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# MULTISTABILITY AND DYNAMIC SCENARIOS IN THE PREY–PREDATOR–SUPERPREDATOR MODEL

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**Abstract:** In mathematical models of population dynamics, the appearance of a continuum of solutions is a rare situation. We analyze a multistability in the system of differential equations describing the prey-predator-superpredator dynamics. The cosymmetric approach is applied to derive a continuous family of equilibria for Beddington-DeAngelis functional response. The case of multistability was detected analytically and the destruction of the family of equilibria was studied. Our results exhibit memory of the disappeared family of equilibria and its impact on dynamic scenarios. Two-parameter bifurcation diagrams were built numerically for cosymmetric and general cases.

**Keywords:** mathematical ecology, prey–predator–superpredator, differential equations, cosymmetry, multistability.

## 1 Introduction

Actual ecological problems require the development of models describing the interaction of many populations. Among them, three-species systems are the basis of food chain analysis [1], including the models where superpredator

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eats prey and predator. Such models are known by several names: "intraguild predation", "prey-predator-top-predator", "trophic level omnivory", and "three-species food web" [2, 3, 4]. Recent studies explore different approaches: stochastic modeling [5], delay effects [6], etc. Several models with a superpredator were developed to investigate the disease processes [2]. There exist approaches by which the superpredator population may be divided into several ages; see, for example, [7] with two stages. Dynamic scenarios and chaotic behavior were found in a cyclic three-species system of prey, predator, and superpredator [8, 9, 10] and four-species cyclic ecosystem [11]. Recently, works have appeared that develop an approach based on Beddington-DeAngelis functional response [12, 13].

Vital problems require a study of the coexistence of species and the possibility of multiple scenarios for population system evolution. Research in physics and biology has yielded important results about multistability and its influence on dynamics and processes [14, 15]. Multistability in predator-prey systems was examined in [16, 17] by using the cosymmetry theory [18]. Particularly, an appearance of a family of oscillatory regimes was found in [16]. When the cosymmetry breaks, the destruction of a family of equilibria may be analyzed with the selective function approach [19].

We consider a trophic chain consisting of prey $x(t)$, predator $y(t)$, and superpredator $z(t)$, with Beddington-DeAngelis functional response. If the predator and superpredator hunt the prey independently, the corresponding system of autonomous differential equations may be written as follows:

$$\begin{aligned}
\frac{dx}{dt} &= \frac{x(1-x)}{f_1} - \frac{xy+xz}{f_2}\\
\frac{dy}{dt} &= \frac{-\mu_1 y - \lambda_1 y^2}{f_1} + \frac{\eta_1 xy}{f_2} - \frac{d_1 yz}{f_3}\\
\frac{dz}{dt} &= \frac{-\mu_2 z - \lambda_2 z^2}{f_1} + \frac{\eta_2 xz}{f_2} + \frac{d_2 yz}{f_3}
\end{aligned} \tag{1}$$

where logistic law is taken for the prey, $\mu_1, \mu_2$ are the natural mortality rates of predator and superpredator. The negative feedback because of intraspecific competition among predator and superpredator is represented by $\lambda_1$ and $\lambda_2$, respectively. The parameters $\eta_1, \eta_2$ characterize the consumption of prey by the predator and superpredator, and $d_1, d_2$ define the consumption of a predator by the superpredator. To realize the Beddington-DeAngelis type functional response [20, 21] for different species in (1), we use the following functions

$$f_j = 1 + a_j x + b_j y + c_j z, \quad (j = 1, 2, 3) \tag{2}$$

System (1) with $f_1 = 1$ was considered in [13] to study competitive exclusion and coexistence in an intraguild predation model. The scenario of multistability was found in [17] for $f_j = 1$ $(j = 1, 2, 3)$. In these works, the case $\lambda_1 = \lambda_2 = 0$ was analyzed.

The paper is organized as follows. In Section 2, we consider the equilibrium points of the system (1) and discuss their stability properties. In Section 3, we get the conditions for a nontrivial cosymmetry and find the parameters that provide a continuous family of equilibria. The various forms of Beddington-DeAngelis function response were used to analyze the possibilities of the family of equilibria disintegration in Section 4. In Section 5, we perform numerical simulation to illustrate our results on the family of equilibria and its destruction. Since there are many parameters in the problem, a complete analysis is not possible and we focus primarily on a number of characteristic cases. Finally, in Section 6, a summary discussion is given to conclude our research.

## 2 Equilibrium points and local stability analysis

System (1) has one trivial equilibrium $E_0 = (0, 0, 0)$ and one axial equilibrium $E_1 = (1, 0, 0)$, irrespective of any parametric restriction. There are some boundary equilibria: the superpredator-absent equilibrium $E_2$ and the predator-absent equilibrium $E_3$. Additionally, equilibrium with all species $E_4$ and other limit cycles might exist.

Firstly, we consider the case $f_1 = f_2 = f_3$. The superpredator–absent equilibrium exists when $\eta_1 > \mu_1$:

$$E_2 = \left(\frac{\lambda_1 + \mu_1}{\lambda_1 + \eta_1}, \frac{\eta_1 - \mu_1}{\lambda_1 + \eta_1}, 0\right) = (x_2, y_2, 0) \tag{3}$$

When $\eta_2 > \mu_2$ the predator-absent equilibrium exists

$$E_3 = \left(\frac{\lambda_2 + \mu_2}{\lambda_2 + \eta_2}, 0, \frac{\eta_2 - \mu_2}{\lambda_2 + \eta_2}\right) = (x_3, 0, z_3) \tag{4}$$

The interior equilibrium $E_4 = (x_4, y_4, z_4)$ corresponds to the scenario when all three interacting species will survive:

$$\begin{aligned}
x_4 &= \frac{1}{a}\left(d_1 d_2 + \lambda_1\lambda_2 - d_1\mu_2 + \lambda_2\mu_1 + d_2\mu_1 + \lambda_1\mu_2\right) \\
y_4 &= \frac{1}{a}(-\mu_1 + \eta_1 x_3 - d_1 z_3) \\
z_4 &= \frac{1}{a}(-\mu_2 + \eta_2 x_2 + d_2 y_2) \\
a &= (d_1 d_2 + \lambda_1\lambda_2 - d_1\eta_2 + d_2\eta_1 + \eta_1\lambda_2 + \eta_2\lambda_1)
\end{aligned} \tag{5}$$

Here we use the values of $x_2$, $y_2$, $x_3$ and $z_3$, given by (3) and (4).

We consider the local stability of equilibria on the boundaries. The Jacobian matrix evaluated at $E_1$ is

$$J_{E_1} = \frac{1}{a_1 + 1}\begin{bmatrix} -1 & -1 & -1 \\ 0 & \eta_1 - \mu_1 & 0 \\ 0 & 0 & \eta_2 - \mu_2 \end{bmatrix} \tag{6}$$

Thus, the equilibrium $E_1$ is asymptotically stable if $\eta_1 < \mu_1$ and $\eta_2 < \mu_2$. Otherwise, it is a saddle if $\eta_1 > \mu_1$ or $\eta_2 > \mu_2$.

**Proposition 1.** *The equilibrium $E_2$ is asymptotically stable if and only if:*

$$A_1 = d_2(\eta_1 - \mu_1) + \eta_2(\lambda_1 + \mu_1) - \mu_2(\lambda_1 + \eta_1) < 0 \tag{7}$$

*Proof.* The Jacobian matrix at $E_2$ is given by:

$$J_{E_2} = \frac{1}{a_1 x_2 + b_1 y_2 + 1}\begin{bmatrix} -x_2 & -x_2 & -x_2 \\ \eta_1 y_2 & -\lambda_1 y_2 & -d_1 y_2 \\ 0 & 0 & d_2 y_2 + \eta_2 x_2 - \mu_2 \end{bmatrix} \tag{8}$$

One eigenvalue of $J_{E_2}$ is defined explicitly

$$\sigma_3(E_2) = \frac{d_2 y_2 + \eta_2 x_2 - \mu_2}{a_1 x_2 + b_1 y_2 + 1} = \frac{A_1}{(\lambda_1 + \eta_1)(a_1 x_2 + b_1 y_2 + 1)} \tag{9}$$

and the other two eigenvalues are the roots of the characteristic polynomial for the top left sub-matrix $J_{E_2}$

$$P_2(\sigma) = \sigma^2 + \frac{\lambda_1 y_2 + x_2}{a_1 x_2 + b_1 y_2 + 1}\sigma + \frac{x_2 y_2(\eta_1 + \lambda_1)}{(a_1 x_2 + b_1 y_2 + 1)^2} \tag{10}$$

Since $x_2$, $y_2$, and all parameters in $P_2(\sigma)$ are positive, the stability of $E_2$ is affected by the numerator of $\sigma_3(E_2)$. So, the solution $E_2$ is asymptotically stable when $A_1 < 0$. □

**Proposition 2.** *The equilibrium $E_3$ is asymptotically stuble if and only if:*

$$A_2 = \eta_2(d_1 + \mu_1) - \mu_2(d_1 + \eta_1) + \lambda_2(\mu_1 - \eta_1) > 0 \tag{11}$$

*Proof.* The Jacobian matrix at $E_3$ is given by:

$$J_{E_3} = \frac{1}{a_1 x_3 + c_1 z_3 + 1}\begin{bmatrix} -x_3 & -x_3 & -x_3 \\ 0 & -d_1 z_3 + \eta_1 x_3 - \mu_1 & 0 \\ \eta_2 z_3 & d_2 z_3 & -\lambda_2 z_3 \end{bmatrix} \tag{12}$$

One eigenvalue of $J_{E_3}$ is defined explicitly

$$\sigma_2(E_3) = -\frac{d_1 z_3 - \eta_1 x_3 + \mu_1}{a_1 x_3 + c_1 z_3 + 1} = -\frac{A_2}{(\lambda_2 + \eta_2)(a_1 x_3 + c_1 z_3 + 1)} \tag{13}$$

and the other two eigenvalues are the roots of the characteristic polynomial for the 2x2 sub-matrix $J_{E_3}$

$$P_3(\sigma) = \sigma^2 + \frac{\lambda_2 z_3 + x_3}{a_1 x_3 + c_1 z_3 + 1}\sigma + \frac{x_3 z_3(\eta_2 + \lambda_2)}{(a_1 x_3 + c_1 z_3 + 1)^2} \tag{14}$$

Since $x_3$, $z_3$, and all parameters in $P_3(\sigma)$ are positive, the solution $E_3$ is asymptotically stable when $A_2 > 0$. □

Conditions (7) and (11) determine the stability of equilibria $E_2$ and $E_3$ in parameter space. For defining the intersection of domains of stability, we transform (7) and (11) to equations:

$$d_2(\eta_1 - \mu_1) + \eta_2(\lambda_1 + \mu_1) - \mu_2(\lambda_1 + \eta_1) = 0 \tag{15}$$

$$\eta_2(d_1 + \mu_1) - \mu_2(d_1 + \eta_1) + \lambda_2(\mu_1 - \eta_1) = 0 \tag{16}$$

and determine the values of $\mu_2$ and $\eta_2$:

$$\mu_2 = \frac{d_2(d_1+\mu_1)+\lambda_2(\lambda_1+\mu_1)}{d_1-\lambda_1}, \quad \eta_2 = \frac{d_2(d_1+\eta_1)+\lambda_2(\eta_1+\lambda_1)}{d_1-\lambda_1} \tag{17}$$

One can see that $\mu_2$ and $\eta_2$ are defined in terms of all the parameters of the system (1). This point corresponds to the intersection of the stability boundaries $E_2$ and $E_3$. After fixing $d_1$, $d_2$, $\eta_1$, $\mu_1$, $\lambda_1$, and $\lambda_2$, we can draw these stability domains on the parameter plane $\mu_2$ and $\eta_2$. We will focus our analysis mainly on these parameters.

## 3 Family of equilibria

In [18], the notion of cosymmetry was introduced to explain the appearance of a continuous family of steady states (extreme multistability) in the system of autonomous first-order differential equations. Cosymmetry is also a nontrivial vector field orthogonal to the right-hand side of the system $F$. If the system of differential equations has an equilibrium $E$ and $L(E) \neq 0$ (without additional degeneracy), then the equilibrium $E$ belongs to the family of equilibria. The nontrivial cosymmetry of the system produces a continuous family of equilibria with a stability spectrum that varies along the family.

The theory of the cosymmetric defect and the selective equation were introduced for the analysis of nearly cosymmetric situations [19]. We apply this technique to study the destruction of the family of equilibria.

**Proposition 3.** *The vector*

$$L = [yz, c_1xz, c_2xy]^T, \quad c_1 = -\frac{1}{d_1} - c_2\frac{\lambda_2}{d_1}, \quad c_2 = \frac{-\lambda_1+d_1}{\lambda_1\lambda_2+d_1d_2} \tag{18}$$

*will be the cosymmetry of the system (1) when $f_1 = f_2 = f_3$ and conditions on the parameters (17) are held.*

*Proof.* Multiplying the right side of system (1) on cosymmetry (18) and using condition on functions $f_j$, we get:

$$\begin{aligned} < F, L >= \frac{xyz}{f_1}\Big[1 - x - y - z + c_1(-\mu_1 - \lambda_1 y + \eta_1 x - d_1 z) \\ + c_2(-\mu_2 - \lambda_2 z + \eta_2 x + d_2 y)\Big] \end{aligned} \tag{19}$$

After substitution (18) to (19) and simplification, we obtain $< F, L >= 0$. This means that the vector function $L$ is orthogonal to the right-hand side of the system (1), i.e., $L$ is a cosymmetry of the system. □

**Proposition 4.** *System (1) under conditions $f_1 = f_2 = f_3$ and (17) has a continuous family of stable equilibria.*

$$Q = \left\{x \in \left[\frac{\lambda_1+\mu_1}{\lambda_1+\eta_1}, \quad \frac{d_1+\mu_1}{d_1+\eta_1}\right], y = y_Q(x), z = z_Q(x)\right\} \tag{20}$$

*where:*

$$y_Q(x) = \frac{d_1 + \mu_1 - x(d_1 + \eta_1)}{d_1 - \lambda_1}, \quad z_Q(x) = \frac{(\eta_1 + \lambda_1)x - \lambda_1 - \mu_1}{d_1 - \lambda_1} \tag{21}$$

*Proof.* By direct substitution of $Q$ to (1) and using the conditions of Proposition, we check that $Q$ are equilibria. The Jacobian matrix at the family of equilibria (20) is given by:

$$J_Q = \frac{1}{f_1} \begin{bmatrix} -x & x & -x \\ y\eta_1 & -y\lambda_1 & -yd_1 \\ z\eta_2 & zd_2 & -z\lambda_2 \end{bmatrix} \tag{22}$$

The characteristic equation for $J_Q$ is written as:

$$\sigma^3 + A\sigma^2 + B\sigma = 0$$

where

$$A = \frac{\lambda_1 y + \lambda_2 z + x}{f_1}$$
$$B = \frac{1}{f_1^2}\left[xy(\eta_1 + \lambda_1) + xz(\eta_2 + \lambda_2) + yz(d_1 d_2 + \lambda_1\lambda_2)\right] \tag{23}$$

The zero root $\sigma_1 = 0$ corresponds to neutral stability along the family $Q$. Since $A, B > 0$, the equilibria of the family $Q$ are stable. □

One can see that the stability spectrum varies throughout the family. This is a characteristic property of cosymmetric systems.

## 4 Destruction of the family of equilibria

To analyze the destruction of the family of equilibria via violation of Proposition 2 conditions, we use the definitions of a cosymmetric defect and a selective function [19]. For the differential equation

$$\dot{W} = F(W) + G(W, \varepsilon) \tag{24}$$

in a Hilbert space $H$, the cosymmetric defect is defined as

$$D(W, \varepsilon) = < G(W, \varepsilon), L(W) >, \tag{25}$$

where $L$ is the cosymmetry of the vector field $F$ and the perturbation is given by the operator $G(W, \varepsilon)$ such that $G(W, 0) = 0$. It was proven in [19] that the non-degenerate solution of a selective equation means the existence of a branch of solutions with the parameter $\varepsilon$.

Now we consider some cases of family Q destruction. We test violation of conditions (17) and nonequal functions $f_j$.

**Proposition 5.** *Let $f_1 = f_2 = f_3$ and $\mu_2 = \widehat{\mu_2} + \varepsilon_1, \eta_2 = \widehat{\eta_2} + \varepsilon_2$ where $\widehat{\mu_2}$ and $\widehat{\eta_2}$ satisfy (17) and $\varepsilon_1^2 + \varepsilon_2^2 > 0$, then the family of equilibria (20) is destroyed and there exist three solutions: the predator-absent, the superpredator-absent, or all three species coexistence.*

*Proof.* Firstly, we calculate the cosymmetric defect for (1) taking in account that $f_2 = f_1$ and $f_3 = f_1$:

$$D = xyz\frac{(\varepsilon_2 x - \varepsilon_1)(d_1 - \lambda_1)}{f_1(d_1 d_2 + \lambda_1\lambda_2)} \tag{26}$$

The selective function is obtained by the substitution (20) to (26)

$$S(x) = xy_Q(x)z_Q(x)\frac{(d_1 - \lambda_1)^2(\varepsilon_2 x - \varepsilon_1)}{g_1} \tag{27}$$

where $y_Q(x)$ and $z_Q(x)$ are taken according to (21)

$$\begin{aligned} g_1 =& \lambda_1 x(c_1 - a_1) + d_1 x(a_1 - b_1) - \eta_1 x(b_1 - c_1) + \lambda_1(-1 - c_1) \\ &+ d_1(1 + b_1) + \mu_1(b_1 - c_1)(d_1 d_2 + \lambda_1\lambda_2) \end{aligned} \tag{28}$$

The selective equation $S(x) = 0$ has four solutions: $x = 0$, $z_Q(x) = 0$, $y_Q(x) = 0$, and $x = \frac{\varepsilon_1}{\varepsilon_2}$. The root $x = 0$ has no biological sense. The solution $z_Q(x) = 0$ gives a member of the family $Q$ corresponding to the equilibrium without superpredator $(E_2)$.

$$x = \frac{\lambda_1 + \mu_1}{\lambda_1 + \eta_1}, \quad y = \frac{\eta_1 - \mu_1}{\eta_1 + \lambda_1}, \quad z = 0 \tag{29}$$

Similarly, for $y_Q(x) = 0$, we come to equilibrium without a predator

$$x = \frac{d_1 + \mu_1 + \varepsilon_1 R}{d_1 + \eta_1 + \varepsilon_2 R}, \quad y = 0, \quad z = \frac{\eta_1 - \mu_1 - (\varepsilon_1 - \varepsilon_2)R}{d_1 + \eta_1 + \varepsilon_2 R} \tag{30}$$

$$R = \frac{d_1 - \lambda_1}{d_2 + \lambda_2}$$

which tends to $E_3$ when $\varepsilon_1, \varepsilon_2 \to 0$. The solution

$$x = \frac{\varepsilon_1}{\varepsilon_2}, \quad y = \frac{\varepsilon_2(d_1 + \mu_1) - \varepsilon_1(d_1 + \eta_1)}{\varepsilon_2(d_1 - \lambda_1)}, \quad z = \frac{\varepsilon_1(\eta_1 + \lambda_1) - \varepsilon_2(\mu_1 + \lambda_1)}{\varepsilon_2(d_1 - \lambda_1)} \tag{31}$$

corresponds to the survival of three species. □

**Proposition 6.** *Let* $f_2 = f_3 = 1 + a(x + y + z)$, $f_1 = \frac{f_2}{1+\varepsilon(x+y+z)}$ *and parameters* $\mu_2$, $\eta_2$ *satisfy (17), then the family of equilibria (20) is destroyed, and there exist two nontrivial solutions: the predator-absent and the superpredator-absent.*

*Proof.* The cosymmetric defect for (1) may be written as:

$$D = -xyz\frac{(x + y + z)x\varepsilon}{1 + a(x + y + z)} \tag{32}$$

The selective function is obtained by the substitution (20) to (32)

$$S(x) = -xy_Q(x)z_Q(x)\frac{\varepsilon x}{1 + a} \tag{33}$$

The solution $x = 0$ has no biological sense. The other solutions $z_Q(x) = 0$ and $y_Q(x) = 0$ correspond to (3) and (4), respectively. Thus, we obtain only two equilibria: $E_2$ (without superpredtor $z = 0$) or $E_3$ (without predtor $y = 0$). □

A more difficult situation occurs when $f_1 = 1$, $f_2 \neq f_3$, and $\mu_2$, $\eta_2$ satisfy (17). The cosymmetric defect is given by:

$$D_1 = xyz\left[x + 3 - \frac{x-y-z}{f_2} + \frac{d_1d_2(y+z)}{f_3(d_1d_2+\lambda_1\lambda_2)} + \frac{-\lambda_1d_2y+\lambda_2d_1z}{f_2^2f_3(d_1d_2+\lambda_1\lambda_2)}\right] \tag{34}$$

The selective function is obtained by the substitution (20) to (34):

$$\begin{aligned} S_1(x) = xyz\Bigg[&\frac{(\eta_1x-\mu_1)(d_1\lambda_2-d_2\lambda_1)+\lambda_1(x-1)(d_1d_2+d_1\lambda_2)}{f_2^2f_3} \\ &+\frac{1-2x}{f_2}+\frac{d_1d_2(1-x)}{f_3(d_1d_2+\lambda_1\lambda_2)}+x+3\Bigg] \end{aligned} \tag{35}$$

Because full analysis of the selective equation is difficult, we assume that $f_1 = 1$, $f_2 = f_3$. The cosymmetric defect is rewritten as:

$$D_2 = -xyz\left[\frac{f_2-1}{f_2}\left(x - z + c_1(\lambda_1y - d_1z)\right)\right] \tag{36}$$

and we come to the selective function

$$S_2(x) = \frac{-xyz(f_2-1)(h_0+h_1x)}{(d_1d_2+\lambda_1\lambda_2)(d_1-\lambda_1)f_2} \tag{37}$$

where

$$h_0 = -\mu_1(d_1\lambda_2+d_2\lambda_1) - 2\lambda_1\lambda_2d_1 - d_1d_2\lambda_1 \tag{38}$$

$$h_1 = x\left[\eta_1(d_1\lambda_2+d_2\lambda_1) + \lambda_1\lambda_2(3d_1-2\lambda_1) + d_1^2d_2\right] \tag{39}$$

The zeros of the selective function (37) correspond to (3), (4), and three species solutions:

$$x = \frac{1}{r}\left(d_1d_2\lambda_1 + \lambda_1\lambda_2(2d_1-\lambda_1) + \mu_1(d_1\lambda_2+d_2\lambda_1)\right) \tag{40}$$

$$y = \frac{1}{r}(d_1d_2(d_1+\mu_1) + d_1\lambda_2(\eta_1-\mu_1) + \lambda_1\lambda_2(d_1-\eta_1+2\mu_1)) \tag{41}$$

$$z = \frac{1}{r}(d_1d_2(\lambda_1+\mu_1) + d_2\lambda_1(\mu_1-\eta_1) + \lambda_1\lambda_2(\lambda_1-\eta_1+2\mu_1)) \tag{42}$$

$$r = d_1^2d_2 + \lambda_1\lambda_2(3d_1-2\lambda_1) + \eta_1(d_1\lambda_2+d_2\lambda_1) \tag{43}$$

It is clear that the solution $f_2 = 1$ for (37) leads to $f_1 = f_2 = f_3 = 1$. So, this case corresponds to the existence of the family of equilibria

**Remark 1.** *When $f_1 = 1$, $f_3 = f_2$, and $\lambda_1 = \lambda_2 = 0$, we come to the system studied in [13]. In this case, we have*

$$S_3(x) = -x^2y_Q(x)z_Q(x)\frac{f_2-1}{f_2} \tag{44}$$

*The zeros of the selective function $z_Q(x) = 0$ and $y_Q(x) = 0$ correspond to equilibria (3) and(4), respectively. The solution $f_2 = 1$ leads to cosymmetry and a family of equilibria [17].*

## 5 Numerical simulation

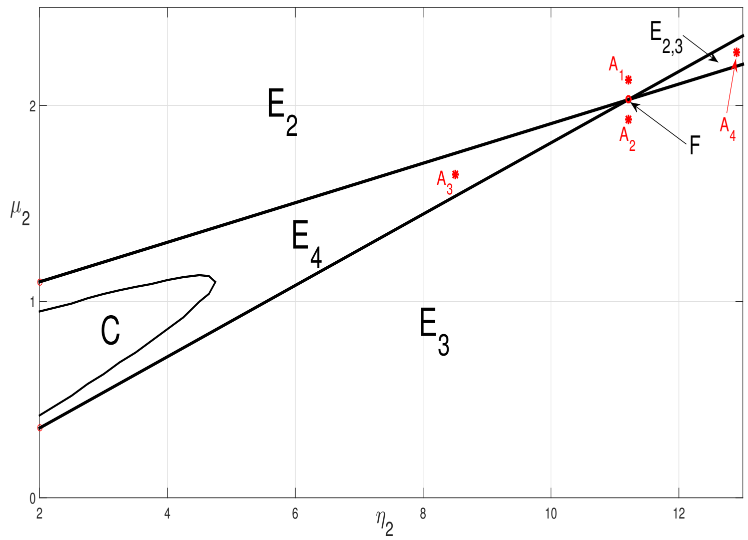



FIG. 1. Two-parameter bifurcation diagram with respect to $\eta_2$ and $\mu_2$, $E_j$ ($j = 2,3,4$) regions of monostability, $E_{2,3}$ – the region of bistability, $C$ – the region of limit cycles, point $F$ corresponds to the family of equilibria; $\mu_1 = 1$, $\eta_1 = 10$, $d_1 = 1$, $d_2 = 1$, $\lambda_1 = 0.01$, $\lambda_2 = 0.01$ and $a_j = b_j = c_j = 0.1$ ($j = 1,2,3$).

Let us illustrate the theoretical considerations in the previous sections with numerical results. We fix some parameters: $\mu_1 = 1$, $\eta_1 = 10$, $d_1 = 1$, $d_2 = 1$, $\lambda_1 = 0.01$, $\lambda_2 = 0.01$, $a_j = b_j = c_j = 0.1$, and take $\mu_2$, $\eta_2$ satisfying (17). Fig. 1 shows the regime map on the parameter plane $\eta_2$ and $\mu_2$. Symbol $E_j$ marks the stability domain for the equilibrium $E_j$, $j = 2,3,4$, see Propositions 1 and 2. Stable equilibria $E_2$ or $E_3$ coexist for the parameter values within the bistability region $E_{2,3}$. The domains $E_2$, $E_3$, $E_4$, and $E_{23}$ share a point $F$, which corresponds to the family of equilibria. The symbol $C$ denotes the region of values for which limit cycles exist. This region was obtained through a computational experiment. A map similar to Fig. 1 was presented in [22], but without mentioning a family of equilibria and bistability.

In Fig. 1, we see that the competitive exclusion of the predator occurs when crossing the stability boundary for the equilibrium with the coexistence of all three species ($E_4$) and the region where bistability is realized (region $E_{23}$). Thus, region $E_2$ ($E_3$) corresponds to the parameter values at which the superpredator (predator) dies out, regardless of the initial conditions.

However, there are parameter values (region of bistability $E_{23}$) for which the extinction of the superpredator and predator depends on its initial amount.

The family $Q$ (4) (point $F$ in Fig. 1) contains only stable equilibria; see Proposition 4. Fig. 2 demonstrates that trajectories converge oscillatorily towards the family of equilibria from different initial conditions. The family of equilibria is drawn by the black line $AE_2$.

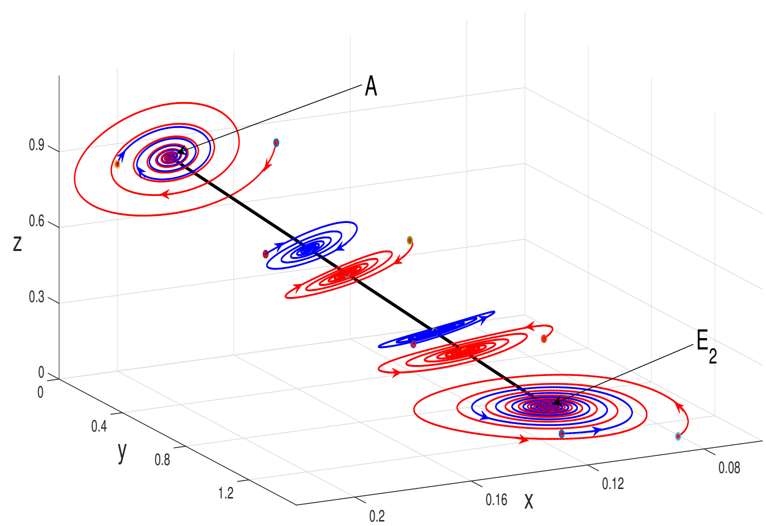



FIG. 2. Convergence to equilibria of the family $Q$ (black line) from different initial points (circles); $\mu_1 = 1$, $\eta_1 = 10$, $d_1 = 1$, $d_2 = 1$, $\lambda_1 = 0.01$, $\lambda_2 = 0.01$ and $a_j = b_j = c_j = 0.1$ $(j = 1, 2, 3)$.

We draw the basin of attraction of the system (1) for family $Q$. In order to find on the plane $z$ =const, we divide the family of equilibria $Q$ into six colors [red, green, cyan, blue, yellow, and black]; see Fig. 3. One can see variance in basins sizes depending on the initial condition. It can be seen that the corresponding to different parts of the family sectors assemble to the straight line $x = y = 0$. We stress that the order of colors is kept both for the family and for sectors on planes $z = const$. For a plane with minimal $z$, the largest sector corresponds to the section of the family near equilibrium $E_2$ (red color), and for the level $z_3$, this sector is minimal.

When cosymmetry conditions are broken, destruction of the family occurs. We examine different scenarios of it, i.e., $\mu_2$ and $\eta_2$ are not satisfied (17) or under different functions $f_j$ (2), see Table 1 and Figs. 4 – 9.

Now we illustrate the result of Proposition 5 and take $f_1 = f_2 = f_3 = 1 + 0.1(x + y + z)$. As shown in Fig. 4, the superpredator extincts when $\mu_2$ increasing ($\varepsilon_1 > 0$, $\varepsilon_2 = 0$). It leads to the establishment of a stable equilibrium $E_2$. Trajectories initiated near the family $Q$ converge towards

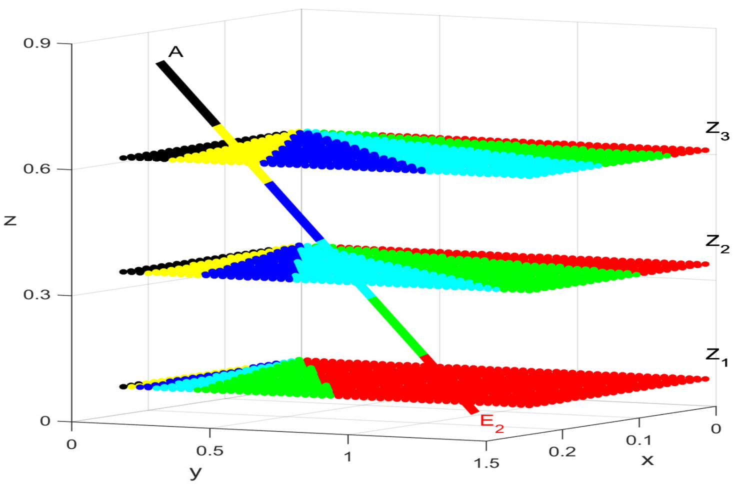



FIG. 3. Family of equilibria $AE_2$ and several planar basins of attraction of the system (1) in $z_1 = 0.63$, $z_2 = 0.37$, and $z_3 = 0.1$; $\mu_1 = 1$, $\eta_1 = 10$, $d_1 = 1$, $d_2 = 1$, $\lambda_1 = 0.01$, $\lambda_2 = 0.01$, and $a_j = b_j = c_j = 0.1$ $(j = 1, 2, 3)$.

$E_2$ (depicted by the red). Conversely, a decreasing in $\mu_2$ ($\varepsilon_1 < 0$, $\varepsilon_2 = 0$) results in the elimination of the predator: blue trajectories tend to a stable equilibrium $E_3$. Stability of $E_4$ demonstrates Fig. 5a, where parameters $\mu_2 = 1.65, \eta_2 = 8.5$ respond the point $A_3$ in Fig. 1. The node-node bistability is shown in Fig. 5b when two stable equilibria coexist. This case corresponds to the point $A_4$ ($\mu_2 = 2.27, \eta_2 = 12.9$) in Fig. 1. The dependence on the initial point takes place. One can observe different regime realizations: equilibrium $E_2$ (death of the superpredator) or equilibrium $E_3$ (death of the predator). The green line corresponds to unstable equilibrium $E_4$.

The destruction of the family under different $f_j$ was partially analyzed by Propositions 5 and 6. Here we present the results of the numerical simulation. Fig. 6 shows bifurcation diagrams for several cases when a family of equilibria is destroyed, namely cases 4, 5, and 6 from Table 1.

When $f_1 = 1$, $f_2 = f_3$, we find that the family of stable equilibria annihilates and only the equilibrium $E_2$ is stable (case 1 in Table 1). The same was obtained for the case 4, see Fig. 6a. Then we fix $f_1$, $f_3$, and change the function $f_2$. Increasing the parameter $a_2$ to 0.5 gives stable equilibrium $E_3$. For $c_2 = 0$ the equilibrium $E_4$ becomes steady (case 3 in Table 1). So, one can see multiple scenarios in the vicinity of the disappeared family of equilibria.

The bistability occurs with an increasing $a_2$ (case 5 in Table 1, see Figs. 6b, 7a). As seen in Fig. 7a, boundary equilibria $E_2$ and $E_3$ (the death of a superpredator or a predator) are both stable, while interior equilibrium $E_4$ (three

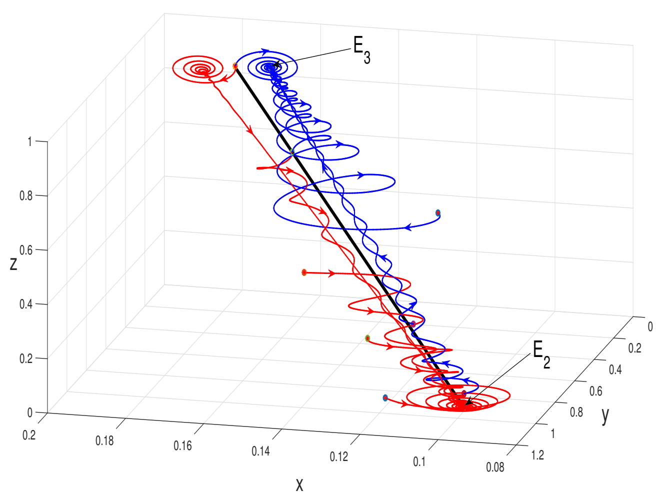
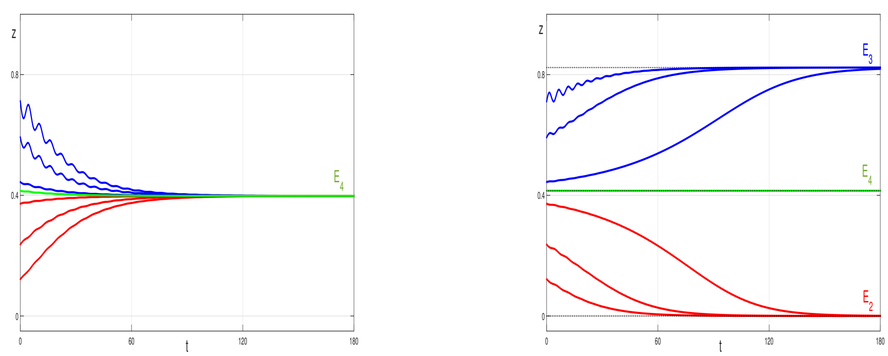



FIG. 4. Phase portraits after destruction of the family of equilibria (black line $AE2$), $\mu_2 = \widehat{\mu_2} + 0.1$ (red), $\mu_2 = \widehat{\mu_2} - 0.1$ (blue), parameters $\widehat{\mu_2}$, $\eta_2$ satisfy (17); $\mu_1 = 1$, $\eta_1 = 10$, $d_1 = 1$, $d_2 = 1$, $\lambda_1 = 0.01$, $\lambda_2 = 0.01$, $a_j = b_j = c_j = 0.1$ $(j = 1, 2, 3)$.




a b

FIG. 5. Graph of superpredator after the destruction of the family of equilibria: $a$) Convergence to the isolated equilibrium $E_4$, parameters $\mu_2$ and $\eta_2$ do not satisfy relations (17) $\mu_2 = 1.65$, $\eta_2 = 8.5$, $b$) Node-node bistability $\mu_2 = 2.27, \eta_2 = 12.9$ (point $A_4$ in Fig.1a); $\mu_1 = 1$, $\eta_1 = 10$, $d_1 = 1$, $d_2 = 1$, $\lambda_1 = 0.01$, $\lambda_2 = 0.01$, $a_j = b_j = c_j = 0.1$ $(j = 1, 2, 3)$.

species coexist) is unstable. This takes place close to the family of equilibria that has disappeared. One can see funnel trajectories tending to equilibria

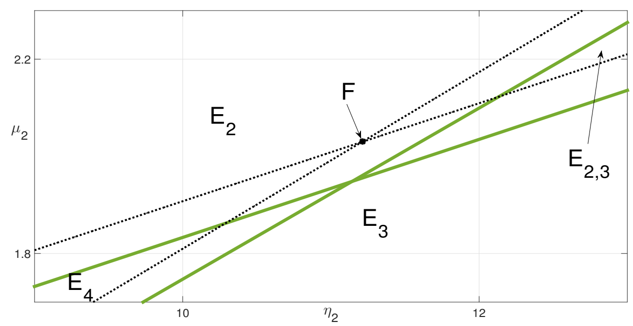
$E_2$ and $E_3$ from different initial points taken on the line corresponding to the family $Q$.

For fixed $f_1 = 1$, $f_2 = 1 + 0.9x$, and $a_3 = 0$, depending on the parameters $b_3$ and $c_3$, there exist scenarios with stable equilibria $E_j$ ($j = 2, 3, 4$) and bistability. As an example, when $b_3 = 0.05$ and $c_3 = 0.2$ (case 6 in Table 1 and Fig. 6c), the equilibrium $E_4$ (three non-zero species) is stable; see Fig. 7b. Note that equilibria $E_2$ and $E_3$ are stable on the planes $z = 0$ and $y = 0$, respectively.

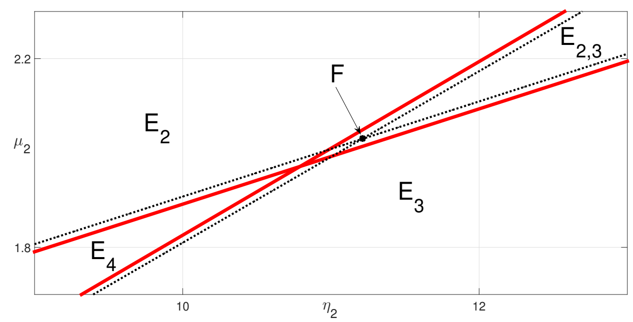
| $No$ | $f_1$ | $f_2$ | $f_3$ | Attractors |
|---|---|---|---|---|
| 1 | 1 | $1 + 0.1(x + y + z)$ | $1 + 0.1(x + y + z)$ | $E_2$ |
| 2 | 1 | $1 + 0.5x + 0.1(y + z)$ | $1 + 0.1(x + y + z)$ | $E_3$ |
| 3 | 1 | $1 + 0.5x + 0.1y$ | $1 + 0.1(x + y + z)$ | $E_4$ |
| 4 | 1 | $1 + 0.1x$ | $1 + 0.1(x + y + z)$ | $E_2$ |
| 5 | 1 | $1 + 0.9x$ | $1 + 0.1(x + y + z)$ | $E_2$, $E_3$ |
| 6 | 1 | $1 + 0.9x$ | $1 + 0.05y + 0.2z$ | $E_4$ |
| 7 | $1 + \frac{x+y+z}{10}$ | $1 + 0.5x + \frac{y+z}{100}$ | $1 + \frac{x+y}{10} + 0.06z$ | cycle, cycle |
| 8 | $1 + \frac{x+z}{10} + 0.01y$ | $1 + 0.5x + \frac{y+z}{100}$ | $1 + \frac{x+y}{10} + 0.06z$ | $E_2$, cycle |

TABLE 1. Different Beddington-DeAngelis functional responses break a family of equilibria, parameters $\eta_2$, $\mu_2$ satisfy (17); $\mu_1 = 1$, $\eta_1 = 10$, $d_1 = 1$, $d_2 = 1$, $\lambda_1 = 0.01$, $\lambda_2 = 0.01$.

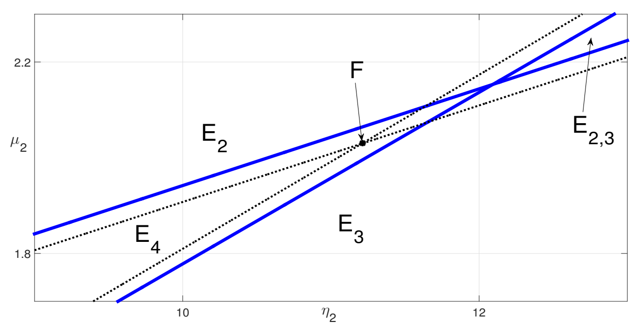
For case 7 in Table 1, we have obtained cycle-cycle bistability around unstable equilibria $E_2$ (red) and $E_3$ (blue), see Fig. 8 and Fig. 9a. The phase portrait in Fig. 9a demonstrates the convergence of trajectories (red and blue) to limit cycles (black). Fig. 9b shows the node-cycle bistability: the limit cycle (black) on the plane $y = 0$ and the stable equilibrium $E_2$. So, the destruction of the family of equilibria exhibits several types of bistability: node-node, node-cycle, and cycle-cycle.




a

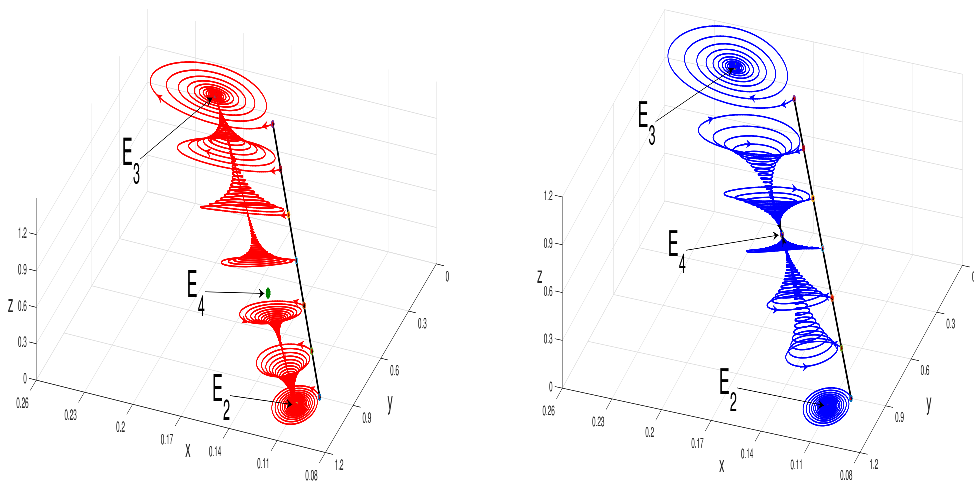



b



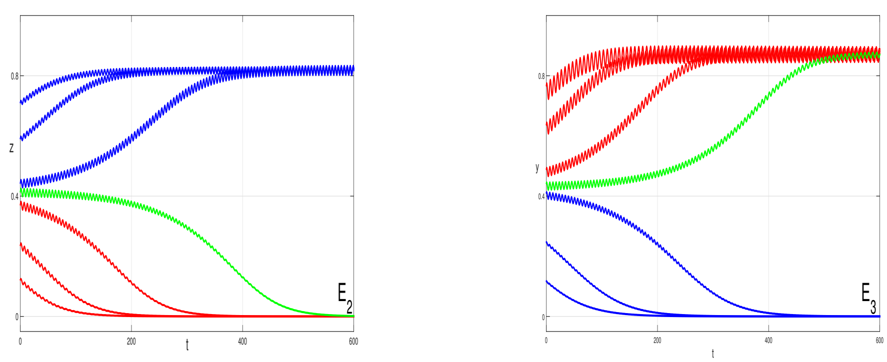

c

FIG. 6. Comparison of bifurcation diagrams for cosymmetric (dot lines) and cases from the table (color lines): $E_j$ ($j = 2, 3, 4$) – the regions of equilibrium stability, $E_{2,3}$ – the region of bistability, point $F$ corresponds to the family of equilibria $f_j = 1+0.1x+0.1y+0.1z$ ($j = 1, 2, 3$). $a$), $b$) and $c$) are cases 4, 5, and 6 in Table 1 respectively.




a b

FIG. 7. Dynamics after destruction of the family of equilibria (black line $AE2$) for different $f_j$: $a$) case 5 in Table 1, $b$) case 6 in Table 1.

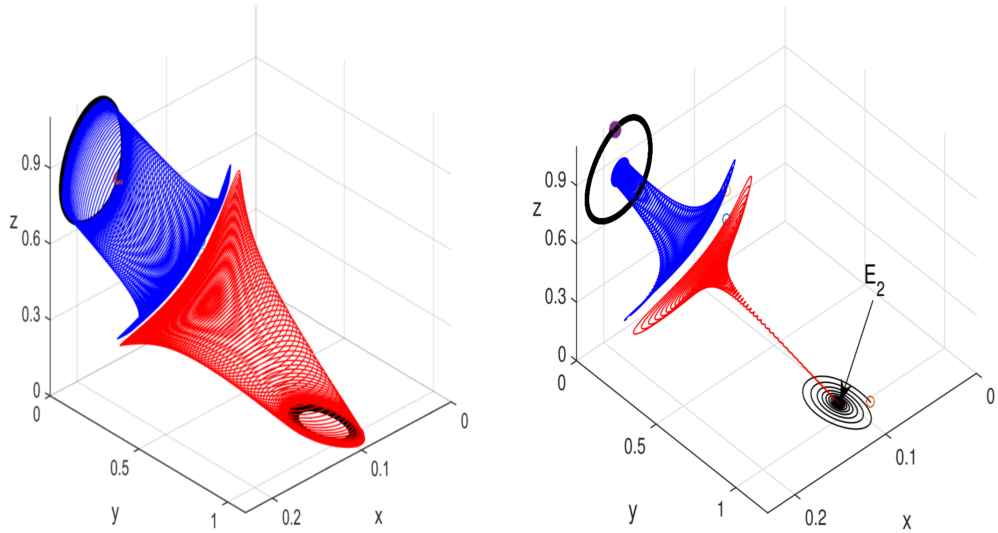



a b

FIG. 8. Cycle-cycle bistability after the destruction of the family of equilibria. Graph of superpredator ($a$) and predator ($b$), case 7 in Table 1.

## 6 Conclusions

The cosymmetry in a three-species model with a classical Lotka-Volterra functional response was studied in [17]. Here, we analyze a prey, predator, and superpredator model with Beddington-DeAngelis functional response [20, 21] for all three involving species. Multistability in the form of a continuous family of equilibria was found for the case of identical functional




a b

FIG. 9. Phase portraits after the destruction of the family of equilibria: *a*) cycle-cycle bistability, case 7 in Table 1. *b*) node-cycle bistability, case 8 in Table 1.

responses and additional conditions on parameters $\eta_2$ and $\mu_2$. We analyzed different scenarios of family destruction, used numerical analysis, and plotted two-parameter bifurcation diagrams for two parameters characterizing the dynamics of the superpredator: the death rate of the superpredator $\mu_2$ and the consumption of prey by the superpredator $\eta_2$. Then we analyze scenarios with different functional responses.

Given model can describe the interaction of species in aquatic communities [23, 24], namely systems of phytoplankton, zooplankton, and fish. Another field concerns terrestrial communities with small vertebrates (birds and lizards), which are consumers of both spiders and herbivorous insects [25].

The future steps of the dynamics study in a prey, predator, and superpredator model may concern various environmental conditions, including spatial heterogeneity [26] and seasonality of factors. Examples of cosymmetry and multistability in inhomogeneous predator-prey model were given in [27].

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