Mathematics

https://www.aimspress.com/journal/Math

AIMS Mathematics, 9(11): 30263–30297.
DOI: 10.3934/math.20241461
Received: 13 August 2024
Revised: 19 September 2024
Accepted: 10 October 2024
Published: 24 October 2024

Research article

Bifurcation analysis for the coexistence in a Gause-type four-species food web model with general functional responses

Jorge Luis Ramos-Castellano[1], **Miguel Angel Dela-Rosa**[2,*] and **Iván Loreto-Hernández**[2]

[1] División Académica de Ciencias Básicas, Universidad Juárez Autónoma de Tabasco, Km. 1, Carretera Cunduacán-Jalpa de Méndez, c.p. 86690, Cunduacán, Tabasco, México

[2] División Académica de Ciencias Básicas, Consejo Nacional de Humanidades, Ciencias y Tecnologías-Universidad Juárez Autónoma de Tabasco, Km. 1, Carretera Cunduacán-Jalpa de Méndez, c.p. 86690, Cunduacán, Tabasco, México

* **Correspondence:** Email: madelarosaca@conahcyt.mx.

Abstract: The dynamics of an ordinary differential equations (ODEs) system modelling the interaction of four species (one prey or resource population, two mesopredator populations, and one super-predator population) was analyzed. It was assumed that the functional responses for each interaction were general. We showed parameter conditions that ensured that the differential system underwent a supercritical Hopf bifurcation or a Bogdanov-Takens bifurcation, from which the coexistence of the four species was guaranteed. In addition, the results were illustrated by several applications, where the prey had a logistic growth rate. For the interaction of the mesopredators and prey, we considered classical Holling-type functional responses, and for the rest of the interactions, we proposed certain generalized functional responses similar to the well-known "Beddington-DeAngelis" or "Crowley-Martin" functional responses. At the end, some numerical simulations were given.

Keywords: four-dimensional food web model; Hopf bifurcation; Bogdanov-Takens bifurcation; coexistence of species; generalized functional responses
Mathematics Subject Classification: 37G15, 34C60, 92D25

1. Introduction

There are wide interactions between populations forming an ecosystem in nature, which depend on the ecological and biological aspects or processes, whose study incorporates several parameters. For instance, the depredation between the species has been of interest in both the ecological and mathematical points of view, see [1]. Besides, the dynamical analysis of ordinary differential equations (ODEs) mathematical models with population interactions is a current research topic that contributes to the literature on deterministic ecology models [1,2].

The depredation interactions could be of several types: Predator-prey, tritrophic, intraguild, and food webs that involve more than three species. Roughly speaking, in the deterministic modeling of population dynamics by means of ODE systems the coexistence of the involved populations is of great relevance, which can be guaranteed by showing the existence of different kinds of stable limit sets.

In the two-dimensional case, there is a perspective due to Lotka and Volterra that assumes that a population prey with density x with a Malthusian growth rate is the source of a predator population with density y whose interaction is the result of a direct attack measured by a linear functional response $f_1(x)$ [1–3]. This model has inspired a kind of generalized Gause-type models, where a positive smooth function $h_1(x)$ captures the prey growth rate, and the functional response is not necessarily a linear function; in this sense, other ecological factors could be considered, like the predator satiety and the defense group of prey, etc. [4]. The mathematical expression for the corresponding model is:

$$\begin{aligned} \frac{dx}{dt} &= h_1(x) - bf_1(x)y, \\ \frac{dy}{dt} &= cf_1(x)y - dy, \end{aligned} \tag{1.1}$$

where c and d are the efficiency conversion coefficient and the mortality predator rate, respectively.

On the other hand, there are recent works in which the three dimensional case takes place, which focus on three-dimensional ODE systems for modeling tritrophic (Figure 1 shows the energy transference) or intraguild interactions* (Figure 2 shows the energy transference). In this respect, let us recall some works. The model in this occasion is of the form:

$$\begin{aligned} \frac{dx}{dt} &= h_1(x) - f_1(x)y - g_1(x)z, \\ \frac{dy}{dt} &= (c_1 f_1(x) - d_1)y - g_2(y)z, \\ \frac{dz}{dt} &= (e_1 g_1(x) + e_2 g_2(y) - d_2)z. \end{aligned} \tag{1.2}$$

This model collects the intraguild interactions, where MP and SP are specialists. Here, we have the smooth functions $f_1(x)$, $g_1(x)$, and $g_2(y)$ as functional responses for the interactions P-MP, MP-SP, and P-SP, respectively. Moreover, when the term $g_1(x)z$ does not appear in the first equation, one recovers the tritrophic case. Here, c_1, e_1 and e_2 measure the efficiency conversion coefficients; d_1 and d_2 are the mortality predators rates.

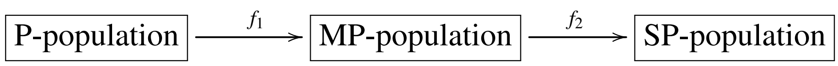


Figure 1. A tritrophic flow energy transference.

*Here, the interactions are between one prey P with population density x, one predator MP, and a super-predator SP, with population densities y and z, respectively.

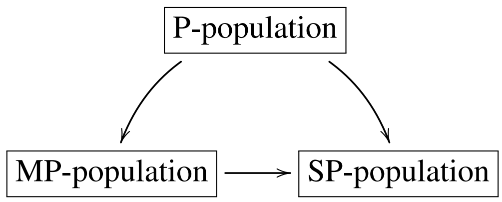


Figure 2. An intraguild predation flow energy transference.

In order to be more precise in the motivation for the main results in the present paper, let us recall some works in this direction. In [5], the authors studied a tritrophic model and showed the coexistence of the species by the existence of a stable limit cycle that emerges from a Hopf bifurcation. In [6] the authors made an analysis of a tritrophic model, showing parameter conditions for guaranteeing that the differential system exhibits a Bogdanov-Takens bifurcation; moreover, in the case of Holling functional responses, the coexistence of the three species was shown by means of the existence of stable limit cycles. On the other hand, several tritrophic models were studied in [7–10] by assuming that a superpredator feeds from the prey. In all these research works, the authors showed the coexistence of the involved species guaranteeing the existence of invariant stable limit sets via a Hopf, a Bautin, or a zero-Hopf bifurcation.

On the other hand, there is a vast diversity of food web interactions in nature, due to which, for population dynamics studies, it is necessary to incorporate models with more than three species. There are not enough of such models, because it is difficult to carry out an exhaustive mathematical analysis by means of the usual methods. In this regard, there are few works focusing on this subject. For instance, in [11] an intraguild type model was studied, in which four species interact, namely, a prey, two middle predators, and a superpredator. The authors proved the coexistence of all the species by showing the existence of stable limit sets through a Hopf or a Hopf-Hopf bifurcation.

Thus, the aim of the present manuscript is to deal with the dynamical analysis of a Gause-type four-dimensional food web model modelling the interaction of four species: One prey (P), two middle predators (MP1 and MP2), and one superpredator (SP1); besides, it is considered that such interactions are governed by general functional responses and by the general growth rate for the prey (see Figure 3).

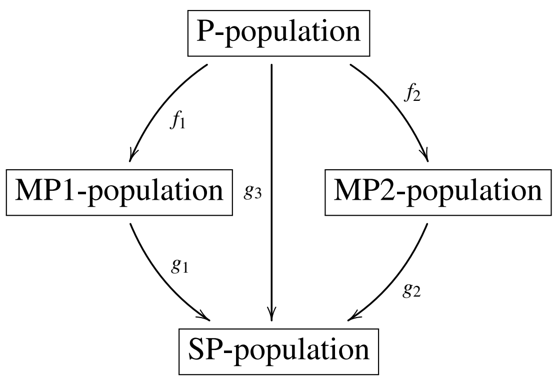


Figure 3. A four-species food web energy transference.

2. Food web model formulation and novelty of the main results

In this manuscript, based on the work in [12] (cf. [13]) we revisit a Gause-type model that considers the presence of one prey (P) or resource population, two predator populations (MP1 and MP2), and one superpredator population (SP), and the functional responses for each interaction are quite general.

For clarity in the model of interest, we will fix the following notation: w represents the prey population density that is consumed by two predators with population densities x and y, respectively; these predators are predated by other superpredator species with population density z which also feed from the prey. Now one has the following ecological premises:

- The intrinsic prey growth rate without predation populations is measured by the term $R_1 wh(w)$, where $h(w)$ is a positive smooth function (R_1 is as in Table 1).
- The population interactions MP1-P and MP2-P are given by smooth positive functions depending only on the density w: $f_1(w), f_2(w)$.
- The population interactions SP-P, SP-MP1, and SP-MP2 are given by smooth positive functions depending on the densities w, x and y :

$$g_1(w,x,y), g_2(w,x,y), \text{ and } g_3(w,x,y).$$

- The interaction model is Gause-type, where each predator-prey interaction as above is carried out by direct attack, which means that each mesopredator and the superpredator are specialists.

Derived from the above premises, we have that the model interaction will consider nine dimensionless parameters whose ecological meaning is given in Table 1.

Table 1. Parameter meanings for the food web model (2.1).

Parameter	Ecological Meaning
R_1	Intrinsic growth rate of prey P
c_1 and c_2	Efficiency conversion of predators MP1 and MP2
e_1	Efficiency conversion of interaction SP-P
e_2 and e_3	Efficiency conversions of interactions SP-MP1 and SP-MP2
d_1, d_2, and d_3	Mortality rates of predators and super-predator

Specifically, the mathematical model is given for the following ODEs:

$$\begin{aligned}
\frac{dw}{dt} &= R_1 wh(w) - f_1(w)x - f_2(w)y - g_1(w,x,y)z, \\
\frac{dx}{dt} &= x(c_1 f_1(w) - d_1) - g_2(w,x,y)z, \\
\frac{dy}{dt} &= y(c_2 f_2(w) - d_2) - g_3(w,x,y)z, \\
\frac{dz}{dt} &= z(e_1 g_1(w,x,y) + e_2 g_2(w,x,y) + e_3 g_3(w,x,y) - d_3).
\end{aligned} \tag{2.1}$$

For ecological consistency, the set of interest for the analysis of differential system (2.1) is $\Omega := \{(w, x, y, z) \in \mathbb{R}^4 : w > 0,\ x > 0,\ y > 0,\ z > 0\}$.

On the other hand, in order to distinguish our main contribution to the present paper, it is important to note the results by [12, 13], in which the authors obtained dynamical analysis for special cases of model (2.1).

In fact, in [13] , the authors proposed and analyzed model (2.1). It is worth mentioning that they assumed that the prey growth rate is logistic, the functional responses f_1 and f_2 are Holling of type II, the smooth positive functions g_1, g_2, and g_3 depend on w, x, and y and are a kind of modified "Holling II" functional response, that is, they are of the form:

$$g_i(w, x, y) = \frac{a_{i+1} w}{1 + b_2 w + b_3 x + b_4 y}.$$

Moreover, they showed the existence of an equilibrium point which could be stable. Finally, by numerical simulations, a stable limit cycle was exhibited.

On the other hand, in [12], the authors made an analysis of model (2.1) by the weak hypothesis that the prey growth rate $Rwh(w)$ is logistic, the interaction functional responses f_1 and f_2 are Holling of type II, $g_1(w, x, y)$ depends only on the prey w, and it is of Holling type II, the functional responses $g_2(w, x, y)$ and $g_3(w, x, y)$ depend only on w and are Holling type I (that is, they are of the Lotka-Volterra type). They showed the existence of several equilibrium points, and determined their stability. They also proved that a Hopf bifurcation takes place.

2.1. Novelty and main contribution of our results

The novelty of our present work lies in the fact that we obtained analytical results instead of only numerical ones. For this, we used the approach in Kuznetsov et al. In the following, we will summarize the content of our main contribution to the present manuscript:

- Our main results provide a more general dynamical analysis for model (2.1) that extends those obtained in the aforementioned works.
- The principal part of our contribution is that we consider that the functional responses are general and depend on the population densities (w, x, y) and some other conditions at the equilibria, which allow us to prove our main results in the present manuscript (see Theorems 5 and 9): Independent of the functional responses, here are parameter conditions to ensure that the differential system undergoes a supercritical Hopf bifurcation or a non-degenerate (codimension two) Bogdanov-Takens bifurcation.
- As a consequence of our main theorems, the coexistence of the four species is guaranteed. This is the relevant ecological aspect that we are looking for in this manuscript.
- Besides, the major novelty of our manuscript is that the theoretical results are stated for quite general functional responses[†]:
  - (i) Here, we have a tool for making numerical simulations that illustrates the phases of the dynamical behaviors that the differential system could have.
  - (ii) For the numerical results, we make the explicit assumption of having a logistic growth rate for prey, which allows us to explore a wide variety of examples.

[†]They could be explicit and are considered as certain generalized functional responses similar to the well-known functional responses of "Beddington-DeAngelis" or "Crowley-Martin".

(iii) Our examples involve some aspects of ecological relevance (for instance, satiety in predators, predator interference, a defense group in the prey, and competence between predators), see Section 5.

3. Dynamical analysis via a Hopf bifurcation

3.1. Equilibrium points and a criterion for stability

The following proposition provides a criterion to show the existence of equilibria whose entries are all positive, and hence one has the existence of at least one equilibrium point for differential system (2.1) inside Ω.

Proposition 1. *Let $p = (w_0, x_0, y_0, z_0)$ be a point in Ω. If the parameters of system (2.1) satisfy*

$$R_1 = \frac{x_0 f_1(w_0) + y_0 f_2(w_0) + z_0 g_1(w_0, x_0, y_0)}{w_0 h(w_0)}, \quad c_1 = \frac{d_1 x_0 + z_0 g_2(w_0, x_0, y_0)}{x_0 f_1(w_0)}, \tag{3.1}$$
$$c_2 = \frac{d_2 y_0 + z_0 g_3(w_0, x_0, y_0)}{y_0 f_2(w_0)}, \text{ and } d_3 = e_1 g_1(w_0, x_0, y_0) + e_2 g_2(w_0, x_0, y_0) + e_3 g_3(w_0, x_0, y_0),$$

then p is an equilibrium point.

Proof. First, we note that all the parameters in system (2.1) are positive; therefore, in order to determine the equilibria in Ω for differential system (2.1), we solve the following algebraic system:

$$\begin{aligned} &R_1 w h(w) - f_1(w) x - f_2(w) y - g_1(w, x, y) z = 0, \\ &x (c_1 f_1(w) - d_1) - g_2(w, x, y) z = 0, \\ &y (c_2 f_2(w) - d_2) - g_3(w, x, y) z = 0, \\ &z (e_1 g_1(w, x, y) + e_2 g_2(w, x, y) + e_3 g_3(w, x, y) - d_3) = 0. \end{aligned} \tag{3.2}$$

In fact, in the above system, we solve the first equation in terms of R_1, the second one in terms of c_1, the third one in terms of c_2, and the fourth one in terms of d_3. Hence, the result is obtained. □

3.2. Conditions for simplifying the dynamical analysis

In order to make the dynamical analysis simpler and with the aim to simplify the massive computations that we need to carry out, it will be assumed that the functional responses and their derivatives take special values when they are evaluated at the entries of the equilibrium point p in Proposition 1. That is, from now on, we will assume that the system of equations given in Appendix A.1 is satisfied by p.

3.3. Stability result for the equilibrium points

The proof of the following stability result for the equilibrium points is contained in Appendix A.2.

Proposition 2. *Suppose that the hypotheses on Proposition 1 hold, and that the following additional parameter conditions are satisfied*

$$f_2'(10y_0) > 0, \quad \partial_w g_1(10y_0, 6y_0, y_0) > 0,$$

$$d_2 = \frac{33}{10} y_0 f_2'(10y_0), \quad e_1 = e_3 = \frac{f_2'(10y_0)}{10\partial_w g_1(10y_0, 6y_0, y_0)}, \qquad (3.3)$$
$$e_2 = \frac{121 f_2'(10y_0)}{120\partial_w g_1(10y_0, 6y_0, y_0)} \text{ and } z_0 = \frac{y_0 f_2'(10y_0)}{\partial_w g_1(10y_0, 6y_0, y_0)},$$

and $d_1 > d_{10} := \frac{386660234 y_0 f_2'(10y_0)}{122003525}$. *Then, p is a locally asymptotically stable equilibrium point for system* (2.1).

3.4. H-bifurcation conditions

At first, assuming that the parameter conditions given in Proposition 1 and Eq (3.3) are valid, we will consider differential system (2.1) as a 1-parameter continuous dynamical system with respect to d_1. In the following lemmas, we will show the necessary conditions under which differential system (2.1) undergoes a Hopf bifurcation.

Lemma 3. *If the hypotheses in Proposition 1 and Eq* (3.3) *are satisfied, then by making* $d_1 = d_{10}$, *the linear approximation of system* (2.1) *at p,* $M(p)$, *has eigenvalues:*

$$\lambda_{1,2} = \pm i\omega, \quad \lambda_{3,4} = \left(-\frac{7}{2} \pm \frac{1}{4} i \sqrt{\frac{588151373}{3485815}}\right) y_0 f_2'(10y_0),$$

where $\omega = \sqrt{\frac{99}{5600}} y_0 f_2'(10y_0) > 0$.

Proof. Let $\Sigma(d_1)$ be as in the proof of Proposition 2. From the proof of this proposition, we have that the characteristic polynomial for $M(p, d_1)$ is $\mathrm{pol}(\lambda)$. Hence, the desired factorization for $\mathrm{pol}(\lambda)$ is obtained by solving $\Sigma(d_1) = 0$, which is obtained if $d_1 = d_{10}$. Finally, the proof follows from [9, Lemma 2.1(ii)]. □

Lemma 4. *If the hypotheses of Lemma 3 hold, the Hopf transversal condition is verified:* $\frac{\partial Re(\lambda_{1,2})}{\partial d_1}(d_{10}) \neq 0$.

Proof. Under the hypotheses, the linear approximation $M_p(d_1)$ is given in the proof of Proposition 2. Now, in Appendix A.3, we compute a pair of eigenvectors for $M_p(d_{10})$ and its transpose $\left(M_p(d_{10})\right)^T$, corresponding to the eigenvalues iw_0 and $-iw_0$, respectively. Therefore, on using a formula in [14, pag. 189], one computes the derivative of the real part of $\lambda_{1,2}$ which provides the transversal condition given by $\frac{\partial \mathrm{Re}(\lambda_{1,2})}{\partial d_1}(d_{10})$ as:

$$-\frac{541898550987885837837824810289209375 0 f_2'(10y_0)^2}{79212074629289676919 29\,(3400000481284371 04\partial_w g_1(10y_0, 6y_0, y_0)^2 + 6527530581280625 f_2'(10y_0)^2)}.$$

□

3.5. H-Main result

We are ready to state one of the main results in the present manuscript.

Theorem 5 (H-Main theorem)**.** *If the hypotheses of Lemma 3 hold and* $l(p, d_{10}) \neq 0$, *then system* (2.1) *undergoes an H-bifurcation at p with respect to* d_1 *and bifurcation value* d_{10}.

Proof. The proof is obtained by the following procedure:

- First, from Lemmas 3 and 4, the necessary Hopf (H) bifurcation conditions are valid. In fact, the existence of a simple pair of purely imaginary eigenvalues and the transversal condition are verified.
- Now, from the hypotheses of Lemma 3, the first Lyapunov coefficient $l(p, d_{10})$ for system (2.1) is computed by using the Kuznetsov formulae [14, 15] but its mathematical expression is very huge, so we omit it here[‡].
- Finally, from the well-known Andronov-Hopf theorem [14, 15], it follows that:
  i) If $l(p, d_{10})$ is not zero, then then differential system (2.1) undergoes an H-bifurcation.
  ii) The H-bifurcation is supercritical whenever $l(p, d_{10}) < 0$, and it is subcritical if $l(p, d_{10}) > 0$.
- As a consequence of the above, one has the desired result.

□

4. Dynamical analysis via a Bogdanov-Takens bifurcation

In this section, the dynamics of differential system (2.1) will be analyzed by means of a Bogdanov-Takens (BT) bifurcation.

Now, from Section 3.1, one obtains parameter conditions for the existence of an equilibrium point $p \in \Omega$ of differential system (2.1), which will be the main starting hypothesis of Theorem 9. Besides, in the case of a Hopf bifurcation, Proposition 2 proved the local stability of p.

In the following subsections, we will show the work that contains both the hypothesis and preliminary results necessary to state the second main result of this manuscript.

4.1. Conditions for simplifying the BT-dynamical analysis

In order to simplify the BT-bifurcation analysis, from now on, we will suppose that:

- **BTBC1:** This means that the conditions in Appendix A.1 are valid;
- **BTBC2:** This means that the hypotheses in Proposition 1 hold;
- **BTBC3:** Here we suppose that the following additional conditions are valid:

$$f_2'(w_0) = \frac{z_0 \partial_w g_1(w_0, x_0, y_0)}{y_0}, \quad e_2 = \frac{121 f_2'(10y_0)}{120 \partial_w g_1(10y_0, 6y_0, y_0)}, \quad e_1 = e_3 = \frac{f_2'(10y_0)}{12 \partial_w g_1(10y_0, 6y_0, y_0)}.$$

Under the above conditions, differential system (2.1) has as linear approximation $\mathcal{J}(w, x, y, z)$ at any point (w, x, y, z) given by

$$\begin{pmatrix} -xf_1'(w) - yf_2'(w) - T_0 & -f_1(w) - z\partial_x g_1(w, x, y) & -f_2(w) - z\partial_y g_1(w, x, y) & -g_1(w, x, y) \\ xf_1'(w)T_1 - z\partial_w g_2(w, x, y) & -d_1 - z\partial_x g_2(w, x, y) + f_1(w)T_1 & -z\partial_y g_2(w, x, y) & -g_2(w, x, y) \\ yf_2'(w)T_2 - z\partial_w g_3(w, x, y) & -z\partial_x g_3(w, x, y) & -d_2 - z\partial_y g_3(w, x, y) + f_2(w)T_2 & -g_3(w, x, y) \\ zT_3 & zT_4 & zT_5 & T_6 - \frac{39}{5}T_7 \end{pmatrix},$$

$$T_0 = z\partial_w g_1(w, x, y) + \frac{8\,(h(w) + wh'(w))\,T_7}{5y_0 h'(10y_0)}, \quad T_1 = \frac{6d_1 y_0 + 6T_7 y_0}{120 y_0 T_7}, \quad T_2 = \frac{d_2 y_0 + T_7 y_0}{20 y_0 T_7},$$

[‡]The explicit mathematical expression for the Lyapunov coefficient will be given in the applications contained in Section 5.

$$T_3 = \frac{z_0\partial_w g_1(w,x,y)}{12y_0} + \frac{121z_0\partial_w g_2(w,x,y)}{120y_0} + \frac{z_0\partial_w g_3(w,x,y)}{12y_0},$$
$$T_4 = \frac{z_0\partial_x g_1(w,x,y)}{12y_0} + \frac{121z_0\partial_x g_2(w,x,y)}{120y_0} + \frac{z_0\partial_x g_3(w,x,y)}{12y_0},$$
$$T_5 = \frac{z_0\partial_y g_1(w,x,y)}{12y_0} + \frac{121z_0\partial_y g_2(w,x,y)}{120y_0} + \frac{z_0\partial_y g_3(w,x,y)}{12y_0},$$
$$T_6 = \frac{z_0 g_1(w,x,y)}{12y_0} + \frac{121z_0 g_2(w,x,y)}{120y_0} + \frac{z_0 g_3(w,x,y)}{12y_0},$$
$$T_7 = z_0\partial_w g_1(10y_0, 6y_0, y_0).$$

As a particular case, one obtains that the linear approximation at the equilibrium point p becomes

$$\mathcal{J}(p) = \begin{pmatrix} -8T_7 & \dfrac{-235T_7}{12} & -15T_7 & \dfrac{-20y_0T_7}{z_0} \\ \dfrac{6y_0T_7+6d_1y_0}{20y_0} + \dfrac{3T_7}{40} & \dfrac{1}{2}T_7 & \dfrac{3}{2}T_7 & -\dfrac{6y_0T_7}{z_0} \\ \dfrac{y_0T_7+d_2y_0}{20y_0} + \dfrac{T_7}{80} & \dfrac{1}{24}T_7 & \dfrac{1}{2}T_7 & -\dfrac{y_0T_7}{z_0} \\ \dfrac{z_0T_7}{150y_0} & \dfrac{671z_0T_7}{1440y_0} & -\dfrac{151z_0T_7}{80y_0} & 0 \end{pmatrix}. \tag{4.1}$$

4.2. Predators' mortality rates as BT-bifurcation parameters

In order to prove the presence of a BT-bifurcation, we will consider that differential system (2.1) is a two-parameter family with respect to the predators mortality rates d_1 and d_2; hence, the linear approximation at the equilibrium point $p = (w_0, x_0, y_0, z_0)$ given in (4.1) will be denoted by $\mathcal{J}(p, d_1, d_2)$. These assumptions allow us to have the following necessary BT-condition, and its proof is contained in Appendix C.1.

Lemma 6. *If the hypotheses in Proposition 1 are valid,*

$$d_{10} = \frac{70940543z_0\partial_w g_1(10y_0, 6y_0, y_0)}{8309764} > 0 \textit{ and } d_{20} = \frac{73066255z_0\partial_w g_1(10y_0, 6y_0, y_0)}{8309764} > 0,$$

then the eigenvalues of $\mathcal{J}(p, d_{10}, d_{20})$ *are*

$$\lambda_{1,2} = 0, \quad \lambda_{3,4} = \left(-\frac{7}{2} \pm i\frac{11}{4}\sqrt{\frac{37917221}{6232323}}\right) z_0\partial_w g_1(10y_0, 6y_0, y_0). \tag{4.2}$$

4.3. BT-Main results for the food web model

In this subsection, following the ideas in [16] (cf. [6]), we will show the non-degeneracy conditions under which system (2.1) undergoes a Bogdanov-Takens bifurcation at p with respect to the predators' mortality rates d_1 and d_2.

4.3.1. Simplification of the food web model

Let d_{10} and d_{20} be as in Lemma 6. The existence of a positive equilibrium point p is guaranteed by the parameter conditions given in (3.1) of Proposition 1, and in particular the parameters c_1 and c_2 depend on the predator mortality rates according to the following formulas:

$$c_1(d_1) = \frac{d_1 x_0 + z_0 g_2(w_0, x_0, y_0)}{x_0 f_1(w_0)} \text{ and } c_2(d_2) = \frac{d_2 y_0 + z_0 g_3(w_0, x_0, y_0)}{y_0 f_2(w_0)}.$$

Now, by considering the values $c_1(d_{10})$ and $c_2(d_{20})$, we have that model (2.1) becomes:

$$\begin{aligned} \frac{dw}{dt} &= R_1 w h(w) - f_1(w)x - f_2(w)y - g_1(w, x, y)z, \\ \frac{dx}{dt} &= x(c_1(d_{10}) f_1(w) - d_1) - g_2(w, x, y)z, \\ \frac{dy}{dt} &= y(c_2(d_{20}) f_2(w) - d_2) - g_3(w, x, y)z, \\ \frac{dz}{dt} &= z(e_1 g_1(w, x, y) + e_2 g_2(w, x, y) + e_3 g_3(w, x, y) - d_3). \end{aligned} \tag{4.3}$$

Hence, p is an equilibrium point of system (4.3) if and only if $(d_1, d_2) = (d_{10}, d_{20})$.
Convention: From now on,

$$\mathcal{G}(w, x, y, z, d_1, d_2)$$

will denote the coordinates of the vector field associated to system (4.3), and

$$\tau(w, x, y, z, d_1, d_2) \text{ and } \delta(w, x, y, z, d_1, d_2)$$

will be the trace and the determinant of the Jacobian matrix

$$\mathcal{J}(w, x, y, z, d_1, d_2)$$

of $\mathcal{G}$, respectively.

It is worth mentioning that the non-degeneracy conditions and the so-called quadratic coefficients were computed by means of the formulae of Guckenheimer-Kuznetsov (see [17] and cf. [16, Theorem A.1] and [6]). These formulas were implemented in routines inside the software Mathematica.

4.3.2. Regularity BT-condition for the food web model

The regularity condition is obtained by computing the determinant $\mathbf{Reg_0}$ of the Jacobian for the map

$$\mathcal{F} : (w, x, y, z, d_1, d_2) \mapsto (\mathcal{G}(w, x, y, z, d_1, d_2), \tau(w, x, y, z, d_1, d_2), \delta(w, x, y, z, d_1, d_2)) \tag{4.4}$$

at (p, d_{10}, d_{20}). The mathematical expression of $\mathbf{Reg_0}$ is huge, so we will omit it here, but it will be given explicitly in the applications as we will see later. In this sense, we can state the following result.

Proposition 7. *If the hypotheses in Proposition 1 are verified for system* (4.3)*, then the map* (4.4) *is regular at* (p, d_{10}, d_{20}) *if and only if* $\mathbf{Reg_0}$ *is a non-zero real number.*

4.3.3. Computation of the BT-quadratic coefficients

The following result provides us with explicit mathematical expressions for the BT-quadratic coefficients, which are computed by using the normalized BT-eigenvectors given in Appendix C.2. Here, the formulaes of Guckenheimer-Kuznetsov were used (see [17] and cf. [16, Theorem A.1] and [6]).

Proposition 8. *If the hypotheses in Proposition 1 are valid, then the quadratic coefficints at* (p, d_{10}, d_{20}) *are:*

$$\begin{aligned} \mathbf{a}_0 &= -\frac{(59 z_0 \partial_w g_1(10y_0,6y_0,y_0))^2((-2z_0\mathbf{a_{00}}+\mathbf{a_{01}})h'(10y_0)+\mathbf{a_{02}})}{270004092645550915208000h'(10y_0)}, \\ \mathbf{b}_0 &= \frac{59\partial_w g_1(10y_0,6y_0,y_0)((-2z_0\mathbf{b_{00}}+\mathbf{b_{01}})h'(10y_0)+\mathbf{b_{02}})}{19607423994153610587503247464900h'(10y_0)}; \end{aligned} \tag{4.5}$$

where $\mathbf{a_{00}}, \mathbf{a_{01}}, \mathbf{a_{02}}, \mathbf{b_{00}}, \mathbf{b_{01}}$*, and* $\mathbf{b_{02}}$ *are as in Appendix C.3.*

In terms of Propositions 8 and 7, we now proceed to state the second main result in this manuscript.

Theorem 9 (BT-Main theorem)**.** *Suppose that the hypotheses in proposition 1 hold, and that* $\mathbf{Reg_0}$ *and* $\kappa = \mathbf{a}_0\mathbf{b}_0$ *are non-zero real numbers. Then system* (4.3) *undergoes a Bogdanov-Takens bifurcation at* p *with respect to the parameters* d_1 *and* d_2, *with bifurcation value* (d_{10}, d_{20}).

Proof. From Lemma 6, the linear approximation of system (4.3) at p has the eigenvalues as in (4.2) if $(d_1, d_2) = (d_{10}, d_{20})$. Besides, since $\mathbf{Reg_0}$ and κ are non-zero real numbers, the result is proved by the BT-Theorem in [17] (cf. [16, Theorem A.1] and [6]). □

5. H-validation results and numerical simulations

In this section, we will show how the H-Main Theorem 5 and its proof are applied to concrete examples for guaranteeing the coexistence of the four populations. On considering differential system (2.1), let us begin by stating the following main hypotheses that allow us to provide interesting examples:

- The prey has a specific logistic growth rate, that is, the intrinsic prey growth function is $R_1 w h(w) = R_1 w \left(1 - \frac{w}{k_1}\right)$, where k_1 is the carrying capacity of the prey.
- The functional responses f_1 and f_2 can be Holling of type II or IV, which measure the satiety or the defense group of the prey population.
- Under the above premises, we propose the following cases according to the type of functional responses that

  $$g_1(w, x, y), g_2(w, x, y), \text{ and } g_3(w, x, y)$$

  could be:

  i) **Case H1:** Predators and the superpredator have satiety and interference through generalized Holling II functional responses (see Falconi et al. [18] and cf. [13]).
  ii) **Case H2:** The prey has a defense group, while predators and the superpredator have defense and interference, all through generalized Holling II or IV functional responses[§].

[§]These generalized functional responses are inspired by the similar ones that were used in Falconi et al. [18], Maghool et al. and [19] (cf. [13]).

iii) **Case H3:** The prey has a defense group and predators have defense, interference, or intrinsic competence, all through generalized Holling IV functional responses (see Falconi et al. [18], Maghool et al. [19]).

5.1. Case H1: Satiety and interference between predators

In this case, the specific functional responses are:

$$f_1(x) = \frac{a_1 x}{b_1 + x}, \quad f_2(x) = \frac{a_2 x}{b_2 + x}, \quad g_1(w,x,y) = \frac{\alpha_1 w}{\beta_1 + \gamma_1 w + \delta_1 x + \eta_1 y},$$
$$g_2(w,x,y) = \frac{\alpha_2 x}{\beta_2 + \gamma_2 w + \delta_2 x + \eta_2 y}, \quad g_3(w,x,y) = \frac{\alpha_3 y}{\beta_3 + \gamma_3 w + \delta_3 x + \eta_3 y}.$$

Substitution of the above explicit functions implies that system (2.1) will have many new parameters. Therefore, in order for the conditions in Appendix A.1 to be satisfied, we make the following additional parameter assignments:

$$w_0 = 10y_0, \quad x_0 = 6y_0, \quad k_1 = 20y_0, \quad b_1 = b_2 = 10y_0,$$

$$a_2 = a_1, \quad \alpha_2 = \frac{\alpha_1\beta_2}{2\beta_1}, \quad \alpha_3 = \frac{\alpha_1\beta_3}{2\beta_1}, \quad \gamma_1 = \frac{2\beta_1}{5y_0},$$

$$\gamma_2 = \frac{\beta_2}{10y_0}, \quad \gamma_3 = \frac{\beta_3}{10y_0}, \quad \delta_1 = \frac{\beta_1}{6y_0}, \quad \delta_2 = \frac{2\beta_2}{3y_0},$$

$$\delta_3 = \frac{\beta_3}{3y_0}, \quad \eta_1 = \frac{2\beta_1}{y_0}, \quad \eta_2 = \frac{2\beta_2}{y_0}, \quad \eta_3 = \frac{4\beta_3}{y_0}.$$

From these assignments and the computations in Appendix B.1, we have that the corresponding differential system undergoes a supercritical Hopf bifurcation and hence the existence of a stable limit cycle takes place.

5.1.1. Numerical simulations for Case H1

For visualizing the coexistence of the four species by a stable limit cycle, we consider the following parameter values for the free parameters in Case H1 in Subsection 5.1 that we have as a consequence of the above formulae:

$$a_1 = 40, \quad \beta_1 = \beta_2 = \beta_3 = 1, \quad y_0 = 10, \quad \alpha_1 = 2.$$

Therefore, $p = (100, 60, 10, 8)$ and $d_{10} = \frac{386660234}{122003525}$. According to the above explicit formulae, the parameters for numerically validating the H-Main Theorem for differential system (2.1) are given in Table 2, from which, numerically, the transversal condition holds since $\frac{\partial \mathrm{Re}(\lambda_{1,2})(d_{10})}{\partial d_1} < 0$. This means that $\mathrm{Re}(\lambda)$ is a decreasing function[¶] on d_1. Moreover, there is a stable limit cycle coming from a supercritical Hopf bifurcation, because the first Lyapunov coefficient becomes $l_1(d_{10}) = -0.0306563$.

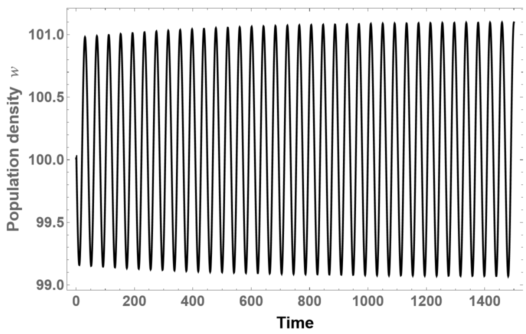
[¶]If $d_1 > d_{10}$, the equilibrium point p is locally asymptotically stable and if $d_1 < d_{10}$, it becomes unstable from which one ensures that a stable limit cycle emerges.

Table 2. Numerical validation for the H-Main Theorem: Case H1.

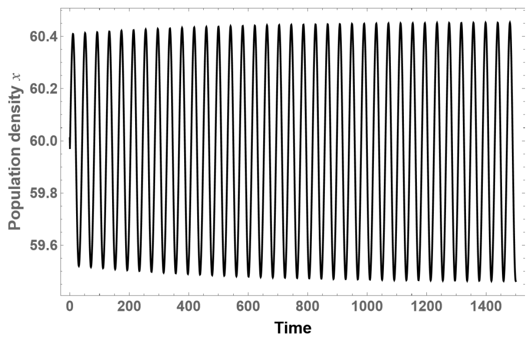
Specific parameter values for numerical simulation in Case H1	
Equilibrium point entries	$w_0 = 100,\ x_0 = 60,\ y_0 = 10,\ z_0 = 8$
Hypotheses of Proposition 1	$R_1 = 32,\ c_1 = \frac{405954979}{1952056400},\ c_2 = \frac{43}{200},\ d_3 = \frac{163}{20}$
Conditions (3.3) in Proposition 2	$d_2 = \frac{33}{10},\ e_1 = e_3 = \frac{2}{25},\ e_2 = \frac{121}{50},\ d_1 > d_{10}$
Carrying capacity of prey	$k_1 = 200$
MP1 and MP2 parameters of functional responses	$a_1 = a_2 = 40,\ b_1 = b_2 = 100$
SP parameters of functional responses	$\alpha_1 = 2, \alpha_2 = \alpha_3 = 1,\ \beta_1 = \beta_2 = \beta_3 = 1,\ \gamma_1 = \frac{1}{25}, \gamma_2 = \gamma_3 = \frac{1}{100},$
	$\delta_1 = \frac{1}{60},\ \delta_2 = \frac{1}{15},\ \delta_3 = \frac{1}{30},\ \eta_1 = \eta_2 = \frac{1}{5},\ \eta_3 = \frac{2}{5}$
H-Bifurcation value	$d_{10} = \frac{386660234}{122003525} = 3.16925$
Transversal condition and Lyapunov coefficient	$\frac{\partial \mathrm{Re}(\lambda_{1,2})(d_{10})}{\partial d_1} = -0.00127211,\ l_1(p, d_{10}) = -0.0306563$

5.1.2. Coexistence by numerical detection of a stable limit cycle

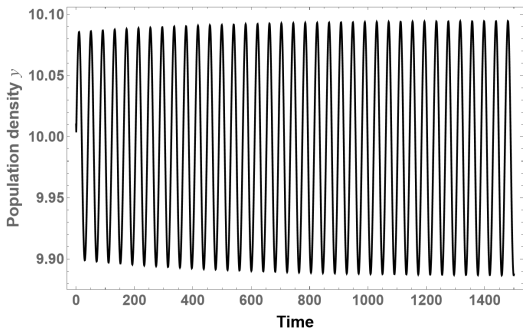
From the above numerical parameter assignments, we make the small perturbation $d_1 = d_{10} - \frac{1}{10^2}$, and we take the initial condition in the phase space $q = \left(w_0 + \frac{1}{10^2}, x_0 + \frac{1}{10^2}, y_0 + \frac{1}{10^2}, z_0 + \frac{1}{10^2}\right)$ whose trajectory tends to a stable limit cycle with projection to the hyperspace given by $\mathbb{R}^3_{(x,y,z)} \simeq \{(0, x, y, z)\}$. In Figure 4, we show the time series for the four populations and the limit cycle projection.



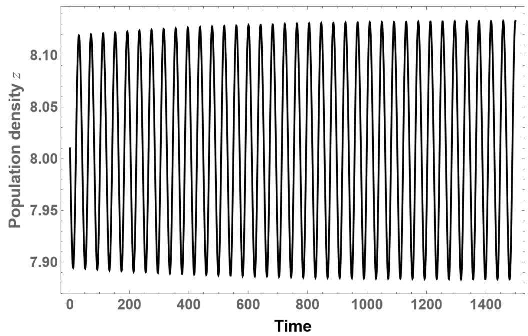
(a) Population density w



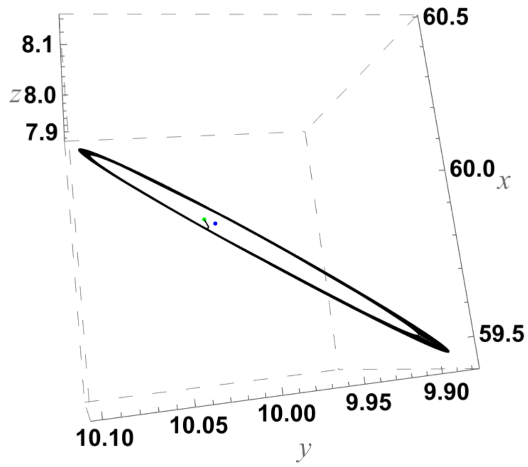
(b) Population density x



(c) Population density y



(d) Population density z



(e) Projection of the stable limit cycle

Figure 4. Population densities and the projection of the stable limit cycle in Case H1.

5.2. *Case H2: Group defenses and predators' interference*

In this case, the specific functional responses are:

$$f_1(x) = \frac{a_1 x}{b_1 + x^2}, \quad f_2(x) = \frac{a_2 x}{b_2 + x^2}, \quad g_1(w,x,y) = \frac{\alpha_1 w}{\beta_1 + \gamma_1 w^2 + \delta_1 x + \eta_1 y},$$
$$g_2(w,x,y) = \frac{\alpha_2 x}{\beta_2 + \gamma_2 w + \delta_2 x^2 + \eta_2 y}, \quad g_3(w,x,y) = \frac{\alpha_3 y}{\beta_3 + \gamma_3 w + \delta_3 x + \eta_3 y^2}.$$

Substitution of the above explicit functions implies that system (2.1) will have many new parameters. Therefore, in order for the conditions in Appendix A.1 to be satisfied, we make the following additional parameter assignments:

$$\begin{array}{llll} w_0 = 10y_0, & x_0 = 6y_0, & k_1 = 20y_0, & b_1 = b_2 = 300y_0^2, \\ a_1 = a_2, & \alpha_2 = \dfrac{5\alpha_1\gamma_2}{6\delta_1}, & \alpha_3 = \dfrac{5\alpha_1\gamma_3}{2\delta_1}, & \gamma_1 = \dfrac{3\delta_1}{25y_0}, \\ \beta_1 = 18y_0\delta_1, & \beta_2 = 30y_0\gamma_2, & \beta_3 = 30y_0\gamma_3, & \delta_2 = \frac{5\gamma_2}{9y_0}, \\ \delta_3 = \dfrac{10\gamma_3}{3}, & \eta_1 = 12\delta_1, & \eta_2 = 20\gamma_2, & \eta_3 = \dfrac{20\gamma_3}{y_0}. \end{array}$$

From these assignments and the computations in Appendix B.2 along with the above results, the corresponding differential system undergoes a supercritical Hopf bifurcation and hence there is a stable limit cycle. Therefore, the coexistence of the four species takes place.

5.2.1. Numerical simulations for Case H2

For visualizing the coexistence of the four species by a stable limit cycle, we consider the following parameter values for the free parameters in Case H2 in Subsection 5.1 that we have as a consequence of the above formulae:

$$a_2 = 7000, \quad \delta_1 = \gamma_2 = \gamma_3 = 1, \quad y_0 = 10, \quad \alpha_1 = 90.$$

Therefore, $p = \left(100, 60, 10, \frac{28}{3}\right)$ and $d_{10} = \frac{193330117}{69716300}$. According to the above explicit formulae, the parameters for numerically validating the H-Main Theorem for differential system (2.1) are given in Table 3, from which, numerically, the transversal condition holds since $\frac{\partial \mathrm{Re}(\lambda_{1,2})(d_{10})}{\partial d_1} < 0$. This means that $\mathrm{Re}(\lambda)$ is a decreasing function[‖] on d_1. Moreover, there is a stable limit cycle coming from a supercritical Hopf bifurcation, because the first Lyapunov coefficient becomes $l_1(d_{10}) = -0.0652417$.

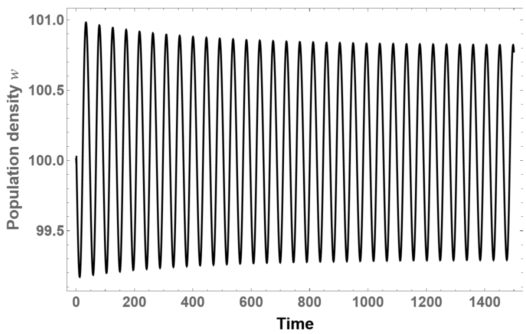
Table 3. Numerical validation for the H-Main Theorem: Case H2.

Specific parameter values for the numerical simulation in Case H2	
Equilibrium point entries	$w_0 = 100$, $x_0 = 60$, $y_0 = 10$, $z_0 = 9.3333$
Hypotheses of Proposition 1	$R_1 = 28$, $c_1 = 0.208463$, $c_2 = 0.215$, $d_3 = 7.13125$
Conditions (3.3) in Proposition 2	$d_2 = 2.8875$, $e_1 = e_3 = 0.93333$, $e_2 = 0.941111$, $d_1 > d_{10}$
Carrying capacity of prey	$k_1 = 200$
MP1 and MP2 parameters of functional responses	$a_1 = a_2 = 7000$, $b_1 = b_2 = 30000$
SP parameters of functional responses	$\alpha_1 = 90, \alpha_2 = 75$, $\alpha_3 = 75$, $\beta_1 = 180$, $\beta_2 = \beta_3 = 300$, $\gamma_1 = 0.012$, $\gamma_2 = \gamma_3 = 1$,
	$\delta_1 = 1$, $\delta_2 = 0.0555556$, $\delta_3 = 3.33333$, $\eta_1 = 12$, $\eta_2 = 20$, $\eta_3 = 2$
H-Bifurcation value	$d_{10} = 2.7731$
Transversal condition and Lyapunov coefficient	$\frac{\partial \mathrm{Re}(\lambda_{1,2})(d_{10})}{\partial d_1} = -0.00172392$, $l_1(p, d_{10}) = -0.0652417$

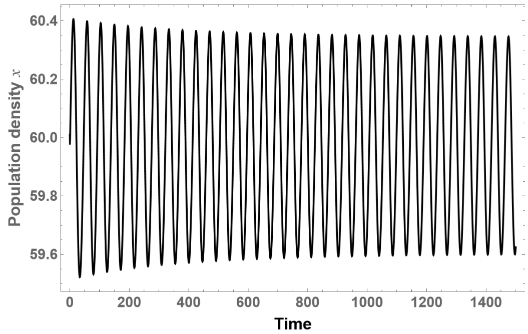
[‖]If $d_1 > d_{10}$, the equilibrium point p is locally asymptotically stable and if $d_1 < d_{10}$, it becomes unstable from which one ensures that a stable limit cycle emerges.

5.2.2. Coexistence by numerical detection of a stable limit cycle: Case H2

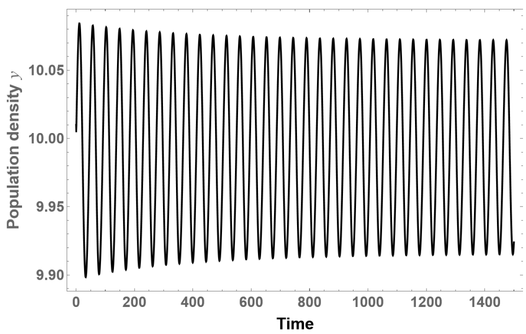
From the above numerical parameter assignments, we make the small perturbation $d_1 = d_{10} - \frac{1}{10^2}$, and we take the initial condition in the phase space $q = \left(w_0 + \frac{1}{10^2}, x_0 + \frac{1}{10^2}, y_0 + \frac{1}{10^2}, z_0 + \frac{1}{10^2}\right)$ whose trajectory tends to a stable limit cycle with projection to the hyperspace given by $\mathbb{R}^3_{(x,y,z)} \simeq \{(0, x, y, z)\}$. Figure 5 shows the time series for the four populations and the limit cycle projection.



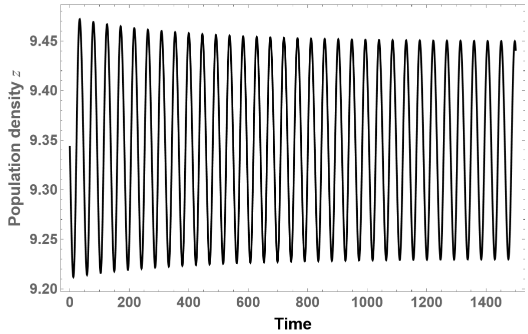
(a) Population density w



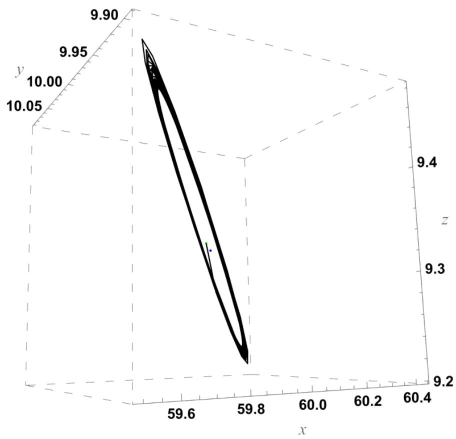
(b) Population density x



(c) Population density y



(d) Population density z



(e) Projection of the stable limit cycle

Figure 5. Population densities time series and the projection of the stable limit cycle in Case H2.

5.3. *Case H3: Defense group, competence, and interference*

In this case, the specific functional responses are:

$$f_1(x) = \frac{a_1 x}{b_1 + x^2}, \quad f_2(x) = \frac{a_2 x}{b_2 + x^2}, \quad g_1(w,x,y) = \frac{\alpha_1 w}{\beta_1 + \gamma_1 w^2 + \delta_1 x^2 + \eta_1 y},$$
$$g_2(w,x,y) = \frac{\alpha_2 x}{\beta_2 + \gamma_2 w + \delta_2 x^2 + \eta_2 y^2}, \quad g_3(w,x,y) = \frac{\alpha_3 y}{\beta_3 + \gamma_3 w + \delta_3 x + \eta_3 y^2}.$$

Substitution of the above explicit functions implies that system (2.1) will have many new parameters. Therefore, in order for the conditions in Appendix A.1 to be satisfied, we make the following additional parameter assignments:

$$w_0 = 10y_0, \ x_0 = 6y_0, \ k_1 = 20y_0, \ b_1 = b_2 = 300y_0^2, \ a_1 = a_2,$$
$$\alpha_2 = \frac{7\alpha_1\beta_2}{16\beta_1}, \ \alpha_3 = \frac{7\alpha_1\beta_3}{12\beta_1}, \ \gamma_1 = \frac{\beta_1}{175y_0^2}, \ \gamma_2 = \frac{\beta_2}{40y_0}, \ \gamma_3 = \frac{\beta_3}{30y_0},$$
$$\delta_1 = \frac{\beta_1}{252y_0^2}, \ \delta_2 = \frac{\beta_2}{72y_0^2}, \ \delta_3 = \frac{\beta_3}{9y_0}, \ \eta_1 = \frac{4\beta_1}{7y_0}, \ \eta_2 = \frac{\beta_2}{4y_0^2}, \ \eta_3 = \frac{2\beta_3}{3y_0^2}.$$

From these assignments and the computations in Appendix B.3, we have that the differential system undergoes a supercritical Hopf bifurcation and there is a stable limit cycle. Hence, the coexistence of the four species takes place.

5.3.1. Numerical simulations for Case H3

For visualizing the coexistence of the four species by a stable limit cycle, we consider the following parameter values for the free parameters in Case H3 in Subsection 5.1 that we have as a consequence of the above formulae:

$$a_1 = 6020, \quad \beta_1 = \beta_2 = \beta_3 = 1, \quad y_0 = 10, \quad \alpha_1 = 1.$$

Therefore, $p = \left(100, 60, 10, \frac{86}{25}\right)$ and $d_{10} = \frac{8313195031}{3485815000}$. According to the above explicit formulae, the parameters for numerically validating the H-Main Theorem for differential system (2.1) are given in Table 4, from which, numerically, the transversal condition holds since $\frac{\partial \mathrm{Re}(\lambda_{1,2})(d_{10})}{\partial d_1} < 0$. This means that $\mathrm{Re}(\lambda)$ is a decreasing function** on d_1. Moreover, there is a stable limit cycle coming from a supercritical Hopf bifurcation, because the first Lyapunov coefficient becomes $l_1(p, d_{10}) = -0.111732$.

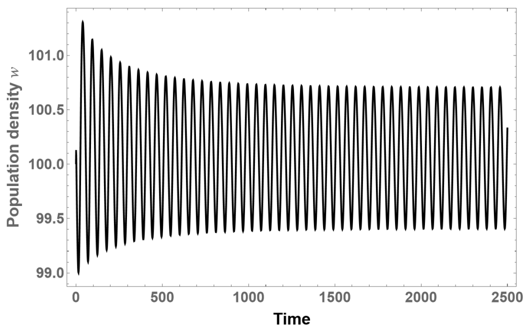
**If $d_1 > d_{10}$, the equilibrium point p is locally asymptotically stable and if $d_1 < d_{10}$, it becomes unstable from which one ensures that a stable limit cycle emerges.

Table 4. Numerical validation for the H-Main Theorem: Case H3.

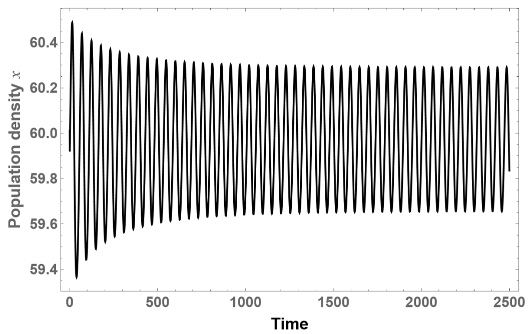
Specific parameter values for the numerical simulation in Case H3	
Equilibrium point entries	$w_0 = 100,\ x_0 = 60,\ y_0 = 10,\ z_0 = 3.44$
Hypotheses of Proposition 1	$R_1 = 24.08,\ c_1 = 0.207798,\ c_2 = 0.215,\ d_3 = 6.13288$
Conditions (3.3) in Proposition 2	$d_2 = 2.48325,\ e_1 = e_3 = 0.0344,\ e_2 = 0.346867,\ d_1 < d_{10}$
Carrying capacity of prey	$k_1 = 200$
MP1 and MP2 parameters of functional responses	$a_1 = a_2 = 6020,\ b_1 = b_2 = 30000$
SP parameters of functional responses	$\alpha_1 = 1,\ \alpha_2 = 0.4375,\ \alpha_3 = 0.583333,\ \beta_1 = \beta_2 = \beta_3 = 1,\ \gamma_1 = 0.0000571429,$ $\gamma_2 = 0.0025,\ \gamma_3 = 0.00333333,\ \delta_1 = 0.0000396825,\ \delta_2 = 0.000138889,\ \delta_3 = 0.0111111,$ $\eta_1 = 0.0571429,\ \eta_2 = 0.0025,\ \eta_3 = 0.00666667$
H-Bifurcation value	$d_{10} = 2.38486$
Transversal condition and Lyapunov coefficient	$\frac{\partial \mathrm{Re}(\lambda_{1,2})(d_{10})}{\partial d_1} = -0.000237563,\ l_1(p, d_{10}) = -0.111732$

5.3.2. Coexistence by numerical detection of a stable limit cycle

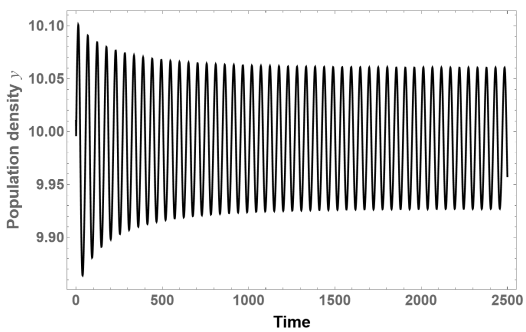
From the above numerical parameter assignments, we make the small perturbation $d_1 = d_{10} - \frac{1}{10^2}$, and we take the initial condition in the phase space $q = \left(w_0 + \frac{1}{10^2}, x_0 + \frac{1}{10^2}, y_0 + \frac{1}{10^2}, z_0 + \frac{1}{10^2}\right)$ whose trajectory tends to a stable limit cycle with projection to the hyperspace given by $\mathbb{R}^3_{(x,y,z)} \simeq \{(0, x, y, z)\}$. Figure 6 shows the time series for the four populations and the limit cycle projection.



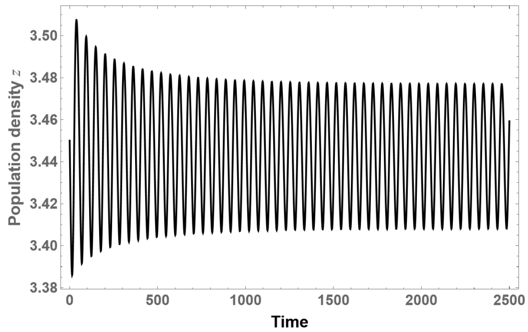
(a) Population density w



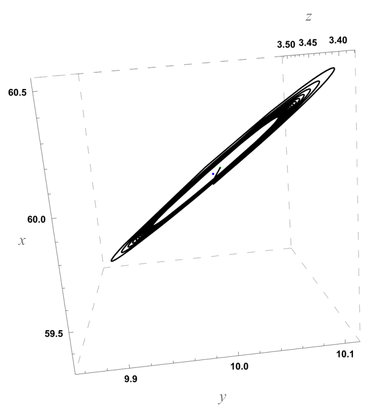
(b) Population density x



(c) Population density y



(d) Population density z



(e) Projection of the stable limit cycle

Figure 6. Population densities time series and the projection of the stable limit cycle in Case H3.

6. BT-validations results and numerical simulations

In this subsection, we will give some applications that illustrate the results in Propositions 7 and 8, and Theorem 9. In order to be more precise and in a self-contained way, in the applications we are interested in, let us make the premises that provide interesting examples. In fact, on considering the differential system (4.3), we assume that:

- The prey has a specific growth rate given by a logistic one, that is, the intrinsic prey growth function is $R_1 wh(w) = R_1 w\left(1 - \dfrac{w}{k_1}\right)$, where k_1 is the carrying capacity of the prey.
- The functional responses f_1 and f_2 can be Holling types II or IV, measuring the satiety or the defense group of the prey population;
- Under the above premises, we propose the following cases according to the type of functional responses $g_1(w, x, y), g_2(w, x, y)$, and $g_3(w, x, y)$:
  a) **Case BT1:** Predators and the superpredator have satiety and interference through generalized Holling II functional responses.
  b) **Case BT2:** The prey has a defense group, while predators and the superpredator have defense and interference, all through generalized Holling II or IV functional responses.

6.1. Case BT1: Satiety and interference between predators

In this case, according to the hypotheses, the functional responses are similar to the ones used in Case H1 in Subsection 5.1.

Substitution of the above explicit functions implies that system (4.3) will have many new parameters. Therefore, in order for the conditions in Subsection 4.1 to be satisfied, we make the following additional parameter assignments:

$$\begin{array}{lllll} e_2 = \dfrac{121z_0}{120y_0}, & w_0 = 10y_0, & x_0 = 6y_0, & \alpha_2 = \dfrac{\alpha_1\eta_2}{2\eta_1}, & \alpha_3 = \dfrac{3\alpha_1\delta_3}{\eta_1}, \\ \beta_1 = \dfrac{y_0\eta_1}{2}, & \beta_2 = \dfrac{y_0\eta_2}{2}, & \beta_3 = 3y_0\delta_3, & \gamma_1 = \dfrac{\eta_1}{5}, & \gamma_2 = \dfrac{\eta_2}{20}, \\ \gamma_3 = \dfrac{3\delta_3}{10}, & \delta_1 = \dfrac{\eta_1}{12}, & \delta_2 = \dfrac{\eta_2}{3}, & \eta_3 = 12\delta_3, & k_1 = 20y_0, \\ \multicolumn{5}{l}{b_1 = b_2 = 10y_0, \quad a_1 = a_2 = \dfrac{5z_0\alpha_1}{y_0\eta_1}, \quad e_1 = e_3 = \dfrac{z_0}{12y_0}.} \end{array} \tag{6.1}$$

From these assignments and the computations in Appendix D.1, we have that $\mu := \text{sign}(\kappa) = -1$. Hence, we have the existence of a stable limit cycle which comes from a supercritical Hopf bifurcation or a homoclinic bifurcation. This allows us to obtain the coexistence of the four species by a stable limit cycle.

6.1.1. Numerical simulations for Case BT1

In the following, some numerical results are given to illustrate the results in Section 6. From the conditions in (6.1), differential system (4.3) has the free parameters α_1, η_1, η_2 and δ_3 and the free constants z_0 and y_0. In order to obtain the numerical simulations, we set:

$$z_0 = 10, \quad y_0 = 11, \quad \alpha_1 = \eta_1 = \eta_2 = \delta_3 = 1.$$

From these conditions and according to the main Theorem 9, the parameter values for the depending parameters are shown in Table 5. Now, taking the vector perturbation $(d_{10}, d_{20}) + \left(\frac{1}{10^4}, \frac{1}{10^5}\right) =$

(0.970015, 0.999134), there is a saddle equilibrium point:

$$p_1 = (166.327, 30.3503, 0, 16.0185),$$

at which the corresponding linear approximation has eigenvalues

$$\lambda_{1,2} = -0.397727 \pm 0.770803i \text{ and } \lambda_{3,4} = 0.0000267485 \pm 0.00138117i.$$

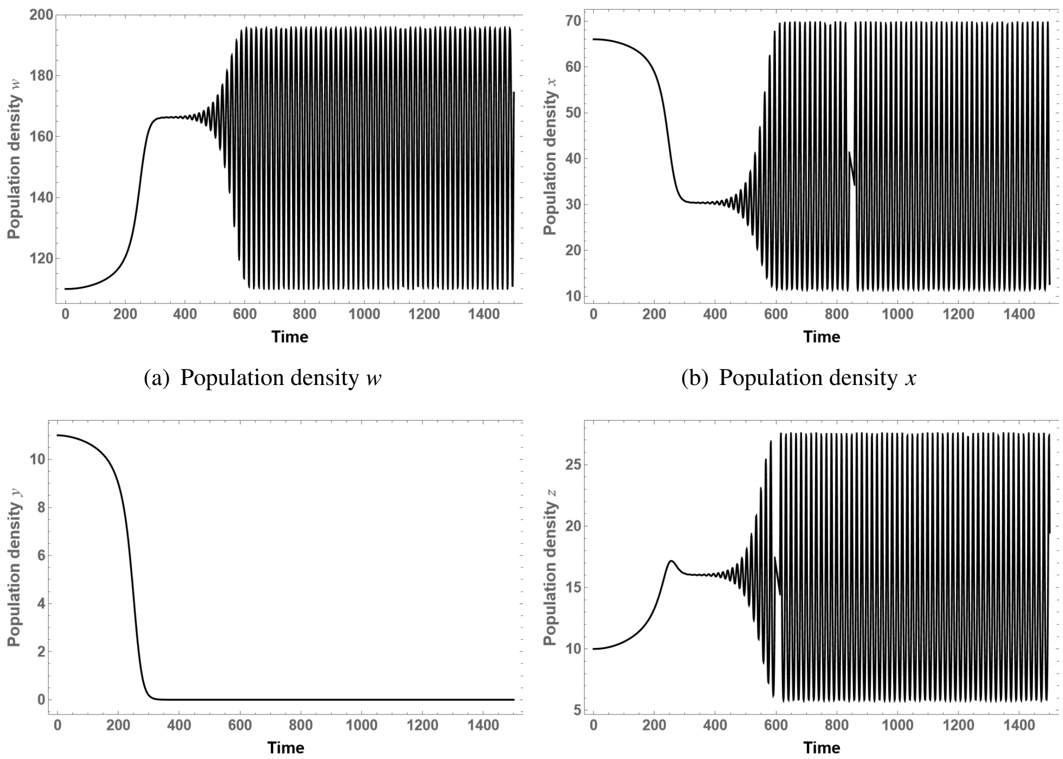
Table 5. Numerical validation for the BT-Main Theorem: Case BT1.

Specific parameter values for the numerical simulation in Case BT1	
Equilibrium point entries	$w_0 = 110$, $x_0 = 66$, $y_0 = 11$, $z_0 = 10$
Hypotheses of Proposition 1	$R_1 = 3.63636$, $c_1 = 0.476851$, $c_2 = 0.489641$, $d_3 = 0.886364$
Carrying capacity of prey	$k_1 = 220$
MP1 and MP2 parameters of functional responses	$a_1 = a_2 = 4.54545$, $b_1 = b_2 = 110$
SP parameters of functional responses	$e_2 = 0.916667$, $\alpha_2 = 0.5$, $\alpha_3 = 3$, $\beta_1 = \beta_2 = 5.5$, $\beta_3 = 33$, $\gamma_1 = 0.2$, $\gamma_2 = 0.05$, $\gamma_3 = 0.3$, $\delta_1 = 0.08333$, $\delta_2 = 0.3333$, $\eta_3 = 12$, $e_1 = e_3 = 0.0757576$
BT-Bifurcation value	$d_{10} = 0.970115$, $d_{20} = 0.999184$
Quadratic coefficients and κ	$\mathbf{a_0} = -4.59307 \times 10^{-6}$, $\mathbf{b_0} = 0.00015748$, $\kappa = -7.23315 \times 10^{-10}$
Regularity condition	$Reg_0 = 0.00122321$

Moreover, taking as an initial condition

$$p_0 = (10y_0, 6y_0, y_0, z_0) + \left(\frac{1}{10^3}, \frac{1}{10^3}, \frac{1}{10^3}, \frac{1}{10^3}\right),$$

we have an orbit inside a small neighborhood of p_1, tending to a limit set in which the three populations w, x, and z coexist by means of a stable limit cycle, and the population y extincts. Figure 7 shows the corresponding time series for each population density.



(a) Population density w (b) Population density x

(c) Population density y (d) Population density z

Figure 7. Population densities time series in the Case BT1.

6.2. Case BT2: Group defenses and predators' interference

In this case, according to the hypotheses, the functional responses are similar to the ones used in Case H2 in Subsection 5.2.

Substitution of the above explicit functions implies that system (4.3) will have many new parameters. Therefore, in order for the conditions in Subsection 4.1 to be satisfied, we make the following additional parameter assignments:

$$
\begin{aligned}
&e_2 = \frac{121 z_0}{120 y_0}, \quad w_0 = 10 y_0, \quad x_0 = 6 y_0, \quad \alpha_2 = \frac{\alpha_1 \eta_2}{2\eta_1}, \quad \alpha_3 = \frac{3\alpha_1\delta_3}{\eta_1},\\
&\beta_1 = \frac{3 y_0 \eta_1}{2}, \quad \beta_2 = \frac{3 y_0 \eta_2}{2}, \quad \beta_3 = 9 y_0 \delta_3, \quad \gamma_1 = \frac{\eta_1}{100 y_0}, \quad \gamma_2 = \frac{\eta_2}{20},\\
&\gamma_3 = \frac{3\delta_3}{10}, \quad \delta_1 = \frac{\eta_1}{12}, \quad \delta_2 = \frac{\eta_2}{36 y_0}, \quad \eta_3 = \frac{6\delta_3}{y_0}, \quad k_1 = 20 y_0,\\
&b_1 = b_2 = 300 y_0^2, \quad a_1 = a_2 = \frac{100 z_0 \alpha_1}{\eta_1}, \quad e_1 = e_3 = \frac{z_0}{12 y_0}.
\end{aligned}
\tag{6.2}
$$

These assignments and the computations in Appendix D.2 have that $\mu := \text{sign}(\kappa) = -1$. Hence, we have the existence of a stable limit cycle which comes from a supercritical Hopf bifurcation or a homoclinic bifurcation. This allows us to obtain the coexistence of the four species by a stable limit cycle.

6.2.1. Numerical simulations for Case BT2

In the following, some numerical results are given for illustrating the results in Section 6. From the conditions in (6.2), the differential system (4.3) has free parameters α_1, η_1, η_2, and δ_3, and free constants z_0 and y_0. In this case, we consider the assignments:

$$z_0 = 10, \quad y_0 = 11, \quad \alpha_1 = \eta_1 = \eta_2 = \delta_3 = 1.$$

According to the main Theorem 9, Table 6 shows the parameter values for the depending parameters.

Table 6. Numerical validation for the BT-Main Theorem: Case BT2.

Specific parameter values for the numerical simulation in Case BT2	
Equilibrium point entries	$w_0 = 110$, $x_0 = 66$, $y_0 = 11$, $z_0 = 10$
Hypotheses of Proposition 1	$R_1 = 3.63636$, $c_1 = 0.476851$, $c_2 = 0.489641$, $d_3 = 0.886364$
Carrying capacity of prey	$k_1 = 220$
MP1 and MP2 parameters of functional responses	$a_1 = a_2 = 1000$, $b_1 = b_2 = 36300$
SP parameters of functional responses	$e_2 = 0.916667$, $\alpha_2 = 0.5$, $\alpha_3 = 3$, $\beta_1 = \beta_2 = 16.5$, $\beta_3 = 99$,
	$\gamma_1 = 0.000909091$, $\gamma_2 = 0.05$, $\gamma_3 = 0.3$, $\delta_1 = 0.08333$, $\delta_2 = 0.00252525$,
	$\eta_3 = 0.545455$, $e_1 = e_3 = 0.0757576$
BT-Bifurcation value	$d_{10} = 0.970115$, $d_{20} = 0.999184$
Quadratic coefficients and κ	$\mathbf{a_0} = -4.34412 \times 10^{-6}$, $\mathbf{b_0} = 0.000325726, \kappa = -1.41499 \times 10^{-9}$
Regularity condition	$\mathbf{Reg_0} = 0.000743216$

Taking the perturbation

$$(d_{10}, d_{20}) + \left(\frac{1}{10^{28}}, \frac{1}{10^{26}}\right) = (0.970115, 0.999184),$$

there is a saddle equilibrium point

$$p_2 = (142.88, 47.0907, 4.81109, 15.7472),$$

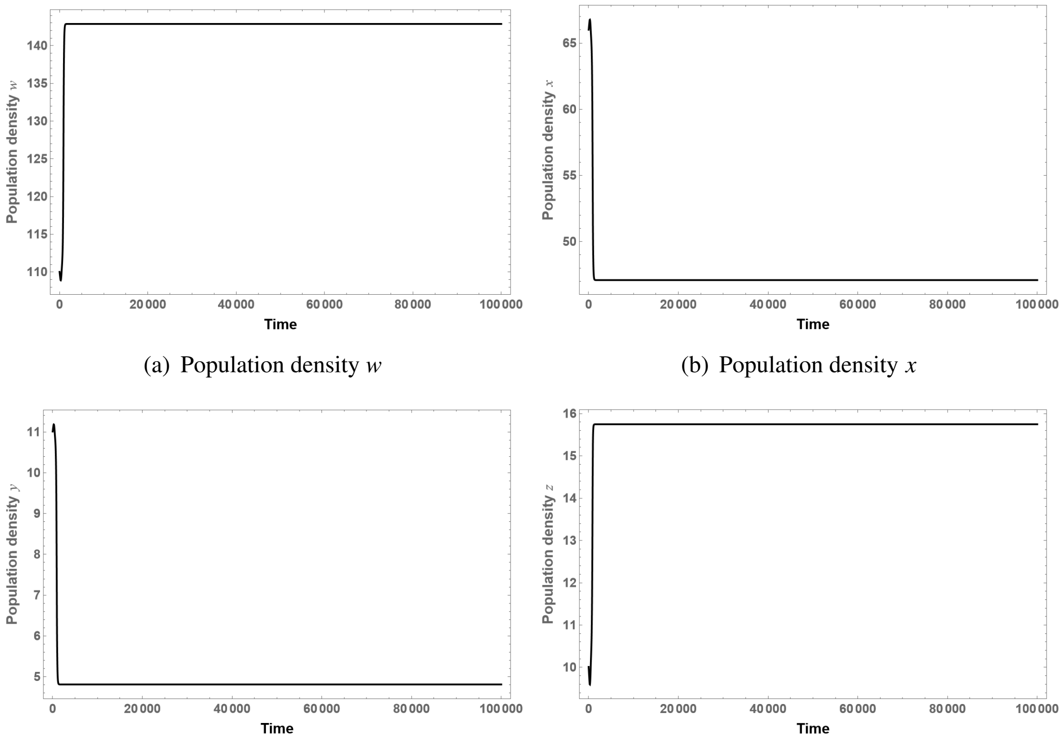
at which the corresponding linear approximation has eigenvalues

$$\lambda_{1,2} = -0.397727 \pm 0.770803i, \quad \lambda_{3,4} = -4.34379 \times 10^{-27} \pm 3.07689 \times 10^{-14} i.$$

Moreover, taking the initial condition

$$p_0 = (10y_0, 6y_0, y_0, z_0) + \left(\frac{1}{10^2}, \frac{1}{10^2}, \frac{1}{10^2}, \frac{1}{10^2}\right),$$

we obtain an orbit tending to p_2. Figure 8 shows the corresponding time series for each population density.



(a) Population density w (b) Population density x

(c) Population density y (d) Population density z

Figure 8. Population densities time series in Case BT2.

7. Discussion and concluding remarks

A four-species food web model consisting of a prey P, two mesopredators MP1 and MP2, and a superpredator SP was modeled by a four-dimensional nonlinear autonomous ordinary differential equation system given by (2.1). This model is Gause-type, and therefore MP1, MP2, and SP are specialists, that is, the survival of the mesopredators only depends on the source, and the survival of the SP only depends on the mesopredators. The dynamical analysis and the species coexistence for the differential system has been studied by other authors using specific functional responses and a concrete growth rate of the prey; therefore, the main goal in the present manuscript was to provide a study of the coexistence of the species as far as possible independent of both the growth rate of prey P and the functional responses involved in the populations interactions. This philosophic reasoning allowed us to obtain the Theorems 5 and 9, which have general statements showing sufficient conditions on the parameters to ensure that the system undergoes a Hopf or a Bogdanov-Takens bifurcation.

These analytical results could be validated by considering functional responses that incorporate several ecological premises, which, for a Hopf bifurcation, we collect in the Cases H1–H3 (see Subsection 5); and for a BT-bifurcation, we have the Cases BT1–BT2 (see Subsection 6).

The ecological aspects that we have considered in the applications[††] give us interesting results, both theoretically and numerically, and hence, they serve as a contribution to the literature on ecological modeling for population dynamics.

The numerical results allow us to show that the coexistence of the species is feasible, specifically, we have[‡‡]:

- Numerical H-results: See Subsubsections 5.1.1, 5.2.1, and 5.3.1.
- Numerical BT-results: See Subsubsections 6.1.1 and 6.2.1.

We want to finalize this discussion by observing that our study could be more general by considering the following aspects:

i) Using a similar approach as was made in the present paper, it is possible to show both analytically and numerically that food web model (2.1) undergoes a zero-Hopf and a double Hopf bifurcation. The results will be in a forthcoming paper from the authors.

ii) We will explore an improved biological adapted approach, which consists of introducing the intrinsic notion of time delays, in some or all of the equations appearing in our differential food web model. This allows us to have another system inside the ecological delay differential equations (DDEs) theory, see [20]. Using this new approach, some specific ecological conditions can be explored, which depends on periods of time for performing a biological process or for efficiency of depredation. Besides, it is well known that in predator-prey models, delays are central for studying "ad-hoc" population behaviors, for instance, in nature the predator could not know the position or the velocity information of the prey population instantly. We will consider this kind of generalization in our four-dimensional food web model (2.1) or in a linear system associated with it. This work will be the content of a forthcoming paper, where specific aspects of study are the strong delay-independent stability and the time-delayed feedback control. Some references in this respect are [21, 22], and the references therein.

Author contributions

Jorge Luis Ramos-Castellano: Methodology, Investigation, Formal analysis, Software, Writing-Original Draft; Miguel Angel Dela-Rosa: Conceptualization, Methodology, Formal Analysis, Investigation, Software, Writing-Review and Editing; Iván Loreto-Hernández: Conceptualization, Methodology, Formal Analysis, Investigation, Software, Writing-Review and Editing. All authors have read and approved the final version of the manuscript for publication

Acknowledgements

The first author gives thanks to the Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT) for the financial support through a Mexican doctoral scholarship. The authors greatly

[††]The mesopredators and the superpredator have satiety and interference through generalized functional responses with similar properties as the Holling of type II or IV; or the prey has a defense group, and the mesopredators and the superpredator have defense and interference; or the prey has a defense group, and the mesopredators have defense, interference, or intrinsic competence.

[‡‡]The approach that we have used in this manuscript for obtaining the main results is relevant, because all of them were obtained by focusing on the explicit formulae for parameters and the mathematical expression for guaranteeing the hypotheses of an H-bifurcation (transversal condition and the first Lyapunov coefficient) and of a BT-bifurcation (regularity condition and the quadratic coefficients).

thank the anonymous reviewers for their valuable comments made on previous versions of this manuscript, which helped to improve the presentation of the obtained results.

Conflict of interest

The authors declare that they have no conflict of interest to disclose.

References

1. J. D. Murray, *Mathematical biology I. An Introduction*, Interdisciplinary Applied Mathematics, New York: Springer-Verlag, 2002. https://doi.org/10.1007/b98868
2. M. Kot, *Elements of mathematical ecology*, Cambridge: Cambridge University Press, 2001. https://doi.org/10.1017/CBO9780511608520
3. F. Brauer, C. Castillo-Chávez, *Mathematical models in population biology and epidemiology*, New York: Springer-Verlag, 2001. https://doi.org/10.1007/978-1-4614-1686-9
4. G. T. Skalski, J. F. Gilliam, Functional responses with predator interference viable alternatives to the Holling type II model, *Ecology*, **82** (2001), 3083–3092. https://doi.org/10.2307/2679836
5. G. Blé, I. Loreto-Hernández, Limit cycles in a tritrophic food chain model with general functional responses, *Int. J. Nonlinear Sci. Num.*, **23** (2022), 449–460. https://doi.org/10.1515/ijnsns-2019-0175
6. G. Blé, V. Castellanos, M. A. Dela-Rosa, Bifurcation analysis of a Kolmogorov type tritrophic model, *Acta Appl. Math.*, **181** (2022). https://doi.org/10.1007/s10440-022-00520-y
7. F. E. Castillo-Santos, M. A. Dela-Rosa, I. Loreto-Hernández, Existence of a limit cycle in an intraguild food web model with Holling type II and logistic growth for the common prey, *Appl. Math.*, **8** (2017), 358–376. https://doi.org/10.4236/am.2017.83030
8. G. Blé, V. Castellanos, I. Loreto-Hernández, Stable limit cycles in an intraguild predation model with general functional responses, *Math. Method Appl. Sci.*, **45** (2022), 2219–2233. https://doi.org/10.1002/mma.7921
9. G. Blé, M. A. Dela-Rosa, I. Loreto-Hernández, Stability analysis of a tritrophic model with stage structure in the prey population, *J. Nonlinear Sci. Appl.*, **12** (2019), 765–790. http://dx.doi.org/10.22436/jnsa.012.12.01
10. G. Blé, I. Loreto-Hernández, Two-dimensional attracting torus in an intraguild predation model with general functional responses and logistic growth rate for the prey, *J. Appl. Anal. Comput.*, **11** (2021), 1557–1576. https://doi.org/10.11948/20200282
11. G. Blé, C. Guzmán-Arellano, I. Loreto-Hernández, Coexistence in a four-species food web model with general functional responses, *Chaos Soliton. Fract.*, **153** (2021), 111555. https://doi.org/10.1016/j.chaos.2021.111555
12. A. Mondal, A. K. Pal, G. P. Samanta, Stability analysis of a complex four species food-web model, *Filomat*, **36** (2022), 99–123. https://doi.org/10.2298/FIL2201099M
13. S. Gakkhar, A. Priyadarshi, S. Banerjee, Complex behaviour in four species food-web model, *J. Biol. Dynam.*, **6** (2012), 440–456. https://doi.org/10.1080/17513758.2011.618547

14. Y. A. Kuznetsov, *Elements of applied bifurcation theory*, New York: Springer, 1998.
15. Y. A. Kuznetsov, Andronov-Hopf bifurcation, *Scholarpedia*, **1** (2006), 1858. https://doi.org/10.4249/scholarpedia.1858
16. G. Blé, M. A. Dela-Rosa, Bogdanov-Takens bifurcation in a Leslie type tritrophic model with general functional responses, *Acta Appl. Math.*, **169** (2020), 361–382. https://doi.org/10.1007/s10440-019-00302-z
17. J. Guckenheimer, Y. A. Kuznetsov, Bogdanov-Takens bifurcation, *Scholarpedia*, **2** (2007), 1854. https://doi.org/10.4249/scholarpedia.1854
18. M. Falconi, Y. Vera-Damián, C. Vidal, Predator interference in a Leslie-Gower intraguild predation model, *Nonlinear Anal. Real.*, **51** (2020), 102974. https://doi.org/10.1016/j.nonrwa.2019.102974
19. F. H. Maghool, R. K. Naji, The dynamics of a tritrophic Leslie-Gower food-web system with the effect of fear, *J. Appl. Math.*, **2021** (2021), 2112814. https://doi.org/10.1155/2021/2112814
20. H. Smith, *An introduction to delay differential equations with applications to the life sciences*, New York: Springer, 2011. https://doi.org/10.1007/978-1-4419-7646-8
21. J. Z. Cai, Q. B. Gao, Y. F. Liu, A. G. Wu, Generalized Dixon resultant for strong delay-independent stability of linear systems with multiple delays, *IEEE T. Automat. Contr.*, **69** (2024), 2697–2704. https://doi.org/10.1109/TAC.2023.3337691
22. Q. B. Gao, R. Cepeda-Gomez, N. Olgac, A test platform for cognitive delays: Target tracking problem with multiple time-delayed feedback control, *Int. J. Dynam. Control*, **2** (2014), 77–85. https://doi.org/10.1007/s40435-014-0077-6

Appendix

A. Mathematical conditions for the Hopf bifurcation analysis

A.1. Necessary mathematical conditions to make our dynamical analysis simpler

$$
\begin{aligned}
w_0 &= 10y_0, & x_0 &= 6y_0,\\
h(w_0) &= -w_0 h'(w_0), & f_1(w_0) &= 2w_0 f_1'(w_0),\\
f_2(w_0) &= 2w_0 f_2'(w_0), & g_1(w_0,x_0,y_0) &= 2w_0\partial_w g_1(w_0,x_0,y_0),\\
g_2(w_0,x_0,y_0) &= 2x_0\partial_x g_2(w_0,x_0,y_0), & g_3(w_0,x_0,y_0) &= 2y_0\partial_y g_3(w_0,x_0,y_0),\\
\partial_w g_2(w_0,x_0,y_0) &= -\frac{3}{40}\partial_w g_1(w_0,x_0,y_0), & \partial_x g_2(w_0,x_0,y_0) &= \frac{1}{2}\partial_w g_1(w_0,x_0,y_0),\\
\partial_y g_2(w_0,x_0,y_0) &= -\frac{3}{2}\partial_w g_1(w_0,x_0,y_0), & \partial_w g_3(w_0,x_0,y_0) &= -\frac{\partial_w g_1(w_0,x_0,y_0)}{80},\\
\partial_x g_3(w_0,x_0,y_0) &= -\frac{\partial_w g_1(w_0,x_0,y_0)}{24}, & \partial_y g_3(w_0,x_0,y_0) &= \frac{1}{2}\partial_w g_1(w_0,x_0,y_0),\\
\partial_x g_1(w_0,x_0,y_0) &= -\frac{5}{12}\partial_w g_1(w_0,x_0,y_0), & \partial_y g_1(w_0,x_0,y_0) &= -5\partial_w g_1(w_0,x_0,y_0),\\
f_1'(w_0) &= f_2'(w_0).
\end{aligned}
$$

A.2. *Proof of Proposition 2*

We have that the hypotheses of Proposition 2 and Section A.1 hold. The parameters d_2, e_1, e_2, e_3 and z_0 satisfy the conditions (3.3). Therefore, the linear approximation, $M(p)$, for system (2.1) at p is given by

$$\begin{pmatrix} -8y_0 f_2'(10y_0) & \frac{-235}{12} y_0 f_2'(10y_0) & -15y_0 f_2'(10y_0) & -20y_0 \partial_w g_1(10y_0, 6y_0, y_0) \\ \frac{3}{40}\left(4d_1 + 5y_0 f_2'(10y_0)\right) & \frac{1}{2} y_0 f_2'(10y_0) & \frac{3}{2} y_0 f_2'(10y_0) & -6y_0 \partial_w g_1(10y_0, 6y_0, y_0) \\ \frac{91}{400} y_0 f_2'(10y_0) & \frac{1}{24} y_0 f_2'(10y_0) & \frac{1}{2} y_0 f_2'(10y_0) & -y_0 \partial_w g_1(10y_0, 6y_0, y_0) \\ \frac{37 y_0 f_2'(10y_0)^2}{1600 \partial_w g_1(10y_0, 6y_0, y_0)} & \frac{11 y_0 f_2'(10y_0)^2}{24 \partial_w g_1(10y_0, 6y_0, y_0)} & -\frac{157 y_0 f_2'(10y_0)^2}{80 \partial_w g_1(10y_0, 6y_0, y_0)} & 0 \end{pmatrix}.$$

From this, the corresponding characteristic polynomial is

$$\begin{aligned} \mathrm{pol}(\lambda) &= A_{01}\lambda^4 + A_{11}\lambda^3 + A_{21}\lambda^2 + A_{31}\lambda + A_{41}, \text{ where} \\ A_{11} &= 7y_0 f_2'(10y_0), \quad A_{21} = \frac{1}{160} y_0 f_2'(10y_0)\left(940d_1 + 671 y_0 f_2'(10y_0)\right), \\ A_{31} &= \frac{99}{800} {y_0}^3 f_2'(10y_0)^3, \\ A_{41} &= \frac{{y_0}^3 f_2'(10y_0)^3 \left(632227 y_0 f_2'(10y_0) - 197860 d_1\right)}{12800}. \end{aligned}$$

Set

$$\begin{aligned} \Sigma(d_1) &:= {A_{11}}^2 A_{41} - A_{11}A_{21}A_{31} + {A_{31}}^2 \\ &= \frac{y_0^5 f_2'(10y_0)^5 \left(386660234 y_0 f_2'(10y_0) - 122003525 d_1\right)}{160000}. \end{aligned}$$

Then we have that $\Sigma(d_1) < 0$ and $A_{i1} > 0,\ i = 1, \ldots, 4$, whenever

$$d_1 > d_{10} := \frac{386660234 y_0 f_2'(10y_0)}{122003525}.$$

By the Routh-Hurwitz test (cf. [9, Lemma 2.1(i)]), the proof is completed.

A.3. *Eigenvectors for $M_p(d_{10})$ in Lemma 4*

$$\begin{aligned} q_1 &= \frac{1}{s_0}\left(\frac{s_3}{s_1}\partial_w g_1(10y_0, 6y_0, y_0), \frac{s_4 \partial_w g_1(10y_0, 6y_0, y_0)}{5s_2}, -\frac{s_5}{s1}\partial_w g_1(10y_0, 6y_0, y_0), s_6 f_2'(10y_0)\right), \\ q_2 &= \left(\frac{s_1 s_9 s_0}{160 s_7 \partial_w g_1(10y_0, 6y_0, y_0)}, -\frac{3485815 i s_2 s_0}{432 s_7 \partial_w g_1(10y_0, 6y_0, y_0)}, \frac{5 s_1 s_{10} s_0}{72 s_7 \partial_w g_1(10y_0, 6y_0, y_0)}, \frac{5 s_2 s_{11} s_0}{18 s_7 f_2'(10y_0)}\right), \\ s_0 &= \sqrt{3400000481284371104 \partial_w g_1(10y_0, 6y_0, y_0)^2 + 6527530581280625 f_2'(10y_0)^2}, \quad s_1 = \sqrt{1492006990007}, \\ s_2 &= \sqrt{10444048930049}, \quad s_3 = 27886520\sqrt{7}\left(8627174 + 33441 i\sqrt{154}\right), \end{aligned}$$

$s_4 = 72\left(-57161314102613 - 170600447467i\sqrt{154}\right)$, $s_5 = 4i\sqrt{7}\left(33166645833\sqrt{154} - 6156878697763i\right)$,
$s_6 = 25\sqrt{10444048930049}$, $s_7 = 128116047502161657\sqrt{154} - 11490886977720227i$,
$s_8 = 128116047502161657\sqrt{154} - 11490886977720227i$, $s_9 = 1787\sqrt{22} + 4460i\sqrt{7}$,
$s_{10} = 2919\sqrt{22} + 683096i\sqrt{7}$, $s_{11} = 915\sqrt{154} + 20452i$.

B. Application of the H-Main results

B.1. *For Case H1*

The validation of the H-main Theorem is obtained according to the following:

- The existence of a positive equilibrium point: The parameter conditions in Proposition 1 are satisfied and given by:

$$R_1 = \frac{4a_1}{5}, \ c_1 = \frac{1}{20} + \frac{2d_1}{a_1}, \ c_2 = \frac{43}{200}, \ d_3 = \frac{163a_1}{800}.$$

- The stability test for the equilibrium point holds and the hypotheses in Proposition 2 become:

$$d_2 = \frac{33a_1}{400}, \ e_1 = \frac{a_1\beta_1}{25y_0\alpha_1}, \ e_2 = \frac{121a_1\beta_1}{300y_0\alpha_1}, \ e_3 = \frac{a_1\beta_1}{25y_0\alpha_1}, \ \text{and} \ d_1 > d_{10} = \frac{193330117a_1}{2440070500}.$$

- The bifurcation value and the equilibrium point: From Proposition 2,

$$p = \left(10y_0, 6y_0, y_0, \frac{2a_1\beta_1}{5\alpha_1}\right) \text{ and } d_{10} = \frac{193330117a_1}{2440070500}.$$

- The necessary condition for having an H-bifurcation: If $d_1 = d_{10}$, Lemma 3 implies that

$$\lambda_{1,2} = \pm i\omega_0, \ \lambda_{3,4} = \left(-\frac{7}{80} \pm \frac{1}{160}i\sqrt{\frac{588151373}{3485815}}\right)a_1, \ \omega_0 = \frac{3}{800}\sqrt{\frac{11}{14}}a_1.$$

- Transversal H-condition: From Lemma 4, $\dfrac{\partial \mathrm{Re}\left(\lambda_{1,2}\right)}{\partial d_1}(d_{10})$ is

$$-\frac{21675942039515433513512992411568375\,0a_1{}^2\beta_1{}^2}{792120746292896769 1929\left(261101223251225a_1{}^2\beta_1{}^2 + 85000012032109276\alpha_1{}^2y_0{}^2\right)}.$$

- The first Lyapunov coefficient: In the proof of the H-Main Theorem, we emphasized that the huge formulae for the first Lyapunov coefficient were omitted and hence we restrict ourselves to provide them explicitly in the examples. Using the Kuznetsov formulae [14, 15], one has

$$l(p, d_{10}) = -\frac{\sigma_1\sqrt{\frac{7}{22}}\alpha_1{}^2}{\sigma_2\left(261101223251225a_1{}^2\beta_1{}^2 + 85000012032109276\alpha_1{}^2y_0{}^2\right)};$$

$$\sigma_1 = 246296960006717632481797512246682474680410099893274125748603156340906855 7;$$

$$\sigma_2 = 52668874174960567100578262605555245119208296332878304 08.$$

B.2. For Case H2

The validation of the H-main Theorem is obtained according to the following:

- The existence of a positive equilibrium point: the parameter conditions in Proposition 1 are satisfied and given by

$$R_1 = \frac{a_2}{25y_0}, \quad c_1 = \frac{1}{20} + \frac{40d_1y_0}{a_2}, \quad c_2 = \frac{43}{200}, \; d_3 = \frac{163a_2}{16000y_0}.$$

- The stability test for the equilibrium point holds and the hypotheses in Proposition 2 become:

$$d_2 = \frac{33a_2}{8000y_0}, \; e_1 = \frac{3a_2\delta_1}{250y_0\alpha_1}, \quad e_2 = \frac{121a_2\delta_1}{1000y_0\alpha_1}, \quad e_3 = \frac{3a_2\delta_1}{250y_0\alpha_1}, \; d_1 > d_{10}.$$

- The bifurcation value and the equilibrium point: from Proposition 2,

$$p = \left(10y_0, 6y_0, y_0, \frac{3a_2\delta_1}{25\alpha_1}\right) \text{ and } d_{10} = \frac{193330117a_2}{48801410000y_0}.$$

- The necessary condition for having an H-bifurcation: If $d_1 = d_{10}$, Lemma 3 implies that

$$\lambda_{1,2} = i\omega_0 \quad \lambda_{3,4} = \frac{\left(-\frac{7}{2} \pm \frac{1}{4}i\sqrt{\frac{588151373}{3485815}}\right)a_2}{800y_0}, \; \omega_0 = \frac{3}{16000}\sqrt{\frac{11}{14}}a_2.$$

- Transversal H-condition: From Lemma 4, $\frac{\partial \mathrm{Re}(\lambda_{1,2})}{\partial d_1}(d_{10})$ is

$$-\frac{867037681580617340540519696462735 0a_2{}^2\delta_1{}^2}{880134162547663076881(340000048128437104y_0{}^2\alpha_1{}^2 + 93996440370441a_2{}^2\delta_1{}^2)}.$$

- The first Lyapunov coefficient: Using the Kuznetsov formulae, one has

$$l(p_0, d_{10}) = -\frac{\sigma_1\sqrt{\frac{7}{22}}\alpha_1{}^2}{\sigma_2\left(93996440370441a_2{}^2\delta_1{}^2 + 340000048128437104\alpha_1{}^2y_0{}^2\right)};$$

$$\sigma_1 = 649948627352984750779096160569506149815372011870035421638445940200357 17;$$

$$\sigma_2 = 162558253626421503396846489523318657775334247940982 42.$$

B.3. For Case H3

The validation of the H-main Theorem is according to the following:

- The existence of a positive equilibrium point: The parameter conditions in Proposition 1 are satisfied and given by

$$R = \frac{a_1}{25y_0}, \quad c_1 = \frac{1}{20} + \frac{40d_1y_0}{a_1}, \quad c_2 = \frac{43}{200}, \quad d_3 = \frac{163a_1}{16000y_0}.$$

- The stability test for the equilibrium point holds and the hypotheses in Proposition 2 become:

$$d_2 = \frac{33a_1}{8000y_0}, \ e_1 = \frac{a_1\beta_1}{1750y_0^2\alpha_1}, \quad e_2 = \frac{121a_1\beta_1}{21000y_0^2\alpha_1}, \quad e_3 = \frac{a_1\beta_1}{1750y_0^2\alpha_1}, \ d_1 > d_{10}.$$

- The bifurcation value and the equilibrium point: From Proposition 2,

$$p = \left(10y_0, 6y_0, y_0, \frac{a_1\beta_1}{175y_0\alpha_1}\right) \text{ and } d_{10} = \frac{193330117a_1}{48801410000y_0}.$$

- The necessary condition for having H-bifurcation: If $d_1 = d_{10}$, Lemma 3 implies that

$$\lambda_{1,2} = i\omega_0 \quad \text{and} \quad \lambda_{3,4} = \frac{\left(-\frac{7}{2} \pm \frac{1}{4}i\sqrt{\frac{588151373}{3485815}}\right)a_1}{800y_0}, \ \omega_0 = \frac{3}{16000}\sqrt{\frac{11}{14}\frac{a_1}{y_0}}.$$

- Transversal H-condition: From Lemma 4 $\frac{\partial \mathrm{Re}(\lambda_{1,2})}{\partial d_1}(d_{10})$ is

$$-\frac{123862525940088191505788528066105 0a_1{}^2\beta_1{}^2}{792120746292896769 1929(2380000336899059728y_0{}^2\alpha_1{}^2 + 1492006990007a_2{}^2\beta_1{}^2)}.$$

- The first Lyapunov coefficient: Once again, using the Kuznetsov formulae, one has

$$l(p, d_{10}) = -\frac{\sigma_1\sqrt{\frac{7}{22}}y_0^2\alpha_1{}^2}{\sigma_2\left(1492006990007a_1{}^2\beta_1{}^2 + 2380000336899059728\alpha_1{}^2y_0{}^4\right)};$$
$$\sigma_1 = 565595098433391594607010631370851 2$$
$$4700222673386391223596191092151023 83\ 861;$$
$$\sigma_2 = 11970198676127401613767786955808010254365521893835978 2.$$

C. Necessary BT-conditions for the web model

In order to begin with the BT-analysis, in the following lemma, the necessary BT-conditions will be stated. Before making the principal analysis, let us denote by P_λ the characteristic polynomial of the linear approximation of system (2.1) at p. The characteristic polynomial is

$$P_\lambda = \lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4. \tag{C.1}$$

A necessary condition to have a BT-bifurcation is that there are $\lambda_3, \lambda_4 \in \mathbb{C}$ such that we have the factorization

$$\begin{aligned}\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 &= \lambda^2(\lambda - \lambda_3)(\lambda - \lambda_4)\\ &= (\lambda^2 - (\lambda_3 + \lambda_4)\lambda + \lambda_3\lambda_4)\lambda^2\\ &= \lambda^4 - (\lambda_3 + \lambda_4)\lambda^3 + \lambda_3\lambda_4\lambda^2,\end{aligned}$$

that is,

$$A_3 = A_4 = 0, \;\; A_2 = \lambda_3\lambda_4, \;\text{ and }\; A_1 = -(\lambda_3 + \lambda_4). \tag{C.2}$$

Then, by a direct computation, the next result follows.

Lemma 10. *If the coefficients of P_λ satisfy the conditions in* (C.2)*, $A_1 > 0$ and $A_2 > 0$, then its roots are*

$$\lambda_{1,2} = 0, \quad \lambda_3 = \frac{-A_1 - \sqrt{A_1^2 - 4A_2}}{2}, \quad \textit{and} \quad \lambda_4 = \frac{-A_1 + \sqrt{A_1^2 - 4A_2}}{2}. \tag{C.3}$$

Remark 11. *From the hypotheses of Lemma 10:*

- *If $A_1^2 - 4A_2 > 0$, then $-\sqrt{A_1^2 - 4A_2} < 0$ and $-A_1 < 0$, hence λ_3 is a negative real number. Moreover,*

$$A_1^2 - 4A_2 < A_1^2 \iff \sqrt{A_1^2 - 4A_2} < A_1 \iff \sqrt{A_1^2 - 4A_2} - A_1 < 0.$$

  Therefore, λ_4 is a negative real number, too.
- *If $A_1^2 - 4A_2 < 0$, then $\lambda_3, \lambda_4 \in \mathbb{C}$ with $Re(\lambda_3) = Re(\lambda_4) = -\frac{A_1}{2} < 0$.*

C.1. Proof of Lemma 6

The linear approximation of system (2.1) at p has characteristic polynomial

$$P_\lambda(d_1, d_2) = \lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4, \qquad \text{where}$$

$$\begin{aligned}&A_0 = 1, \;\; A_1 = 7z_0\partial_w g_1(10y_0, 6y_0, y_0),\\ &A_2 = \frac{1}{96}z_0\partial_w g_1(10y_0, 6y_0, y_0)\left(145z_0\partial_w g_1(10y_0, 6y_0, y_0) + 564d_1 + 72d_2\right),\\ &A_3 = \frac{z_0^2\partial_w g_1(10y_0, 6y_0, y_0)^2\left(12649z_0\partial_w g_1(10y_0, 6y_0, y_0) + 88d_1 - 1524d_2\right)}{1920},\\ &A_4 = -\frac{z_0^3\partial_w g_1(10y_0, 6y_0, y_0)^3\left(3561z_0\partial_w g_1(10y_0, 6y_0, y_0) + 28907d_1 - 28471d_2\right)}{1920}.\end{aligned} \tag{C.4}$$

From Lemma 10, it follows that $P_\lambda(d_1, d_2) = \lambda^2(\lambda - \alpha_1)(\lambda - \alpha_2)$ if and only if $A_3 = A_4 = 0$. On the other hand, by making the assignments $d_1 = d_{10}$ and $d_2 = d_{20}$, the result follows, where $\alpha_1 = \lambda_3$ and $\alpha_2 = \lambda_4$.

C.2. Normalized BT-eigenvectors for proof of Proposition 8

Using the Guckenheimer-Kuznetsov formulae and the software Mathematica (see [17] and cf. [16, Appendix A] and [6]), we compute the normalized eigenvectors for $\mathcal{J}(p, d_{10}, d_{20})$ and $\mathcal{J}^T(p, d_{10}, d_{20})$:

$$q_0 = (q_{01}, q_{02}, q_{03}, q_{04}), \quad q_1 = (q_{11}, q_{12}, q_{13}, q_{14});$$

$$\begin{aligned}
q_{01} &= -\frac{3677070570 y_0 \partial_x g_1(10y_0, 6y_0, y_0)}{5809519049}, \quad q_{02} = \frac{2507454216 y_0 \partial_x g_1(10y_0, 6y_0, y_0)}{5809519049},\\
q_{03} &= \frac{606034548 y_0 \partial_x g_1(10y_0, 6y_0, y_0)}{5809519049}, \quad q_{04} = -\frac{2877826539 z_0 \partial_x g_1(10y_0, 6y_0, y_0)}{11619038098},\\
q_{11} &= \frac{115161850296718878660 60 y_0}{3678805762295631219709 z_0}, \quad q_{12} = -\frac{793073125542183384 8520 y_0}{3678805762295631219709 z_0},\\
q_{13} &= -\frac{1434464608597924651548 y_0}{3678805762295631219709 z_0}, \quad q_{14} = \frac{4351305094969314954798}{3678805762295631219709},\\
p_1 &= \left(\frac{109 z_0}{17700 y_0}, -\frac{28907 z_0}{21240 y_0}, \frac{28471 z_0}{3540 y_0}, 1\right),\\
p_0 &= \left(0, -\frac{1519549}{231516 y_0 \partial_w g_1(10y_0, 6y_0, y_0)}, \frac{1480963}{38586 y_0 \partial_w g_1(10y_0, 6y_0, y_0)}, \frac{4438}{6431 z_0 \partial_w g_1(10y_0, 6y_0, y_0)}\right).
\end{aligned}$$

C.3. Terms for the quadratic coefficients in Proposition 8

$$\begin{aligned}
\mathbf{a_{00}} = {} & 96083802551532096 y_0 \partial_y^2 g_1(10y_0, 6y_0, y_0) + 795089113623108864 y_0 \partial_x \partial_y g_1(10y_0, 6y_0, y_0)\\
& + 1644831599641714944 y_0 \partial_x^2 g_1(10y_0, 6y_0, y_0) - 8873565668350863105 \partial_w g_1(10y_0, 6y_0, y_0)\\
& - 1165962976143497280 y_0 \partial_w \partial_y g_1(10y_0, 6y_0, y_0) - 4824145405372037760 y_0 \partial_w \partial_x g_1(10y_0, 6y_0, y_0)\\
& + 3537197804511027600 y_0 \partial_w^2 g_1(10y_0, 6y_0, y_0) + 2949805563447597120 y_0 \partial_y^2 g_2(10y_0, 6y_0, y_0)\\
& + 24409507414573774080 y_0 \partial_x \partial_y g_2(10y_0, 6y_0, y_0) + 50496892032924391680 y_0 \partial_x^2 g_2(10y_0, 6y_0, y_0)\\
& - 3579546169561088160 0 y_0 \partial_w \partial_y g_2(10y_0, 6y_0, y_0) - 148102912018022467200 y_0 \partial_w \partial_x g_2(10y_0, 6y_0, y_0)\\
& + 108593181011598922000 y_0 \partial_w^2 g_2(10y_0, 6y_0, y_0) - 990943345787689728 0 y_0 \partial_y^2 g_3(10y_0, 6y_0, y_0)\\
& - 82000112977469675520 y_0 \partial_x \partial_y g_3(10y_0, 6y_0, y_0) - 169636805093356369920 y_0 \partial_x^2 g_3(10y_0, 6y_0, y_0)\\
& + 120249534464931110400 y_0 \partial_w \partial_y g_3(10y_0, 6y_0, y_0) + 497529725262673996800 y_0 \partial_w \partial_x g_3(10y_0, 6y_0, y_0)\\
& - 364802654977681968000 y_0 \partial_w^2 g_3(10y_0, 6y_0, y_0);\\
\mathbf{b_{00}} = {} & 4176349552521202149970551 36 y_0 \partial_y^2 g_1(10y_0, 6y_0, y_0) + 4181605554814705668293497152 y_0 \partial_x \partial_y g_1(10y_0, 6y_0, y_0)\\
& + 10151922900977566424314375680 y_0 \partial_x^2 g_1(10y_0, 6y_0, y_0) - 8782283295019253626571796 15 \partial_w g_1(10y_0, 6y_0, y_0)\\
& - 6090728136122323311124787160 y_0 \partial_w \partial_y g_1(10y_0, 6y_0, y_0)\\
& - 29603352702257865402807468240 y_0 \partial_w \partial_x g_1(10y_0, 6y_0, y_0)\\
& + 21580373074016479704338355300 y_0 \partial_w^2 g_1(10y_0, 6y_0, y_0)\\
& + 28874872513114782000828206 40 y_0 \partial_y^2 g_2(10y_0, 6y_0, y_0)
\end{aligned}$$

$$+461729173321160250675813379 20y_0\partial_x\partial_y g_2(10y_0,6y_0,y_0)$$
$$+14160931730064974517345312768 0y_0\partial_x^2 g_2(10y_0,6y_0,y_0)$$
$$-66439199506043649506337659800y_0\partial_w\partial_y g_2(10y_0,6y_0,y_0)$$
$$-41006744919175285608951582600 0y_0\partial_w\partial_x g_2(10y_0,6y_0,y_0)$$
$$+29681599885829894120297351050 0y_0\partial_w^2 g_2(10y_0,6y_0,y_0)$$
$$+15500682198414711104279800320y_0\partial_y^2 g_3(10y_0,6y_0,y_0)$$
$$+53424146993221012497259875840y_0\partial_x\partial_y g_3(10y_0,6y_0,y_0)$$
$$-44310622013710573340404915200y_0\partial_x^2 g_3(10y_0,6y_0,y_0)$$
$$-82615020512826474158497675200y_0\partial_w\partial_y g_3(10y_0,6y_0,y_0)$$
$$+11228848247348562618951779520 0y_0\partial_w\partial_x g_3(10y_0,6y_0,y_0)$$
$$-69376432530706260133488324000y_0\partial_w^2 g_3(10y_0,6y_0,y_0);$$
$$\mathbf{b_{01}} = 881955063312443959598555800 50y_0^2 f_1''(10y_0) - 8700287856736824442227328162 5y_0^2 f_2''(10y_0);$$
$$\mathbf{b_{02}} = 64879172730106024136557430400y_0 z_0\partial_w g_1(10y_0,6y_0,y_0)h''(10y_0).$$

D. Application of the BT-Main results

D.1. For Case BT1

The validation of the BT-Main Theorem is according to the following:

- The existence of a positive equilibrium point: The parameter conditions in Proposition 1 are satisfied and given by:

$$R_1 = \frac{4z_0\alpha_1}{y_0\eta_1},\ \ c_1 = \frac{79250307}{166195280},\ \ c_2 = \frac{81376019}{166195280},\ \ d_3 = \frac{39z_0\alpha_1}{40y_0\eta_1}.$$

- The bifurcation value and the equilibrium point: From Lemma 6,

$$p = (10y_0, 6y_0, y_0, z_0),\ \ d_{10} = \frac{70940543z_0\alpha_1}{66478112y_0\eta_1},\quad \text{and}\quad d_{20} = \frac{73066255z_0\alpha_1}{66478112y_0\eta_1}.$$

- The necessary condition for having a BT-bifurcation: If $d_1 = d_{10}$ and $d_2 = d_{20}$, Lemma 6 implies that

$$\lambda_{1,2} = 0,\ \ \lambda_{3,4} = \frac{\left(-\frac{7}{16} \pm \frac{11}{32}i\sqrt{\frac{37917221}{6232323}}\right)\alpha_1 z_0}{y_0\eta_1}.$$

- Regularity BT-condition: From Proposition 7 and using the software Mathematica,

$$\mathbf{Reg_0} = \frac{3062663712947293z_0^7\alpha_1^7}{1284845926229213184y_0^7\eta_1^7}.$$

- The quadratic coefficients: From Proposition 8, one has

$$\mathbf{a_0} = -\frac{338050197175353927327z_0^2\alpha_1^3}{5529683817380882743459840y_0^3\eta_1^3} \text{ and } \mathbf{b_0} = \frac{38258699630807074116090133395 63z_0\alpha_1^2}{200780021700132972416033254040 5760y_0^2\eta_1^2}.$$

D.2. *For Case BT2*

The validation of the BT-Main Theorem is according to the following:

- The existence of a positive equilibrium point: The parameter conditions in Proposition 1 are satisfied and given by:

$$R_1 = \frac{4z_0\alpha_1}{y_0\eta_1}, \quad c_1 = \frac{79250307}{166195280}, \quad c_2 = \frac{81376019}{166195280}, \quad d_3 = \frac{39z_0\alpha_1}{40y_0\eta_1}.$$

- The bifurcation value and the equilibrium point: From Lemma 6,

$$p = (10y_0, 6y_0, y_0, z_0), \quad d_{10} = \frac{70940543z_0\alpha_1}{66478112y_0\eta_1}, \text{ and } d_{20} = \frac{73066255z_0\alpha_1}{66478112y_0\eta_1}.$$

- The necessary condition for having a BT-bifurcation: If $d_1 = d_{10}$ and $d_2 = d_{20}$, Lemma 6 implies that

$$\lambda_{1,2} = 0, \quad \lambda_{3,4} = \frac{\left(-\frac{7}{16} \pm \frac{11}{32} i \sqrt{\frac{37917221}{6232323}}\right)\alpha_1 z_0}{y_0\eta_1}.$$

- Regularity BT-condition: From Proposition 7 and using the software Mathematica,

$$\mathbf{Reg_0} = \frac{93043312663486 09\alpha_1^7 z_0^7}{6424229631146065920\eta_1^7 y_0^7}.$$

- The quadratic coefficients: From Proposition 8, one has

$$\mathbf{a_0} = -\frac{319727305666717874403\alpha_1^3 z_0^2}{552968381738088274345 9840\eta_1^3 y_0^3} \text{ and } \mathbf{b_0} = \frac{158265999847087714604369738 9907\alpha_1^2 z_0}{40156004340026594483206650808 1152\eta_1^2 y_0^2},$$

AIMS Press