

DYNAMICS OF A COMPETITIVE LOTKA–VOLTERRA SYSTEMS IN \mathbb{R}^3

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ABSTRACT. We provide the phase portraits of the 3-dimensional competitive Lotka–Volterra systems

$$\dot{x} = x(a - x - y - z), \quad \dot{y} = y(b - x - y - z), \quad \dot{z} = z(c - x - y - z),$$

for all the values of the parameters a , b and c with $0 < a < b < c$ in the positive octant of the Poincaré ball.

1. INTRODUCTION AND STATEMENT OF THE MAIN RESULTS

We say that a polynomial vector field $X = (P(x, y, z), Q(x, y, z), R(x, y, z))$ in \mathbb{R}^3 is quadratic if the maximum of the degrees of the polynomials P , Q and R is 2. A Lotka–Volterra system in \mathbb{R}^3 is a quadratic polynomial vector field X with x a factor of P , y a factor of Q , and z a factor of R .

The Lotka–Volterra systems, were initially proposed as a model for studying the interactions between species in two dimension, developed independently by Alfred J. Lotka in 1925 [17] and by Vito Volterra in 1926 [24]. Later on in 1936 Kolmogorov [13] extended these systems to arbitrary dimension and arbitrary degree, these kinds of extended differential systems are called Kolmogorov systems.

The Lotka–Volterra systems can model many natural phenomena such as the time evolution of conflicting species in biology [19], chemical reactions [9], hydrodynamics [5], economics [23], the coupling of waves in laser physics [14], the evolution of electrons, ions and neutral species in plasma physics [15], etc. The interest in the 3-dimensional Lotka–Volterra systems becomes more important after the work of Brenig and Goriely [3, 4], because they proved that many other differential systems, coming from physics, biology, chemistry and economics, can be transformed, using a quasimonomial formalism, into 3-dimensional Lotka–Volterra systems.

In general the dynamics of the Lotka–Volterra systems are far from being understood, although some dynamics for special families of these systems have been revealed (see [1], [2], [16], [25], [26]). Thus for instance, the theory

2010 *Mathematics Subject Classification.* Primary 34C07, Secondary 34C08.

Key words and phrases. Lotka–Volterra systems, integrability, phase portraits, Poincaré ball, competitive Lotka–Volterra systems.

on cooperative or competitive systems was developed by Hirsch in the papers [10]-[11], where he proved that these systems generically exhibits a global attractor which lies on a 2-dimensional manifold.

In this work we consider the following class of competitive Lotka–Volterra systems

$$(1) \quad \begin{aligned} \dot{x} &= x(a - x - y - z), \\ \dot{y} &= y(b - x - y - z), \\ \dot{z} &= z(c - x - y - z), \end{aligned}$$

which depends on the three parameters a , b and c such that $0 < a < b < c$. Here the dot denotes derivative with respect to the time t . We recall that a general 3-dimensional Lotka–Volterra system

$$\begin{aligned} \dot{x} &= x(a - a_1x - a_2y - a_3z), \\ \dot{y} &= y(b - b_1x - b_2y - b_3z), \\ \dot{z} &= z(c - c_1x - c_2y - c_3z), \end{aligned}$$

is called *competitive* if all its parameters a, a_i, b, b_i, c, c_i for $i = 1, 2, 3$ are positive.

The competitive systems are of interest for their applications in nature, these system can describe the dynamics of two or more species competing for the same limited food source; for the territory (which is related to food resources too), or in some way inhibit each other their growth. In competitive systems it is assumed always that the growth of each species is directly proportional to the number of individuals of the species (see [8]). For more details on the competitive systems see the mentioned papers of Hirsch [10]-[11].

For a survey of competitive and related types of systems see the book by Freedman (1980) [8]. Only very special competitive systems have the desirable property that every trajectory converges to an equilibrium as $t \rightarrow +\infty$.

The region of ecological interest in competitive systems is the first octant of \mathbb{R}^3 and the infinity of this region, that will be studied using the Poincaré compactification (see section 2).

An *invariant* is a first integral depending on the time. The invariants of the form $f(x, y, z)e^{st}$ with $s \in \mathbb{R} \setminus \{0\}$ are called *Darboux invariants*. The existence of a Darboux invariant allows to obtain information on the α -limits and ω -limits of the orbits of the differential system. So when they exist, they play an important role in the study of the dynamics of a differential system.

Note that system (1) has the Darboux invariant

$$(2) \quad I(x, y, z) = e^{(2c-b-a)t} \frac{xy}{z^2},$$

because on the solutions $(x(t), y(t), z(t))$ of system (1) we have

$$\frac{\partial I}{\partial x}\dot{x} + \frac{\partial I}{\partial y}\dot{y} + \frac{\partial I}{\partial z}\dot{z} + \frac{\partial I}{\partial t} = 0.$$

For more information about the Darboux invariants see Theorem 8.7 of [7]. Note that if $2c = a + b$, then I is a first integral of system (1), but this situation will not be considered here because under the assumption that $0 < a < b < c$ we always have that $2c > a + b$.

The objective of this work is to describe the dynamics of the Lotka–Volterra systems (1) in the positive octant of \mathbb{R}^3 adding the infinity, i.e. we are interest in describe the dynamics of system (1) on the region

$$D = \{(x, y, z) \in \mathbb{D}^3 : x \geq 0, y \geq 0, z \geq 0\}$$

of the Poincaré ball \mathbb{D}^3 .

Roughly speaking the Poincaré ball \mathbb{D}^3 is the closed unit ball centered at the origin of \mathbb{R}^3 , where its interior is identified with \mathbb{R}^3 and its boundary \mathbb{S}^2 is defined as the infinity \mathbb{R}^3 , in the sense that in the space \mathbb{R}^3 we can go to or come from the infinity in as many directions as points has the 2–dimensional sphere \mathbb{S}^2 . A polynomial differential system in \mathbb{R}^3 , i.e. in the interior of \mathbb{D}^3 can be extended to the its boundary \mathbb{S}^2 in a unique analytic way, this extension is called the Poincaré compactification of a polynomial differential system, because it was done by first time by Poincaré in [22] for the polynomial differential systems in \mathbb{R}^2 , for its extension to polynomial differential systems in \mathbb{R}^3 see [6]. For a brief introduction to Poincaré compactification see section 2.

We say that two compactified polynomial differential systems on the Poincaré ball \mathbb{D}^3 are *topologically equivalent* if there is a homeomorphism of \mathbb{D}^3 which send orbits of one system into orbits of the other system preserving or reversing the orientation of all+ the orbits.

In the next theorem we describe the phase portrait on the positive octant of the Poincaré ball, i.e. on D , of the 3–dimensional competitive Lotka–Volterra systems (1).

Theorem 1. *For every 3–dimensional competitive Lotka–Volterra system (1) the following statements hold.*

- (a) *Its phase portraits on the three invariant faces $x = 0$, $y = 0$ and $z = 0$ in the positive octant of the Poincaré ball are topologically equivalent to the ones of Figure 1(a).*
- (b) *All the points at the infinity in the positive octant of the Poincaré ball are equilibrium points. Every one of these infinite equilibria is the α –limit of a unique orbit not contained at infinity.*

- (c) *The plane $\Pi(x, y, z) = bcx + acy + abz - abc = 0$ is invariant by the flow of system. The phase portrait of the system on this plane is topologically equivalent to the one described in Figure 1(b).*
- (d) *Let $\phi_t(q)$ be the solution of the system such that $\phi_t(q) = q$ with q in the interior of the positive octant and satisfying that $\Pi(q) \neq 0$.*
- (d.1) *Then $\phi_t(q)$ tends to the attractor point $(0, 0, c)$ when $t \rightarrow +\infty$.*
- (d.2) *If $\Pi(q) < 0$, then $\phi_t(q)$ tends to the repeller $(0, 0, 0)$ when $t \rightarrow -\infty$.*
- (d.3) *If $\Pi(q) > 0$, then when $t \rightarrow -\infty$ the orbit $\phi_t(q)$ tends to some infinite equilibrium point contained in the boundary of the positive octant of the Poincaré ball.*

This work is organized as follows. In section 2 we present some basic definitions and some preliminary results necessary to prove Theorem 1. In section 3 we prove Theorem 1.

2. PRELIMINARIES

2.1. Poincaré compactification of \mathbb{R}^3 . In order to give a detailed proof of Theorem 1 we need the Poincaré compactification.

We consider a polynomial vector field $\mathcal{X} = (P, Q, R)$ associated to the polynomial differential system

$$\dot{x} = P(x, y, z), \quad \dot{y} = Q(x, y, z), \quad \dot{z} = R(x, y, z).$$

The degree n of \mathcal{X} is defined as $n = \max\{\deg(P), \deg(Q), \deg(R)\}$.

Now we shall describe the equations of the Poincaré compactification of a polynomial differential system in \mathbb{R}^3 .

We consider the local charts (U_k, ϕ_k) and (V_k, ψ_k) for $k = 1, 2$ on the disc \mathbb{D}^3 defined by

$$\begin{aligned} U_k &= \{x = (x_1, x_2, x_3) \in \mathbb{D}^3 : x_k > 0\}, \\ V_k &= \{x = (x_1, x_2, x_3) \in \mathbb{D}^3 : x_k < 0\}, \end{aligned}$$

where the diffeomorphisms $\phi_k : U_k \rightarrow \mathbb{R}^3$ for $k = 1, 2, 3$ are

$$\begin{aligned} \phi_1(x) &= \left(\frac{x_2}{x_1}, \frac{x_3}{x_1}, \frac{1}{x_1} \right) = (z_1, z_2, z_3), & \phi_2(x) &= \left(\frac{x_1}{x_2}, \frac{x_3}{x_2}, \frac{1}{x_2} \right) = (z_1, z_2, z_3), \\ \phi_3(x) &= \left(\frac{x_1}{x_3}, \frac{x_2}{x_3}, \frac{1}{x_3} \right) = (z_1, z_2, z_3), \end{aligned}$$

and $\psi_k(x) = -\phi_k(x)$.

Note that the coordinates (z_1, z_2, z_3) have different meaning depending on local chart, but the points of the infinity, i.e. the points of the boundary \mathbb{S}^2 of \mathbb{D}^3 all have the coordinate $z_3 = 0$.

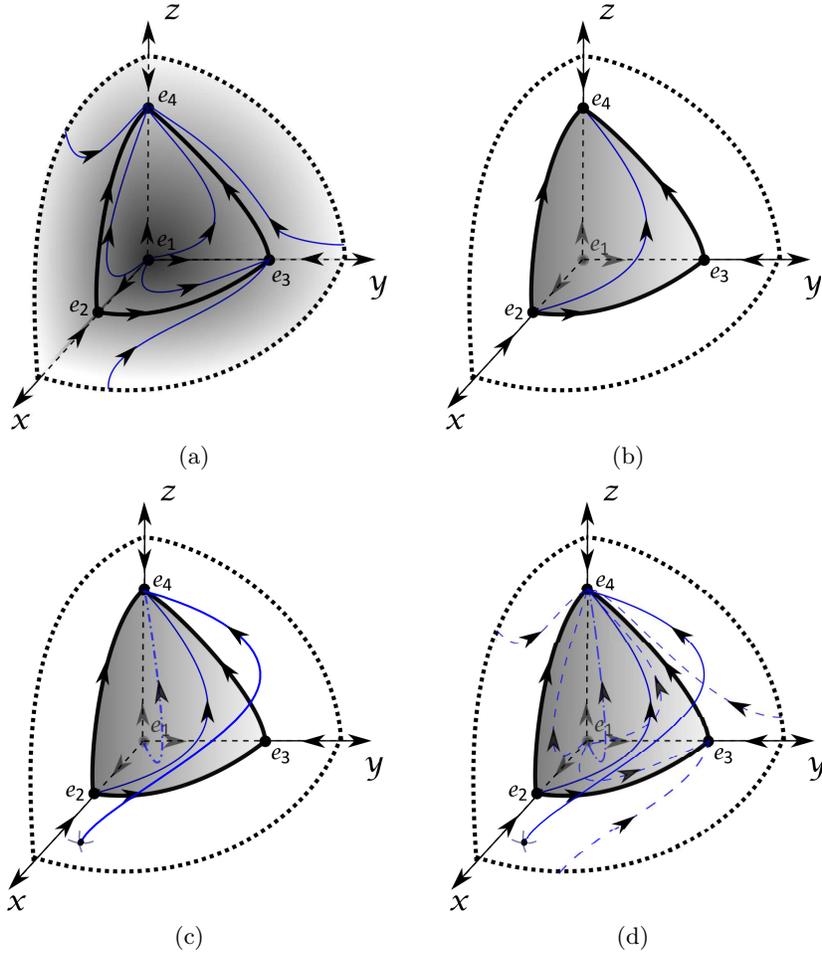


FIGURE 1. The phase portraits of system (1) in the positive first octant of the Poincaré ball. (a) On the boundaries $x = 0$, $y = 0$ and $z = 0$. (b) On the invariant plane $\Pi : bcx + bcy + abz - abc = 0$. (c) In the interior of the Poincaré ball, considering one orbit passing for q such that $\Pi(q) < 0$, other with $\Pi(q) = 0$ and other with $\Pi(q) > 0$. (d) Phase portrait in the first octant of the Poincaré ball, the dashed lines are in the boundaries, the dashed and dotted line satisfied $\Pi(q) < 0$.

Now we give the expression of the compactified vector field $p(\mathcal{X})$ of the polynomial vector field $X = (P, Q, R)$ in each local chart. The expression of the compactified analytical vector field $p(\mathcal{X})$ of \mathcal{X} of degree n on the local chart U_1 of \mathbb{D}^3 is

$$(3) \quad z_3^n (-z_1 P(z) + Q(z), -z_2 P(z) + R(z), -z_3 P(z)),$$

where $z = (1/z_3, z_1/z_3, z_2/z_3)$.

In a similar way the expression of $p(\mathcal{X})$ in U_2 is

$$(4) \quad z_3^n (-z_1 Q(z) + P(z), -z_2 Q(z) + R(z), -z_2 Q(z)),$$

where $z = (z_1/z_3, 1/z_3, z_2/z_3)$.

Finally the vector field $p(\mathcal{X})$ in U_3 is

$$(5) \quad z_3^n (-z_1 R(z) + P(z), -z_2 R(z) + Q(z), -z_2 R(z)),$$

where $z = (z_1/z_3, z_2/z_3, 1/z_3)$.

The singular points of $p(\mathcal{X})$ which are on the boundary \mathbb{S}^2 of \mathbb{D}^3 (at $z_3 = 0$) are called *infinite singular points*, and we call *finite singular points* to the ones which are in the interior of \mathbb{D}^3 .

From equations (3), (4) and (5) it follows that the infinity \mathbb{S}^2 of the Poincaré disc is invariant under the flow of the compactified vector field $p(\mathcal{X})$. For studying its infinite singular points we only need to study the ones that are on the local chart U_1 , in U_2 with $z_1 = 0$, and the origin of the local chart U_3 in case that this be a singular point.

The expression for $p(\mathcal{X})$ in the local chart V_k is the same as in U_k multiplied by $(-1)^{n-1}$. Therefore the infinite singular points appear on pairs diametrically opposite on \mathbb{S}^2 with the same stability if n is odd and with the opposite stability if n is even. For more details on the Poincaré compactification in \mathbb{R}^3 see [6].

As we said in the introduction two compactified polynomial differential systems on the Poincaré ball \mathbb{D}^3 are *topologically equivalent* if there is a homeomorphism of \mathbb{D}^3 sending orbits of one to the other system, either preserving or reversing the orientation of all the orbits.

2.2. Poincaré compactification of \mathbb{R}^2 . See chapter 5 of [7] for the expressions of the compactified vector field of a polynomial differential system in \mathbb{R}^3 .

Now we shall see how to characterize the phase portrait of a compactified vector field $p(X)$ in the Poincaré disc \mathbb{D}^2 defined by the invariant planes $x = 0$, $y = 0$ and $z = 0$.

Let Y be the restriction of the Lotka–Volterra system (1) on some of the invariant planes $x = 0$, $y = 0$ and $z = 0$. A *separatrix* of $p(Y)$ is an orbit which is either an equilibrium point, or a trajectory which lies in the boundary of a hyperbolic sector of a finite or an infinite equilibrium point, or any orbit contained in \mathbb{S}^1 (the boundary of D^2 , i.e. the infinity of the plane), or a limit cycle. Neumann [20] proved that the set formed by all separatrices of $p(Y)$, denoted by $S(p(Y))$ is closed.

The open connected components of $\mathbb{D}^2 \setminus S(p(Y))$ are called canonical regions of Y or of $p(Y)$. A *separatrix configuration* is the union of $S(p(Y))$ plus one orbit chosen in each canonical region. Two separatrix configurations $S(p(Y))$ and $S(p(\mathcal{Y}))$ are *topologically equivalent* if there is an orientation preserving or reversing homeomorphism which maps the trajectories of $S(p(Y))$ into the trajectories of $S(p(\mathcal{Y}))$. The following result is due to Markus [18], Neumann [20] and Peixoto [21], who found it independently.

Theorem 2. *The phase portraits in the Poincaré disc \mathbb{D}^2 of two compactified polynomial vector fields $p(Y)$ and $p(\mathcal{Y})$ are topologically equivalent, if and only if, their separatrix configurations $S(p(Y))$ and $S(p(\mathcal{Y}))$ are topologically equivalent.*

3. PHASE PORTRAITS OF SYSTEM (1)

In this section we study all the phase portraits of the 3–dimensional Lotka–Volterra systems (1) in the positive octant of the Poincaré ball. Initially we study the finite and infinite singular points as function of the parameters a , b and c .

First note that system (1) has always the three invariant planes $x = 0$, $y = 0$ and $z = 0$.

We start with the study of the infinite singular points, for this purpose we use the Poincaré compactification. System (1) in local chart U_1 is

$$(6) \quad \dot{z}_1 = z_1 z_3 (b - a), \quad \dot{z}_2 = z_2 z_3 (c - a), \quad \dot{z}_3 = z_3 (1 + z_1 + z_2 - a z_3),$$

in the local chart U_2 is

$$(7) \quad \dot{z}_1 = z_1 z_3 (a - b), \quad \dot{z}_2 = z_2 z_3 (c - b), \quad \dot{z}_3 = z_3 (1 + z_1 + z_2 - b z_3),$$

and in the local chart U_3 is

$$(8) \quad \dot{z}_1 = z_1 z_3 (a - c), \quad \dot{z}_2 = z_2 z_3 (b - c), \quad \dot{z}_3 = z_3 (1 + z_1 + z_2 - c z_3).$$

From systems (6), (7) and (8) we get that all the points at infinity (i.e. all the points having the coordinate $z_3 = 0$) are equilibrium points. Moreover, the eigenvalues of the linear part of those systems at these equilibrium points have always one positive eigenvalue, and the eigenvalue 0 with multiplicity two. So by the theory of normal hyperbolicity (see for instance [12]) every equilibrium point is the α –limit of a unique orbit. Roughly speaking, the whole infinity of the positive octant in the Poincaré ball is a repeller. In short we have proved statement (b) of Theorem 1.

Now we study the finite singular points. System (1) has four finite equilibria: namely

$$e_1 = (0, 0, 0), \quad e_2 = (a, 0, 0), \quad e_3 = (0, b, 0) \text{ and } e_4 = (0, 0, c).$$

The linear matrix of system (1) is

$$(9) \quad M = \begin{pmatrix} a - 2x - y - z & -x & -x \\ -y & b - x - 2y - z & -y \\ -z & -z & c - x - y - 2z \end{pmatrix}.$$

Since the eigenvalues at the origin of the matrix M are a , b and c , the origin is a repeller.

The eigenvalues of M at e_2 are $-a$, $b - a$ and $c - a$, so taking into account their eigenvectors the equilibrium e_2 has an 1-dimensional stable manifold contained in the positive x -axis, and a 2-dimensional unstable manifold. Moreover the equilibrium e_2 restricted to the planes $y = 0$ and $z = 0$ is a saddle.

The eigenvalues of M at e_3 are $a - b$, $-b$ and $c - b$, so taking into account their eigenvectors the equilibrium e_3 has a 2-dimensional stable manifold contained in the positive quadrant of the plane $z = 0$ (restricted to this plane e_3 is a stable node), and an 1-dimensional unstable manifold contained in the positive quadrant of the plane $x = 0$ (restricted to this plane e_3 is a saddle).

Finally the eigenvalues of M at e_4 are $a - c$, $b - c$ and $-c$, therefore e_4 is an attractor.

We note that the finite equilibria are all on the boundary of the positive octant of \mathbb{R}^3 , more precisely at the origin and on the positive axes of this octant.

We shall study the phase portrait of system (1) on the three faces $x = 0$, $y = 0$ and $z = 0$ of the closed positive octant in the Poincaré ball. Taking into account the local phase portraits of the finite equilibria on these three faces, and that the axes x , y and z are invariant (i.e. if an orbit has point on some of these axes it is contained in that axis), then we obtain the phase portraits described in Figure 1(a). This completes the proof of statement (a) of Theorem 1.

Now we shall study the phase portrait of system (1) in the interior of the positive octant.

First we shall prove that the plane $\Pi(x, y, z) = bcx + acy + abz - abc = 0$ that contains the three equilibria e_2 , e_3 and e_4 is invariant by the flow of system (1). Indeed, since

$$\frac{f\Pi}{dt} = D[\Pi, x]\dot{x} + D[\Pi, y]\dot{y} + D[\Pi, z]\dot{z} = -(x + y + z)\Pi,$$

on the points (x, y, z) where $\Pi(x, y, z) = 0$ its derivative with respect to the time t also is zero, consequently the plane $\Pi(x, y, z) = 0$ is invariant by the flow of system (1).

An easy analysis of the phase portrait of system (1) restricted to the invariant plane $\Pi(x, y, z) = 0$, provides that this phase portrait is the one shown in Figure 1(b). Note that isolating z from the invariant plane $\Pi = 0$ and substituting it into the differential system (1) we get the system:

$$(10) \quad \begin{aligned} \dot{x} &= x \left(a - c + \left(\frac{c}{b} - 1 \right) y \right) + x^2 \left(\frac{c}{a} - 1 \right), \\ \dot{y} &= y \left(b - c + \left(\frac{c}{a} - 1 \right) x \right) + y^2 \left(\frac{c}{b} - 1 \right). \end{aligned}$$

System (10) has three equilibria: an attractor at the origin, a repeller in $(a, 0)$, and a saddle in $(0, b)$; the infinity is filled of equilibria.

We have already studied the phase portrait on the invariant planes $x = 0$, $y = 0$ and $z = 0$, then we need to study the orbit of a point $q = (x, y, z)$ for $xyz \neq 0$ such that $\Pi(q) = 0$. On this plane Π , there exist a finite saddle in $(0, b)$, a repeller in $(a, 0)$, and an attractor in $(a, 0)$. This and the continuity of the solutions implies that the point q has its α -limit in $(a, 0)$ and its ω -limit in $(0, 0)$. Thus, we have that the phase portrait on the invariant plane $\Pi \subset \mathbb{R}^3$ is the one shown in Figure 1(b). Note that we must consider the correspondence $(0, 0) \rightarrow (0, 0, c)$, $(a, 0) \rightarrow (a, 0, 0)$ and $(0, b) \rightarrow (0, b, 0)$.

This completes the proof of statement (c) of Theorem 1.

From Figure 1(b) it follows that the 2–dimensional unstable manifold of the equilibrium e_2 restricted to the positive octant is contained in the plane $\Pi(x, y, z) = 0$; and that the 2–dimensional stable manifold of the equilibrium e_3 restricted to the positive octant is contained in the plane $z = 0$.

The next lemma completes the phase portrait of the competitive Lotka–Volterra system (1), proving statement (d) of Theorem 1.

Lemma 3. *Let $\phi_t(q) = (x(t), y(t), z(t))$ be the solution of the Lotka–Volterra system (1) such that $\phi_t(q) = q$ with $q = (x, y, z)$ in the interior of the positive octant and satisfying that $\Pi(q) \neq 0$.*

- (a) *Then $\phi_t(q) \rightarrow e_4$ when $t \rightarrow +\infty$.*
- (b) *If $\Pi(q) < 0$, then $\phi_t(q) \rightarrow e_1$ when $t \rightarrow -\infty$.*
- (c) *If $\Pi(q) > 0$, then when $t \rightarrow -\infty$ the orbit $\phi_t(q)$ tends to some infinite equilibrium point contained in the boundary of the positive octant inside the Poincaré ball.*

Proof. Considering the Darboux invariant (2) and a point $q = (x, y, z)$ in the interior of the Poincaré ball, it holds that $I(q) = cte \notin \{0, \pm\infty\}$. We want to remark that due to the fact that we only consider the vector field defined in the first octant of the compactified ball (in a compact), all its solutions are defined in the maximal interval $(-\infty, +\infty)$ of time.

Now for the Darboux invariant $I = e^{(2c-a-b)t}xyz^{-2}$, and since $2c-a-b > 0$ we obtain the following relations

$$(11) \quad \lim_{t \rightarrow +\infty} e^{(2c-a-b)t} \rightarrow +\infty; \quad \lim_{t \rightarrow -\infty} e^{(2c-a-b)t} \rightarrow 0.$$

Due to the fact that this Darboux invariant it is constant on the orbits, this implies that we needs satisfies that $\lim_{t \rightarrow +\infty} xyz^{-2} \rightarrow 0$, then the ω -limit must be in $x = 0$, or $y = 0$, or in $z = \infty$. Since the infinity is a repeller, the ω -limit must be the equilibrium point $e_4 = (0, 0, c)$ which is the unique attractor in $\{x = 0\} \cup \{y = 0\}$. This proves statement (a) of Lemma 3.

On the other hand the α -limit, according with the second expression in (11), is conditioned by the relation $\lim_{t \rightarrow -\infty} xyz^{-2} \rightarrow \infty$, then can be in $x \rightarrow \infty$, or $y \rightarrow \infty$, or $z \rightarrow 0$. We recall that the plane Π is invariant under the flow, then a orbit passing for q such that $\Pi(q) < 0$ must have their α -limit on e_1 (we know that e_1 is the unique repeller (even more is the unique equilibrium) on the region $\Pi(q) < 0$), and an orbit passing for a point q with $\Pi(q) > 0$ has it α -limit at the infinity, because there are not finite equilibria on this region and the infinity is a repeller. These affirmations prove statements (b) and (c) of Lemma 3. Figure 1(c) shows one orbit in each region $\Pi(q) > 0$, $\Pi(q) = 0$ and $\Pi(q) < 0$. \square

In short the phase portrait of system (1) in the first octant is as is shown in Figure 1(d).

ACKNOWLEDGEMENTS

The first author is partially supported by the Ministerio de Economía, Industria y Competitividad, Agencia Estatal de Investigación grants MTM2016-77278-P (FEDER) and MDM-2014-0445, the Agència de Gestió d'Ajuts Universitaris i de Recerca grant 2017SGR1617, and the H2020 European Research Council grant MSCA-RISE-2017-777911.

The second author is supported by CONICYT PCHA / Postdoctorado en el extranjero Becas Chile / 2018 - 74190062.

REFERENCES

- [1] J. Alavez-Ramírez, G. Blé, V. Castellanos, and J. Llibre. On the global flow of a 3-dimensional Lotka-Volterra system. *Nonlinear Anal.*, 75(10):4114–4125, 2012.
- [2] G. Blé, V. Castellanos, J. Llibre, and I. Quilantán. Integrability and global dynamics of the May-Leonard model. *Nonlinear Anal. Real World Appl.*, 14(1):280–293, 2013.
- [3] L. Brenig. Complete factorisation and analytic solutions of generalized lotka-volterra equations. *Physics Letters A*, 133(7):378–382, 1988.
- [4] L. Brenig and A. Goriely. Universal canonical forms for time-continuous dynamical systems. *Phys. Rev. A*, 40:4119–4122, Oct 1989.

- [5] F. H. Busse. Transition to turbulence via the statistical limit cycle route. In H. Haken, editor, *Chaos and Order in Nature*, pages 36–44, Berlin, Heidelberg, 1981. Springer Berlin Heidelberg.
- [6] A. Cima and J. Llibre. Bounded polynomial vector fields. *Trans. Amer. Math. Soc.*, 318(2):557–579, 1990.
- [7] F. Dumortier, J. Llibre, and J. C. Artés. *Qualitative theory of planar differential systems*. Universitext. Springer-Verlag, Berlin, 2006.
- [8] H. I. Freedman. *Deterministic mathematical models in population ecology / H.I. Freedman*. M. Dekker New York, 1980.
- [9] R. Hering. Oscillations in lotkavolterra systems of chemical reactions. *J. Math. Chem.*, 5:197–202, 1990.
- [10] M. W. Hirsch. Systems of differential equations which are competitive or cooperative. I. Limit sets. *SIAM J. Math. Anal.*, 13(2):167–179, 1982.
- [11] M. W. Hirsch. Systems of differential equations that are competitive or cooperative. VI. A local C^r closing lemma for 3-dimensional systems. *Ergodic Theory Dynam. Systems*, 11(3):443–454, 1991.
- [12] M. W. Hirsch, C. C. Pugh, and M. Shub. *Invariant manifolds*. Lecture Notes in Mathematics, Vol. 583. Springer-Verlag, Berlin-New York, 1977.
- [13] A. Kolmogorov. Sulla teoria di volterra della lotta per lesistenza. *Giornale dell Istituto Italiano degli Attuari*, 7:74–80, 1936.
- [14] W. E. Lamb. Theory of an optical maser. *Phys. Rev.*, 134:A1429–A1450, Jun 1964.
- [15] G. Laval and R. Pellat. Plasma physics (les houches). *Proc. Summer School of Theoretical Physics*, page 261, 1975.
- [16] J. Llibre and D. Xiao. Limit cycles bifurcating from a non-isolated zero-Hopf equilibrium of three-dimensional differential systems. *Proc. Amer. Math. Soc.*, 142(6):2047–2062, 2014.
- [17] A. J. Lotka. Elements of physical biology. *Science Progress in the Twentieth Century (1919-1933)*, 21(82):341–343, 1926.
- [18] L. Markus. Global structure of ordinary differential equations in the plane. *Trans. Amer. Math. Soc.*, 76:127–148, 1954.
- [19] R. M. May. *Stability and complexity in model ecosystems*. Princeton University Press Princeton, N.J, 1973.
- [20] D. A. Neumann. Classification of continuous flows on 2-manifolds. *Proc. Amer. Math. Soc.*, 48:73–81, 1975.
- [21] M. M. Peixoto. On the classification of flows on 2-manifolds. In *Dynamical systems (Proc. Sympos., Univ. Bahia, Salvador, 1971)*, pages 389–419. Academic Press, New York, 1973.
- [22] H. Poincaré. Sur les courbes définies par une équation différentielle. *Oeuvres Complètes*, 1:Theorem XVII, 1928.
- [23] S. Solomon and P. Richmond. Stable power laws in variable economies; lotka-volterra implies pareto-zipf. *The European Physical Journal B - Condensed Matter and Complex Systems*, 27(2):257–261, May 2002.
- [24] V. Volterra. Variazioni e fluttuazioni del numero dindividui in specie animali conviventi. *Memoire della R. Accademia Nazionale dei Lincei.*, CCCCXXIII(II):558–560, 1926.
- [25] E. C. Zeeman and M. L. Zeeman. An n -dimensional competitive Lotka-Volterra system is generically determined by the edges of its carrying simplex. *Nonlinearity*, 15(6):2019–2032, 2002.
- [26] E. C. Zeeman and M. L. Zeeman. From local to global behavior in competitive Lotka-Volterra systems. *Trans. Amer. Math. Soc.*, 355(2):713–734, 2003.

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