t)$ can be easily deduced from the fourth equation of model (2.2). Also, if $x(0) = x_0 > 0$, then $x(t) > 0$ for all $t > 0$. The same argument is valid for components $y(t), z(t)$ and $a(t)$. Hence, $R_+^{4,0}$, the interior of R_+^4, is an invariant set for model (2.2). And the planes x–y, x–z and x–z are also invariant. Our next task is to study the boundedness of the solutions of model (2.2).

To simplify the calculations, we apply the following transformations to model (2.2):

$$x \to \frac{x}{K}, \quad y \to c_1 K y, \quad z \to \beta z, \quad a \to \frac{a}{c_1 K}.$$

Model (2.2) then becomes

$$\begin{aligned} \frac{dx}{dt} &= x[r(1-x) - ay], \\ \frac{dy}{dt} &= y(max - ma^2 z - d_1), \\ \frac{dz}{dt} &= z(na^2 y - d_2), \\ \frac{da}{dt} &= \xi(x - 2az), \end{aligned} \tag{3.2}$$

where the number of parameters is reduced from eight to six and the two non-dimensional parameters m and n can be defined in terms of the original parameters:

$$m = c_1^2 K^2, \quad n = c_1 c_2 \beta K.$$

Due to the uniform persistence of model (3.2), there exists a time T such that $x(t), y(t), z(t), a(t) > \tilde{c}(0 < \tilde{c} < 1)$ for $t > T$. From the first equation of model (3.2) and considering the non-negativity of components y and a, we have $dx/dt \leqslant rx(1-x)$. The usual comparison theory [10] tells us that $x(t) \leqslant 1$ as $t \to \infty$. Denote $S_1 = mnx + ny + mz$. Assuming $d_1 \leqslant d_2$,

$$\frac{dS_1}{dt} = -mnd_1 x - d_1 ny - d_2 mz + mnrx - mnrx^2 + mnd_1 x \leqslant -d_1 S_1 + mn[(r + d_1)x - rx^2] \leqslant -d_1 S_1 + b_1,$$

where

$$b_1 = \begin{cases} \frac{mn(r+d_1)^2}{4r}, & \text{if } d_1 < r; \\ mnd_1, & \text{if } d_1 \geqslant r. \end{cases} \tag{3.3}$$

Note that the values of d_1 and d_2 do not affect the boundedness of x, y and z. From the inequality above, we have

$$S_1 \leqslant S_1(0)\exp(-d_1 t) + \frac{b_1(1 - \exp(-d_1 t))}{d_1}.$$

Moreover, we have $\limsup_{t\to\infty} S_1(t) \leqslant b_1/d_1$, which is independent of initial values and equivalent to $\limsup_{t\to\infty}(mnx(t) + ny(t) + mz(t)) \leqslant b_1/d_1$. The variables x, y and z are thus ultimately bounded regardless of the value of the dynamic trait a. Denote $S_2 = x + a$. Then when $t > T$,

$$\begin{aligned} \frac{dS_2}{dt} &= rx - rx^2 - axy + \xi x - 2\xi az \leqslant rx - rx^2 + \xi x + 2\tilde{c}\xi x - 2\tilde{c}\xi x - 2\xi az < -2\tilde{c}\xi(x + a) + (r + \xi + 2\tilde{c}\xi)x - rx^2 \\ &\leqslant -2\tilde{c}\xi S_2 + b_2, \end{aligned}$$

where

$$b_2 = \begin{cases} \frac{(r+\xi+2\tilde{c}\xi)^2}{4r}, & \text{if } \xi + 2\tilde{c}\xi < r; \\ \xi + 2\tilde{c}\xi, & \text{if } \xi + 2\tilde{c}\xi \geqslant r. \end{cases} \tag{3.4}$$

Define $b_3 = 2\tilde{c}\xi$. From the inequality above, we conclude that

$$x(t) + a(t) < (x_0 + a_0)\exp(-b_3 t) + \frac{b_2(1 - \exp(-b_3 t))}{b_3}.$$

Therefore, we have $\limsup_{t\to\infty}(x(t) + a(t)) < b_2/b_3$, which is also independent of initial values.

Lemma 3.2. *All solutions initiating in $R_+^{4,0}$ are bounded, with an ultimate bound.*

In order to find the local stability of the positive equilibrium of model (3.2) we have to calculate the Jacobian matrix J at this equilibrium. The positive equilibrium for model (3.2) is $E^*(x^*, y^*, z^*, a^*)$, where

$$x^* = \frac{2d_1nr}{d_2m + 2d_1nr}, \quad y^* = \frac{d_2m^2nr^2}{(d_2m + 2d_1nr)^2},$$
$$z^* = \frac{d_1mn^2r^2}{(d_2m + 2d_1nr)^2}, \quad a^* = \frac{d_2m + 2d_1nr}{mnr}.$$

The Jacobian matrix of (3.2) at E^* is

$$J = \begin{pmatrix} -rx^* & -a^*x^* & 0 & -x^*y^* \\ ma^*y^* & 0 & -ma^{*2}y^* & y^*(mx^* - 2ma^*z^*) \\ 0 & na^{*2}z^* & 0 & \frac{2d_2z^*}{a^*} \\ \xi & 0 & -2\xi a^* & -2\xi z^* \end{pmatrix},$$

whose characteristic equation is

$$\lambda^4 + A\lambda^3 + B\lambda^2 + C\lambda + D = 0, \tag{3.5}$$

where

$$A = \frac{2d_1nr^2}{d_2m + 2d_1nr} + \frac{2d_1mn^2r^2\xi}{(d_2m + 2d_1nr)^2},$$
$$B = \frac{2d_1d_2mr}{d_2m + 2d_1nr} + \frac{2d_1mn^2r^2\xi(2d_2 + r)}{(d_2m + 2d_1nr)^2},$$
$$C = \frac{2d_1^2d_2nr^2}{d_2m + 2d_1nr} + \frac{2d_1d_2mn^2r^2\xi}{(d_2m + 2d_1nr)^2} + \frac{4d_1^2d_2mn^2r^3\xi(m + 2nr)}{(d_2m + 2d_1nr)^3},$$
$$D = \frac{2d_1^2d_2mn^2r^3\xi}{(d_2m + 2d_1nr)^2}.$$

Notice that zero is not the root of (3.5). From the Routh–Hurwitz criteria [11], all the real parts of roots for (3.5) are negative if and only if

$$ABC - A^2D > C^2, \tag{3.6}$$

which is equivalent to

$$\begin{aligned} &16d_1^4d_2n^4r^4 + 8d_1^3d_2mn^3r^3(4d_2 + n\xi) + 4d_1^2d_2mn^2r^2[6md_2^2 + 3mnd_2\xi \\ &\quad + 2nr\xi(m + 2nr + n^2\xi)] + 2d_1mnr[4d_2^4m^2 + 3d_2^3m^2n\xi + 2d_2mn^4r\xi^3 \\ &2n^3r^3(m + 2nr)\xi^2 + 4d_2^2mnr(m + 2nr + n^2\xi)\xi] + m^2[d_2^5m^2 + d_2^4m^2n\xi \\ &\quad + 2d_2^2mn^4r\xi^3 + 2n^4r^3(m + 2nr)\xi^3 + 2d_2n^3r^2(m + 2nr)(r + 2n\xi)\xi^2 \\ &\quad + 2d_2^3mnr(m + 2nr + n^2\xi)\xi] > 0. \end{aligned} \tag{3.7}$$

Inequality (3.6) or (3.7) always holds for any positive parameters in (3.2), and thus the positive equilibrium E^* is locally stable.

4. Analysis of global stability

When the positive equilibrium E^* is locally asymptotically stable, it is of interest to know its basin of attraction. In particular, we would like to know if its basin of attraction includes all the points in the feasible region, namely, if E^* is globally asymptotically stable. The difficulty associated with this problem is largely due to the lack of practical tools. The method of Lyapunov functions is most commonly applied (see [10]). However, its application is often hindered by the fact that global Lyapunov functions are difficult to construct and there is no general approach to construct them. Another method to prove global stability is to use the higher Poincare–Bendixon theory (see [12]). This approach depends crucially on the fact that the system studied is competitive. But model (2.2) or (3.2) is not a competitive system. Therefore, to investigate the global stability of the positive equilibrium E^*, we now apply the high-dimensional Bendixson criterion of Li and Muldowney [13], which we briefly summarize next.

Let $D \subset R^n$ be an open set and function $F : X \mapsto F(X) \in R^n$ be C^1 for $X \in D$. Consider the differential equation

$$\frac{dX}{dt} = F(X). \tag{4.1}$$

As shown in [13], to derive a high-dimensional Bendixson criterion, it is sufficient to show that the second compound equation

$$\frac{\mathrm{d}Z}{\mathrm{d}t} = \frac{\partial F^{[2]}}{\partial X}(X(t, X_0))Z(t) \tag{4.2}$$

with respect to a solution $X(t, X_0) \in D$ of system (4.1) is equi-uniformly asymptotically stable, namely, for each $X_0 \in D$, system (4.2) is uniformly asymptotically stable, and the exponential decay rate is uniform for X_0 in each compact subset of D, where $D \subset R^n$ is an open connected set. Here $\partial F/\partial X^{[2]}$ is the second additive compound matrix of the Jacobian matrix $\partial F/\partial X$. It is a $\binom{n}{2} \times \binom{n}{2}$ matrix, and thus (4.2) is a linear system of dimension $\binom{n}{2}$ (see [14,15] for details).

For a general 4×4 matrix

$$A = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{pmatrix},$$

its second additive compound matrix $A^{[2]}$ is

$$A^{[2]} = \begin{pmatrix} a_{11}+a_{22} & a_{23} & a_{24} & -a_{13} & -a_{14} & 0 \\ a_{32} & a_{11}+a_{33} & a_{34} & a_{12} & 0 & -a_{14} \\ a_{42} & a_{43} & a_{11}+a_{44} & 0 & a_{12} & a_{13} \\ -a_{31} & a_{21} & 0 & a_{22}+a_{33} & a_{34} & -a_{24} \\ -a_{41} & 0 & a_{21} & a_{43} & a_{22}+a_{44} & a_{23} \\ 0 & -a_{41} & a_{31} & -a_{42} & a_{32} & a_{33}+a_{44} \end{pmatrix}. \tag{4.3}$$

The equi-uniform asymptotic stability of (4.2) implies the exponential decay of the surface area of any compact two-dimensional surface in D. If D is simply connected, this excludes the existence of any invariant simple closed rectifiable curve in D, including periodic orbits.

Proposition 4.1 [13]. *Let $D \subset R^n$ be a simply connected region. Assume that the family of linear systems (4.2) is equi-uniformly asymptotically stable. Then*

(a) D contains no simple closed invariant curves, including periodic orbits, homoclinic orbits, heteroclinic cycles;
(b) each semi-orbit in D converges to a single equilibrium.

In particular, if D is positively invariant and contains a unique equilibrium $\overline{X}$, then $\overline{X}$ is globally asymptotically stable in D.

The required uniform asymptotic stability of the family of linear systems (4.2) can be proved by constructing a suitable Lyapunov function. For instance, (4.2) is equi-uniformly asymptotically stable if there exists a positive definite function $V(Z)$, such that $\mathrm{d}V(Z)/\mathrm{d}t|_{(4.2)}$ is negative definite, and V and $\mathrm{d}V/\mathrm{d}t|_{(4.2)}$ are both independent of X_0.

In order to prove the global stability of the positive equilibrium in model (2.2) or (3.2), we first make the following assumption.

(**H**) There exist positive numbers $\varpi, \theta, \vartheta, \rho$ and σ such that

$$\max\left\{c_{11} + \frac{c_{12}\varpi}{\theta} + c_{13}\varpi + \frac{c_{15}\varpi}{\rho},\quad \frac{c_{21}\theta}{\varpi} + c_{22} + c_{23}\theta + \frac{c_{24}\theta}{\vartheta} + \frac{c_{26}\theta}{\sigma},\quad \frac{c_{32}}{\theta} + c_{33} + \frac{c_{35}}{\rho},\quad \frac{c_{42}\vartheta}{\theta} + c_{44} + \frac{c_{45}\vartheta}{\rho} + \frac{c_{46}\vartheta}{\sigma},\right.$$
$$\left.\frac{c_{51}\rho}{\varpi} + c_{53}\rho + \frac{c_{54}\rho}{\vartheta} + c_{55} + \frac{c_{56}\rho}{\sigma},\quad \frac{c_{62}\sigma}{\theta} + \frac{c_{65}\sigma}{\rho} + c_{66}\right\} < 0.$$

For model (3.2), denote $X = (x, y, z, a)^T$ and

$$F(X) = (x[r(1-x) - ay],\quad y(max - ma^2z - d_1),\quad z(na^2y - d_2),\quad \xi(x - 2az))^T.$$

We then have

$$\frac{\partial F}{\partial X} = \begin{pmatrix} r - 2rx - ay & -ax & 0 & -xy \\ may & max - ma^2z - d_1 & -ma^2y & mxy - 2mayz \\ 0 & na^2z & na^2y - d_2 & 2nayz \\ \xi & 0 & -2\xi a & -2\xi z \end{pmatrix},$$

and we assume that

$$\frac{\partial F^{[2]}}{\partial X} = \begin{pmatrix} b_{11} & b_{12} & b_{13} & b_{14} & b_{15} & b_{16} \\ b_{21} & b_{22} & b_{23} & b_{24} & b_{25} & b_{26} \\ b_{31} & b_{32} & b_{33} & b_{34} & b_{35} & b_{36} \\ b_{41} & b_{42} & b_{43} & b_{44} & b_{45} & b_{46} \\ b_{51} & b_{52} & b_{53} & b_{54} & b_{55} & b_{56} \\ b_{61} & b_{62} & b_{63} & b_{64} & b_{65} & b_{66} \end{pmatrix}.$$

By (4.3), we obtain that

$$\begin{aligned}
&b_{11} = r - d_1 - 2rx - ay + max - ma^2z, \quad b_{12} = -ma^2y, \quad b_{13} = mxy - 2mayz, \quad b_{14} = 0,\\
&b_{15} = xy, \quad b_{16} = 0, \quad b_{21} = na^2z, \quad b_{22} = r - d_2 - 2rx - ay + na^2y, \; b_{23} = 2nayz,\\
&b_{24} = -ax, \quad b_{25} = 0, \quad b_{26} = xy, \quad b_{31} = 0, \quad b_{32} = -2\xi a, \; b_{33} = r - 2rx - ay - 2\xi z,\\
&b_{34} = 0, \quad b_{35} = -ax, \quad b_{36} = 0, \quad b_{41} = 0, \quad b_{42} = may, \quad b_{43} = 0,\\
&b_{44} = -d_1 - d_2 + max - ma^2z + na^2y, \quad b_{45} = 2nayz, \; b_{46} = -mxy + 2mayz,\\
&b_{51} = -\xi, \quad b_{52} = 0, \quad b_{53} = may, \quad b_{54} = -2\xi a, \; b_{55} = -d_1 + max - ma^2z - 2\xi z,\\
&b_{56} = -ma^2y, \quad b_{61} = 0, \quad b_{62} = -\xi, \quad b_{63} = 0, \quad b_{64} = 0, \; b_{65} = na^2z, \quad b_{66} = -d_2 + na^2y - 2\xi z.
\end{aligned}$$

The second compound system

$$\begin{pmatrix} \dot z_1 \\ \dot z_2 \\ \dot z_3 \\ \dot z_4 \\ \dot z_5 \\ \dot z_6 \end{pmatrix} = \frac{\partial F^{[2]}}{\partial X} \begin{pmatrix} z_1 \\ z_2 \\ z_3 \\ z_4 \\ z_5 \\ z_6 \end{pmatrix}$$

then becomes

$$\begin{aligned}
\dot z_1 &= (r - d_1 - 2rx - ay + max - ma^2z)z_1 - ma^2yz_2 + (mxy - 2mayz)z_3 + xyz_5,\\
\dot z_2 &= na^2zz_1 + (r - d_2 - 2rx - ay + na^2y)z_2 + 2nayzz_3 - axz_4 + xyz_6,\\
\dot z_3 &= -2\xi az_2 + (r - 2rx - ay - 2\xi z)z_3 - axz_5,\\
\dot z_4 &= mayz_2 + (-d_1 - d_2 + max - ma^2z + na^2y)z_4 + 2nayzz_5 + (-mxy + 2mayz)z_6,\\
\dot z_5 &= -\xi z_1 + mayz_3 - 2\xi az_4 + (-d_1 + max - ma^2z - 2\xi z)z_5 - ma^2yz_6,\\
\dot z_6 &= -\xi z_2 + na^2zz_5 + (-d_2 + na^2y - 2\xi z)z_6,
\end{aligned} \tag{4.5}$$

where $X(t) = (x(t), y(t), z(t), a(t))^T$ is an arbitrary solution of model (3.2) with $X_0(t) = (x_0(t), y_0(t), z_0(t), a_0(t))^T \in R_+^{4,0}$. Set

$$W(Z) = \max\{\varpi|z_1|, \theta|z_2|, |z_3|, \vartheta|z_4|, \rho|z_5|, \sigma|z_6|\}.$$

Direct calculations lead to the following inequalities:

$$\begin{aligned}
&\frac{\mathrm{d}^+}{\mathrm{d}t}\varpi|z_1| \leqslant c_{11}\varpi|z_1| + \frac{c_{12}\varpi}{\theta}\theta|z_2| + c_{13}\varpi|z_3| + \frac{c_{15}\varpi}{\rho}\rho|z_5|,\\
&\frac{\mathrm{d}^+}{\mathrm{d}t}\theta|z_2| \leqslant \frac{c_{21}\theta}{\varpi}\varpi|z_1| + c_{22}\theta|z_2| + c_{23}\theta|z_3| + \frac{c_{24}\theta}{\vartheta}\vartheta|z_4| + \frac{c_{26}\theta}{\sigma}\sigma|z_6|,\\
&\frac{\mathrm{d}^+}{\mathrm{d}t}|z_3| \leqslant \frac{c_{32}}{\theta}\theta|z_2| + c_{33}|z_3| + \frac{c_{35}}{\rho}\rho|z_5|,\\
&\frac{\mathrm{d}^+}{\mathrm{d}t}\vartheta|z_4| \leqslant \frac{c_{42}\vartheta}{\theta}\theta|z_2| + c_{44}\vartheta|z_4| + \frac{c_{45}\vartheta}{\rho}\rho|z_5| + \frac{c_{46}\vartheta}{\sigma}\sigma|z_6|,\\
&\frac{\mathrm{d}^+}{\mathrm{d}t}\rho|z_5| \leqslant \frac{c_{51}\rho}{\varpi}\varpi|z_1| + c_{53}\rho|z_3| + \frac{c_{54}\rho}{\vartheta}\vartheta|z_4| + c_{55}\rho|z_5| + \frac{c_{56}\rho}{\sigma}\sigma|z_6|,\\
&\frac{\mathrm{d}^+}{\mathrm{d}t}\sigma|z_6| \leqslant \frac{c_{62}\sigma}{\theta}\theta|z_2| + \frac{c_{65}\sigma}{\rho}\rho|z_5| + c_{66}\sigma|z_6|,
\end{aligned} \tag{4.6}$$

in which $\mathrm{d}^+/\mathrm{d}t$ denotes the right-hand derivative and

$$\begin{aligned}
&c_{11} = r - d_1 - 2r\tilde{c} - \tilde{c}^2 + \frac{m(1+2\tilde{c})^2}{16\tilde{c}^2}, \quad c_{12} = -m\tilde{c}^3, \quad c_{13} = \frac{m^2(d_1+r)^2}{4d_1 r},\\
&c_{15} = \frac{m(d_1+r)^2}{4d_1 r}, \quad c_{21} = \frac{n^2(d_1+r)^2(1+2\tilde{c})^4}{4^5\tilde{c}^4 d_1 r}, \quad c_{22} = r - d_2 - 2r\tilde{c} + \frac{mn(d_1+r)^2(1+2\tilde{c})^4}{4^5\tilde{c}^4 d_1 r},\\
&c_{23} = \frac{mn^2(d_1+r)^4(1+2\tilde{c})^2}{128\tilde{c}^2 d_1^2 r^2}, \quad c_{24} = -\tilde{c}^2, \quad c_{26} = \frac{m(d_1+r)^2}{4d_1 r}, \quad c_{32} = -2\xi\tilde{c},\\
&c_{33} = r - 2r\tilde{c} - 2\xi\tilde{c}, \quad c_{35} = -\tilde{c}^2, \quad c_{42} = \frac{m^2(d_1+r)^2(1+2\tilde{c})^2}{64\tilde{c}^2 d_1 r},\\
&c_{44} = -d_1 - d_2 + \frac{m(1+2\tilde{c})^2}{16\tilde{c}^2} + \frac{mn(d_1+r)^2(1+2\tilde{c})^4}{4^5\tilde{c}^4 d_1 r}, \quad c_{45} = \frac{mn^2(d_1+r)^4(1+2\tilde{c})^2}{128\tilde{c}^2 d_1^2 r^2},\\
&c_{46} = -m\tilde{c}^2 + \frac{m^2 n(d_1+r)^4(1+2\tilde{c})^2}{128\tilde{c}^2 d_1^2 r^2}, \quad c_{51} = -\xi, \quad c_{53} = \frac{m^2(d_1+r)^2(1+2\tilde{c})^2}{64\tilde{c}^2 d_1 r},\\
&c_{54} = -2\xi\tilde{c}, \quad c_{55} = -d_1 + \frac{m(1+2\tilde{c})^2}{16\tilde{c}^2} - 2\xi\tilde{c}, \quad c_{56} = -m\tilde{c}^3, \quad c_{62} = -\xi,\\
&c_{65} = \frac{n^2(d_1+r)^2(1+2\tilde{c})^4}{4^5\tilde{c}^4 d_1 r}, \quad c_{66} = -d_2 + \frac{mn(d_1+r)^2(1+2\tilde{c})^4}{4^5\tilde{c}^4 d_1 r} - 2\xi\tilde{c}.
\end{aligned} \tag{4.7}$$

Therefore,

$$\frac{\mathrm{d}^+}{\mathrm{d}t} W(Z(t)) \leqslant \psi W(Z(t)),$$

with

$$\begin{aligned}
\psi = \max\Bigg\{ &c_{11} + \frac{c_{12}\varpi}{\theta} + c_{13}\varpi + \frac{c_{15}\varpi}{\rho}, \quad \frac{c_{21}\theta}{\varpi} + c_{22} + c_{23}\theta + \frac{c_{24}\theta}{\vartheta} + \frac{c_{26}\theta}{\sigma}, \quad \frac{c_{32}}{\theta} + c_{33} + \frac{c_{35}}{\rho}, \quad \frac{c_{42}\vartheta}{\theta} + c_{44} + \frac{c_{45}\vartheta}{\rho} + \frac{c_{46}\vartheta}{\sigma},\\
&\frac{c_{51}\rho}{\varpi} + c_{53}\rho + \frac{c_{54}\rho}{\vartheta} + c_{55} + \frac{c_{56}\rho}{\sigma}, \quad \frac{c_{62}\sigma}{\theta} + \frac{c_{65}\sigma}{\rho} + c_{66}\Bigg\}.
\end{aligned}$$

Thus, under hypothesis (**H**), and by the boundedness of solution of model (3.2), there exists a positive constant τ such that $\psi \leqslant -\tau < 0$, and thus

$$W(Z(t)) \leqslant W(Z(s))\exp(-\tau(t-s)), \quad t \geqslant s > 0.$$

This establishes the equi-uniform asymptotic stability of the second compound system (4.5), and hence the positive equilibrium E^* of model (3.2) is globally stable following from Proposition 4.1. We summarize the above analysis in the following theorem.

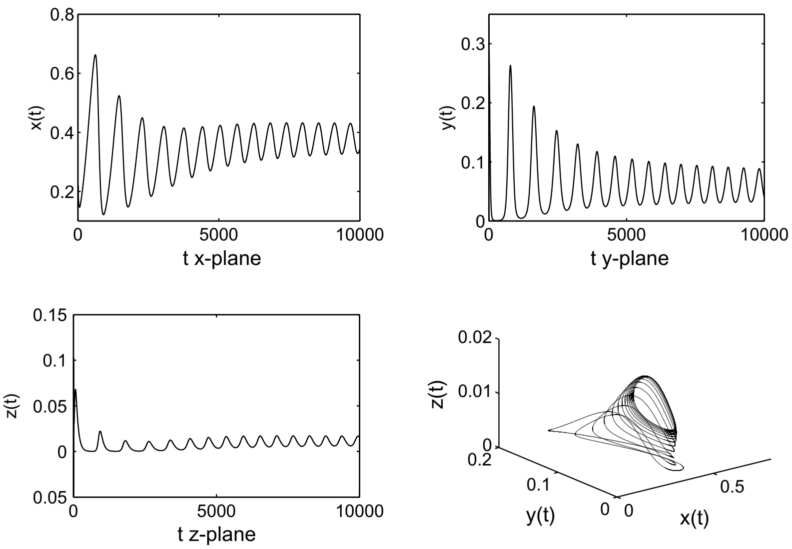

Fig. 1. Numerical simulations of the dynamics of species x, y and z in model (2.2) or (3.2) showing global stability.

Theorem 4.2. *If hypothesis (H) is satisfied, then model (2.2) or (3.2) has no non-trivial periodic solutions. Furthermore, the positive equilibrium E^* is globally stable in $R_+^{4,0}$.*

Based on the local stability analysis in Section 3 and Theorem 4.2, we next carry out numerical simulations of the dynamics of species x, y and z (see Fig. 1) to illustrate its global stability through an example. We use the following parameter values in the original model (2.2): $r = 2, K = 4, c_1 = c_2 = \beta = 1/2, d_1 = 1, d_2 = 5, \xi = 14$ (we also take $\tilde{c} = 1/4$). From the non-dimensional transformation in Section 3 we know that $m = 1, n = 1/2$. We also know that the positive equilibrium E^* is locally stable from Section 3. We then substitute the above parameter values into (4.7), and obtain

$$\begin{aligned}
&c_{11} = 2.1875, \quad c_{12} = -0.0156, \quad c_{13} = 1.1250, \quad c_{15} = 1.1250, \quad c_{21} = 1.4238, \quad c_{22} = -1.1524,\\
&c_{23} = 1.4238, \quad c_{24} = -0.0625, \quad c_{26} = 1.1250, \quad c_{32} = -8.1667, \quad c_{33} = -6.2500, \quad c_{35} = -0.0625,\\
&c_{42} = 2.5312, \quad c_{44} = -0.9024, \quad c_{45} = 1.4238, \quad c_{46} = 2.7851, \quad c_{51} = -14, \quad c_{53} = 2.5312,\\
&c_{54} = -7, \quad c_{55} = -5.75, \quad c_{56} = -0.0156, \quad c_{62} = -14, \quad c_{65} = 1.4238, \quad c_{66} = -9.1524.
\end{aligned}$$

The positive numbers $\varpi = 1.0000, \theta = 0.0030, \vartheta = 0.0001, \rho = 1.0000$ and $\sigma = 1.0000$ are such that

$$\max\{-1.8841, -1.1404, -2728.5458, -0.0583, -74669.9011, -4674.3953\} < 0.$$

Therefore the positive equilibrium E^* is globally stable (see Fig. 1).

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