

Hopf and zip bifurcation in a specific $(n+1)$ -dimensional competitive system

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Abstract

In this work we study the occurrence of *Andronov-Hopf and zip bifurcation* in a concrete $(n+1)$ -dimensional predator-prey system modelling the competition among n species of predators for one species of prey. This is a generalization of results by Farkas (1984).

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1 Introduction

The *zip bifurcation* phenomenon was introduced by Farkas [5] in 1984 for a three dimensional prey-predator system. The model was not at structurally stable although it illustrated the intuitively evident fact that at low values of the carrying capacity K both predators might survive but as K grew only one of them survives. Recently (see [1], [8]) the phenomenon was generalized to a four dimensional ODE system.

The purpose of this paper is to study the occurrence of periodic orbits generated by *Andronov-Hopf bifurcation* in an ODE system modelling the competition among n species of predators for a single prey. Specifically, we will consider the system

$$\begin{cases} \dot{S} &= \gamma(1 - \frac{S}{K})S - \sum_{i=1}^n m_i f_i(S)x_i \\ \dot{x}_i &= (m_i f_i(S) - d_i)x_i, \quad i = 1, 2, \dots, n, \end{cases} \quad (1)$$

where S denotes the quantity of prey, x_i denotes the quantity of predator i and $f_i(S) = \frac{S}{a_i + S}$ is the functional response of predator i . All other parameters in (1) are assumed to be non-negative and represent

- γ : *intrinsic growth rate of prey*
- K : *carrying capacity of the environment*
- m_i : *maximal birth rate of predator i*

- d_i : mortality of predator i
- a_i : half saturation constant of predator i .

Also, we study in the same model the phenomenon of *zip bifurcation*.

In the next section we study the equilibrium points for the system and we prove its dissipativeness. In Section 3 we establish the conditions under which the Andronov-Hopf bifurcation occurs and finally in Section 4 we determine conditions for the occurrence of zip bifurcation in the model.

2 Equilibrium points

First we show that system (1) is dissipative before studying its equilibrium points.

Proposición 2.1. *Any solution of the system (1) with initial values $S^0 > 0$, $x_i^0 > 0$, $i = 1, 2, \dots, n$ is bounded in $[0, \infty]$.*

We first observe that any solution of (1) whose initial value has positive components remains with positive components, as long as the solution exists. We will prove that the solution exists for all time $t \geq 0$ and there exists a bounded set J in \mathbb{R}_+^{n+1} which attracts the solutions starting on any bounded set in \mathbb{R}_+^{n+1} . Let $d_0 = \min\{d_1, \dots, d_n\}$ and $V(S, x_1, \dots, x_n) = S + x_1 + \dots + x_n$. If $z(t) = (S(t), x_1(t), \dots, x_n(t))$ is a solution of (1), then as long as it exists, we have

$$\frac{d}{dt}V(z(t)) = \gamma\left(1 - \frac{S(t)}{K}\right)S(t) - \sum_{i=1}^n d_i x_i(t).$$

Since $S\left(1 - \frac{S}{K}\right) \leq \frac{K}{4}(1 + d_0)^2 - d_0 S$ for all $S \in \mathbb{R}$, we have

$$\frac{d}{dt}V(z(t)) \leq -\gamma d_0 S(t) - \sum_{i=1}^n d_i x_i(t) + \frac{K}{4}(1 + d_0)^2.$$

Letting $\alpha = \min\{d_0, \gamma d_0\}$, we have

$$\frac{d}{dt}V(z(t)) \leq -\alpha V(z(t)) + \frac{K}{4}(1 + d_0)^2$$

and therefore

$$V(z(t)) \leq V(z(0))e^{-\alpha t} + \frac{K}{4\alpha}(1 + d_0)^2,$$

as long as the solution exists. If B is a bounded set contained in \mathbb{R}_+^{n+1} , then there exists $R > 0$ such that $V(z(0)) \leq R$. Let $t_0 = \frac{1}{\alpha} \log \frac{K(1+d_0)^2}{4\alpha R}$ and $z(0) \in B$. For $t \geq t_0$, we have

$$V(z(t)) \leq R \frac{K(1+d_0)^2}{4\alpha R} + \frac{K}{4\alpha}(1 + d_0)^2 \leq \frac{K(1+d_0)^2}{2\alpha}.$$

This implies that any solution is defined for $t \geq 0$ and the compact set

$$J = \left\{ (S, x_1, \dots, x_n) : S \geq 0, x_1 \geq 0, \dots, x_n \geq 0 \text{ and } S + x_1 + \dots + x_n \leq \frac{K(1+d_0)^2}{2\alpha} \right\}$$

attracts all bounded set B . Therefore the system is dissipative and its global attractor is contained in J .

Now, we discuss the equilibrium points of (1), that is the solutions of the system

$$\begin{aligned} \gamma \left(1 - \frac{S}{K}\right) S - \sum_{i=1}^n m_i f_i(S) x_i &= 0 \\ (m_i f_i(S) - d_i) x_i &= 0, i = 1, 2, \dots, n. \end{aligned} \quad (2)$$

For $i = 1, \dots, n$, let $\lambda_i = \frac{a_i d_i}{m_i - d_i}$ the prey *threshold quantity* for species i . Then, aside from the obvious solutions $(S, x_1, \dots, x_n) = (0, 0, \dots, 0)$ and $(S, x_1, \dots, x_n) = (K, 0, \dots, 0)$, equation (2) has biologically interesting solutions only if $m_i > d_i$ and $\lambda_1 = \dots = \lambda_n$. Henceforth we assume that $m_i > d_i$ and $\lambda_1 = \dots = \lambda_n = \lambda$, i.e, the n species have equal prey threshold although they achieve this by different means.

With these notations and hypotheses, the system (1) can be written as

$$\begin{cases} \dot{S} &= \gamma \left(1 - \frac{S}{K}\right) S - \sum_{i=1}^n m_i f_i(S) x_i \\ \dot{x}_i &= \beta_i g_i(S) x_i, \end{cases} \quad (3)$$

where $g_i(S) = \frac{S-\lambda}{a_i+S}$, $\beta_i = m_i - d_i$ and $i = 1, 2, \dots, n$.

The equilibrium points of system (3) are the origin $(S, x_1, \dots, x_n) = (0, 0, \dots, 0)$, the point $(S, x_1, \dots, x_n) = (K, 0, \dots, 0)$ and the points of $(n-1)$ -dimensional hyperplane

$$\begin{aligned} H &= \{(S, x_1, \dots, x_n) \in \mathbb{R}^{n+1} : S = \lambda, \\ &\quad \frac{m_1}{a_1+\lambda} x_1 + \dots + \frac{m_n}{a_n+\lambda} x_n = \gamma \left(1 - \frac{\lambda}{K}\right), x_i \geq 0, i = 1, \dots, n\} \end{aligned} \quad (4)$$

To study the stability of these equilibrium points, observe that the Jacobian matrix $J(S, x_1, \dots, x_n)$ of the system (3) is

$$\begin{pmatrix} \gamma \left(1 - \frac{2S}{K}\right) - \sum_{i=1}^n m_i f'_i(S) x_i & m_1 f_1(S) & m_2 f_2(S) & \dots & m_{n-1} f_{n-1}(S) & m_n f_n(S) \\ g'_1(S) x_1 & g_1(S) & 0 & \dots & 0 & 0 \\ g'_2(S) x_2 & 0 & g_2(S) & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ g'_{n-1}(S) x_{n-1} & 0 & 0 & \dots & g_{n-1}(S) & 0 \\ g'_n(S) x_n & 0 & 0 & \dots & 0 & g_n(S) \end{pmatrix}.$$

So, it is easy to see that $(S, x_1, \dots, x_n) = (0, 0, \dots, 0)$ is unstable, with an n -dimensional stable manifold and a one-dimensional unstable manifold. Now, $(S, x_1, \dots, x_n) = (K, 0, \dots, 0)$ is asymptotically stable if $K < \lambda$ and unstable if $K > \lambda$ with a 1-dimensional stable manifold and an n -dimensional unstable manifold. Note that if $K < \lambda$, then H is empty, and if $K = \lambda$ then $H = \{0\}$. It is known (see [10] and [3]) that

$$K > \lambda \quad (5)$$

is a necessary condition for the survival of each predator. Therefore (5) will also be assumed from now on. In the next section we fix our attention to the study of stability of the equilibrium points belonging to H .

3 Occurrence of Andronov-Hopf and zip bifurcation

In this section, we study the stability of the points in H . The study will be separated in two cases; one of them is when we consider $a = a_1 = a_2 = \dots = a_n$, that is, all predators have the same functional response and the other case is $a_1 < a_2 < \dots < a_n$, that is, the predators have different functional responses.

3.1 Andronov-Hopf bifurcation

In the following, we consider the case $a = a_1 = a_2 = \dots = a_n$. Thus the system (3) takes the form

$$\begin{cases} \dot{S} &= \gamma(1 - \frac{S}{K})S - \sum_{i=1}^n \frac{m_i x_i}{a + S} S \\ \dot{x}_i &= \beta_i \frac{S - \lambda}{a + S} x_i. \end{cases}$$

Since $\lambda_1 = \dots = \lambda_n = \lambda$, we have $\frac{m_1}{d_1} = \dots = \frac{m_n}{d_n}$. Introducing the variable $\rho_i = \frac{d_{i+1}}{d_i} = \frac{m_{i+1}}{m_i}$, $i = 1, 2, \dots, n-1$ we obtain

$$m_{i+1} = m_i \rho_i, \quad i = 1, 2, \dots, n-1. \quad (6)$$

We also have $\rho_i = \frac{\beta_{i+1}}{\beta_i}$. Hence, we can write

$$\begin{cases} \rho_1 &= \frac{\beta_2}{\beta_1} &\Rightarrow \beta_2 = \rho_1 \beta_1 \\ \rho_2 &= \frac{\beta_3}{\beta_2} &\Rightarrow \beta_3 = \rho_2 \beta_2 &\Rightarrow \beta_3 = \rho_1 \rho_2 \beta_1 \\ \vdots & & \\ \rho_{n-1} &= \frac{\beta_n}{\beta_{n-1}} &\Rightarrow \beta_n = \rho_{n-1} \beta_{n-1} &\Rightarrow \beta_n = \rho_1 \rho_2 \dots \rho_{n-1} \beta_1. \end{cases} \quad (7)$$

Similarly, we get

$$\begin{cases} m_2 = m_1\rho_1 \\ m_3 = m_2\rho_2 & \Rightarrow m_3 = \rho_1\rho_2m_1 \\ \vdots \\ m_n = m_{n-1}\rho_{n-1} & \Rightarrow m_n = \rho_1\rho_2\rho_{n-1}m_1. \end{cases} \quad (8)$$

Considering the expressions in (7) and (8), the system (3.1) can be written in the form

$$\begin{cases} \dot{S} = \gamma\left(1 - \frac{S}{K}\right)S - \frac{x_1 + \rho_1x_2 + \rho_1\rho_2x_3 + \dots + \rho_{n-1}x_n}{a+S}m_1S \\ \dot{x}_1 = \beta_1\frac{S-\lambda}{a+S}x_1 \\ \dot{x}_2 = \rho_1\beta_1\frac{S-\lambda}{a+S}x_2 \\ \dot{x}_3 = \rho_1\rho_2\beta_1\frac{S-\lambda}{a+S}x_3 \\ \vdots \\ \dot{x}_n = \rho_1\rho_2\dots\rho_{n-1}\beta_1\frac{S-\lambda}{a+S}x_n \end{cases} \quad (9)$$

Dividing the third equation in (9) by the second, the fourth by the third and so on, up to dividing the n -th equation by the $(n-1)$ -th, we get the following system

$$\begin{cases} \frac{dx_2}{dx_1} = \rho_1\frac{x_2}{x_1} \\ \frac{dx_3}{dx_2} = \rho_2\frac{x_3}{x_2} \\ \vdots \\ \frac{dx_n}{dx_{n-1}} = \rho_{n-1}\frac{x_n}{x_{n-1}} \end{cases} \quad (10)$$

Integrating each equation in (10) we obtain easily the following first integrals for the system

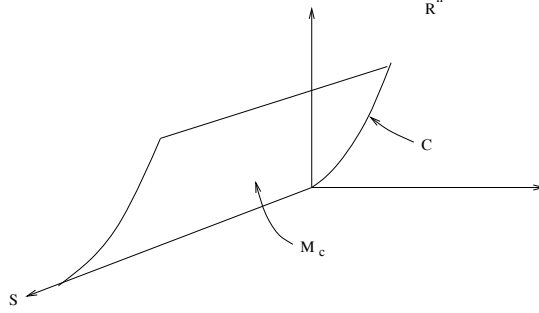
$$V_1(S, x_1, \dots, x_n) = \frac{x_2}{x_1^{\rho_1}}, V_2(S, x_1, \dots, x_n) = \frac{x_3}{x_2^{\rho_2}}, \dots, V_{n-1}(S, x_1, \dots, x_n) = \frac{x_n}{x_{n-1}^{\rho_{n-1}}}.$$

Hence, for each fixed value of $c_i > 0$, $i = 1, 2, \dots, n-1$,

$$\frac{x_2}{x_1^{\rho_1}} = c_1 \quad , \quad \frac{x_3}{x_2^{\rho_2}} = c_2 \quad , \dots \quad , \quad \frac{x_n}{x_{n-1}^{\rho_{n-1}}} = c_{n-1},$$

are invariant $(n-1)$ -dimensional manifolds in \mathbb{R}^n with coordinates (x_1, x_2, \dots, x_n) .

Now, for any $c = (c_1, \dots, c_{n-1})$ with $c_i > 0$ for $i = 1, \dots, n-1$, the intersection of these manifolds is a curve \mathcal{C} in \mathbb{R}^n , which is invariant for the

Figure 1: The manifolds M_c

system (9). A straightforward computation gives the parametric equations of \mathcal{C} , namely

$$\begin{aligned}
 x_2 &= c_1 x_1^{\rho_1} \\
 x_3 &= c_2 x_2^{\rho_2} \quad \Rightarrow \quad x_3 = c_2 c_1^{\rho_2} x_1^{\rho_1 \rho_2} \\
 x_4 &= c_3 x_3^{\rho_3} \quad \Rightarrow \quad x_4 = c_3 c_2^{\rho_3} c_1^{\rho_2 \rho_3} x_1^{\rho_1 \rho_2 \rho_3} \\
 &\vdots \\
 x_n &= c_{n-1} x_{n-1}^{\rho_{n-1}} \quad \Rightarrow \quad x_n = c_{n-1} c_{n-2}^{\rho_{n-1}} c_{n-3}^{\rho_{n-1} \rho_{n-2}} \dots c_1^{\rho_{n-1} \rho_{n-2} \dots \rho_2 \rho_1} x_1^{\rho_1 \rho_2 \dots \rho_{n-1}}.
 \end{aligned} \tag{11}$$

For any $c = (c_1, \dots, c_{n-1}) \in \mathbb{R}_+^{n-1}$, we denote by M_c the invariant manifold

$$M_c = \{(S, x_1, x_2, \dots, x_n) \in \mathbb{R}^{n+1} : S \geq 0 \text{ and } x_1, x_2, \dots, x_n \text{ satisfy (11)}\}. \tag{12}$$

Then, the family $\{M_c : c \in \mathbb{R}_+^{n-1}\}$ is a two-dimensional foliation of the first octant of \mathbb{R}^{n+1} and each leaf is the image of the embedding $h_c : \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R}^{n+1}$ given by

$$h_c(S, x_1) = (S, x_1, x_2(x_1), \dots, x_n(x_1)). \tag{13}$$

For a fixed $c = (c_1, c_2, \dots, c_{n-1})$ with $c_i > 0$, $i = 1, 2, \dots, n-1$, we study the restriction of the system (9) to the manifold M_c , parametrized by S and x_1 . Taking into account (11), this restriction is given by

$$\left\{ \begin{array}{l}
 \dot{S} = \gamma \left(1 - \frac{S}{K}\right) S - \frac{(x_1 + \rho_1 c_1 x_1^{\rho_1} + \rho_1 \rho_2 c_2 c_1^{\rho_2} x_1^{\rho_1 \rho_2} + \dots + \rho_1 \rho_2 \dots \rho_{n-1} c_{n-1} c_{n-2}^{\rho_{n-1}} \dots c_1^{\rho_1 \rho_2 \dots \rho_{n-1}} x_1^{\rho_1 \rho_2 \dots \rho_{n-1}}) m_1 S}{a+S} \\
 \dot{x}_1 = \beta_1 \frac{S-\lambda}{a+S} x_1
 \end{array} \right.$$

The introduction of the new parameters

$$\begin{aligned}
 \eta_1 &= \rho_1; \quad \eta_2 = \rho_1 \rho_2; \quad \dots; \quad \eta_{n-1} = \rho_1 \rho_2 \dots \rho_{n-1} \\
 \alpha_1 &= c_1 \rho_1; \quad \alpha_2 = c_2 c_1^{\rho_2} \rho_1 \rho_2; \quad \dots; \quad \alpha_{n-1} = c_{n-1} c_{n-2}^{\rho_{n-1}} \dots c_1^{\rho_2 \rho_3 \dots \rho_{n-1}} \rho_1 \rho_2 \rho_{n-1}
 \end{aligned}$$

carries the previous system into

$$\begin{cases} \dot{S} = \gamma(1 - \frac{S}{K})S - \frac{x_1 + \alpha_1 x_1^{\eta_1} + \alpha_2 x_1^{\eta_2} + \dots + \alpha_{n-1} x_1^{\eta_{n-1}}}{a+S} m_1 S \\ \dot{x}_1 = \beta_1 \frac{S-\lambda}{a+S} x_1. \end{cases} \quad (14)$$

The equilibrium points of (14) are $(S, x_1) = (0, 0)$, $(S, x_1) = (K, 0)$ and the single intersection point $(S, x_1) = (\lambda, \xi_1)$, where $x_1 = \xi_1$ is the unique positive solution of the equation

$$\begin{aligned} x_1 + \rho_1 c_1 x_1^{\rho_1} + \rho_1 \rho_2 c_2 c_1^{\rho_2} x_1^{\rho_1 \rho_2} + \dots + \\ \rho_1 \rho_2 \dots \rho_{n-1} c_{n-1} c_{n-2}^{\rho_{n-1}} \dots c_1^{\rho_1 \rho_2 \dots \rho_{n-1}} x_1^{\rho_1 \rho_2 \dots \rho_{n-1}} = \frac{\gamma(a+\lambda)(K-\lambda)}{m_1 K}, \end{aligned} \quad (15)$$

or, equivalently,

$$x_1 + \alpha_1 x_1^{\eta_1} + \alpha_2 x_1^{\eta_2} + \dots + \alpha_{n-1} x_1^{\eta_{n-1}} = \frac{\gamma(a+\lambda)(K-\lambda)}{m_1 K}. \quad (16)$$

Geometrically, the nontrivial equilibrium point of (14) is described as follows: ξ_1 is the second component of the point $(\lambda, \xi_1, \dots, \xi_n)$ obtained as the transversal intersection of the manifolds H and M_c . The other components are given by

$$\begin{cases} \xi_2 = c_1 \xi_1^{\rho_1} \\ \xi_3 = c_2 c_1^{\rho_2} \xi_1^{\rho_1 \rho_2} \\ \xi_4 = c_3 c_2^{\rho_3} c_1^{\rho_2 \rho_3} \xi_1^{\rho_1 \rho_2 \rho_3} \\ \vdots \\ \xi_n = c_{n-1} c_{n-2}^{\rho_{n-1}} c_{n-3}^{\rho_{n-1} \rho_{n-2}} \dots c_1^{\rho_1 \rho_2 \dots \rho_{n-1}} \xi_1^{\rho_1 \rho_2 \dots \rho_{n-1}}. \end{cases} \quad (17)$$

The Jacobian matrix of the system (14) is

$$J_I(S, x_1) = \begin{pmatrix} \gamma(1 - \frac{S}{K}) - \frac{\gamma S}{K} + \frac{x_1 + \sum_{i=1}^{n-1} \alpha_i x_i^{\eta_i}}{(a+S)^2} m_1 a & 1 + \sum_{i=1}^{n-1} \alpha_i \eta_i x_i^{\eta_i-1} \\ \frac{a+\lambda}{a+S} \beta_1 x_1 & -\frac{i=1}{a+S} m_1 S \\ & \frac{S-\lambda}{a+S} \beta_1 \end{pmatrix}$$

Since

$$J_I(\theta, \theta) = \begin{pmatrix} \gamma & 0 \\ 0 & -\frac{\beta_1 \lambda}{a} \end{pmatrix} \text{ and } J_I(K, \theta) = \begin{pmatrix} -\gamma & -\frac{m_1 K}{a+K} \\ 0 & \frac{(K-\lambda)\beta_1}{a+K} \end{pmatrix},$$

both $(S, x_1) = (0, 0)$ and $(S, x_1) = (K, 0)$ are saddle points if $K > \lambda$.

To study the stability of $(S, x_1) = (\lambda, \xi_1)$, where ξ_1 is the only positive solution of (16), we will consider K as a bifurcation parameter. Next, we will show that (14) undergoes an Andronov-Hopf bifurcation around $(S, x_1) = (\lambda, \xi_1)$. The following theorem concerns it.

Teorema 3.1. *If $\lambda < K < a + 2\lambda$, then the equilibrium $(S, x_1) = (\lambda, \xi_1)$ of system (14) is globally asymptotically stable inside the positive quadrant. Moreover, for $\lambda < K < a + 2\lambda$, (14) does not have closed orbits inside the positive quadrant. Finally, at $K = a + 2\lambda$ the system undergoes an Andronov-Hopf Bifurcation, i.e. there is $\delta > 0$ such that for $K \in (a + 2\lambda, a + 2\lambda + \delta)$, the system (14) has an orbitally asymptotically stable limit cycle surrounding (λ, ξ_1) .*

First, we translate (λ, ξ_1) to the origin by the change of coordinates

$$y_1 = S - \lambda y_2 = x_1 - \xi_1, \quad (18)$$

where ξ_1 satisfies (16). System (14) becomes

$$\begin{cases} \dot{y}_1 = \gamma(y_1 + \lambda)\left(1 - \frac{y_1 + \lambda}{K}\right)S - \\ \quad - \frac{y_2 + \xi_1 + \alpha_1(y_2 + \xi_1)^{\eta_1} + \alpha_2(y_2 + \xi_1)^{\eta_2} + \dots + \alpha_{n-1}(y_2 + \xi_1)^{\eta_{n-1}}}{a + y_1 + \lambda} m_1(y_1 + \lambda) \\ \dot{y}_2 = \beta_1 \frac{y_1}{a + y_1 + \lambda} (y_2 + \xi_1) \end{cases} \quad (19)$$

The Jacobian matrix of the previous system is

$$J_2(y_1, y_2) = \begin{pmatrix} \frac{\partial f_1(y_1, y_2)}{\partial y_1} & \frac{\partial f_1(y_1, y_2)}{\partial y_2} \\ \frac{\partial f_2(y_1, y_2)}{\partial y_1} & \frac{\partial f_2(y_1, y_2)}{\partial y_2} \end{pmatrix},$$

where,

$$\begin{aligned} f_1(y_1, y_2) &= \gamma(y_1 + \lambda)\left(1 - \frac{y_1 + \lambda}{K}\right)S + \\ &\quad - \frac{y_2 + \xi_1 + \alpha_1(y_2 + \xi_1)^{\eta_1} + \alpha_2(y_2 + \xi_1)^{\eta_2} + \dots + \alpha_{n-1}(y_2 + \xi_1)^{\eta_{n-1}}}{a + y_1 + \lambda} m_1(y_1 + \lambda) \end{aligned}$$

$$f_2(y_1, y_2) = \beta_1 \frac{y_1}{a + y_1 + \lambda} (y_2 + \xi_1).$$

Since ξ_1 satisfies (16), we obtain

$$J_2(0, 0) = \begin{pmatrix} \frac{\gamma\lambda(K - 2\lambda - a)}{K(a + \lambda)} & \frac{(1 + \alpha_1\eta_1\xi_1^{\eta_1 - 1} + \dots + \alpha_{n-1}\eta_{n-1}\xi_1^{\eta_{n-1} - 1})\lambda m_1}{a + \lambda} \\ \frac{\beta_1\xi_1}{a + \lambda} & 0 \end{pmatrix}.$$

Hence, the characteristic polynomial associate to $J_2(0, 0)$ is

$$\begin{aligned} P(\mu) &= \mu^2 + \frac{\gamma\lambda(a + 2\lambda - K)}{K(a + \lambda)}\mu \\ &\quad + \frac{\beta\xi_1(1 + \alpha_1\eta_1\xi_1^{\eta_1 - 1} + \dots + \alpha_{n-1}\eta_{n-1}\xi_1^{\eta_{n-1} - 1})\lambda m_1}{(a + \lambda)^2} \end{aligned}$$

and its eigenvalues are

$$\begin{aligned} \mu_{1,2}(K) &= \frac{\frac{\gamma\lambda(K-a-2\lambda)}{K(a+\lambda)}}{2} \\ &\pm \frac{\sqrt{\left(\frac{\gamma\lambda(K-a-2\lambda)}{K(a+\lambda)}\right)^2 - 4 \frac{(\xi_1 + \alpha_1 \eta_1 \xi_1^{\eta_1} + \dots + \alpha_{n-1} \eta_{n-1} \xi_1^{\eta_{n-1}}) \beta_1 \lambda m_1}{(a+\lambda)^2}}}{2}. \end{aligned}$$

Therefore, the origin $(y_1, y_2) = (0, 0)$ is asymptotically stable if $\lambda < K < a + 2\lambda$ and unstable when $K > a + 2\lambda$.

To show that system (19), and consequently the system (14), does not have closed orbits in the positive quadrant for $\lambda < K < a + 2\lambda$, we apply Dulac's Criterion (see [4]). Consider the function $h(S, x_1) = \frac{x_1^q(a+S)}{S}$, where q is a constant to be appropriately chosen. A straightforward computation leads to

$$\left(\frac{\partial f(S, x_1)}{\partial S} + \frac{\partial g(S, x_1)}{\partial x_1} \right) h(S, x_1) = \frac{\gamma K - 2\gamma S - \gamma a + \frac{\beta_1 K(q+1)(S-\lambda)}{S}}{K} x_1^q,$$

were $f(S, x_1) = \gamma(1 - \frac{S}{K})S - \frac{x_1 + \alpha_1 x_1^{\eta_1} + \alpha_2 x_1^{\eta_2} + \dots + \alpha_{n-1} x_1^{\eta_{n-1}}}{a+S} m_1 S$ and $g(y_1, y_2) = \beta_1 \frac{S-\lambda}{a+S} x_1$.

Taking q such that $2\gamma\lambda = \beta_1 K(q+1)$ we get

$$\left(\frac{\partial f(S, x_1)}{\partial S} + \frac{\partial g(S, x_1)}{\partial x_1} \right) h(S, x_1) = \frac{K - a - 2\lambda - \frac{2(S-\lambda)^2}{S}}{K} \gamma x_1^q.$$

Hence, for $S > \lambda$ and $K < a + 2\lambda$, $\left(\frac{\partial f(S, x_1)}{\partial S} + \frac{\partial g(S, x_1)}{\partial x_1} \right) h(S, x_1) < 0$, so, by Dulac's Criterion, the system (19) does not admit periodic orbits inside the positive quadrant of \mathbb{R}^2 . Thus, if $K < a + 2\lambda$, the equilibrium $(S, x_1) = (\lambda, \xi_1)$ will be globally asymptotically stable for solutions with initial conditions inside the positive quadrant.

To complete the proof, we need to verify the hypotheses of Andronov - Hopf's Theorem to show that at $K = K_0 = a + 2\lambda$, the system (19), and consequently the system (14), undergoes a Hopf bifurcation. First, we note that at $K = K_0$, we have $\mu_{1,2}(K_0) = \pm i\omega_0$, where

$$\omega_0 = \frac{\left[(\xi_1 + \alpha_1 \eta_1 \xi_1^{\eta_1} + \dots + \alpha_{n-1} \eta_{n-1} \xi_1^{\eta_{n-1}}) \beta_1 \lambda m_1 \right]^{\frac{1}{2}}}{a + \lambda} > 0. \quad (20)$$

Therefore, there exists $\delta > 0$ such that the eigenvalues $\mu_{1,2}(K)$ are nonreal and complex conjugate. Furthermore,

$$\frac{d}{dK} \operatorname{Re} \mu(K_0) = \frac{\gamma}{2(a + 2\lambda)(a + \lambda)} > 0. \quad (21)$$

In the following, we are going to compute the first Liapunov coefficient to determine the supercriticality of the periodic orbit generate by the Hopf bifurcation. To do this, we shall use the technique given in [12] (see also [9]).

A straightforward computation shows that at $K = K_0$ the eigenvectors of $J_2(0, 0)$ associated to $\mu_{1,2}(K_0)$ are $q_{1,2} = (\pm i\Delta, 1)$, where $\Delta = \frac{\omega_0(a+\lambda)}{\beta_1\xi_1}$. The eigenvectors of the transposed $J_2(0, 0)^T$ associated to $\mu_1(K_0)$ is $p_1 = (-\frac{i}{\Delta}, 1)$ and the associated to $\mu_2(K_0)$ is $p_2 = (\frac{i}{\Delta}, 1)$.

Expanding the righthand side of system (19) in power series around $(y_1, y_2) = (0, 0)$ at $K = K_0$ we are led to

$$\left\{ \begin{array}{l} \dot{y}_1 = -\frac{\left(1 + \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i-1}\right) m_1 \lambda}{a+\lambda} y_2 - \frac{\gamma \lambda}{a+\lambda} y_1^2 - \frac{1 + \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i-1}}{(a+\lambda)^2} y_1 y_2 - \\ \frac{m_1 \lambda \sum_{i=1}^{n-1} \alpha_i \eta_i (\eta_i - 1) \xi_1^{\eta_i-1}}{(a+\lambda)^3} y_2^2 - \frac{\gamma a}{K} y_1^3 + \frac{a+(a+\lambda) \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i-1}}{(a+\lambda)^3} y_1^2 y_2 - \\ \frac{a m_1 \sum_{i=1}^{n-1} \alpha_i \eta_i (\eta_i - 1) \xi_1^{\eta_i-1}}{2((a+\lambda)^2)} y_1 y_2^2 - \frac{m_1 \lambda \sum_{i=1}^{n-1} \alpha_i \eta_i (\eta_i - 1) (\eta_i - 2) \xi_1^{\eta_i-2}}{6(a+\lambda)} y_2^3 + O(|y|^4) \\ \dot{y}_2 = \frac{\beta_1 \xi_1}{a+\lambda} y_1 - \frac{\beta_1 \xi_1}{(a+\lambda)^2} y_1^2 + \frac{\beta_1}{a+\lambda} y_1 y_2 + \frac{\beta_1 \xi_1}{(a+\lambda)^3} y_1^3 - \frac{\beta_1}{(a+\lambda)^2} y_1^2 y_2 + O(|y|^4) \end{array} \right. \quad (22)$$

Denote the coefficients of the vector field associated to \dot{y}_1 by

$$\begin{aligned} a_0 &= 0, & a_1 &= 0, \\ a_2 &= -\frac{\left(1 + \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i-1}\right) m_1 \lambda}{a+\lambda}, & a_3 &= -\frac{\gamma \lambda}{K(a+\lambda)} \\ a_4 &= -\frac{m_1 a \left(1 + \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i-1}\right)}{(a+\lambda)^2}, & a_5 &= -\frac{m_1 \lambda \sum_{i=1}^{n-1} \alpha_i \eta_i (\eta_i - 1) \xi_1^{\eta_i-1}}{2(a+\lambda)}, \\ a_6 &= -\frac{\gamma a}{K(a+\lambda)^2}, & a_7 &= \frac{1 + \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i-1}}{(a+\lambda)^3}, \\ a_8 &= -\frac{a m_1 \sum_{i=1}^{n-1} \alpha_i \eta_i (\eta_i - 1) \xi_1^{\eta_i-1}}{2((a+\lambda)^2)}, & a_9 &= -\frac{m_1 \lambda \sum_{i=1}^{n-1} \alpha_i \eta_i (\eta_i - 1) (\eta_i - 2) \xi_1^{\eta_i-2}}{6(a+\lambda)} \end{aligned}$$

and the coefficients of the vector field associated to \dot{y}_2 by

$$\begin{aligned}
b_0 &= 0 & b_1 &= \frac{\beta_1 \xi_1}{a+\lambda} & b_2 &= 0 \\
b_3 &= -\frac{\beta_1 \xi_1}{(a+\lambda)^2} & b_4 &= \frac{\beta_1}{a+\lambda} & b_5 &= 0 \\
b_6 &= \frac{\beta_1 \xi_1}{(a+\lambda)^3} & b_7 &= -\frac{\beta_1}{(a+\lambda)^2} & b_8 &= 0 & b_9 &= 0.
\end{aligned}$$

Letting $Y = (y_1, y_2)$ and $F(Y, 0) = (F_1(Y, 0), F_2(Y, 0))$, we can write the system (22) as $\dot{Y} = J_3(0, 0)Y + F(Y, 0)$, where

$$\begin{aligned}
F_1(Y, 0) &= a_0 + a_1 y_1 + a_2 y_2 + a_3 y_1^2 + a_4 y_1 y_2 + a_5 y_2^2 + a_6 y_1^3 + a_7 y_1^2 y_2 \\
&\quad + a_8 y_1 y_2^2 + a_9 y_2^3 + O(|Y|^4), \\
F_2(Y, 0) &= b_0 + b_1 y_1 + b_2 y_2 + b_3 y_1^2 + b_4 y_1 y_2 + b_5 y_2^2 + b_6 y_1^3 + b_7 y_1^2 y_2 \\
&\quad + b_8 y_1 y_2^2 + b_9 y_2^3 + O(|Y|^4),
\end{aligned}$$

or, equivalently,

$$F(Y, 0) = \frac{1}{2}B(Y, Y) + \frac{1}{6}C(Y, Y, Y) + O(|Y|^4),$$

where

$$\begin{aligned}
B(Y, Y) &= (2a_3 y_1^2 + 2a_4 y_1 y_2 + 2a_5 y_2^2, 2b_3 y_1^2 + 2b_4 y_1 y_2) \\
C(Y, Y, Y) &= (6a_6 y_1^3 + 6a_7 y_1^2 y_2 + 6a_8 y_1 y_2^2 + 6a_9 y_2^3, 6b_1 y_1^3 + 6b_7 y_1^2 y_2).
\end{aligned}$$

It is known (see, e.g. [12]) that the first Liapunov number $l_1(0)$ of (22) is given by

$$l_1(0) = \frac{1}{2\omega_0} \operatorname{Re}(ig_{20}g_{11} + \omega_0 g_{21}),$$

where $g_{20} = \langle p, B(q, q) \rangle$, $g_{11} = \langle p, B(q, \bar{q}) \rangle$, $g_{21} = \langle p, C(q, q, \bar{q}) \rangle$ and $\langle \cdot, \cdot \rangle$ stands for the inner product in \mathbb{C} .

A straightforward computation shows

- $B(q, q) = (-2a_3 \Delta^2 + 2i\Delta a_4 + 2a_5, -2\Delta^2 b_3 + 2i\Delta b_4)$
- $B(q, \bar{q}) = (2a_3 \Delta^2 + 2a_5, 2\Delta^2 b_3)$
- $C(q, q, \bar{q}) = (6a_6 i \Delta^3 + 2a_7 \Delta^2 + 2a_8 i \Delta + 6a_9, 6b_1 i \Delta^3 + 2b_7 i \Delta)$.

Consequently,

- $g_{20}(0) = ia_3 \Delta + a_4 - i\frac{a_5}{\Delta} - b_3 \Delta^2 + ib_4 \Delta$
- $ig_{20}(0) = -a_3 \Delta + ia_4 + \frac{a_5}{\Delta} - ib_3 \Delta^2 - b_4 \Delta$
- $g_{11}(0) = -ia_3 \Delta - \frac{ia_5}{\Delta} + b_3 \Delta^2$

- $ig_{20}(0)g_{11}(0) = ia_3^2\Delta^2 + a_3a_4\Delta - ia_3a_5 - a_3b_3\Delta^3 + ia_3b_4\Delta^2 + ia_3a_5 + \frac{a_4a_5}{\Delta} - a_5b_3\Delta - \frac{ia_5^2}{\Delta^2} + ia_5b_4 - a_3b_3\Delta^3 + ia_4b_3\Delta^2 + a_5b_3\Delta - ib_3^2\Delta^3 - b_3b_4\Delta^3$
- $\omega_0g_{21}(0) = 3\omega_0a_6\Delta^2 - i\omega_0a_7\Delta + \omega_0a_8 - 3i\omega_0a_9 + 3i\omega_0b_1\Delta^3 + \omega_0b_7\Delta^2$

and, therefore,

$$\begin{aligned} l_1(0) &= \frac{1}{2\omega_0^2} \left(a_3a_4\Delta - a_3b_3\Delta^3 + \frac{a_4a_5}{\Delta} - a_5b_3\Delta - a_3b_3\Delta^3 + a_5b_3\Delta - b_3b_4\Delta^3 + 3\omega_0a_6\Delta^2 + \omega_0a_8 + \omega_0b_7\Delta^2 \right) \\ &= \frac{1}{2\omega_0^2} \left(a_3a_4\Delta - 2a_3b_3\Delta^3 + \frac{a_4a_5}{\Delta} - b_3b_4\Delta^3 + 3\omega_0a_6\Delta^2 + \omega_0a_8 + \omega_0b_7\Delta^2 \right) \end{aligned} \quad (23)$$

Taking into account the expressions for a_i , b_i , and Δ ($i = 1, 2, \dots, 9$), we have

$$-2\Delta^3 a_3 b_3 = -2 \frac{\omega_0(a+\lambda)^3}{\beta_1^3 \xi_1^3} \frac{\gamma\lambda}{K(a+\lambda)} \frac{\beta_1 \xi_1}{(a+\lambda)^2} = -2 \frac{\omega_0^3 \gamma \lambda}{K \beta_1^2 \xi_1^2}$$

and

$$\omega_0 b_7 \Delta^2 - b_3 b_4 \Delta^3 = -\frac{\omega_0^3 (a+\lambda)^2}{\beta_1^2 \xi_1^2} \frac{\beta_1}{(a+\lambda)^2} + \frac{\omega_0^3 (a+\lambda)^3}{\beta_1^3 \xi_1^3} \frac{\beta_1}{a+\lambda} \frac{\beta_1 \xi_1}{(a+\lambda)^2} = 0.$$

From (20), we have

$$\frac{\omega_0^2 (a+\lambda)^2}{\beta_1} = m_1 \lambda (\xi_1 + \alpha_1 \eta_1 \xi_1^{\eta_1} + \dots + \alpha_{n-1} \eta_{n-1} \xi_1^{\eta_{n-1}})$$

and this leads to

$$\begin{aligned} \frac{a_4 a_5}{\Delta} &= \frac{\beta_1}{\omega_0(a+\lambda)} \frac{m_1 a \left(\xi_1 + \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i} \right)}{(a+\lambda)^2} \frac{m_1 \lambda \sum_{i=1}^{n-1} \alpha_i \eta_i (\eta_i - 1) \xi_1^{\eta_i - 1}}{2(a+\lambda)} \\ &= \frac{m_1 a \omega_0}{2(a+\lambda)^2} \sum_{i=1}^{n-1} \alpha_i \eta_i (\eta_i - 1) \xi_1^{\eta_i - 1} \end{aligned}$$

and therefore $\frac{a_4 a_5}{\Delta} + \omega_0 a_8 = 0$. Furthermore,

$$\begin{aligned} \Delta a_3 a_4 &= \frac{\omega_0 \gamma a}{K \beta_1 \xi_1 (a+\lambda)^2} \left(1 + \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i - 1} \right) m_1 \lambda \\ &= \frac{\omega_0 \gamma a}{K \beta_1 \xi_1^2 (a+\lambda)^2} \left(\xi_1 + \sum_{i=1}^{n-1} \alpha_i \eta_i \xi_1^{\eta_i} \right) m_1 \lambda \\ &= \frac{\omega_0 \gamma a}{K \beta_1 \xi_1^2 (a+\lambda)^2} \frac{\omega_0^2 (a+\lambda)^2}{K \beta_1} = \frac{\omega_0^3 \gamma a}{K \beta_1^2 \xi_1^2}. \end{aligned}$$

From the previous equation, $\Delta a_3 a_4 + 3\omega_0 \Delta^2 a_6 = -2 \frac{\omega_0^3 \gamma a}{K \beta_1^2 \xi_1^2}$. Thus

$$l_1(0) = -2 \frac{\omega_0 \gamma a}{K \beta_1^2 \xi_1^2} < 0.$$

Hence, the system (19), and consequently the system (14), undergoes a supercritical Hopf bifurcation and the orbit generated by the bifurcation

exists for $a + 2\lambda < K < a + 2\lambda + \delta$ ($\delta > 0$) and is orbitally asymptotically stable. The proof is complete.

3.2 Zip bifurcation

In the following, we are going to consider the case $a_1 < a_2 < \dots < a_n$. These conditions and $\lambda_1 = \lambda_2 = \dots = \lambda_n$ imply that $b_1 < \dots < b_n$. In fact, $\frac{a_1 d_1}{m_1 - d_1} = \dots = \frac{a_n d_n}{m_n - d_n} \Rightarrow \frac{a_1}{b_1 - 1} = \dots = \frac{a_n}{b_n - 1} \Rightarrow \frac{a_i}{a_{i+1}} = \frac{b_i - 1}{b_{i+1} - 1} < 1$, $i = 1, 2, \dots, n - 1$, and therefore $b_i < b_{i+1}$, $i = 1, 2, \dots, n - 1$.

Denote by $J = J(S, x_1, \dots, x_n)$ the Jacobian matrix of the system (3) and

$$j = \gamma \left(1 - \frac{S}{K}\right) - \frac{\gamma S}{K} - \sum_{i=1}^n \frac{m_i a_i}{(a_i + S)^2} x_i, \text{ so}$$

$$J = \begin{pmatrix} j & -\frac{m_1 S}{a_1 + S} & -\frac{m_2 S}{a_2 + S} & \cdots & -\frac{m_{n-1} S}{a_{n-1} + S} & -\frac{m_n S}{a_n + S} \\ \frac{\beta_1 (a_1 + \lambda)}{(a_1 + S)^2} x_1 & \frac{\beta_1 (S - \lambda)}{a_1 + \lambda} & 0 & \cdots & 0 & 0 \\ \frac{\beta_2 (a_2 + \lambda)}{(a_2 + S)^2} x_2 & 0 & \frac{\beta_2 (S - \lambda)}{a_2 + \lambda} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \frac{\beta_{n-1} (a_{n-1} + \lambda)}{(a_{n-1} + S)^2} x_{n-1} & 0 & 0 & \cdots & \frac{\beta_{n-1} (S - \lambda)}{a_{n-1} + \lambda} & 0 \\ \frac{\beta_n (a_n + \lambda)}{(a_n + S)^2} x_n & 0 & 0 & \cdots & 0 & \frac{\beta_n (S - \lambda)}{a_n + \lambda} \end{pmatrix}$$

Computing $J(\lambda, \xi_1, \dots, \xi_n)$ at a point $(\lambda, \xi_1, \dots, \xi_n) \in H$, we get

$$J = \begin{pmatrix} -\frac{\gamma \lambda}{K} + \lambda \sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i & -\frac{m_1 \lambda}{a_1 + \lambda} & -\frac{m_2 \lambda}{a_2 + \lambda} & \cdots & -\frac{m_{n-1} \lambda}{a_{n-1} + \lambda} & -\frac{m_n \lambda}{a_n + \lambda} \\ \frac{\beta_1 \xi_1}{a_1 + \lambda} & 0 & 0 & \cdots & 0 & 0 \\ \frac{\beta_2 \xi_2}{a_2 + \lambda} & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \frac{\beta_{n-1} \xi_{n-1}}{a_{n-1} + \lambda} & 0 & 0 & \cdots & 0 & 0 \\ \frac{\beta_n \xi_n}{a_n + \lambda} & 0 & 0 & \cdots & 0 & 0 \end{pmatrix}$$

since $\gamma \left(1 - \frac{\lambda}{K}\right) - \sum_{i=1}^n \frac{m_i a_i}{(a_i + \lambda)^2} \xi_i = \sum_{i=1}^n \frac{m_i a_i}{a_i + \lambda} \xi_i - \sum_{i=1}^n \frac{m_i a_i}{(a_i + \lambda)^2} \xi_i = \lambda \sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i$,

according to (4).

The characteristic polynomial of $J(\lambda, \xi_1, \dots, \xi_n)$ is given by

$$P(\mu) = \mu^{n-1} \left[\mu^2 + \mu \left(\frac{\lambda \gamma}{K} - \lambda \sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i \right) + \lambda \sum_{i=1}^n \frac{m_i \beta_i}{(a_i + \lambda)^2} \xi_i \right]. \quad (24)$$

In fact, we have

$$\det(\mu - J) = \left(\mu - \lambda \sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i + \frac{\lambda \gamma}{K} \right) \mu^n + \frac{m_1 \lambda}{a_1 + \lambda} \Delta_{12} + \frac{m_2 \lambda}{a_2 + \lambda} \Delta_{13} + \dots + \frac{m_n \lambda}{a_n + \lambda} \Delta_{1n} \quad (25)$$

where $\Delta_{1j} = (-1)^{j+1} \det(\mu - J)_{1j}$ and $\det(\mu - J)_{1j}$ is the determinant of the submatrix $(\mu - J)_{1j}$ gotten from $\mu - J$ eliminating the line 1 and the column j , $j = 2, 3, \dots, n+1$, i.e

$$\Delta_{1j} = (-1)^{j+1} \begin{pmatrix} & & & & & \text{col}(j-1) & \text{col}(j+1) & & & & \\ -\frac{\beta_1 \xi_1}{a_1 + \lambda} & \mu & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 & \\ -\frac{\beta_2 \xi_2}{a_2 + \lambda} & 0 & \mu & 0 & \dots & 0 & 0 & \dots & 0 & 0 & \\ -\frac{\beta_3 \xi_3}{a_3 + \lambda} & 0 & 0 & \mu & \dots & 0 & 0 & \dots & 0 & 0 & \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \dots & \vdots & \vdots & \\ -\frac{\beta_{n-1} \xi_{n-1}}{a_{n-1} + \lambda} & 0 & 0 & 0 & \dots & 0 & 0 & \dots & \mu & 0 & \\ -\frac{\beta_n \xi_n}{a_n + \lambda} & 0 & 0 & 0 & \dots & 0 & 0 & \dots & 0 & \mu & \end{pmatrix}$$

$$\text{So } \Delta_{12} = (-1)^3 [(-1)^2 (-\frac{\beta_1 \xi_1}{a_1 + \lambda}) \mu^{n-2}] = \frac{\beta_1 \xi_1}{a_1 + \lambda} \mu^{n-1}; \quad \Delta_{13} = \frac{\beta_2 \xi_2}{a_2 + \lambda} \mu^{n-1}; \\ \Delta_{14} = \frac{\beta_3 \xi_3}{a_3 + \lambda} \mu^{n-1} \dots \Delta_{1n} = \frac{\beta_n \xi_n}{a_n + \lambda} \mu^{n-1}.$$

Thus, the characteristic polynomial of $J(\lambda, \xi_1, \dots, \xi_n)$ is given as in (24). This means that each equilibrium point in H has 0 as an eigenvalue with multiplicity $n-2$ and two eigenvalues with negative real part if the polynomial between brackets in (24) is stable (respectively, positive real part if the same polynomial is unstable). Observe that if $\lambda < K < a_1 + 2\lambda$, we have

$$\sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i \leq \frac{1}{a_1 + \lambda} \gamma (1 - \frac{\lambda}{K}) < \frac{1}{a_1 + \lambda} (1 - \frac{\lambda}{a_1 + 2\lambda}) < \frac{\gamma}{K},$$

since $a_i + 2\lambda < a_{i+1} + 2\lambda$, $i = 1, 2, \dots, n$. Similarly, if $K > a_n + 2\lambda$, then

$$\sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i > \frac{\gamma}{k}.$$

Therefore the polynomial between brackets in (24) is stable if

$$\lambda < K < a_1 + 2\lambda \quad \text{since} \quad \sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i < \frac{\gamma}{k} \quad (26)$$

and unstable if

$$K > a_n + 2\lambda \quad \text{since} \quad \sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i > \frac{\gamma}{k}. \quad (27)$$

Consider the following hyperplane

$$H_1 = \{(\lambda, \xi_1, \dots, \xi_n) \in \mathbb{R}^{n+1} : \sum_{i=1}^n \frac{m_i}{(a_i + \lambda)^2} \xi_i = \frac{\gamma}{k}\} \quad (28)$$

With the previous comments we can state the following theorem

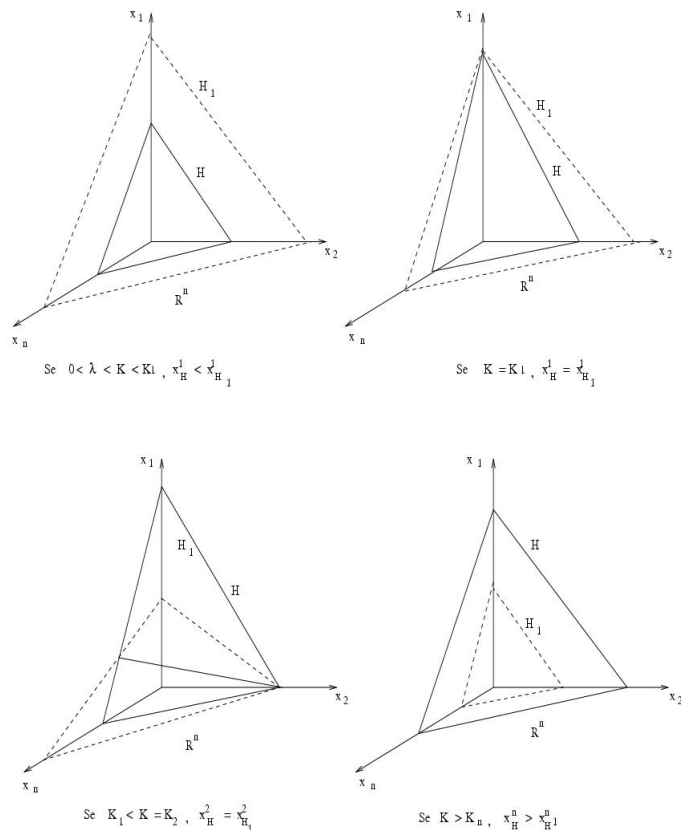


Figure 2: Hyperplane's Intersections

Teorema 3.2. *Let us assume that $0 < \lambda < K$, $\gamma, \beta_i, m_i, a_i$ are positive and $a_1 < a_2 < \dots < a_n$. If the carrying capacity K of the environment satisfies $K < a_1 + 2\lambda$, then all equilibrium points in H are Liapunov stable, in the sense that there is a neighborhood of H such that all the solutions in this neighborhood are attracted by H ; if $K > a_n + 2\lambda$, then the equilibrium points are unstable. Furthermore, if K is increased from one extreme to the other one of the interval $(a_1 + 2\lambda, a_n + 2\lambda)$ then the hyperplane intersection of H and H_1 is traveling through H from the vertex on the axis x_n to the vertex x_1 and the equilibria left behind get destabilized; For $a_1 + 2\lambda < K < a_n + 2\lambda$ this hyperplane intersection divides H in two parts, "the upper one" is a repeller and "the lower one" is an attractor of the system, i.e, the system undergoes a zip bifurcation.*

If $\lambda < K < a_1 + 2\lambda$, then the linearization of (3) around each equilibrium $(\lambda, \xi_1, \dots, \xi_n) \in H$ has zero as an eigenvalue of multiplicity $n-1$ and two eigenvalues with negative real part, according to (26). It implies, by the Theorem of the Invariant Manifolds (see [1] Theorem A.3.1), that through each equilibrium point $(\lambda, \xi_1, \dots, \xi_n) \in H$ pass one $(n-1)$ -dimensional smooth invariant manifold. Further, all the orbits on this manifold tends to $(\lambda, \xi_1, \dots, \xi_n)$ when $t \rightarrow +\infty$. On the other hand, if $K > a_n + 2\lambda$, the equilibrium $(\lambda, \xi_1, \dots, \xi_n)$ are unstable in accordance with (27).

Let us study the more interesting case when K changes from $a_1 + 2\lambda$ to $a_n + 2\lambda$. We will show that when K grows from $a_1 + 2\lambda$ up to $a_n + 2\lambda$, the $(n-1)$ -dimensional hyperplane in \mathbb{R}^{n+1} given in (28) intersect H , and the properties of stability of the equilibrium points in H changes. We will denote the intercepts coordinates of H with the coordinate axes by $(x_H^1, 0, 0, \dots, 0)$, $(0, x_H^2, 0, \dots, 0)$, ..., $(0, 0, 0, \dots, x_H^n)$ and of H_1 by $(x_{H_1}^1, 0, 0, \dots, 0)$, $(0, x_{H_1}^2, 0, \dots, 0)$, ..., $(0, 0, 0, \dots, x_{H_1}^n)$. Observe that $x_H^i = \frac{\gamma(a_i+\lambda)(K-\lambda)}{m_i K}$ is an increasing function of K ; on the other hand, $x_{H_1}^i = \frac{\gamma(a_i+\lambda)^2}{m_i K}$ is a decreasing function of K ; furthermore, as the function $K(a) = a + 2\lambda$ is increasing in the interval $a \in [0, a_n + 2\lambda]$ we have $\lambda < K_1 < K_2 < \dots < K_n$. A simple calculation shows that if $\lambda < K < K_i$ then $x_H^i < x_{H_1}^i$ and $x_H^i = x_{H_1}^i$ at $K = K_i$ for $i = 1, 2, \dots, n$. Hence, for $\lambda < K < K_1$ the hyperplane H is below H_1 and reach H_1 at $K = K_1$.

In this case, inequality (26) is valid for all points in H implying that all his points are stable (when we change K in the interval $\lambda < K < K_1$ the hyperplane H and H_1 are dislocated parallel). When K is increased beyond K_1 , the hyperplane H cuts into H_1 and reach $x_H^2 = x_{H_1}^2$ at $K = K_2$, reach $x_H^3 = x_{H_1}^3$ at $K = K_3$ and so on up to reach $x_H^n = x_{H_1}^n$ at $K = K_n$. For $K > K_n$, the hyperplane H_1 cuts the hyperplane H outside the positive octant so that now H_1 will be below H (see Figure 2). In the process in that part of H which is already above the hyperplane H_1 the condition (27) holds. This mean that the equilibrium on this part of the hyperplane have a $(n-1)$ - dimensional unstable manifold which fill a neighborhood of this part of H . The proof is complete.

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