

Global dynamics of a family of 3-D Lotka–Volterra Systems

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Abstract

In this paper we analyse the flow of a family of three dimensional Lotka-Volterra systems restricted to an invariant and bounded region. We conclude that the behaviour of the flow in the interior of this region is very simple: either every orbit is a periodic orbit or they move from one boundary to another. We also characterise some of the bifurcations taking place at the boundary of the invariant region.

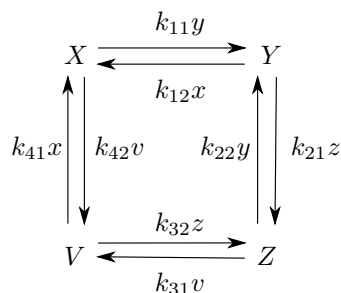
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1 Introduction

Consider a closed chemical system formed by four coexisting macromolecular species denoted by X, Y, Z and V . A macromolecule works in a reaction network far from equilibrium. As discussed by Wyman [19] such reaction can be modeled as a “turning wheel” of one-step transitions of the macromolecule, which circulate in a closed reaction path involving the four possible states. The turning wheels have been proposed by Di Cera et al. [5] as a generic model for macromolecular autocatalytic interactions.

While Di Cera’s model considers unidirectional first order interactions, Murza et al. in [6] consider a closed sequence of chemical equilibria. In their approach the reaction rates were defined as functions of the time dependent product concentrations, multiplied by their reaction rate constants. This type of reaction rates had been introduced in the original Wyman’s paper [19].

Following the closed sequence of chemical equilibria in [6], the autocatalytic chemical reactions between X, Y, Z and V



is governed by the following 4-parameter family of nonlinear differential equations

$$\begin{aligned}
 \dot{x} &= x(k_1y - k_4v), \\
 \dot{y} &= y(k_2z - k_1x), \\
 \dot{z} &= z(k_3v - k_2y), \\
 \dot{v} &= v(k_4x - k_3z).
 \end{aligned} \tag{1}$$

Functions $x(t), y(t), z(t)$ and $v(t)$ are concentrations at time t of the chemical species X, Y, Z, V respectively. The parameters $k_i = k_{i2} - k_{i1}$ for $i = 1, 2, 3, 4$ are differences of pairs of reaction rate constants corresponding to each chemical equilibrium. It can be easily seen that system (1) is identical to the Di Cera's model restricted to $n = 4$, see equation (7) in [5]. In that work, Di Cera claims that this family exhibits self sustained and conservative oscillations only when the parameter $\mathbf{k} = (k_1, k_2, k_3, k_4)$ is in the three dimensional manifold $\mathcal{S} = \{\mathbf{k} \in \mathbb{R}^4 \setminus \{0\} : k_1 k_3 - k_2 k_4 = 0\}$.

Assuming that the conservation of mass $x + y + z + v = 1$ applies to the macromolecular system (1), its kinetic behaviour is described by the three-dimensional differential system

$$\begin{cases} \dot{x} = x(k_1 y - k_4(1 - x - y - z)), \\ \dot{y} = y(k_2 z - k_1 x), \\ \dot{z} = z(-k_2 y + k_3(1 - x - y - z)), \end{cases} \quad (2)$$

restricted to the invariant by the flow bounded region $\mathcal{T} = \{x \geq 0, y \geq 0, z \geq 0, x + y + z \leq 1\}$.

Polynomial system (2) is a particular case of the three-dimensional Lotka-Volterra systems (LVS)

$$\dot{x}_i = x_i \left(a_i + \sum_{j=1}^3 b_{ij} x_j \right), \quad i = 1, 2, 3,$$

which has been extensively studied starting with the pioneer works of Lotka [9] and Volterra [11]. These systems have multiple applications in biochemistry. For instance, enzyme kinetics [19], circadian clocks [7] and genetic networks [13, 12] often produce sustained oscillations modeled with LVS.

Solutions of LVS cannot, in general, be written in terms of elementary functions. So that the search for invariant manifolds, first integrals or/and integrability conditions can be useful to the analysis of the flow. This approach has experimented an increasing popularity over the last few years after the works of Christopher and Llibre [2, 3, 4], which are based on the Darboux's theory of integrability, see for instance [1, 14, 10] and references therein. Unfortunately for systems of dimension greather that 2 the behaviour of the flow is not entirely known, even when the system is integrable. Of course in the case of non-integrable LVS the lack of knowledge is higher and other tools are required. Nevertheless and for special families of parameters, some results concerning to the existence of limit cycles can be found in [15, 16, 17, 18]. Additional results about the number of limit cycles which can appear after perturbation are presented in [8].

In this paper we deal with the global analysis of the flow of system (2) restricted to the region \mathcal{T} . Note that the boundary $\partial\mathcal{T}$ of the region is a three dimensional simplex which is invariant by the flow. This boundary is formed by the union of the following invariant subsets: the invariant faces $\mathcal{X} = \{(x, 0, z) : x > 0, z > 0, x + z < 1\}$, $\mathcal{Y} = \{(0, y, z) : y > 0, z > 0, y + z < 1\}$, $\mathcal{Z} = \{(x, y, 0) : x > 0, y > 0, x + y < 1\}$ and $\Sigma = \{(x, y, z) : x > 0, y > 0, z > 0, x + y + z < 1\}$; and the invariant edges $\mathcal{R}_{xz} = \{(x, 0, 0) : 0 < x < 1\}$, $\mathcal{R}_{xy} = \{(0, 0, z) : 0 < z < 1\}$, $\mathcal{R}_{yz} = \{(0, y, 0) : 0 \leq y \leq 1\}$, $\mathcal{R}_{px} = \{(x, 0, 1 - x) : 0 \leq x \leq 1\}$, $\mathcal{R}_{py} = \{(0, y, 1 - y) : 0 < y < 1\}$ and $\mathcal{R}_{pz} = \{(x, 1 - x, 0) : 0 < x < 1\}$. We remark that the edges \mathcal{R}_{yz} and \mathcal{R}_{px} are closed segments formed by singular points.

In order to make easier the analysis we consider the following subsets in the parameter space: $\mathcal{S}^- = \{\mathbf{k} \in \mathbb{R}^4 : k_1 k_3 - k_2 k_4 < 0\}$, $\mathcal{S}^+ = \{\mathbf{k} \in \mathbb{R}^4 : k_1 k_3 - k_2 k_4 > 0\}$, $\mathcal{NZ} = \{\mathbf{k} \in \mathbb{R}^4 : k_1 k_2 k_3 k_4 \neq 0\}$ and $\mathcal{PS} = \{\mathbf{k} \in \mathbb{R}^4 : k_1 k_2 > 0, k_1 k_3 > 0, k_1 k_4 > 0\}$. We note that \mathcal{S}^- and \mathcal{S}^+ together with \mathcal{S} (defined above) form a partition of the parameter space \mathbb{R}^4 . We also note that the parameter set \mathcal{PS} is a subset of \mathcal{NZ} .

The main result of the paper is summarised in the following theorem.

Theorem 1 (a) Suppose that $\mathbf{k} \in \mathcal{PS} \cap \mathcal{S}$.

(a-1) The open segment

$$R = \left\{ \left(\frac{k_3}{k_4} z, \frac{k_4 - (k_4 + k_3)z}{k_4 + k_1}, z \right) : 0 < z < \frac{k_4}{k_3 + k_4} \right\}$$

is contained in the interior of \mathcal{T} and every point in R is a singular point.

(a-2) Let \mathbf{p} be a point contained in the interior of \mathcal{T} but not in R . Then the orbit $\gamma_{\mathbf{p}}$ through the point \mathbf{p} is a periodic orbit.

(a-3) Each of the two limit sets of every orbit in $\mathcal{X} \cup \Sigma$ is a singular point contained in the edge \mathcal{R}_{px} . Moreover, given two orbits $\gamma_1 \subset \mathcal{X}$ and $\gamma_2 \subset \Sigma$ such that $\omega(\gamma_1) = \alpha(\gamma_2)$, then $\omega(\gamma_2) = \alpha(\gamma_1)$.

- (a-4) Each of the two limit sets of every orbit in $\mathcal{Y} \cup \mathcal{Z}$ is a singular point contained in the edge \mathcal{R}_{yz} . Moreover, given two orbits $\gamma_1 \subset \mathcal{Y}$ and $\gamma_2 \subset \mathcal{Z}$ such that $\omega(\gamma_1) = \alpha(\gamma_2)$, then $\omega(\gamma_2) = \alpha(\gamma_1)$.
- (a-5) The behaviour of the flow in \mathcal{T} is topologically equivalent to the one draw in Figure 1.
- (b) Suppose that $\mathbf{k} \notin \mathcal{PS} \cap \mathcal{S}$ and $\mathbf{k} \neq \mathbf{0}$. The limit sets of every orbit in \mathcal{T} are contained in the boundary of \mathcal{T} . Thus the flow goes from one face to another.

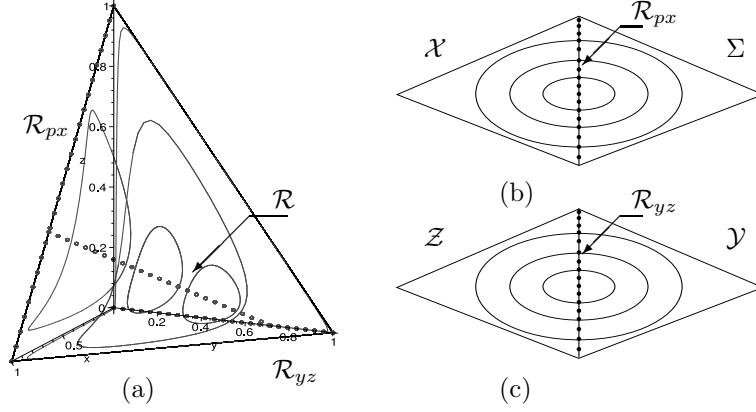


Figure 1: Behaviour of the flow of system (2) for $\mathbf{k} \in \mathcal{PS} \cap \mathcal{S}$: (a) in the interior of \mathcal{T} ; (b) at the edges $\mathcal{X} \cup \Sigma$ and (c) at the edges $\mathcal{Y} \cup \mathcal{Z}$.

We remark that Theorem 1 completely characterises the region in the parameter space where the corresponding system (2) exhibits self sustained oscillations. Thus the necessary conditions $\mathbf{k} \in \mathcal{S}$ for the existence of such behaviour, given by Di Cera et al. [5], are here completed with the necessary and sufficient condition $\mathbf{k} \in \mathcal{PS} \cap \mathcal{S}$. Furthermore this oscillating behaviour in the interior of \mathcal{T} extends to a heteroclinic behaviour at the boundary. Therefore the period function defined in the interior of \mathcal{T} is a non-constant function; it grows by approaching the boundary.

In dimension greater than two, differential systems usually present chaotic motion in the sense that the difference between the initial conditions grows exponentially with time. This is not our case. The dynamic behaviour of family (2) is very simple and non-strange attractors appear. In fact, as showed in Theorem 1(b), in absence of periodic orbits every orbit goes from one side of the boundary of \mathcal{T} to another. Nevertheless, we can remark certain singular situations related to the form and location of the limit sets. One of these limit set configurations is described in the next result. Before stating it we consider the following singular points in the edges \mathcal{R}_{px} and \mathcal{R}_{yz} , respectively

$$\begin{aligned} \mathbf{p}_{px} &= \left(\frac{k_2}{k_1+k_2}, 0, \frac{k_1}{k_1+k_2} \right), & \mathbf{q}_{px} &= \left(\frac{k_3}{k_3+k_4}, 0, \frac{k_4}{k_3+k_4} \right), \\ \mathbf{p}_{yz} &= \left(0, \frac{k_4}{k_1+k_4}, 0 \right), & \mathbf{q}_{yz} &= \left(0, \frac{k_3}{k_3+k_2}, 0 \right). \end{aligned} \quad (3)$$

When \mathbf{k} is in the manifold $\mathcal{PS} \cap \mathcal{S}$, the points \mathbf{p}_{px} and \mathbf{q}_{px} are equal and they coincide with one of the endpoints of the segment R defined in Theorem 1(a-1). Similarly, the points \mathbf{p}_{yz} and \mathbf{q}_{yz} are also equal and they coincide with the other endpoint of R . On the other hand, when $\mathbf{k} \in \mathcal{PS} \setminus \mathcal{S}$, we define the following segments contained in the edges \mathcal{R}_{px} and \mathcal{R}_{yz} , respectively

$$s_{px} = \{ \mathbf{p}_{px} + r(\mathbf{q}_{px} - \mathbf{p}_{px}) : r \in [0, 1] \}, \quad s_{yz} = \{ \mathbf{p}_{yz} + r(\mathbf{q}_{yz} - \mathbf{p}_{yz}) : r \in [0, 1] \}. \quad (4)$$

To clarify the exposition of the next result we introduce the subsets $\mathcal{PS}_+ = \{ \mathbf{k} \in \mathbb{R}^4 : k_i > 0 \}$ and $\mathcal{PS}_- = \{ \mathbf{k} \in \mathbb{R}^4 : k_i < 0 \}$ which form a partition of \mathcal{PS} .

Theorem 2 Suppose that $\mathbf{k} \in \mathcal{PS} \setminus \mathcal{S}$.

- (a) Each of the two limit sets of every orbit in the interior of \mathcal{T} is formed by a singular point contained in the segments s_{px} and s_{yz} . In particular, given a point \mathbf{p} in the interior of \mathcal{T} , if $\mathbf{k} \in \mathcal{PS}_+ \cap \mathcal{S}^+$ or $\mathbf{k} \in \mathcal{PS}_- \cap \mathcal{S}^-$, then $\alpha(\gamma_{\mathbf{p}}) \in s_{yz}$ and $\omega(\gamma_{\mathbf{p}}) \in s_{px}$; and if $\mathbf{k} \in \mathcal{PS}_+ \cap \mathcal{S}^-$ or $\mathbf{k} \in \mathcal{PS}_- \cap \mathcal{S}^+$ then $\alpha(\gamma_{\mathbf{p}}) \in s_{px}$ and $\omega(\gamma_{\mathbf{p}}) \in s_{yz}$.
- (b) Each of the two limit sets of every orbit in $\mathcal{X} \cup \Sigma$ is a singular point contained in the edge \mathcal{R}_{px} . Moreover, given two orbits $\gamma_1 \subset \mathcal{X}$ and $\gamma_2 \subset \Sigma$ such that $\omega(\gamma_1) = \alpha(\gamma_2)$, then $\omega(\gamma_2) \neq \alpha(\gamma_1)$.
- (c) Each of the two limit sets of every orbit in $\mathcal{Y} \cup \mathcal{Z}$ is a singular point contained in the edge \mathcal{R}_{yz} . Moreover, given two orbits $\gamma_1 \subset \mathcal{Y}$ and $\gamma_2 \subset \mathcal{Z}$ such that $\omega(\gamma_1) = \alpha(\gamma_2)$, then $\omega(\gamma_2) \neq \alpha(\gamma_1)$.
- (d) The behaviour of the flow in \mathcal{T} is topologically equivalent to the one drawn in Figure 1.

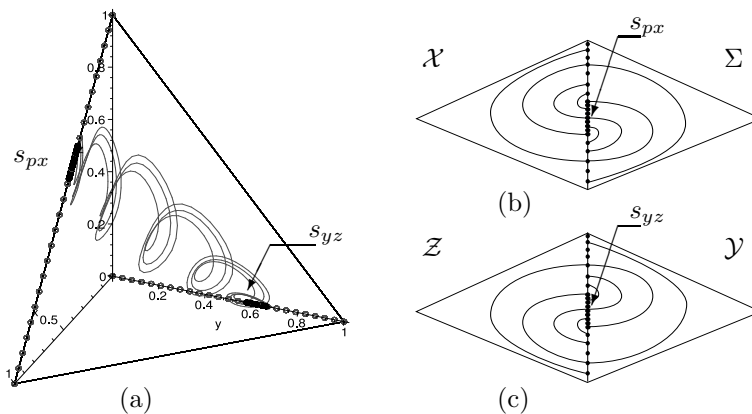


Figure 2: Behaviour of the flow of system (2) for $\mathbf{k} \in \mathcal{PS} \setminus \mathcal{S}$: (a) in the interior of \mathcal{T} ; (b) at the edges $\mathcal{X} \cup \Sigma$ and (c) at the edges $\mathcal{Y} \cup \mathcal{Z}$.

From Theorem 2 we conclude that the bifurcation taking place at the manifold \mathcal{S} is not only characterised by the behaviour of the flow in the interior of \mathcal{T} . In addition it must be described by taking into account the changes of the limit sets s_{yz} and s_{px} at the boundary of \mathcal{T} . Hence when $\mathbf{k} \in \mathcal{PS}_+ \cap \mathcal{S}^+$ the orbits in the faces $\mathcal{Y} \cup \mathcal{Z}$ are organised in spirals around the segment s_{yz} moving away from it; and the orbits in the faces $\mathcal{X} \cup \Sigma$ are organised in spirals around the segment s_{px} approaching it. When $\mathbf{k} \in \mathcal{PS} \cap \mathcal{S}$, the segment s_{yz} reduces to the singular point \mathbf{p}_{yz} and the segment s_{px} reduce to the singular point \mathbf{p}_{px} ; furthermore the flow in the faces $\mathcal{Y} \cup \mathcal{Z}$ and $\mathcal{X} \cup \Sigma$ describes heteroclinic orbits around them. Finally, when $\mathbf{k} \in \mathcal{PS}_+ \cap \mathcal{S}^-$ the orbits in $\mathcal{Y} \cup \mathcal{Z}$ are organised in spiral around the segment s_{yz} approaching it; and the orbits in the faces $\mathcal{X} \cup \Sigma$ are organised in spirals around the segment s_{px} moving away from it. The bifurcation set of system (2) is drawn in Figure 1. From this we conclude that the bifurcation at the boundary is similar to a focus–center–focus bifurcation.

The paper is organised as follows. In Section 2 we analyse the existence and the local behaviour of the singular points both in the interior and in the boundary of \mathcal{T} . In Section 3 we deal with the first integrals of the flow and we characterise the integrability of the flow. Using these first integrals, in Section 4 we analyse the flow at the boundary of \mathcal{T} . In Section 5 and by using again the first integrals we analyse the flow in the interior of \mathcal{T} and we prove the main results of the paper.

2 Singular points

In the following proposition we summarise the results about the existence, location and stability of the singular points of system (2).

Proposition 1 *The half straight lines \mathcal{R}_{px} and \mathcal{R}_{yz} are formed by singular points.*

- (a) *If $\mathbf{k} \in \mathcal{NZ}$ there are no other singular points in the boundary of the simplex.*

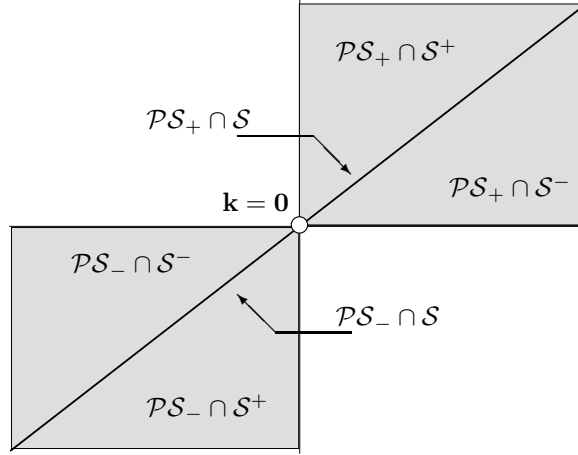


Figure 3: Representation of the bifurcation set in a two dimensional parameter space.

(a-1) Suppose that $\mathbf{k} \in \mathcal{PS} \cap \mathcal{S}$. The open segment

$$R = \left\{ \left(\frac{k_3}{k_4}z, \frac{k_4 - (k_4 + k_3)z}{k_4 + k_1}, z \right) : 0 < z < \frac{k_4}{k_3 + k_4} \right\}$$

is formed by all the singular points in the interior of the region \mathcal{T} . Moreover the jacobian matrix of the vector field evaluated at each of these points has one real eigenvalue equal to zero and two purely imaginary eigenvalues.

(a-2) Suppose that $\mathbf{k} \in \mathcal{NZ} \setminus \{\mathcal{PS} \cap \mathcal{S}\}$. There are no singular points in the interior of region \mathcal{T} .

(b) Suppose that $\mathbf{k} \notin \mathcal{NZ}$ and $\mathbf{k} \neq \mathbf{0}$. There are no singular points in the interior of region \mathcal{T} .

Proof. Straight forward computations show that the half straight lines \mathcal{R}_{px} and \mathcal{R}_{yz} are formed by singular points.

Suppose now that $\mathbf{k} \in \mathcal{NZ}$. Hence none of the components of the parameter \mathbf{k} is zero. In this case the singular points are given by the solutions to the following systems

$$\left. \begin{array}{l} x = 0 \\ yz = 0 \\ z(-k_2y + k_3(1 - y - z)) = 0 \end{array} \right\} \begin{array}{l} -x(1 - x - z) = 0 \\ y = 0 \\ z(1 - x - z) = 0 \end{array}$$

$$\left. \begin{array}{l} x(k_1y - k_4(1 - x - y)) = 0 \\ -yx = 0 \\ z = 0 \end{array} \right\} \begin{array}{l} k_4x + (k_1 + k_4)y + k_4z = k_4 \\ (k_1 + k_4)y + (k_3 + k_4)z = k_4 \\ (k_2k_4 - k_1k_3)(y + z) = k_2k_4 - k_1k_3 \end{array}$$

where in the last one we impose $xyz \neq 0$ to avoid repetitions. From the three first systems it is easy to conclude that there are no other singular points that those in the half straight lines \mathcal{R}_{px} and \mathcal{R}_{yz} . With respect to the last one we distinguish two situations.

First let us suppose that $\mathbf{k} \notin \mathcal{S}$, that is $k_2k_4 - k_1k_3 \neq 0$. From the third equation it follows that $y + z = 1$, and therefore $x = 0$. Since $k_1k_4 \neq 0$ from the first equation we conclude that $y = 0$ and $z = 1$. Hence the singular point is one of the endpoints of the edge \mathcal{R}_{yz} ; i.e. it does not belong to the interior of \mathcal{T} .

Suppose now that $\mathbf{k} \in \mathcal{S}$, that is $k_2k_4 - k_1k_3 = 0$. Thus the linear system is equivalent to the following one

$$\left. \begin{array}{l} k_4x + (k_1 + k_4)y + k_4z = k_4, \\ (k_1 + k_4)y + (k_3 + k_4)z = k_4. \end{array} \right\}$$

If $k_1 + k_4 = 0$, then from the first equation we obtain $x + z = 1$. Therefore $y = 0$ and the singular point belongs to \mathcal{R}_{px} . On the contrary, if $k_1 + k_4 \neq 0$, then there exists a straight line of singular points parametrically defined

by $x = zk_3/k_4$ and $y = (k_4 - (k_3 + k_4)z)/(k_1 + k_4)$. Since the singular points in the interior of \mathcal{T} must satisfy that $x > 0, y > 0, z > 0$ and $x + y + z < 1$, then there exist singular points in the interior of \mathcal{T} if and only if

$$\frac{k_3}{k_4} > 0, \quad \frac{k_3 + k_4}{k_1 + k_4} z < \frac{k_4}{k_1 + k_4}, \quad \frac{k_1}{k_4} \left(\frac{k_3 + k_4}{k_1 + k_4} z \right) < \frac{k_1}{k_1 + k_4}, \quad z > 0.$$

It is easy to check that the previous inequalities are equivalent to

$$\frac{k_3}{k_4} > 0, \quad \frac{k_3 + k_4}{k_1 + k_4} z < \frac{k_4}{k_1 + k_4}, \quad \frac{k_1}{k_4} > 0, \quad z > 0.$$

Since $\mathbf{k} \in \mathcal{S}$ we have $k_1/k_4 = k_2/k_3$. Therefore we conclude that there exist singular points in the interior of \mathcal{T} if and only if all the components of \mathbf{k} have the same sign; that is $\mathbf{k} \in \mathcal{PS}$. In such case these singular points are given by

$$x = \frac{k_3}{k_4} z, \quad y = \frac{k_4 - (k_3 + k_4)z}{k_1 + k_4}, \quad 0 < z < \frac{k_4}{k_1 + k_4}, \quad (5)$$

which proves statement (a-1).

The jacobian matrix of the vector field defined by the differential equation (2) and evaluated at the singular points (5) is given by

$$\begin{pmatrix} k_3 z & (k_2 + k_3)z & k_3 z \\ -k_1 y & 0 & k_2 y \\ -k_3 z & -(k_2 + k_3)z & -k_3 z \end{pmatrix}$$

The characteristic polynomial is equal to $\lambda(\lambda^2 + b) = 0$, where $b = zy(k_1 + k_2)(k_2 + k_3)$. Since $\mathbf{k} \in \mathcal{PS}$ the coefficient b is positive. Then we get one zero eigenvalue and a pair of complex conjugated eigenvalues with zero real part. From this we conclude the statement (a-2).

If $\mathbf{k} \notin \mathcal{NZ}$ and $\mathbf{k} \neq \mathbf{0}$, then at least one of the coordinates of \mathbf{k} is equal to zero and at least one is different from zero. Without loss of generality we suppose that $k_1 = 0$ and $k_2 \neq 0$. From the second equations in (2) we conclude that the singular points are contained in the boundary of \mathcal{T} . This proves the statement (b). ■

Proposition 2 *If $\mathbf{k} \in \mathcal{PS} \setminus \mathcal{S}$, then none singular point in either $\mathcal{R}_{px} \setminus s_{px}$ or $\mathcal{R}_{yz} \setminus s_{yz}$ is the limit set of an orbit in the interior of the region \mathcal{T} .*

Proof. Let \mathbf{p} be a point in the set $\mathcal{R}_{px} \setminus s_{px}$, that is $\mathbf{p} = (x_0, 0, 1 - x_0)$ where either

$$x_0 > \max \left\{ \frac{k_2}{k_1 + k_2}, \frac{k_3}{k_3 + k_4} \right\} \quad \text{or} \quad x_0 < \min \left\{ \frac{k_2}{k_1 + k_2}, \frac{k_3}{k_3 + k_4} \right\}, \quad (6)$$

see expression (3). If we consider a point \mathbf{p} in the set $\mathcal{R}_{yz} \setminus s_{yz}$, the following arguments can be applied in a similar way.

Through the change of variables $\bar{x} = x - x_0$, $\bar{y} = y$ and $\bar{z} = z - 1 + x_0$, system (2) can be written as system $\dot{\bar{\mathbf{x}}} = A\bar{\mathbf{x}} + \mathbf{Q}(\bar{\mathbf{x}})$ where $\bar{\mathbf{x}} = (\bar{x}, \bar{y}, \bar{z})^T$,

$$A = \begin{pmatrix} k_4 x_0 & (k_1 + k_4)x_0 & k_4 x_0 \\ 0 & k_2 - (k_1 + k_2)x_0 & 0 \\ k_3(x_0 - 1) & (k_2 + k_3)(x_0 - 1) & k_3(x_0 - 1) \end{pmatrix} \quad \text{and} \quad \mathbf{Q}(\bar{\mathbf{x}}) = \begin{pmatrix} \bar{x}(k_4 \bar{x} + (k_1 + k_4)\bar{y} + k_4 \bar{z}) \\ \bar{y}(k_2 \bar{z} - k_1 \bar{x}) \\ \bar{z}(-k_3 \bar{x} - (k_2 + k_3)\bar{y} - k_3 \bar{z}) \end{pmatrix}.$$

The eigenvalues of the matrix A are $\lambda_1 = 0, \lambda_2 = (k_3 + k_4)x_0 - k_3$ and $\lambda_3 = k_2 - x_0(k_1 + k_2)$. From (6) it is easy to conclude that $\lambda_2 \lambda_3 < 0$. Therefore there exists a regular matrix P such that $PAP^{-1} = \text{diag}\{0, \lambda_2, \lambda_3\}$.

Going through the change of coordinates $\mathbf{x}_p = P\bar{\mathbf{x}}$ the system can be rewritten as

$$\begin{cases} \dot{x}_p = \frac{k_2 z_p - k_3 y_p}{k_1 k_4 x_0} (k_4 k_1 x_p + k_1(x_0 - 1)(k_3 + k_4)y_p + k_4(x_0 - 1)(k_2 + k_4)z_p) \\ \dot{y}_p = \frac{y_p}{k_1 k_4 x_0} ((\lambda_2 - (k_3 + k_4)x_p)k_1 k_4 x_0 + k_1(k_3^2(1 - x_0) + k_4^2 x_0)y_p + k_4(k_1 k_4 x_0 + k_2 k_3(1 - x_0))z_p) \\ \dot{z}_p = \frac{z_p}{k_1 k_4 x_0} ((\lambda_3 + (k_2 + k_1)x_p)k_1 k_4 x_0 - k_1(k_1 k_4 x_0 + k_2 k_3(1 - x_0))y_p - k_2(k_2^2(1 - x_0) + k_1^2 x_0)z_p) \end{cases} \quad (7)$$

System (7) have two invariant planes $\{y_p = 0\}$ and $\{z_p = 0\}$ intersecting at a straight line formed by singular points, which corresponds with the segment \mathcal{R}_{px} . The direction of the vector field in a sufficiently small neighbourhood of the origin satisfies that

$$\text{sign}(\dot{y}_p) = \text{sign}(y_p)\text{sign}(\lambda_2)$$

$$\text{sign}(\dot{z}_p) = \text{sign}(z_p)\text{sign}(\lambda_3).$$

We conclude that the origin is neither the α -limit set nor the ω -limit set of any orbit in the interior of the regions $\{y_p > 0, z_p > 0\}$, $\{y_p > 0, z_p < 0\}$, $\{y_p < 0, z_p > 0\}$ and $\{y_p < 0, z_p < 0\}$. From this we conclude the proposition. ■

3 Invariant algebraic surfaces and first integrals

In 1878 Darboux showed how to construct first integrals of a planar polynomial vector field possessing sufficient invariant algebraic curves. Recent works improved the Darboux's exposition taking into account other dynamical objects like exponential factors and independent singular points, see [2], [3] and [4] for more details. The extension of the Darboux theory to n -dimensional polynomial differential systems can be found in the work by Llibre and Rodríguez [10]. A brief introduction to the three dimensional case can be found in [1]

Following [1] a first integral of system (2) is a real function F non-constant over the region \mathcal{T} and such that the level surfaces $\mathcal{F}_C = \{(x, y, z) \in \mathcal{T} : F(x, y, z) = C\}$ are invariants by the flow; that is

$$XF = \frac{\partial F}{\partial x}\dot{x} + \frac{\partial F}{\partial y}\dot{y} + \frac{\partial F}{\partial z}\dot{z} = 0$$

where $(\dot{x}, \dot{y}, \dot{z})$ is the vector field associated to the differential system. Thus the existence of a first integral allows the reduction of the dimension of the problem by one. Moreover, the existence of two independent first integrals allows the integrability of the flow.

Let $f \in \mathbb{R}[x, y, z]$ be a polynomial function. The algebraic surface $f = 0$ is called an invariant algebraic surface of the system (2) if there exists a polynomial $K \in \mathbb{R}[x, y, z]$ such that $Xf = Kf$. The polynomial K is called the cofactor of f . The following result is a corollary of the Theorem 2 in [1].

Theorem 3 *Suppose that the polynomial vector field (2) admits p invariant algebraic surfaces $f_i = 0$ with cofactor K_i for $i = 1, 2, \dots, p$. If there exist $\lambda_i \in \mathbb{R}$ not all zero such that $\sum_{i=1}^p \lambda_i K_i = 0$, then the function $f_1^{\lambda_1} f_2^{\lambda_2} \dots f_p^{\lambda_p}$ is a first integral of the vector field (2).*

The next result summarises the first integrals and the conditions for their existence. Sufficient conditions for the integrability of system (2) are also given.

Proposition 3 *Consider the functions $H(x, y, z) = x^{k_2} z^{k_1}$, $\tilde{H}(x, y, z) = x^{k_3} z^{k_4}$, $V(x, y, z) = y^{k_3} (1 - x - y - z)^{k_2}$ and $\tilde{V}(x, y, z) = y^{k_4} (1 - x - y - z)^{k_1}$.*

- (a) *If $\mathbf{k} \in \mathcal{S} \cap \mathcal{NZ}$, then H, V, \tilde{H} and \tilde{V} are first integrals which satisfy that $\tilde{H}^{k_1} = H^{k_4}$ and $\tilde{V}^{k_3} = V^{k_4}$. Moreover H and V are independent.*
- (b) *If $\mathbf{k} \in \mathcal{S} \setminus \mathcal{NZ}$, then two of the previous functions are first integrals and they are independent.*
- (c) *If $\mathbf{k} \notin \mathcal{S}$, then none of the previous functions is a first integral in \mathcal{T} .*

Proof. Consider the algebraic surfaces $f_1(x, y, z) = x$, $f_2(x, y, z) = y$, $f_3(x, y, z) = z$ and $f_4(x, y, z) = x + y + z - 1$. It is easy to check that $Xf_i = f_i K_i$, with $i = 1, 2, 3, 4$, where $K_1(x, y, z) = k_4 x + (k_1 + k_4)y + k_4 z - k_4$, $K_2(x, y, z) = -k_1 x + k_2 z$, $K_3(x, y, z) = -k_3 x - (k_2 + k_3)y - k_3 z + k_3$ and $K_4(x, y, z) = k_4 x - k_3 z$. Therefore $f_i = 0$ is an invariant surface with cofactor K_i , with $i = 1, 2, 3, 4$.

From Theorem 3, if there exist λ_i not all zero and such that $\sum_{i=1}^4 \lambda_i K_i = 0$, then $F = f_1^{\lambda_1} f_2^{\lambda_2} f_3^{\lambda_3} f_4^{\lambda_4}$ is a first integral of system (2). Since

$$\sum_{i=1}^4 \lambda_i K_i = (\lambda_4 k_4 - \lambda_2 k_1)x + (\lambda_1 k_1 - \lambda_3 k_2)y + (\lambda_2 k_2 - \lambda_4 k_3)z + (\lambda_3 k_3 - \lambda_1 k_4)(1 - x - y - z)$$

the existence of such λ_i is equivalent to the existence of non-trivial solutions of the homogeneous linear systems

$$\begin{pmatrix} k_1 & -k_2 \\ -k_4 & k_3 \end{pmatrix} \begin{pmatrix} \lambda_1 \\ \lambda_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \text{ and } \begin{pmatrix} k_2 & -k_3 \\ -k_1 & k_4 \end{pmatrix} \begin{pmatrix} \lambda_2 \\ \lambda_4 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}. \quad (8)$$

Note that the determinant of both previous systems is equal to $k_1k_3 - k_2k_4$. Therefore when \mathbf{k} belongs to the set \mathcal{S} there exist Darboux type first integrals of system (2).

Under the assumption $\mathbf{k} \in \mathcal{S}$ linear system (8) has the following non-trivial solutions $(\lambda_1, \lambda_2, \lambda_3, \lambda_4) \rightarrow (k_2, 0, k_1, 0), (0, k_3, 0, k_2), (k_3, 0, k_4, 0)$ and $(0, k_4, 0, k_1)$. Therefore the functions $H(x, y, z) = x^{k_2}z^{k_1}$, $V(x, y, z) = y^{k_3}(1 - x - y - z)^{k_2}$, $\tilde{H}(x, y, z) = x^{k_3}z^{k_4}$ and $\tilde{V} = y^{k_4}(1 - x - y - z)^{k_1}$ are first integrals. In fact

$$\begin{aligned} XH &= x^{k_2}z^{k_1}(1 - x - y - z)(k_1k_3 - k_2k_4) & XV &= y^{k_3}(1 - x - y - z)^{k_2}x(k_2k_4 - k_1k_3), \\ X\tilde{H} &= x^{k_3}z^{k_4}(k_1k_3 - k_2k_4)y & X\tilde{V} &= y^{k_4}(1 - x - y - z)^{k_1}(k_2k_4 - k_1k_3)z \end{aligned} \quad (9)$$

which vanish in the whole region \mathcal{T} only when $\mathbf{k} \in \mathcal{S}$.

Consider that $\mathbf{k} \in \mathcal{S} \cap \mathcal{NZ}$. Since every coordinate of \mathbf{k} is different from zero it follows that H, V, \tilde{H} and \tilde{V} are not constant in \mathcal{T} . Therefore all of these functions are first integrals. It is easy to check that $\tilde{H}^{k_1} = H^{k_4}$ and $\tilde{V}^{k_3} = V^{k_4}$. Moreover since $\nabla H(x, y, z) = x^{(k_2-1)}z^{(k_1-1)}(k_2z, 0, k_1x)$ and $\nabla V(x, y, z) = y^{(k_3-1)}(1 - x - y - z)^{(k_2-1)}(-k_2y, k_3(1 - x - y - z) - k_2y, -k_2y)$, both integrals are dependent only at the points satisfying that $k_3(1 - x - y - z) = k_2y$ and $k_2z = k_1x$. Taking into account that $k_2 \neq 0$ it follows that this set has zero Lebesgue measure. Then H and V are two independent first integrals.

Consider now that $\mathbf{k} \in \mathcal{S} \setminus \mathcal{NZ}$. Hence \mathbf{k} has one coordinate which is different from zero. Without loss of generality we assume that $k_1 \neq 0$, the remainder cases follows in a similar way. It is easy to check that H and \tilde{V} are not constant in \mathcal{T} , and therefore they are first integrals. Since $\nabla H(x, y, z) = x^{(k_2-1)}z^{(k_1-1)}(k_2z, 0, k_1x)$ and $\nabla \tilde{V}(x, y, z) = y^{(k_4-1)}(1 - x - y - z)^{(k_1-1)}(-k_1y, k_4(1 - x - y - z) - k_1y, -k_1y)$, both integrals are dependent only at the points satisfying that $k_4(1 - x - y - z) = k_1y$ and $k_2z = k_1x$. Therefore H and \tilde{V} are independent. ■

4 Behaviour at the boundary

As we have proved in Proposition 3 some of the functions H, \tilde{H}, V and \tilde{V} are first integrals over the whole region \mathcal{T} only when $\mathbf{k} \in \mathcal{S}$. Nevertheless the restriction of these functions to a particular face of \mathcal{T} results in a first integral even when $\mathbf{k} \notin \mathcal{S}$. In fact, denoting by $\tilde{H}|_{\mathcal{X}}$ the restriction of the function \tilde{H} to the face \mathcal{X} , from expression (9) it follows that $X\tilde{H}|_{\mathcal{X}} = 0$. Therefore the level curves $\tilde{H}|_{\mathcal{X}} = C^{k_4}$ are invariant by the flow. Under the assumption $k_3k_4 > 0$, these level curves define a foliation of \mathcal{X} whose leaves are given by the arcs of hyperbola $\left\{z = Cx^{-\frac{k_3}{k_4}}\right\}_{0 < C < C^*}$ where

$$C^* = \frac{k_4}{k_4 + k_3} \left(\frac{k_3}{k_4 + k_3} \right)^{\frac{k_3}{k_4}}. \quad (10)$$

Furthermore, every leaf with $0 < C < C^*$ intersects the segment \mathcal{R}_{px} at exactly two points, see Figure 4(a). The value $C = C^*$ leads to a unique intersection point with coordinates $x = k_3/(k_3 + k_4)$ and $z = k_4/(k_3 + k_4)$. Since in the face \mathcal{X} we have $y = 0$, it follows that the point corresponding to C^* is the point \mathbf{q}_{px} defined in (3).

Similarly, the restriction of V, \tilde{V} and H to the faces Y, Z and Σ respectively, are first integrals even when $\mathbf{k} \notin \mathcal{S}$, see expression (9). Consider the changes of variables $(u, v, \alpha, \beta) \rightarrow (y, z, k_2, k_3), (y, x, -k_1, -k_4)$ or (x, y, k_1, k_2) , depending on the face \mathcal{Y}, \mathcal{Z} or Σ we are looking at. Under the assumption $\alpha\beta > 0$, the level curves $V|_{\mathcal{Y}} = C^{k_2}, \tilde{V}|_{\mathcal{Z}} = C^{k_1}$ and $H|_{\Sigma} = C^{k_1}$ define a foliation on the corresponding face, whose leaves are given by the unimodal curves $\left\{v = 1 - u - Cu^{-\frac{\beta}{\alpha}}\right\}_{0 < C < C^*}$ where

$$C^* = \frac{\alpha}{\alpha + \beta} \left(\frac{\beta}{\alpha + \beta} \right)^{\frac{\beta}{\alpha}}.$$

Every leaf with $0 < C < C^*$ intersects the segment $\{v = 0, 0 < u < 1\}$ at exactly two points, see Figure 4(b). The value $C = C^*$ leads to a unique intersection point $(\beta/(\alpha + \beta), 0)$. Going back through the change of variables and adding the variable which does not appear in such change, that intersection point coincides with \mathbf{q}_{yz} , \mathbf{p}_{yz} or \mathbf{p}_{px} depending on the change of variables.

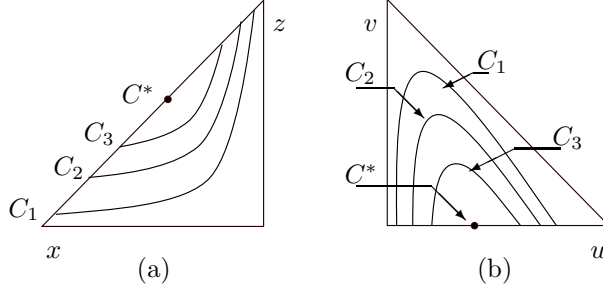


Figure 4: (a) Foliation over the face \mathcal{X} defined by the level curves $\tilde{H}|_{\mathcal{X}} = C^{k_4}$ where $0 < C_1 < C_2 < C_3 < C^*$ and \mathbf{k} in $\mathcal{PS} \setminus \mathcal{S}$. (b) Foliation over the corresponding face of the level curves $H_{\Sigma} = C^{k_1}$ or $V_Y = C^{k_2}$ or $\tilde{V}_Z = C^{k_1}$ where $0 < C_1 < C_2 < C_3 < C^*$ and \mathbf{k} in $\mathcal{PS} \setminus \mathcal{S}$. Note that figure (b) is represented in (u, v) -coordinates.

Using the geometric information of the aforementioned foliations, in the next result we summarise the behaviour of the flow of system (2) at the boundary $\partial\mathcal{T}$ for $\mathbf{k} \in \mathcal{PS}$.

Lemma 1 (a) If $\mathbf{k} \in \mathcal{PS}$, then each of the two limit sets of every orbit contained in $\mathcal{X} \cup \Sigma$ (respectively, $\mathcal{Y} \cup \mathcal{Z}$) is formed by a singular point contained in the edge \mathcal{R}_{px} (respectively, \mathcal{R}_{yz}).

(b) If $\mathbf{k} \in \mathcal{PS} \cap \mathcal{S}$, then for every pair of orbits $\gamma_1 \subset \mathcal{X}$ and $\gamma_2 \subset \Sigma$ (respectively, $\gamma_1 \subset \mathcal{Y}$ and $\gamma_2 \subset \mathcal{Z}$) satisfying that $\omega(\gamma_1) = \alpha(\gamma_2)$, it follows that $\alpha(\gamma_1) = \omega(\gamma_2)$.

(c) If $\mathbf{k} \in \mathcal{PS} \setminus \mathcal{S}$, then for every pair of orbits $\gamma_1 \subset \mathcal{X}$ and $\gamma_2 \subset \Sigma$ (respectively, $\gamma_1 \subset \mathcal{Y}$ and $\gamma_2 \subset \mathcal{Z}$) satisfying that $\omega(\gamma_1) = \alpha(\gamma_2)$, it follows that $\alpha(\gamma_1) \neq \omega(\gamma_2)$.

Proof. We restrict ourselves to consider orbits in the faces $\mathcal{X} \cup \Sigma$. The study of the orbits in the faces $\mathcal{Y} \cup \mathcal{Z}$ follows in a similar way.

Suppose that $\mathbf{k} \in \mathcal{PS}$. Hence $k_3 k_4 > 0$. Therefore every orbit γ_1 in \mathcal{X} is contained in a leaf of the foliation $z = Cx^{-\frac{k_3}{k_4}}$ with $0 < C < C^*$, which is an arc of hyperbola intersecting the edge \mathcal{R}_{px} at exactly two points. Since there are not other singular points in \mathcal{X} , see Proposition 1(a), we conclude that each of the two limit sets of γ_1 is one of these intersection points.

On the other hand we have $k_2 k_1 > 0$. Therefore every orbit γ_2 in Σ is contained in a leaf of the foliation $y = 1 - x - Cx^{-\frac{k_2}{k_1}}$, which is an unimodal curve intersecting the edge \mathcal{R}_{px} at exactly two points. We conclude again that each of the limit sets of γ_2 is one of these intersection points. From this we conclude the statement (a).

Taking into account that Σ is given by the relation $z = 1 - x - y$, we express the leaves in Σ as a function $z(x)$ in the following way $z = Cx^{-\frac{k_2}{k_1}}$.

Let $\mathbf{p} = (x_0, 0, 1 - x_0)$ be a point in the edge \mathcal{R}_{px} . There exist two positive values C_1 and C_2 such that both the leaf $z = C_1 x^{-\frac{k_3}{k_4}}$ in the face \mathcal{X} and the leaf $z = C_2 x^{-\frac{k_2}{k_1}}$ in the face Σ contain the point \mathbf{p} . On the other hand the leaf in the face \mathcal{X} intersects \mathcal{R}_{px} at a new point $(x_1, 0, 1 - x_1)$ and the leaf in the face Σ intersects \mathcal{R}_{px} at a new point $(x_2, 0, 1 - x_2)$. Since two arcs of hyperbola either intersect at most at one point or they coincide, we conclude that $k_3 k_1 = k_4 k_2$ if and only if $x_1 = x_2$. This proves the statements (b) and (c). ■

5 Behaviour in the interior

In this last section we deal with the proof of the main theorems of the paper.

We start by setting the parameter \mathbf{k} in the condition of the Theorem 1(a); that is, $\mathbf{k} \in \mathcal{PS} \cap \mathcal{S}$. Under this assumption system (2) is integrable and the functions H and V are two independent first integrals, see

Proposition 3(a). Since any level surface \mathcal{H}_C is invariant by the flow, we can consider the restriction of the flow to each of these surfaces. Of course this restricted flow is also integrable because the restriction of the function V to \mathcal{H}_C is a first integral.

On the other hand there exists exactly one singular point in the interior of \mathcal{H}_C , which comes from the intersection of the manifold \mathcal{H}_C and the segment R defined in the Proposition 1(a-1). These singular points have a zero eigenvalue and a pair of purely imaginary eigenvalues. We conclude that every orbit in the interior of \mathcal{H}_C , but the singular points, is a periodic orbit. Since this result is independent on the level surface we are working at, it follows that every orbit in the interior of the region \mathcal{T} , but the singular points, is a periodic orbit. The behaviour of the flow at the boundary of \mathcal{T} when $\mathbf{k} \in \mathcal{PS} \cap \mathcal{S}$ can be obtained from Lemma 1(b). This completes the proof of Theorem 1(a).

To prove Theorem 1(b) we consider that $\mathbf{k} \notin \mathcal{PS} \cap \mathcal{S}$ and $\mathbf{k} \neq \mathbf{0}$. We distinguish two situations: first we suppose that $\mathbf{k} \in \mathcal{S} \setminus \mathcal{PS}$. In such case \mathbf{k} belongs to the manifold \mathcal{S} . From Proposition 3 it follows that at least one of the functions H, V, \tilde{H} or \tilde{V} is a first integral. Without loss of generality we can assume that H is a first integral. Hence any level surface \mathcal{H}_C is invariant by the flow and we can consider the restriction of the flow to \mathcal{H}_C . From Proposition 1 there are not singular points in the interior of \mathcal{H}_C . Applying the Poincaré–Bendixson Theorem to the flow in the level surface \mathcal{H}_C , we conclude that the flow goes from the boundary of \mathcal{H}_C to the boundary of \mathcal{H}_C . Since these arguments are independent on the level surface, it follows that the flow goes from the boundary of \mathcal{T} to the boundary of \mathcal{T} .

Suppose now that $\mathbf{k} \notin \mathcal{S}$ and $\mathbf{k} \neq \mathbf{0}$. Since one of the coordinates of \mathbf{k} is different from zero, the level surfaces of at least one of the functions H, V, \tilde{H} and \tilde{V} can be expressed as the graph of an explicit differentiable function. For instance if $k_4 \neq 0$, then $\tilde{\mathcal{H}}_{C^{k_4}}$ is the graph of the function $z = Cx^{-\frac{k_2}{k_4}}$ defined over the face \mathcal{Z} . Each of these level surfaces split the interior of \mathcal{T} into two disjoint connected components. On the other hand since $\mathbf{k} \notin \mathcal{S}$ these level surfaces are not invariant by the flow, see Proposition 3(c). In fact the flow is transversal to them and the direction of the flow through them depends on $\mathbf{k} \in \mathcal{S}^+$ or $\mathbf{k} \in \mathcal{S}^-$, see expression (9). Since as C tends to 0 or to C^* the level surfaces $\tilde{\mathcal{H}}_{C^{k_4}}$ tend to the boundary of \mathcal{T} , we conclude that the flow in the interior of \mathcal{T} goes from one part of the boundary to another part of the boundary. That is the limit sets of every orbit in the interior of \mathcal{T} are contained in $\partial\mathcal{T}$. From this we conclude the Theorem 1(b).

Note that in the previous proof we have only used that the flow crosses through the level surfaces of some of the functions H, V, \tilde{H} or \tilde{V} , always in the same direction. This argumentation results enough to conclude that the limit sets of the orbits in \mathcal{T} are contained in the boundary. To prove Theorem 2 we need to be more precise in the location of these limit sets. To reach this goal we will control the geometry of the level surfaces.

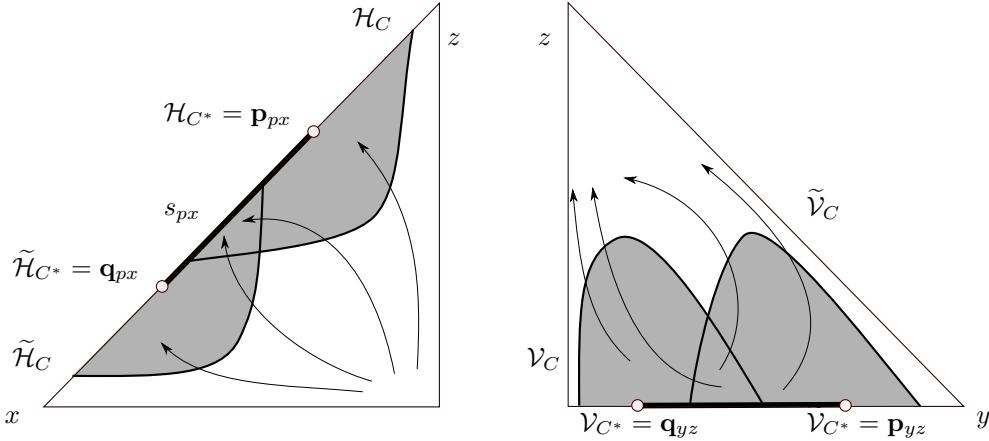


Figure 5: Representation when $\mathbf{k} \in \mathcal{PS}_+ \cap \mathcal{S}^+$ of the positive invariant regions limited by the level surfaces \mathcal{H}_C and $\tilde{\mathcal{H}}_C$; the negative invariant regions limited by the level surfaces \mathcal{V}_C and $\tilde{\mathcal{V}}_C$; the attractor set s_{px} and the repelor set s_{yz} of any given orbit in the interior of the region \mathcal{T} .

Suppose that $\mathbf{k} \in \mathcal{PS}_+ \cap \mathcal{S}^+$. Since $\mathbf{k} \notin \mathcal{S}$ the functions H and \tilde{H} are not first integrals and each level surface \mathcal{H}_C and $\tilde{\mathcal{H}}_C$ splits the region \mathcal{T} into two disjoint regions in such a way that the flow goes from one to the other. In fact since $k_3 k_4 > 0$ the intersection of $\tilde{\mathcal{H}}_C$ with any plane $\{y = y_0 : 0 < y_0 < 1\}$ is an arc of

hyperbola in the (x, z) -plane, see Figure 4(a). Similarly, since $k_1 k_2 > 0$ the intersection of \mathcal{H}_C with any plane $\{y = y_0 : 0 < y_0 < 1\}$ is an arc of hyperbola in the (x, z) -plane. The flow through \mathcal{H}_C and through $\tilde{\mathcal{H}}_C$ has the same direction as the vectors ∇H and $\nabla \tilde{H}$ respectively, see expression (9). Since $k_1 > 0$ the gradient ∇H points to the region containing the point \mathbf{p}_{px} , see the shadowed region in Figure 5. Moreover, since $k_4 > 0$ the gradient $\nabla \tilde{H}$ points to the region containing the point \mathbf{q}_{px} , see Figure 5. Therefore, in Figure 5 the flow moves from the region containing the origin to the shadowed region. On the other hand points in $\mathcal{R}_{px} \setminus s_{px}$ are not limit set of orbits in the interior of \mathcal{T} , see Proposition 2. We conclude that the ω -limit set of any given orbit in the interior of \mathcal{T} is a singular point contained in the segment s_{px} .

On the other hand, since $\mathbf{k} \notin \mathcal{S}$ the functions V and \tilde{V} are not first integrals. Moreover any of the level surfaces \mathcal{V}_C and $\tilde{\mathcal{V}}_C$ splits the region \mathcal{T} into two disjoint regions in such a way that the flow goes from one to the other. The flow through these surfaces has opposite direction to that of the gradients ∇V and $\nabla \tilde{V}$, see expression (9). Since $k_2 > 0$ the gradient ∇V points to the region containing the point \mathbf{q}_{yz} . Similarly, since $k_1 > 0$ the gradient $\nabla \tilde{V}$ points to the region containing the point \mathbf{p}_{yz} . Therefore the flow in the interior of \mathcal{T} comes from the shadowed region in the Figure 5 to the region containing the point $(0, 0, 1)$. Since points in $\mathcal{R}_{yz} \setminus s_{yz}$ are not limit set of orbits in the interior of \mathcal{T} , see Proposition 2, we conclude that the α -limit set of any given orbit in the interior of \mathcal{T} is a singular point contained in the segment s_{yz} , see Figure 5.

As we have just proved when $\mathbf{k} \in \mathcal{PS}_+ \cap \mathcal{S}^+$ the ω -limit set and the α -limit set of any given orbit in the interior of \mathcal{T} is contained in the segments s_{px} and s_{yz} , respectively. Similar arguments apply when $\mathbf{k} \in \mathcal{PS}_- \cap \mathcal{S}^-$. In both cases the behaviour of the flow at the boundary can be obtained from Lemma 1(c). This completes the proof of Theorem 2(a).

Theorem 2(b) follows by noting that a change of the sign of the parameter \mathbf{k} is equivalent to a change in the sign of time in the differential system (2).

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References

- [1] L. CAIRO AND J. LLIBRE, *Darboux integrability for 3D Lotka–Volterra systems*, J. Phys. A: Math. Gen. **33**, (2000), 2395–2406.
- [2] C. J. CHRISTOPHER, *Invariant algebraic curves and conditions for a center*, Proc. R. Soc. Edin. A, **124**, (1994). 1209.
- [3] C. J. CHRISTOPHER AND J. LLIBRE, *Algebraic aspects of integrability for polynomial systems*, Qualit. Theory Dynam. Syst., **1**, (1999). 71–95.
- [4] J. CHAVARRIGA, J. LLIBRE AND J. SOTOMAYOR, *Algebraic solutions for polynomial vector fields with emphasis in the quadratic case*, Expositions Math., **15**, (1999), 161.
- [5] DI CERA, P. E. PHILLIPSON AND J. WYMAN, *Chemical oscillations in closed macromolecular systems*, Proc. Natl. Acad. Sci. U.S., **85**, (1988). 5923–5926.
- [6] A. MURZA, I. OPREA AND G. DANGELMAYR, *Chemical oscillations in a closed sequence of protein folding equilibria*, Libertas Math., **27**, (2007). 125–130.
- [7] R. W. MCCARLEY, J. A. HOBSON, *Neuronal excitability modulation over the sleep cycle: a structural and mathematical model*, Science, **189**, (1975). 58–60.
- [8] M. BOBIENSKI, H. ZOLADEK, *The three-dimensional generalized Lotka–Volterra systems*, Ergod. Th. & Dynam. Sys., **25**, (2005). 759–791.
- [9] A. J. LOTKA, *Analytical Note on Certain Rhythmic Relations in Organic Systems*, Proc. Natl. Acad. Sci. U.S., **6**, (1920). 410–415.

- [10] J. LLIBRE AND G. RODRÍGUEZ, *Invariant hyperplanes and Darboux integrability for d -dimensional polynomial differential systems*, Bull. Sci. Math., **124**, (2000), 599–619.
- [11] V. VOLTERRA, *Leçons sur la Théorie Mathématique de la Lutte pour la vie*, Gautiers Villars, Paris, 1931.
- [12] F. COPPEX, M. DROZ, A. LIPOWSKI, *Extinction dynamics of Lotka-Volterra ecosystems on evolving networks*, Phys. Rev. E, **69**, (2004). 061901.
- [13] S. ALIZON, M. KUCERA, V. A. A. JANSEN, *Competition between cryptic species explains variations in rates of lineage evolution*, Proc. Natl. Acad. Sci. U.S., **105**, (2008). 12382–12386.
- [14] L. CAIRÓ, *Darboux First Integral Conditions and integrability of the 3D Lotka–Volterra System*, J. Non-linear Math. Phys., **7**, (2000), 511-531.
- [15] P. VAN DEN DRIESSCHE AND M. L. ZEEMAN, *Three-dimensional competitive Lotka–Volterra systems with no periodic orbits*, Siam J. Appl. Math., **58**, (1998), 227-234.
- [16] M. L. ZEEMAN, *Hopf bifurcations in competitive three dimensional Lotka–Volterra systems*, Dynam. Stability Systems, **8**, (1993), 189-217.
- [17] M. L. ZEEMAN, *On directed periodic orbits in three-dimensional competitive Lotka–Volterra systems*, in Diff. Equ. and Appl. Bio. and Ind., World Scientific, River Edge, NJ, 1996, 563–572.
- [18] M. W. HIRSCH, *Systems of differential equations that are competitive or cooperative. III: Competing species*, Nonlinearity, **1** (1998), 51–71.
- [19] J. WYMAN, *The turning wheel: A study in steady states*, Proc. Nat. Acad. Sci. USA., **72** (1975), 3983–3987.